Host Plant Limitation of Butterflies in Highly Fragmented Landscapes

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Host plant limitation of butterflies in highly fragmented landscapes

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Abstract:

Insect herbivores can be limited by host plants in two ways: density-dependent competition for food resources, or density-independent search time limitation. Our understanding of density-dependent host plant limitation is relatively well developed and well integrated into conservation plans for at-risk insects. Search time limitation is much less well developed. Here, we explore both mechanisms using empirically-based models of monarch butterfly population dynamics. These mechanisms differ fundamentally in their predictions: Resource competition leads to matching of herbivore densities to host plant densities, and visible competition via consumption of host plants. Search time limitation leads to changes in population growth rate that can cause herbivore numbers to decline when host plant densities are constant. Search time limitation also implies that host plants can limit herbivores, even when many individual plants are uneaten. For monarch butterflies, our calculations suggest that many parts of North America have host plant densities below the threshold for search time limitation, which contrasts with the typical assumption of resource competition. More generally, incorporating search time limitation into conservation plans is important for reframing our understanding of how host plants limit insect herbivores in highly fragmented landscapes.

Introduction:

The assumption that resource limitation drives population declines is threaded throughout applied ecology. For example, hundreds of management programs use food supplementation to augment populations of focal species (Ewen et al. 2015; Ruffino et al. 2014). Similarly, estimates of resource density and/or food availability are the basis for determining if habitat is sufficient to support at-risk species (e.g., Dennis et al. 2003; Lopez-Bao et al. 2010). In nearly all cases, the implicit assumption is that resource limitation acts in a density dependent manner, broadly meaning that the amount of food sets the carrying capacity of animals that can be supported in a particular environment. For example, conservation plans for monarch butterflies include a direct rate of proportionality between the number of stems of their host plant on the landscape and the number of butterflies on the landscape at the end of the breeding season (Johnston et al. 2019; Pleasants 2017; Thogmartin et al. 2017a), derived from density dependent larval survival (Flockhart et al. 2012).

An alternative hypothesis is that resource limitation acts in a density independent way by affecting search time for resources. For example, studies of foraging ungulates assume that forage intake is driven by the rate at which individuals encounter suitable vegetation (Belovsky 1978; Belovsky 1984). If herbivore populations are sparse enough not to affect plant communities, their intake rate will be limited by the encounter rate with suitable plants, not the ratio of consumers to plants. In at least one study of butterflies (Johansson et al. 2007), daily oviposition rates were lower in large flight cages than small experimental ones, implying search time limitation. Indeed, a large body of optimal foraging theory (Mac Arthur and Pianka 1966; Pyke 1984; Pyke et al. 1977) is based on the assumption that search time is a key factor

limiting individual fitness and subsequent population growth rates, even if individuals are not competing directly for resources. Depending on the density of consumers and resources, search time limitation can lead to density independent or density dependent population regulation (Hails and Lawton 1983; Lessells 1985; Stiling 1987). For decades, the importance of search time limitation has been recognized in some fields of applied ecology, including insect biocontrol (Mills and Heimpel 2018).

To date, the notion of search time limitation has not been integrated with our understanding of spatial population dynamics. Nonetheless, the process of animals searching for habitat patches in highly fragmented landscapes is directly analogous to ungulates searching for browse plants or predators searching for prey. This analogy is especially appropriate for specialist insect herbivores, for whom habitat patches are defined by the presence of host plants. Although it is not well-recognized as a limiting factor, search time limitation is a natural outcome of spatial population models that approximate animal movement with diffusion, a longstanding tradition in ecology (Holmes et al. 1994; Ovaskainen and Crone 2009). This property arises because it takes time for animals to move through the landscape, e.g., from one patch of high-quality habitat to another. If specialist insects oviposit at a constant rate in host plant patches (e.g., Fahrig and Paloheimo 1988; Jones et al. 1980; Kareiva 1983), these models directly recapitulate search time models, where search time is an emergent property of the rates of movement through habitat patches and the inter-patch matrix.

In this paper we compare resource limitation via density dependent resource competition vs. density independent search time limitation in a conservation context. Our example is based on the monarch butterfly (*Danaus plexippus plexippus*) in North America. In

North America, migratory monarch butterfly populations have ~4 breeding generations during summer, plus an overwintering generation that migrates to sites in Mexico or California. Monarch butterflies are an interesting case study for several reasons. First, monarch butterflies are specialist herbivores; adults oviposit and larvae feed on milkweeds (*Asclepias* spp). Second, although widespread, monarch butterflies have been in decline and were recently listed as a candidate species under the US Endangered Species Act (U. S. Fish and Wildlife Service 2020). Third, loss of hostplants is thought to be a leading cause of declines (Thogmartin et al. 2017b), and conservation measures are based largely on the assumption density-dependent resource limitation. However, milkweeds are sparse and scattered widely across the landscape, suggesting that search time limitation is also a plausible way in which loss of hostplants could affect population viability. Finally, most vital rates (including movement) throughout the life cycle are estimable from published data, with the caveat that these data come from various locations throughout the monarch's global range. Although our example is framed around monarch butterflies, the mechanisms we explore are general enough that they could apply to any multivoltine insect with high breeding season growth and low overwinter survival.

To make this comparison, we proceed in three steps. First, we review a simplified version of a density-dependent milkweed limitation model that has previously been used to direct monarch butterfly conservation (Flockhart et al. 2015). Second, we present a search-time limitation model of monarch butterflies, based on integrodifference equation models for insect populations in patchy landscapes (Crone et al. 2019; Musgrave and Lutscher 2014). Third, we explore both models numerically to identify host plant densities under which population dynamics are likely to be limited by resource competition vs. search time limitation.

Density dependent host plant limitation:

Flockhart et al. (2015) projected monarch butterfly population dynamics with density-dependent host plant limitation, based on an experimental study (Flockhart et al. 2012) of larval survival as a function of the density of eggs per milkweed stem. This basic mechanism can be expressed using the following relationship to predict population dynamics within the breeding season:

$$N_{t+1} = N_t 0.5 F \theta_L \theta_P \quad \text{Eq. 1}$$

where N_t is the number of monarch butterflies in generation t , F is fecundity (eggs per monarch butterfly, multiplied by 0.5 to scale to female eggs per female monarch butterfly), θ_L is larval survival (from egg to pupation) and θ_P is pupal survival (from pupation to eclosion). Density dependence was incorporated by making larval survival a logistic function of the density of eggs per milkweed stem, i.e.,

$$\theta_L = \theta_F \frac{1}{1 + \exp\left(\beta_1 \frac{e_{t+1}}{M} - \beta_0\right)} \quad \text{Eq. 2}$$

This equation is a standard inverse logit function where survival (θ_L) is a function of the number of eggs (e_{t+1}) per milkweed stem (M), with intercept β_0 and slope of $-\beta_1$, noting that $1/(1+1/\exp(x)) = 1/(1+\exp(-x))$. θ_F is a conversion factor that converts maximum survival in the lab ($\frac{1}{1+\exp(-\beta_0)}$) to realized survival in the field ($\theta_{L,field}$), i.e., $\theta_F = \frac{\theta_{L,field}}{1+\exp(-\beta_0)}$ (see Flockhart et al. 2015). Because eggs are produced by parents in generation, t , $e_{t+1} = N_t F$, and the full recursion equation can be written as

$$N_{t+1} = \frac{N_t 0.5 F \theta_P \theta_F}{1 + \exp\left(\beta_1 \frac{N_t F}{M} - \beta_0\right)} \quad \text{Eq. 3}$$

where all parameters are as defined in eq. 1-2. This model largely recapitulates the well-known Ricker model, although it is not identical because it is based on a logit-linear density dependent relationship between growth rate and density – derived from the standard use of a statistical model for survival – rather than a log-linear density dependent relationship. Solving for carrying capacity (N^* such that $N_{t+1} = N_t$), the equilibrium density of monarch butterflies is proportional to the number of milkweed stems, M :

$$N^* = M \frac{\ln(0.5 F \theta_P \theta_F - 1) + \beta_0}{\beta_1 F} \quad \text{Eq. 4}$$

For parameters relevant to monarch butterflies (Table 1), the low density growth rate (eq 1 solved at the 0-intercept of eq 2) is quite high, ~12.0/generation, which implies rapid growth below carrying capacity. For these parameters, carrying capacity (N^*) is ~0.033 adult female butterflies per milkweed stem (Figure 1A). Flockhart et al. (2015) extended this model to include movement among regions in North America during breeding. Here, we omit this aspect of monarch butterfly life history, for the purposes of comparing density-dependent host plant limitation with search time limitation in general.

Density independent search time limitation:

Musgrave and Lutscher (2014) developed a spatially implicit integrodifference equation model of insect population dynamics in heterogeneous landscapes. Their approach builds on classic reaction-diffusion models analyzed by Shigesada et al. (1986), in which animals move

through heterogeneous landscapes with habitat-specific movement rates (approximated by habitat-specific diffusion coefficients) and habitat-specific population growth rates (Shigesada et al. 1986). One of Shigesada's key insights was that population growth rates depended on the % habitat in a landscape because, in landscapes with low % habitat, animals spend most of their time moving through non-habitat. In other words, search time limitation is an emergent property of reaction-diffusion models applied to spatially heterogeneous landscapes. Another key insight was recognition that these models could be solved for periodic landscapes. In other words, if we are willing to assume that landscapes consist of alternating strips of habitat and non-habitat, we can calculate population growth rates in heterogeneous environments using an equation, rather than a simulation model.

Musgrave and Lutscher extended the general approach to include two key features of insect behavior that make it suitable for analyzing monarch butterfly population dynamics. First, they separated the time scales of movement, adult survival, and oviposition, from juvenile survival. This separation allows organisms to move through non-habitat matrix in which they survive but cannot reproduce (unlike the single population growth rate parameter in classical reaction-diffusion models of population dynamics), and also leads to more accurate estimates of population growth rates (cf. Powell and Zimmermann 2004). Second, they included preference at habitat-type interfaces, an important feature of the biology of many animal species, that is well-documented in butterflies (Brown et al. 2017; Kuefler et al. 2010; Ries and Debinski 2001; Schultz and Crone 2001). These assumptions lead to the following equations for population dynamics in heterogeneous environments:

$$N_{t+1}(x) = \int_{-\infty}^{\infty} K(x, y)p(y)N_t(y)dy \quad \text{Eq. 5}$$

166 Where $N_{t+1}(x)$ is the number of individuals (butterfly eggs) in generation $t+1$ at location x ,
 167 $N_t(y)$ is the number of individuals at some (other) location y in the previous generation, $p(y)$ is
 168 survival from egg to adult at site y , and $K(x, y)$ is a dispersal kernel for reproduction at site x for
 169 individuals born at site y :

$$K(x, y) = \int_0^{\infty} a(x)u(t, x)dt \quad \text{Eq. 6}$$

170 In the dispersal kernel, $a(x)$ is the oviposition rate (eggs/time) of butterflies at location x ; for
 171 simplicity, we consider the special case in which this rate is positive in habitat and 0 in non-
 172 habitat. $u(t, x)$ is the number of adult butterflies at site x at time t , which is a function of
 173 movement $D(x)$, and mortality $m(x)$:

$$\frac{\partial}{\partial t} u(t, x) = \frac{\partial^2}{\partial x^2} (D(x)u(t, x)) - m(x)u(t, x) \quad \text{Eq. 7}$$

174 with preference at patch boundaries, $\bar{z}$, which is a function of the probability of crossing
 175 between habitat and matrix at habitat boundaries. Following Musgrave and Lutscher (2014), if
 176 b is the probability of entering the matrix at boundaries, $\bar{z} = \frac{b}{1-b}$.

177 Musgrave and Lutscher (2014) solved equations 5-7 for periodic landscapes that consist
 178 of parallel strips of alternating high and low quality habitat (Musgrave and Lutscher 2014; see
 179 also Appendix S4 in Crone et al. 2019). Using Musgrave and Lutscher's case "S" (differences in
 180 movement rate but not % time moving in habitat vs. non-habitat), the per-generation growth
 181 rate is the value of λ_{ST} that satisfies:

$$\tan\left(\frac{\sqrt{\frac{m}{D_1}\left(\frac{1}{\lambda_{ST}}\hat{r}_1 - 1\right)}l_1}{2}\right) = \frac{\bar{z}\sqrt{\frac{m}{D_2}}}{\sqrt{\left(\frac{m}{D_1}\frac{1}{\lambda_{ST}}\hat{r}_1 - 1\right)}}\sqrt{\frac{D_2}{D_1}}\tanh\left(\frac{\sqrt{\frac{m}{D_2}}l_2}{2}\right) \quad \text{Eq. 8}$$

where D_1 and D_2 are movement (diffusion) rates in habitat and non-habitat (respectively), $\hat{r}_1$ is the maximum population growth rate if an individual spends its entire life in habitat patches i.e., $\frac{a(x)}{m(x)}$, evaluated for the oviposition rate in habitat patches, and l_1 and l_2 are the relative widths of habitat and non-habitat strips on the periodic landscape, which means the proportion of habitat at landscape scales is $\frac{l_1}{l_1+l_2}$. Eq 8 is a rearrangement of eq. 57 in Musgrave and Lutscher (2014), with a single value of mortality for habitat and non-habitat, no reproduction in non-habitat, and adult butterfly settling rate of 0. (Settling rate is β in Musgrave and Lutscher (2014), and is not used in this paper, following appendix S4 in Crone et al. 2019). We find it convenient to present results of this model in terms of the % habitat on the landscape, $100 \times \frac{l_1}{l_1+l_2}$ and the landscape period, $l_1 + l_2$. In order to relate this model to monarch butterflies, we assume that their milkweed hostplants are “habitat” and areas without milkweed are “non-habitat”. For the calculations in this paper, we used a 1-km period, and explored the effects of % milkweed habitat only. For comparison across models, we convert cover of milkweed habitat to milkweed stems assuming one stem per m^2 (cf. Hartzler 2010).

For parameters relevant to monarch butterflies (Table 1), this model predicts an increasing but nonlinear relationship between population growth rate and milkweed density (Fig 1B). There are two fundamental differences between host-limitation due to search time (this model) and host-limitation due to resource competition (the previous model):

First, in the search-time-limitation model, host plant density affects population growth rate, as opposed to production of individuals (carrying capacity). In practical terms, search-time limitation means that butterfly populations might continue to grow or decline, even when host plant density is not changing. A common assumption of conservation plans (at least for monarch butterflies) is that host plant density determines the number of individuals, which means that if host plant density were constant, butterfly populations would be constant. In the presence of search time limitation, a shift of host plant density to below the threshold for growth would cause populations to decline over time, even if the host plant density remained constant at its new, lower level.

Second, in the search-time-limitation model, the relationship between host plant density and butterfly population growth rate is nonlinear, with a steeper slope at lower host plant densities. In practical terms this relationship means that, in the presence of search-time limitation, a given amount of habitat augmentation has a larger impact on growth rate in areas with low % habitat, i.e., low milkweed cover.

Effects of host plant densities on butterfly population dynamics

To illustrate the contrasting effects density-dependent resource competition vs. search-time limitation for on population viability, we use each to project population dynamics in landscapes with different host plant densities. In the US, most Monarch butterflies have a migratory life cycle, with ~4 summer breeding generations, followed by a migratory generation that overwinters in Mexico (for most butterflies from the eastern and central US) or coastal California (for most butterflies in the western US). Survival during migration and overwintering

is low; and on the order of 0.5% of butterflies that overwinter survive to breed the next spring, and those butterflies often have reduced reproductive success (Table 1).

Density-dependent limitation: In the presence of density dependence, annual population dynamics starting from a population ending one year at carrying capacity can be predicted by:

$$N_0 = \theta_{OW} M \frac{\ln(0.5F\theta_P\theta_F - 1) + \beta_0}{\beta_1 F} \quad \text{Eq. 9a}$$

$$N_1 = \frac{N_0 0.5F\rho\theta_P\theta_F}{1 + \exp\left(\beta_1 \frac{N_0 F \rho}{M} - \beta_0\right)} \quad \text{Eq. 9b}$$

$$N_{t+1} = \frac{N_t 0.5F\theta_P\theta_F}{1 + \exp\left(\beta_1 \frac{N_t F}{M} - \beta_0\right)} \quad \text{for } t > 0 \quad \text{Eq. 9c}$$

where θ_{OW} is survival rate through migration and overwintering, ρ is proportional reduction of fecundity for monarch butterflies from the overwintering generation, and all other parameters are as defined above, noting that the starting population size is determined by the carrying capacity from eq. 4, $M \frac{\ln(0.5F\theta_P\theta_F - 1) + \beta_0}{\beta_1 F}$ (Figure 1A). This method of projecting population dynamics assumes that host plant densities are reset each generation, which could be caused by phenological turnover of host plant species (Yang and Censer 2020) or, in the case of monarch butterflies, movement to other parts of the breeding range.

Model predictions are consistent with the common assumption that end-of-season monarch butterfly population sizes are determined by their carrying capacity in the sense that monarch butterflies are predicted to reach or exceed capacity within three breeding generations (Fig 2A & 3A). This simplified version of a density dependent population model leads to dynamics that overshoot and undershoot equilibrium (Figure 2A). This possibility is not mentioned in most papers about density dependence in monarch butterflies (e.g.,

(Flockhart et al. 2015; Marini and Zalucki 2017, but see Yakubu et al. 2004). Therefore, we compare predictions with and without a population ceiling set at the estimated carrying capacity (Fig 3A). Over multiple years, population driven by density dependent host plant limitation would be expected to remain at the ceiling set by milkweed density (Fig 3B) or, possibly, exhibit multi-year fluctuations around carrying capacity, driven by density dependence (Fig 2B).

Search-time limitation: In the presence of search-time limitation, we can project annual population dynamics using the following equations:

$$N_0 = \theta_{OW} N_{prev} \quad \text{Eq. 10a}$$

$$N_1 = \lambda_\rho N_0 \quad \text{Eq. 10b}$$

$$N_{t+1} = \lambda_{ST} N_t \quad \text{for } t > 0 \quad \text{Eq. 10c}$$

where λ_{ST} is calculated from eq. 8 using breeding season parameters, λ_ρ is calculated from eq 8 using fecundity adjusted for reduced oviposition of the overwintering generation by substituting $\rho \hat{r}_1$ for $\hat{r}_1$, and N_{prev} is the size of the monarch butterfly population at the end of the previous summer. For comparison with density-dependent model predictions, we started one-year projections from the density-dependent carrying capacity, i.e., $N_{prev} =$

$$M \frac{\ln(0.5F\theta_P\theta_F-1)+\beta_0}{\beta_1 F}.$$

The search-time limitation model predicts that, for landscapes with ≥ 15 host plants per Ha, butterfly populations will grow over the course of the year, i.e., exceeding the starting size at the end of the previous year (Fig. 2C & 3C). However, for landscapes with < 15 host plants per Ha, butterfly populations end the year with fewer butterflies than they started with. Not surprisingly, these within-year patterns translate to long-term growth (Fig. 2D), or possibly

growth to a population ceiling (Fig 3D), for populations in landscapes above the host plant threshold for growth (here, ~15 host plants per Ha), and to long-term declines for populations below the host plant threshold for growth.

Discussion

Host plants regulate herbivore populations through both density dependent resource competition and density-independent search time limitation. Spatial models in conservation biology rarely consider the costs of search time for reproductive success; instead, movement and population dynamics are typically treated as separate processes in metapopulation and landscape models (see, e.g., Nathan et al. 2008, Howell et al. 2018, but see McIntire et al. 2007). This is in contrast to decades-old literature in population ecology (reviewed by Dempster 1983) which recognizes that a failure to have enough time to reproduce is a key factor limiting insect populations. Although time-limited butterfly fecundity could be due to in part poor weather for butterfly activity (Doak et al. 2006), it is reasonable to assume that search time limitation is important in at least some species. Together, the possibilities of resource competition and search-time limitation emphasize the fundamental importance of host plant availability in limiting herbivore populations. However, the difference between how these mechanisms act points to the fundamental importance of knowing the conditions under which each mechanism is likely to be important.

The greatest difference between search time limitation and density-dependent resource limitation is that search time limitation affects population growth rate, whereas host plant limitation affects population size. This property means that search time limitation can create

an extinction debt (*sensu* Kuussaari et al. 2009; Tilman et al. 1994). In situations where habitat loss converts a landscape from one in which the maximum population growth rate is positive to one in which it is negative, populations will continue to decline for many years after habitat destruction has stopped, eventually going extinct. Borrowing from metapopulation-based extinction debt models (Hanski and Ovaskainen 2002) it seems likely that such extinction debts will last longest when a population shifts from just above its minimum habitat requirements for positive growth to one in which search time limitation leads to population declines. This kind of situation may explain why monarch butterflies have continued to slowly decline during the past 15 years (Zylstra et al. 2021), even though the amount of milkweed in the landscape seems to have been relatively constant during this period. This possibility contrasts with the conclusions of Zylstra et al. (2021) who inferred that habitat loss was not likely to be the cause of recent monarch butterfly declines, because habitat conditions were relatively constant during a period of population decline.

Of course, both of the models we explore here are simplifications compared to real landscapes. One of the biggest advantages to the search time limitation model presented here is that it is a relatively simple integrodifference equation (IDE) from which estimating a population growth rate is a simple calculation. We believe that this kind of simple calculation is an excellent first step to predicting population dynamics in heterogeneous landscapes, especially when the specific landscape geometry is unknown, or subject to change. Use of simple IDEs is conceptually analogous to the use of structured matrix models (Caswell 2001) in population ecology (see further discussion in Crone et al. 2019). However, this elegance comes with two caveats. The first is that λ_{ST} in eq 8 is an asymptotic growth rate, similar to the long-

term growth rate in a structured matrix model (cf. Caswell 2001, Musgrave and Lutscher 2014). Like projections from matrix models, spatial dynamics of integrodifference models undergo a period of transient dynamics before stabilizing to a steady state growth rate (Caswell et al. 2011). The second caveat is that real landscapes have more complex geometries than the simple periodic landscapes that underpin eq. 8. If monarch butterfly population growth is search time limited, exploring more spatially realistic models would be a useful next step to improving our estimates of growth rates in relation to host plant densities. One advantage of the simple IDE framework is that such models can be solved numerically for particular landscapes and transient dynamics – these solutions are much more mathematically complex than eq 8, but it is still a calculation, not a simulation (see further discussion in Ovaskainen and Crone (2009) in the context of ODEs for spatially heterogeneous landscapes).

One of the most obvious assumptions of the resource-competition models we used in this paper is that host plant density on the landscape is constant from one generation to the next – even within a breeding season. In other words, habitat is reset each generation, and caterpillars only compete within a generation. This assumption may be reasonable for monarch butterflies, in the sense that monarch butterfly populations expand through the landscape during breeding season (Flockhart et al. 2013), with the potential to encounter fresh host plants as the population moves northward. Migration during breeding season could also explain the surprising (but see Yakubu et al. 2004) result that monarch butterfly populations are predicted to overshoot and undershoot carrying capacity. If a monarch butterfly population is expanding to a greater area during each breeding generation, competition could be weaker than predicted by these spatially implicit models. Monarch butterflies have been observed to avoid ovipositing

on plants that already have eggs (Borkin 1982; Zalucki and Kitching 1982b). It is interesting to speculate that this behavior might cause them to expand their ranges more quickly during breeding season, and, under conditions when populations are not search-time limited, reach the population ceiling set by milkweed without overshooting it.

The assumption that habitat is reset between each generation might be less reasonable for non-migratory multivoltine insects, because they inhabit the same landscape during the entire growing season. However, for both migratory and non-migratory species, there may also be phenological turnover within a region such that a butterfly population uses different hostplant species throughout a growing season. It seems unlikely that consumption of host plants would change the qualitative behavior of the resource competition model, in the sense that butterflies would reach (or possibly cycle around) an equilibrium set by host plant densities. If monarch butterflies were limited by resource competition for milkweeds, understanding the mechanisms of competition and inter-generational feedback on milkweed densities would be valuable for tuning the model to make specific predictions about monarch butterfly population dynamics. It could also be ecologically important – and an interesting area of mathematical exploration – to combine resource competition and search time limitation into a single population model.

As a first approximation, we can infer that the transition from search-time limitation to density-dependent resource competition occurs at the density at which populations grow, rather than decline, over multiple years in the presence of search time limitation (Figure 2D). For the parameters we used in this study, this transition occurs at about 15 milkweed stems per hectare for monarch butterflies. Milkweed densities are probably near or below this threshold

in the United States. For example, using estimates from Pleasants & Oberhauser (2013) there is about 13.5 m²/Ha of milkweed cover in agricultural landscapes in Iowa, with habitat-specific cover ranging from 5 m²/Ha in agricultural fields to 99 m²/Ha on roadsides (Supplement 3, Pleasants and Oberhauser 2013). If milkweed cover in this landscape translates to approximately one milkweed stem per m² (in milkweed habitat), then we would expect monarch butterfly populations to be search time limited in this landscape. In a survey of urban cities in the US midwest, Johnston et al. (2019) estimated milkweed densities of 24.1, 26.6, 8.2, and 18.8 stems / Ha of plantable land in Chicago IL, Minneapolis-Saint Paul MN, Kansas City MO, and Austin TX (respectively). Johnston et al. (2019) do not directly report the total proportion of plantable space, but it would need to be greater than 50% for monarchs to be above the threshold for search-time limitation in any of these cities. During surveys of public lands (probably the highest quality lands for monarchs) in Nevada, McKnight (2016) found ~ 25 milkweed stems per Ha, a number only slightly above the threshold for search time limitation; if we account for the smaller size of milkweeds species in the study region, habitat cover is likely well below the threshold for search time limitation (see Supplement 3). These calculations come with the caveat that they represent only a tiny fraction of the total land cover used by monarch butterflies in North America, and that our parameter estimates for monarch butterflies were gathered from scattered sites throughout their global range. Nonetheless, they imply that search time limitation may be the primary way in which milkweed limits monarch butterfly populations in North America.

Despite limited recognition of the role of time costs of movement in spatial conservation models and conservation planning, time constraints are widely recognized as an

important factor limiting populations. Depending on study focus, taxa and era of research, time constraints have alternatively be called discovery time, dispersal time, migration time, or search time (Barnay et al. 1999; Hassell and May 1974; Hassell and Southwood 1978; Waage 1979). These processes emerge from the large diversity of mechanisms by which organisms locate resources including behavioral strategies such as area restricted search (e.g. Kareiva and Odell 1987), visual cues of focal resources and/or physical habitat structure, chemical cues such as from secondary compounds (Li et al. 1997), limited time to find resources (Wajnberg 2006) or densities of conspecifics (Barnay et al. 1999). One challenge to integrating time constraints into conservation planning is that the same basic process has been referred to in many different ways in the scientific literature. Nonetheless, they all boil down to situations in which the individual spends too much time looking for resources to meet its physiological reproductive capacity. We hope this case study inspires more researchers to investigate the importance of search time limitation for population viability in fragmented landscapes. For mathematical biologists interested in IDEs, there are a wide range of avenues for making the basic search-time limitation models more realistic. For ecologists interested in insect conservation, it is important to remember that host plants can limit insect populations, even when many host plants exist – and remain uneaten – in highly fragmented landscapes

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Table 1. Demographic parameters used to create contrasting models with monarch butterflies limited by density dependent survival of eggs on milkweeds (DD) vs. search time limitation based on contact rates with milkweed (ST).				
Parameter	Value	Source	Used in model?	
			DD	ST
m , mortality per second	1.53e-6	calculated from longevity in field cages (23.25 days, Altizer and Oberhauser 1999; their Fig 4.), converted to survival/sec assuming 8 hours of active time/day		X
F , lifetime eggs/female	579.2	Calculated from lifetime fecundity used by Flockhart et al. 2015 (715 eggs), adjusted for mortality in field cages (23.25 days; Altizer & Oberhauser 1999), compared to glassine envelopes (28.7 days; Flockhart et al. 2015); $715 * (23.25/28.7) = 579.2$	X	
β_0 & β_1 , slope and intercept of density-dependent survival	1.0175 -0.1972	(Flockhart et al. 2012)	X	
$\hat{r}$, maximum per-generation growth rate in milkweed habitat	12.05	Calculated from parameters used by Flockhart et al. 2015, adjusted for mortality in field cages (Altizer & Oberhauser 1999); $579.2 * 0.049 * 0.849 * 0.5 = 12.05$ (noting the 0.5 multiplier for female eggs per female)	X	X
p_{max} , max. survival	0.7345	Flockhart et al. 2015, using larval and pupal survival data from (Oberhauser 1997	X	

from egg to adult				
$\bar{z}$, pref at patch edges	0.33	calculated from data in (Zalucki and Kitching 1982a); analysis in Supplement 1		X
D_1 , movement in habitat (m ² /sec)	0.6	Based on data from Zalucki and Kitching (1982a), Fisher et al. (2020), Crone (unpubl); analysis in Supplement 1		X
D_2 , movement in matrix (m ² /sec)	10,000	Estimated from resight data in Nagano et al. (1993); analysis in Supplement 1		X
<i>Additional parameters for full life cycle models</i>				
θ_{ow} , Survival during fall migration & overwintering	0.006	Estimated from resight presented by James et al. (2018; see Suppl. S3 in Crone & Schultz (2021), multiplied by overwintering survival (from Pelton et al. 2019).	X	X
ρ , Reduced fecundity of first breeding generation	0.43	Crone, Schultz, Warchola & Thomas, unpubl. data; see analysis in Supplement 2.	X	X

Figure legends:

Figure 1. Basic predictions model predictions for (A) density-dependent and (B) search-time host plant limitation. In (A) lines represent recruitment curves at different host plant densities, and the dotted line is the 1:1 line. Carrying capacity for each model is the point at which the curve intersects this 1:1 line. In (B) curves represent growth rates calculated for the main breeding generation (λ_{ST}) and the overwintering generation (λ_p). For further discussion of λ_{ST} and λ_p , see “Effects of host plant densities on butterfly population dynamics” in the main text.

Figure 2. Predicted trajectories from models as written, including overcompensating density dependence in the density-dependent models (A&B) and exponential growth in the search-time models (C&D). Left panels (A&C) show changes within one breeding season and right panels (B&D) show dynamics over 15 years. Dotted lines indicate the carrying capacity associated with the density-dependent model for each scenario, which was also used as the starting size.

Figure 3. Predicted trajectories from models with a population ceiling set at the carrying capacity calculated from the resource competition model. Left panels (A&C) show changes within one breeding season and right panels (B&D) show dynamics over 15 years. Dotted lines indicate the carrying capacity associated with the density-dependent model for each scenario, which was also used as the starting size.

(Figure 1)

(Figure 2)

A. Resource competition, within-year

B. Resource competition, among-year

C. Search-time, within-year

D. Search-time, among-year

(Figure 3)

Supplementary Files

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