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Patterns and causes of oviposition in monarch butterflies: Implications for milkweed restoration

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ABSTRACT

Effective habitat restoration requires an understanding of species habitat preferences and the associated mechanisms driving those preferences. We examined the patterns and causes of oviposition preference in the monarch butterfly, a rapidly declining species, in southwestern Ontario at both landscape and milkweed patch spatial scales. Additionally, we measured the abundance of invertebrate predators, parasitoids and parasites across these same spatial scales. Oviposition preference was dependent on both the size of the milkweed patch and the density of milkweed within the patch, as well as landscape type. Small (< 16 m^2), low-density (0.1–2 milkweed per m^2) milkweed patches in agricultural landscape had the highest egg density compared to all types of milkweed patches in non-agricultural and roadside landscapes. Medium-sized patches had the highest predator abundance. Variation in the abundance of parasitoids, and occurrence of parasites of monarch eggs and larvae did not appear to coincide with preferred egg laying habitats. Our results suggest that investing heavily in milkweed restoration in roadside habitats should be done cautiously. Instead, a better strategy may be for managers to develop incentive programs with landowners to plant and maintain milkweeds in agricultural landscapes, which could complement other pollinator initiatives or ecosystem service programs in agricultural landscapes that focus on increasing nectar availability. Our results have important implications for restoring milkweed as an approach to counteract monarch butterflies declines.

1. Introduction

Habitat loss is one of the leading causes of species decline and extinction worldwide (Wilcove et al., 1998; Pimm and Raven, 2000; Ceballos and Ehrlich, 2002; Kerr and Cihlar, 2004; Venter et al., 2006). Although not applicable to all species, one way to mitigate the negative effects of habitat loss is through active habitat restoration (Kareiva and Wennergren, 1995; Fahrig, 1997; Wisdom et al., 2002). However, realizing optimal gains in restoring habitat requires detailed and accurate knowledge of species habitat preferences. It is well known that mobile animals make decisions about where to settle based on multiple spatial scales, from landscapes to microenvironments, with the animal relying on different cues to identify a suitable site (Johnson, 1980). Even if it is known what type of habitat a species prefers and at what spatial scale (Åström et al., 2013; Camaclang et al., 2015; Foit et al., 2016), the spatial configuration of the habitat can also influence settlement patterns (Pulliam et al., 1992; Lewis et al., 1996; Huxel and Hastings, 1999). For example, patch area (Freemark and Merriam, 1986; Davis, 2004; Winter et al., 2006), patch shape (Davis, 2004; Weldon and Haddad, 2005), connectivity (Schadt et al., 2002; O'Brien et al., 2006), fragmentation (Hunter et al., 1995; Pereboom et al., 2008), and habitat heterogeneity (Freemark and Merriam, 1986; Hunter et al., 1995; Heikkinen et al., 2004) have all been shown to influence individual choice (Bergin et al., 2000; Misenhelter and Rotenberry, 2000; DeCesare et al., 2014) and, in some cases, settlement preferences. Additionally, the preference of a species for particular habitat or habitat feature can also depend on the larger spatial scale in which it exists (Mazerolle and Villard, 1999; Boyce et al., 2003; Quevedo et al., 2006; Mayor et al., 2009). Knowledge of what factors can influence species habitat preferences is important for effective restoration.

The eastern North American population of monarch butterflies (*Danaus plexippus* L.; Lepidoptera: Danainae) has declined by 95% in the last 20 years (Brower et al., 2012) and the population is at a high risk of extirpation (Semmens et al., 2016). Butterflies of the last generation of the summer migrate up to 4000 km to the overwintering sites in central Mexico where they congregate in massive clusters in oyamel fir (*Abies religiosa*) forests (Urquhart and Urquhart, 1976; Brower, 1996). In the

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spring, the same individuals mate and migrate north to breeding grounds, and over successive generations that follow, repopulate northern areas (Cockrell et al., 1993; Malcolm et al., 1993; Miller et al., 2012; Flockhart et al., 2013). Summer breeding individuals that live for 2–5 weeks travel comparatively shorter distances in search of nectar, mates, and egg-laying locations (Oberhauser, 2004). Monarchs oviposit – lay their eggs – exclusively on milkweeds of the subfamily Asclepiadoideae (milkweeds), typically singly on the undersides of leaves (Urquhart, 1960) and most commonly one per plant (Zalucki and Kitching, 1982a). Milkweed provides both food and a chemical defense for the developing larvae (Parsons, 1965; Rothschild et al., 1966; Brower, 1984).

While a number of factors have been proposed for the population decline of monarchs, recent population models have shown that monarch abundance is more sensitive to the decline of milkweed, the obligate larval host plant, on the breeding grounds compared to deforestation or rising temperatures on the overwintering grounds in Mexico (Flockhart et al., 2015; Semmens et al., 2016; Pleasants et al., 2017 but see Inamine et al., 2016). The most significant reduction of milkweed has occurred in agricultural fields due to the use of glyphosate herbicides to kill weeds (Pleasants and Oberhauser, 2013). The increase in the use of glyphosate herbicides follows the adoption of genetically modified (GM) crops, notably corn and soybean, altered to be glyphosate-tolerant (Padgette et al., 1996; Duke and Powles, 2008). This has reduced the number of milkweed in North America, most severely in the central midwestern United States (Hartzler, 2010; Pleasants and Oberhauser, 2013; Pleasants, 2017), a significant region of monarch production (Wassenaar and Hobson, 1998; Oberhauser et al., 2001; Pleasants and Oberhauser, 2013; Flockhart et al., 2017a). For example, one study estimated that the 2.2 billion milkweeds present on the landscape in the central Midwest in 1999 had declined by almost 40% by 2014 (Pleasants, 2017). Another study estimated changes in agricultural weed management in Illinois led to an estimated 68% loss of available milkweed for monarchs in the last two decades (Zaya et al., 2017). To counteract the loss of milkweed on the breeding grounds, habitats could be restored to increase the availability of egg laying sites. Thus, it is imperative to understand the causes of monarch butterfly oviposition preference in different landscapes and the spacing of milkweed plants to determine the most effective restoration strategy on the breeding grounds.

To date, studies examining female preferences for oviposition sites have largely consisted of counting eggs and larvae on milkweed in agricultural and non-agricultural landscapes (Oberhauser et al., 2001; Pleasants and Oberhauser, 2013; Kasten et al., 2016). Agricultural landscapes have been shown to contain a higher number of eggs per plant than non-agricultural landscapes (Oberhauser et al., 2001; Pleasants and Oberhauser, 2013). Roadsides, previously categorized as non-agricultural landscape with natural areas, have been proposed as a potentially suitable area for milkweed restoration due to the abundance of roads and availability of land on road margins (Hartzler and Buhler, 2000; Taylor and Shields, 2000; Oberhauser et al., 2001; Hartzler, 2010; Pleasants and Oberhauser, 2013). However, a recent study showed that roadsides have significantly lower egg per plant densities than non-agricultural areas, which included gardens, natural areas, pastures, and old fields (Kasten et al., 2016). There has yet to be a comprehensive study to compare all landscapes concurrently in the same region.

In addition, the mechanisms driving the oviposition preference among landscapes are not well understood. Females may prefer to oviposit in agricultural landscapes over non-agricultural landscapes and roadsides because agricultural landscapes may have fewer invertebrate predators. This pattern could arise from the use of agro-chemicals, specifically insecticides targeted to kill insects, as well as herbicides, which could reduce habitat for invertebrate predators. Conversely, females may prefer non-agricultural landscapes to oviposit due to the greater availability of nectar sources, which may lead to lower foraging times, better lipid reserves and, ultimately, a larger number of eggs laid (Brower et al., 2015).

Monarch oviposition preference could also be influenced by the spatial configuration of habitat, such as the size or density of the milkweed patch. Low-density milkweed patches and single individual milkweed plants have been shown to contain a higher number of eggs per plant than high-density milkweed patches both in agricultural fields (Oberhauser et al., 2001; Pleasants and Oberhauser, 2013) and in natural areas (Zalucki and Kitching, 1982a; Zalucki and Suzuki, 1987). However, this pattern in natural areas has only been shown in Australia where monarchs have been introduced and breed year-round in some regions, and it is not known whether the same pattern would occur in the eastern North American population in a different ecosystem containing different milkweed species. While valuable, these studies also do not explain the possible mechanisms behind these patterns. Females may seek small milkweed patches to avoid natural enemies because large patches may be easier for predators, parasitoids, and parasites to find and could support their populations better than a smaller patch (Zalucki and Kitching, 1982b). A protozoan parasite that monarchs are susceptible to is *Ophryocystis elektroscirrha* (OE), which in heavily infected individuals can result in short adult lifespans, reduced body size, lower mating success, decreased flight ability, and failure to eclose, emerge as an adult properly (Altizer and Oberhauser, 1999; De Roode et al., 2007). The occurrence of OE in monarchs has not been examined in relation to the size of the milkweed patch they inhabit. The rate of OE infection in monarchs could be higher in larger milkweed patches that are frequented by more adult butterflies, potentially increasing the spread of OE to other adults or to milkweed leaves. Investigating which features in the landscape drive oviposition selection could help guide where restoration efforts should be focused.

Here, we examined the factors that drive monarch butterfly oviposition preference by monitoring the number of eggs and larvae in different landscapes (agricultural, non-agricultural, and roadsides) in patches of milkweed, *Ascelpias syriaca*, of varying sizes and densities, and by measuring the abundance of invertebrate predators and parasitoids and the occurrence of the protozoan parasite, OE, in adults that emerged from collected fifth instars. Our hypotheses were considered at two spatial levels: the 'landscape' and 'patch' level. At the landscape level, previous literature suggests that agricultural landscape contains a higher number of eggs per plant than non-agricultural landscape (Oberhauser et al., 2001; Pleasants and Oberhauser, 2013) that may arise because females avoid invertebrate predators, parasites, and parasitoids. We predicted that egg densities would therefore be higher in agricultural landscape compared to non-agricultural landscape and roadsides. Following this same hypothesis, we also predicted that invertebrate predators, parasitoids, and rate of OE infection would be lowest in agricultural landscapes and highest in non-agricultural landscapes due to reduced vegetation biodiversity because of the use of agro-chemicals. At the patch level, prior evidence suggests that low-density patches, single and small milkweed patches, contain higher egg densities than high-density milkweed patches in both agricultural fields (Oberhauser et al., 2001; Pleasants and Oberhauser, 2013) and natural areas (Zalucki and Suzuki, 1987) due to fewer predators, parasitoids, and parasites locating and breeding in small and low-density patches. Thus, we predicted that number of eggs per milkweed would be negatively related (i) to milkweed density in a patch and (ii) to patch size, as measured by monitoring milkweed patches of different sizes and densities in different landscape types. In addition, we predicted that estimated abundance of invertebrate predators and parasitoids, as well as the rate of infection of OE, would be positively related to milkweed density in a patch and to patch size.

2. Methods

2.1. Study sites & experimental design

We conducted our study from Jul 13–Aug 21, 2015, Jul 11–Aug 19, 2016 in Norfolk, Oxford, and Brant Counties in southwestern Ontario,