Dispersal and egg shortfall in Monarch butterflies: what happens when the matrix is cleaned up?

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Abstract. 1. We use an individual-based model describing the life of a monarch butterfly, which utilises milkweeds both aggregated in patches and scattered across the wider landscape as a substrate for laying eggs. The model simplifies the metapopulation of milkweed habitat patches by representing them as a proportion of the overall landscape, with the rest of the landscape considered matrix, which may contain some low density of milkweed plants.

2. The model simulates the number of eggs laid daily by a butterfly as it searches for hosts. The likelihood of finding hosts is related to the density of plants and the search ability of the butterfly. For an empty matrix, remaining in a habitat patch results in more eggs laid. However individuals that are good searchers have almost equivalent success without remaining in a habitat patch. These individuals are most affected by the presence of hosts in the matrix.

3. Given realistic values of habitat patch availability, our model shows that the presence of plants at a low density in the matrix has a substantial impact on the number of eggs laid; removing these plants can reduce lifetime potential fecundity by ca. 20%. These results have implications for monarch butterflies inhabiting agricultural landscapes, in which genetically modified soybean that is resistant to herbicides has resulted in the decimation of milkweeds over large areas.

Key words. Breeding habitat, genetically modified crops, habitat sterilisation, individual movement, models. milkweed patches, roundup ready, searching behaviour.

Introduction

A species population can only persist in an area where births plus immigration exceed deaths and emigration. Such suitable areas are usually considered to constitute the species habitat (Thomas & Kunin, 1999). Increasingly habitats are being fragmented by anthropogenic activities such as agriculture, urbanisation, mining etc. The resulting ensemble of remaining habitat units, variously isolated across a landscape is usually described as a metapopulation for the focal species (e.g. Hanski, 1989; Hanski & Thomas, 1994). The persistence of the species as a whole will depend on a mixture of dynamics within remnant habitat patches and dynamics across such patches, all else being equal (e.g. Hanski, 1989; Hanski *et al*., 1995; Hill *et al*., 1996).

Species persistence will depend on the size and quality of the habitat areas, their spatial distribution, their rates of

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creation and extirpation, and movement amongst such areas. The movement process is then central to persistence and can be broken down into the likelihood of leaving, essentially how the species reacts to habitat edges (Stamps *et al*., 1987; Ries & Debinski, 2001), traversing a potentially treacherous landscape, often dubbed the matrix, and finding new areas (the search process) and utilising them for colonisation (Kitching & Zalucki, 1982; Zalucki & Kitching, 1982d; Ims & Yoccoz, 1997; Revilla & Wiegand, 2008). Implicit in most metapopulation models is the notion that the matrix is empty, or at least negligible as far as the species requirements are concerned.

The ability of animals to perceive and locate resources as they move through the landscape, essentially as they are 'lost in matrix space', will contribute not only to dispersal success in fragmented landscapes, namely finding habitat units (Lima & Zollner, 1996; Conradt *et al*., 2003; Merckx & Van Dyck, 2007), but also their ability to survive and potentially reproduce in the space between 'habitat' patches (below). Empirical information on the perceptual abilities of animals

in real landscapes is limited (Zollner & Lima, 1999; Schooley & Wiens, 2003; Merckx & Van Dyck, 2007). We know from behavioural and electrophysiological studies that insects can perceive resources, such as host plants, from a distance using odour cues and respond accordingly (e.g. Finch & Collier, 2000). These perceptions may be disrupted by many factors and so lead to better or worse localisation of resources (Floater & Zalucki, 2000).

Butterflies have been used as model systems when exploring the interaction of landscape structure and populations persistence. Their habitat requirements are relatively well known and include: host plants for immatures, conditions for immature development, adult food and pharmacological requirements, roosting sites, sites for thermoregulation, mating location, hibernation, and escape from predators (Dover *et al.*, 1997; Walter & Zalucki, 1999; Shreeve *et al.*, 2001; Dennis *et al.*, 2003). The assumption that butterflies do not use the space between habitats has been questioned (Dennis, 2004), although how this space is exploited will depend on the particular species biology (Dennis *et al.*, 2004).

Here we explore the effect of landscape structure and the ability to find habitat and other resources in the matrix, on the potential population persistence of a butterfly via its impact on egg laying. We use a simple modelling approach to infer the effects of host plants growing in the matrix, both in habitat units (host plants at high density) and as single isolated plants, and the ability of the species to find these plants. We then generalise the search function and habitat-leaving rules to potential species persistence in a landscape with various proportions of suitable habitat and matrix 'quality'; density of hosts not in habitat patches. We make the simple point, as has been made by others, that generalisations are likely to be species biology specific, so management decisions based on simple rules may be misleading. We have in mind monarch butterflies, and so infer the potential effects of removing milkweeds in areas between patches of these hosts. The latter is already happening in North America as a consequence of Roundup Ready soybean agriculture (see discussion below).

The study system on which we initially base our model are monarch butterflies, *Danaus plexippus*, in its summer breeding season. This species is a useful test case. The monarch is a vagile species that moves extensively amongst patches of host plants, milkweeds, and almost exclusively species of *Asclepias*. Zalucki (1986, 1993) defined suitable habitat patches as areas of relatively dense milkweed growing in patches of various sizes. Such areas in old fields will usually not only contain milkweed host plants for oviposition and immature development, but also adult nectar plants, roosting sites as well as mates (Bull *et al.*, 1985; Suzuki & Zalucki, 1986). Although local adult monarch density is aggregated around such patches (Zalucki & Suzuki, 1987), *à la* Root's resource concentration hypothesis (Root, 1972), monarchs leave such areas; patch edges are effectively permeable (Zalucki & Kitching, 1982a; Ries & Debinski, 2001). The population that resides outside such habitat patches is substantial (Bull *et al.*, 1985). Based on mark–recapture studies (Zalucki & Kitching, 1985), and modelling adult movement over the lifetime of a female in a landscape with milkweed reflecting realistic distributions

(Zalucki *et al.*, 1981), we showed that females are likely to have an average birth to death distance of ca. 11 km (Zalucki, 1983). The relevant scale or landscape unit for monarch populations is thus an area of ca. 380 km^2 ($\pi \times 11^2$) and the milkweed patches and plants scattered therein. Away from milkweed patch habitat, host plants can be found at various low densities: the matrix is not empty. These scattered 'single isolated plants' are utilised by monarchs as they traverse the landscape (Zalucki & Kitching, 1982b). Such plants can be found along roads and scattered amongst crops and other disturbed areas. Egg numbers per plant in these cases are often high, and returns on eggs in terms of survival to the adult stage are better on single plants than for plants growing in a milkweed patch habitat (Zalucki, 1981a; Zalucki & Kitching, 1982a,b,c; Zalucki & Rochester, 2004).

Our objective here is to partly address what happens to a species persistence if the matrix is cleaned up and made a void, due to say herbicide usage on host plants (milkweeds) growing in agricultural fields. With Roundup Ready soybeans being widely grown in the north-eastern USA, such extirpation of low density milkweeds is occurring. We are in effect creating a landscape in which remnant patches of milkweed may still be present on old fields, and along verges of roadways, but the area in between is being made clean, a situation analogous to a classic metapopulation. We explore some of the consequences of such clearing, at least in theory. Our work is predominantly based on studies of milkweed patch use conducted on Monarchs in south-east Queensland, Australia, where the Monarch breeds year round. No equivalent work has been undertaken in North America but we believe our findings are applicable in general terms to the summer range in North America (Zalucki & Rochester, 2004).

Methods

Model description

The model simulates the egg-laying behaviours of a butterfly over its entire lifespan during a summer generation in a conceptual landscape with suitable egg laying habitat (milkweed plants) distributed throughout. The habitat can be clustered together to form patches and/or spread through the landscape as single plants. The model was constructed in Excel 2003 using a combination of the spreadsheet calculation functions and a VBScript macro to organise the steps. Its structure is summarised in Fig. 1. The model is a simplified version of an individual-based model (Zalucki, 1983) with egg laying per female per day and longevity similar to monarchs (Zalucki, 1981b). The simplification involves how we represent the distribution of milkweed habitat patches within the landscape. Here we assume such patches occupy some proportion of the landscape. The rest is a matrix that may also contain single isolated plants at some low density (see below).

The simulation has the following steps:

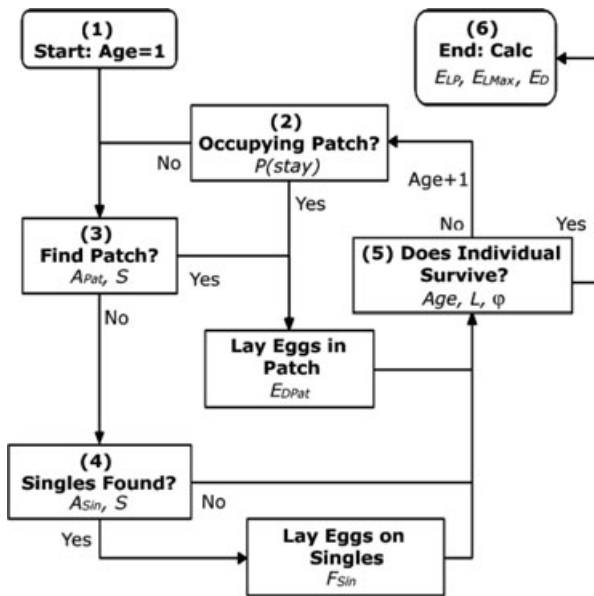1 The butterfly is initialised, age = 1 day, and released into the environment at random with respect to patches. For

Fig. 1. Structure of the model. Italics show the influencing variables.

each day of the butterfly's lifespan (L) it has a maximum number of eggs that can be laid (E_{DPat}) and goes through the same pattern to find host plants upon which to lay them.

2   If the butterfly has previously entered a habitat patch there is a likelihood that it will remain there, P(stay). Newly initialised butterflies have not yet begun searching for habitats at this point and skip this stage. A P(stay) of one results in the butterfly remaining in a habitat patch, assuming it has found one, for the duration of its life. A P(stay) <1 means the butterfly has some chance of leaving the patch habitat. This variable essentially describes the propensity to leave patches or disperse and captures boundary or edge behaviour.

3   A butterfly that has not found a habitat patch, or is not remaining in one, will search for host plant patches and/ or single plants. The probability of a butterfly finding a patch, P(fPat), is based upon the proportion of the environment that has suitable patch habitat (A_{Pat}) and the search ability (S) of the individual:

$$P(\text{fPat}) = A_{Pat}^{S}. \qquad (1)$$

If the value of P(fPat) is greater than a randomly generated number between 0 and 1, then the butterfly has found a habitat patch. If a patch is found, or the butterfly remains in one, it lays E_{DPat} eggs for the day. Search ability, S, measures how well a butterfly can find hosts (as either patches or single plants). When S equals 1, the butterfly effectively searches at random and finds hosts (singles and patches) in proportion to their availability. It should be noted that lower S values result in 'better searchers', and reflects animals that find resources very well, either because of perceptual abilities or resources are more 'apparent'.

4   If no patch is found in the previous step the butterfly commences searching for single plants. The number of single plants found (F_{Sin}) is affected by their density in the matrix (A_{Sin}), the search ability S and the time available for searching ($t = 61$ units):

$$F_{Sin} = t \left(\frac{A_{Sin}}{(2 + A_{Sin})} \right)^{S}. \qquad (2)$$

The time available for searching, t, was calibrated so that the best searchers ($S = 0.1$) lay E_{DPat} eggs at a single plant density of 1 (namely all their eggs). The number of single plants found (F_{Sin}) then impacts upon the number of eggs laid upon them (E_{DSin}):

$$E_{DSin} = 5F_{Sin} \times e^{(-0.07 F_{Sin})} + F_{Sin}. \qquad (3)$$

5   Once eggs are laid, either in a patch or on single plants, the age of the butterfly and its likelihood of survival is checked. If the individual's age hasn't reached its lifespan (L) in days and it survived the day, the age is incremented and a new day begins; the behaviour returns to step 2. If the age of the butterfly is equal to L days or it had died in that time step, it moves on to step 6. The likelihood of survival on any given day, φ, was determined by comparing a random number between 0 and 1, RAND, to φ. If $\varphi >$ RAND the animal has survived.

6   At the end of an individual's life (i.e. when $Age = L$ or $\varphi <$ RAND) the number of eggs laid on each day of the butterfly's life (E_{Day}), either on singles or in patches, are summed and divided by the theoretical maximum number of eggs laid in its life: E_{DPat} eggs per day multiplied by L days, 840 for the intended lifespan of 14 days (see Table 1) to obtain a proportion of the eggs laid during an individuals life (E_{LP}):

$$E_{LP} = \frac{\sum\limits_{D=1}^{14} E_D}{E_{DPat} \times L}. \qquad (4)$$

The model was run in a number of ways in order to explore the parameter space and make predictions for realistic scenarios. The importance of remaining in a patch and the search ability, represented by P(stay) and S respectively, as the behavioural drivers underlying egg laying performance, were examined. A summary of the parameter names and their descriptions can be found in Table 1. These effects were built upon through an examination of the role of singles density A_{Sin} on the proportion of eggs laid E_{LP}. This knowledge was then used to parameterise the model to make predictions for realistic habitats. One hundred replicates of the model were run for all simulation treatments.

Simulation experiments

These simulations examined the interactions between varying parameters on the proportion of eggs laid E_{LP} of the

Table 1. Summary of the parameters used in the model and their descriptions.

Parameter	Description
Age	Age of the individual (days)
A_{Pat}	Proportion of the environment that is suitable habitat patch
A_{Sin}	Density of single plants between suitable habitat or matrix
E_D	Number of eggs laid on each day of the individual's life (60)
E_{DPat}	The number of eggs laid in a habitat patch in a single day
E_{DSin}	The number of eggs laid on single plants in a day
E_{LMax}	The maximum number of eggs it is possible for a butterfly to lay during its lifespan (840)
E_{LP}	The proportion of eggs laid during an individuals lifespan
F_{Sin}	Number of single plants found by the individual in a day
L	Lifespan of the individual (14 days)
φ	Daily survival rate (1)
$P(\text{stay})$	Daily probability that the individual remains in a habitat patch
$P(\text{fPat})$	Daily likelihood of an individual finding a habitat patch
S	Individual search ability
T	Time available to search for single plants in a day (61 units)

simulated butterflies. For all simulation experiments the individuals could lay a maximum of 60 eggs per day (i.e. $E_{DPat} = 60$), spent 61 time units searching for singles per day (i.e. $t = 61$), and had a lifespan of 14 days (i.e. $L = 14$, $\varphi = 1$).

A preliminary examination of daily survival φ indicated that, in its current implementation, the only effect was to reduce the number of eggs laid by the individual (M. P. Zalucki and J. H. Lammers, unpublished results). A potential follow up to this study would be to examine changes in fecundity resulting from habitat influenced survival differences; for example a daily survival rate of 0.8 for searching in the matrix versus 1.0 for remaining in a patch.

The first set of simulations examined the interaction between the likelihood of remaining in a patch, $P(\text{stay})$, and proportion of the landscape area occupied by patch habitat A_{Pat}. Five different values were used for $P(\text{stay})$ (0, 0.25, 0.5, 0.75, 1) and four were used for A_{Pat} (0.25, 0.5, 0.75, 1.0) to form 20

different treatments. Singles density A_{Sin} was set to zero and the search ability of the individuals is assumed to be directly related to the availability of habitat ($S = 1$), namely random search.

The second set of simulations built upon these results by examining the effect of search ability, S at various likelihoods of remaining in a patch $P(\text{stay})$. For these simulations three different values were used for search ability, S (0.1, 0.5, 1) and five were used for $P(\text{stay})$ (0, 0.25, 0.5, 0.75, 1.0) to form 15 treatments. Proportion area of patch habitat A_{Pat} was set to 0.25 and singles density A_{Sin} was maintained at zero.

The third set of simulations examined the effect of small increases to the singles density A_{Sin} in the landscape. Four different levels of singles density A_{Sin} (0, 0.01, 0.1, 0.2) were examined against six proportion areas of patch habitat A_{Pat} (0, 0.2, 0.4, 0.6, 0.8, 1.0) and three different values of search ability S (0.1, 0.5, 1.0), for a total of 72 treatments. For all of these the likelihood of remaining in a patch $P(\text{stay})$ was maintained at 0.5, namely a 50/50 chance of staying or leaving on any 1 day.

The final set of simulations examined the effects of the likelihood of remaining in a patch $P(\text{stay})$ and search ability S on the proportion of eggs laid E_{LP}, if singles density A_{Sin} was cleaned up in a realistic landscape. Five levels of $P(\text{stay})$ (0, 0.25, 0.5, 0.75, 1.0) and three values for S (0.1, 1, 2) were used. Current 'guesstimates' of realistic proportion area of patch habitat A_{Pat} and singles density A_{Sin} are around the 0.05 and 0.01 region, respectively (see Discussion). As such A_{Pat} was set to 0.05, and two levels of A_{Sin} (0.0, 0.01) were used to examine the effect of cleaning up non-patch spaces.

Results

Exploration of the parameter space demonstrated some noteworthy points of the simulation. For modest searchers the model reflects Root's Resource Concentration Hypothesis (Root, 1972), with high likelihoods of remaining in a patch resulting in a higher proportion of eggs laid at all levels of patch availability (Fig. 2a). However, in a metapopulation populated by a highly vagile species, the proportion of eggs laid
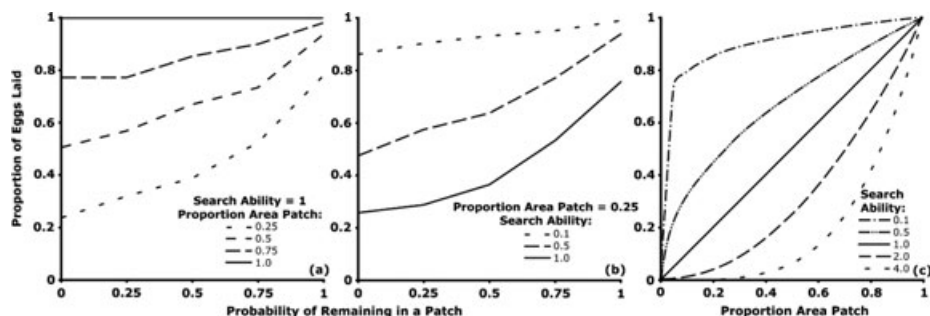

Fig. 2. The effect of various factors on the proportion of eggs laid (E_D) all with no single plants present in the matrix. (a) Depicts the effect of varying the likelihood of staying in a patch, $P(\text{stay})$, for individuals with a search ability equal to chance ($S = 1$). The lines represent different levels of available patch habitat (A_{Pat}). (b) Demonstrates the effect of $P(\text{stay})$ at an A_{Pat} of 0.25. The lines represent different search abilities (S). (c) Depicts the effect of increasing A_{Pat}. The different lines represent individuals with varying S. Good searchers that find resources better than random ($S = 1$) have values of $S < 1$.
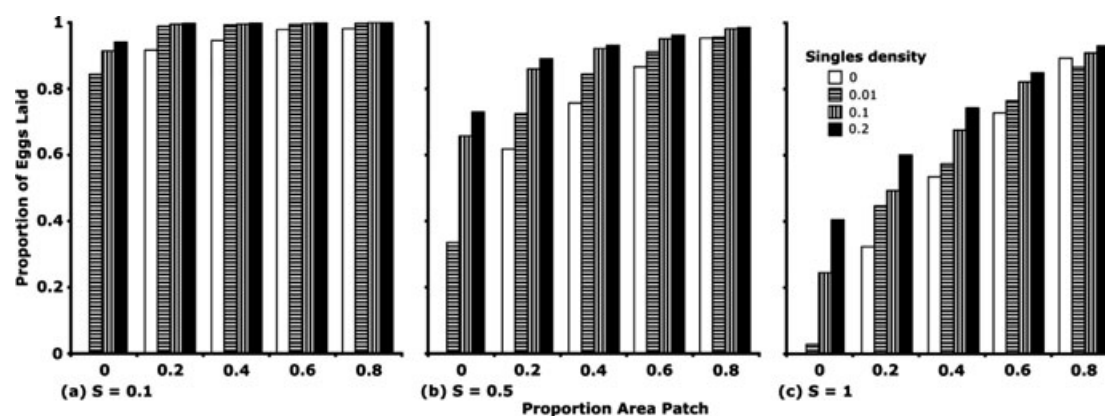
Fig. 3. The effect of the interaction between proportion of available habitat patch (A_{Pat}) and search ability (S, graphs a–c) on the proportion of eggs laid (E_D) at four different levels of single plant density (A_{Sin}, the different columns).

improves with an individual's search ability (Fig. 2c). In this case, being a good searcher has a greater impact on proportion of eggs laid than remaining in a patch (Fig. 2b). The best searchers ($S = 0.1$) are able to lay almost all of their eggs irrespective of whether they remain in a patch (Fig. 2b).

The success of good searchers can be further improved by the inclusion of single plants in the spaces between habitat patches. This is evident in the model through the inclusion of low levels of single plants, and a comparison of their effect on the interactions between search ability and the area of patch available. The presence of singles had an effect on the proportion of eggs laid (Fig. 3). At the smallest singles density ($A_{Sin} = 0.01$), there was a dramatic increase in the proportion of eggs laid by the best searchers ($S = 0.1$) in the environments with low patch availability (Fig. 3). As singles density increases, the biggest improvements in proportion of eggs laid, still occur in the environments with the lowest patch densities, but the greatest improvements were made by individuals with better search abilities than random (i.e. values of S less than 1) (Fig. 3a,b). This was primarily due to the best searchers already being able to lay the majority of their eggs at the lower single plant densities.

Realistic levels of A_{Pat} (around 0.05) do not result in a high proportion of eggs laid by any individuals other than the best

searchers (Fig. 4). In addition these benefited the most from the available singles, increasing the proportion of eggs laid by 22% if they searched for new habitat patches every day ($P(\text{stay}) = 0$) (Fig. 4).

Discussion

Metapopulation theory has become a dominant paradigm in conservation biology during the last 20 years, mainly due to the focus on species persistence due to anthropogenic-induced fragmentation of natural habitats. The general perception has been that the matrix, in which suitable habitat units of the metapopulation sit, is essentially empty.

As Shreeve *et al.* (2004) cogently point out, for butterflies at least, the matrix is not empty, but contains resources which adults may utilise to feed, roost, and reproduce. Here we draw attention to this important observation, as it has implications for how landscapes may be managed. In our simple model we have included searching for oviposition resources or host plants. These we envisage as occupying patches that make up some proportion of the landscape (which we equate with habitat for now) and for single 'isolated' plants at some low density in the matrix. We have in mind Monarch
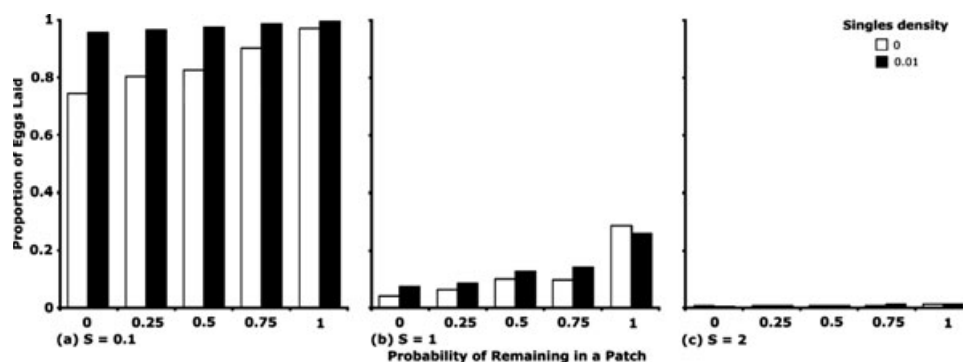

Fig. 4. The effect of varying the likelihood of staying in a patch, $P(\text{stay})$, and search ability (S, graphs a–c) on the proportion of eggs laid (E_D) at a proportion of the landscape with patch (A_{Pat}) of 0.05 and two different levels of single plant density (A_{Sin}, the different columns).

butterflies in their breeding season, but we believe our results have implications for any species that has very leaky habitat patch edges, and hence a high propensity to disperse, and to utilise, if they can find them, resources away from patches, as monarchs do (see Introduction). We do not model an explicit metapopulation structure. Rather the landscape is divided into an area that is 'habitat' as a proportion of the landscape, and the rest is matrix, which may be without (the empty matrix) or with single plant resources at various densities.

As the landscape becomes fragmented (namely the proportion of suitable habitat declines) the key parameters that impact on the proportion of eggs laid are search ability and likelihood of staying in a habitat. Those that stay put and aggregate in habitat patches will do best on average (Fig. 2a), as postulated long ago by Root (1972), unless the whole habitat is in one unit and it too disappears (see, for example, Roff, 1973, 1975). This is essentially where the dynamics of metapopulation persistence comes into its own. Some small likelihood of leaving would be favoured, but finding or search ability in the matrix becomes important, not only for new habitats but also for resources in general.

If the species has a high search ability, then it can find a habitat readily and staying put is no longer as important (Fig. 2b). Such species would tend to be highly vagile, with leaky borders to habitats (e.g. Monarchs). But even for such species a matrix with useable resources can make a big difference to the proportion of eggs laid (Figs 3 and 4). Such species, strictly speaking, can be thought of as patchy populations (Thomas & Kunin, 1999).

Our results have implications for the cleaning up of agricultural landscapes, as crops genetically modified to be herbicide resistant are increasingly planted. Since 1997 some 90% of American farmers have adopted Roundup Ready soybeans occupying some 40.5 million ha of row crop monarch habitat (O. Taylor & K. Oberhauser, pers. comm.). This is about one-third of the potential monarch summer breeding habitat in North America (Brower, 1999). Whereas before such fields contained some milkweeds sufficient for these plants to be considered weeds (Cramer & Burnside, 1982; Hartzler & Buhler, 2000), the increasing use of herbicides is effectively creating an empty matrix (O. Taylor & K. Oberhauser, pers. comm.). Even though conservation-minded consciences might be salved by leaving some fraction of the landscape with habitat, perhaps even a substantial area such as roadsides and the odd old field, an empty matrix may make a big difference for highly dispersive species with good searching capacity, like monarchs (Figs 3 and 4).

For individuals with high search ability, an empty matrix can lead to a ca. 20% reduction in lifetime fecundity (Fig. 4a). This estimate is based on a milkweed patch habitat making up 5% of the landscape, and milkweed throughout the matrix at densities of ca. 1 plant per 100 m^{-2} (density of 0.01 in simulations). Both are likely overestimates. Based on infrared aerial photography Zalucki *et al*. (1981) estimated milkweed in patches made up between 0.6% and 1% of the total land area mapped (400 km^2), at least in Australia. Low density milkweed abundance is even more difficult to estimate, but Oberhauser *et al*. (2001) (prior to the GMO herbicide crops) had estimates

for milkweed that ranged from 0.003 to 0.027 plants per m^{-2} in various 'habitat types' such as corn, other agricultural, edges, and non-agricultural (here we have assumed their higher densities of $0.3 - 3 \text{ m}^{-2}$ are for patches of milkweed). How big a difference a ca. 20% reduction in lifetime fecundity would make to net reproductive rate and population persistence, will depend in part on the relative returns on investment in eggs laid in patches as opposed to plants at low density. We have shown elsewhere that mortality rates due to predation (Zalucki & Kitching, 1982c) and parasitism (Zalucki, 1981a) tend to be higher in patches of milkweed. Mortality due to resource depletion will tend to be higher in single plants, particularly if these plants are small, as there will not be enough resource for a caterpillar to complete development, although females tend to select and lay more eggs on larger plants (Zalucki & Kitching, 1982b).

Here we have used a simplified individual based model to explore the ramifications of searching for and finding resources in a highly simplified landscape. Creating a landscape in which the matrix is truly void, a classic metapopulation, as seems to be happening with herbicided landscapes may be detrimental to the persistence of species with high habitat leaving rates.

Strictly speaking for a wide-ranging species like the Monarch, whose typical movement distances are much greater than typical distances between patches of host plants, a metapopulation context is inappropriate. The Monarch population is sampling a patchy distribution of host plants across the wider landscape. The realistic host-plant distributions modelled show the potential impact of resource distributions on fecundity (egg shortfall) in this species. Thus even for a wide-ranging species like the Monarch, the increasing extirpation of host plants outside clearly defined areas of suitable habitat, can have a major effect on population dynamics. Similarly Thomas (2000) showed that the most pronounced declines in British butterflies had occurred not for the least or most dispersive species, but for those with intermediate dispersal range and (usually) patchily distributed resources.

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