

**AN EVALUATION OF BUTTERFLY GARDENS AS
RESTORATION TOOLS USING THE MONARCH BUTTERFLY
*DANAUS PLEXIPPUS***

by

Brian Thomas Cutting

A thesis submitted to the Faculty of the University of Delaware in partial fulfillment
of the requirements for the degree of Master of Science in Entomology

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Approved: _____
Douglas W. Tallamy, Ph.D.
Professor in charge of thesis on behalf of the Advisory Committee

Approved: _____
Douglas W. Tallamy, Ph.D.
Chair of the Department of Entomology and Wildlife Ecology

Approved: _____
Robin Morgan, Ph.D.
Dean of the College of Agriculture and Natural Resources

Approved: _____
Charles G. Riordan, Ph.D.
Vice Provost for Graduate and Professional Education

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ABSTRACT

As human influence continues to expand into natural areas, the ecological systems that support biodiversity and human populations are failing; most land has been transformed from functional habitat into unsustainable landscapes that suit current human needs. Residential areas are often managed to meet aesthetic and cultural norms, but wildlife gardening holds promise as an acceptable method for sharing human dominated landscapes with plants and animals. In particular, butterfly gardening with suitable host plants can attract breeding Lepidoptera to residential properties, and support higher trophic levels in the process. Despite the popularity of this movement, few studies have evaluated the usefulness of gardens to wildlife by measuring the fitness of multiple stadia of target insects. One study has shown that, if managed improperly, gardens could be ecological traps which are attractive as oviposition targets but support higher mortality, thereby lowering regional populations of the very organisms that they are intended to conserve. I studied the monophagous monarch butterfly *Danaus plexippus* L. and how it is affected by butterfly gardens containing its *Asclepias* host plants. I found increased oviposition on milkweed in gardens over milkweed in natural areas. There was no difference in total sub-adult survival between garden and natural sites, and differences in survival of eggs and larvae were not consistent through the two years of the study. It is likely that isolated

patches of milkweed, as are often found in gardens, are more frequently encountered by ovipositing females, and larval mortality factors are density independent. These results suggest that butterfly gardens with milkweed may serve as source habitats for monarchs, and would thus be useful as a restoration tool for this specie

Chapter 1

INTRODUCTION

Butterfly Gardening and Habitat Restoration

Home gardens represent both opportunities and challenges to restoration ecologists. In the United States alone, residential areas cover an estimated 38 million hectares (Lubowski et al., 2006). In adherence to social norms and pressure from industry advertising, most residences are landscaped in a stereotypical fashion dominated by Eurasian cool season turf grasses and introduced ornamental plants that provide few ecological services, and poor habitat (Jenkins, 1994; Blair and Launer, 1997; Milesi et al., 2005; Tallamy, 2009). For example, a survey in Pennsylvania, Maryland and Delaware found that 92% of the residential landscape was lawn, 79% of the existing plants were alien, and managed landscapes contained only 10% of the tree biomass found in nearby woodlots (Tallamy et al., submitted). In the face of the global extinction crisis (Butchart et al., 2010), an effort is underway to educate and encourage homeowners to manage their land in a way that increases its value as wildlife habitat (Miller and Hobbs, 2002; Tallamy, 2009).

Providing habitat for Lepidoptera (butterflies and moths) is a restoration goal that many hobbyist gardeners have readily adopted. In addition to the aesthetic value of conspicuous and charismatic butterflies, these insects are important targets for restoration because of their function as pollinators (Kearns et al., 1998) and their crucial role in food webs (Burghardt et al., 2010). Despite the musings of a magazine

article that “Butterflies appear out of thin air when you grow [flowers]” (McKeon, 2009), gardeners are becoming increasingly aware that most Lepidoptera can only reproduce and develop on specific host plants with which they have coevolved (Bernays and Graham, 1988; Ehrlich and Raven, 1964). Butterfly gardeners are incorporating larval host plants in addition to the nectar-rich flowers that are traditionally used to attract adults to landscapes. This represents a paradigm shift from butterfly gardening as a hobby based only on aesthetics and entertainment towards intentional and biologically relevant restoration of habitat in traditionally sterile urban and suburban landscapes.

Personal observations by gardeners and researchers alike have led to the assumption that planting appropriate host plants in butterfly gardens will support reproduction and development of Lepidoptera, and can boost regional population numbers. Some studies have found support for this assumption, but have done so by only quantifying adult visitation rather than the production of caterpillars within butterfly garden habitats (Mathew and Anto, 2007; Konvicka and Kadlec, 2011). The assumption that more host plants in the landscape leads to more butterflies has been largely unchallenged despite evidence that in some landscape settings, butterfly gardens may have little to no impact on populations of Lepidoptera beyond aiding dispersal to suitable habitat (Vickery, 1995). For certain species it has even been suggested that gardens with host plants may function as ‘ecological traps’ that have a detrimental effect on population size rather than boosting regional butterfly abundance (Levy and Connor, 2004). Thus, from a conservation perspective, the need to quantify the conservation value of residential butterfly gardens is obvious and immediate.

Source – Sink Habitats Vs Ecological Traps

The concept of the ecological trap pre-dates but is related to source-sink theory (Gates and Gysel, 1978). All landscapes are heterogeneous at some scale and present a variety of habitat conditions. Varied resources and pressures dictate that for any given organism, some patches will be ‘good’ habitat that supports high fecundity and survival, while other patches that are less supportive will be associated with higher mortality and lower reproductive success. Pulliam (1988) defined a source habitat as a ‘good’ patch where birth is greater than death, and emigration is greater than immigration (a net exporter of individuals to the population); the converse, a sink habitat, is a net importer of organisms from the population. He recognized that organisms may regularly live and breed in sink habitats, and therefore the classification of a source or a sink may be influenced as much by its spatial relationship to other habitat patches as it is by conditions within the patch. Furthermore, a matrix of sources and sinks jointly may support a larger and more stable regional metapopulation than would sources alone (Hanski and Simberloff, 1997; Holt, 1997; Pulliam, 1988)

A third classification within the source-sink framework is that of a pseudo-sink: a habitat patch that has high rates of immigration into the site (Watkinson and Sutherland, 1995). If immigration is halted, the local population will decrease to a level where density-dependent mortality factors are reduced, and the patch becomes a source (Watkinson and Sutherland, 1995). Pseudo-sinks have been demonstrated in populations of butterflies when a source was destroyed, and multiple nearby pseudo-sinks became lower level sources (Boughton, 1999).

An ecological trap is a poor quality 'sink' habitat that preferentially draws immigrants from better quality habitat (Gates and Gysel, 1978). Typically, a trap is the result of anthropogenic change to which organisms are maladapted; given enough time, the presence of a trap will theoretically lead to extinction of a population (Battin, 2004). A hypothetical example of an ecological trap would be a house with several bird feeders as well as a colony of feral cats; birds could be drawn to the patch because of the abundance of food resources, and subsequently be subjected to unsustainably high predation.

Ecological traps have been demonstrated in several species, including a Lycaenid butterfly that preferentially oviposits in restored wetlands where periodic human-controlled flooding kills larvae and leads to a seven-fold reduction in survival (Severns, 2011). In a study on a Californian population of pipevine swallowtail (*Battus philenor* L.), Levy and Connor (2004) found lower rates of oviposition and lower rates of survival in gardens than in areas where the pipevine (*Aristolochia californica*) host plant was naturally occurring. They concluded that gardens could be functioning as ecological traps for that species, and discouraged their use for restoration purposes (Levy and Connor, 2004). If the restoration of ecosystem function within human-dominated landscapes is to succeed, we must ensure that recommendations to homeowners and land managers do not encourage the development of ecological traps. More research is needed to understand the conditions under which residential butterfly gardens serve as sources, sinks, or ecological traps for local species of Lepidoptera.

Objectives

Using an eastern population of monarch butterflies, *Danaus plexippus* L., and residential gardens as a model system, the objective of this study was to provide insight into whether intentional butterfly gardening should play a role in habitat restoration and efforts to conserve Lepidoptera. Central to this objective was identifying if butterfly gardens serve as ecological traps. To accomplish this, monarch oviposition and egg and larval survival rates were compared on milkweed host plants in butterfly gardens and in natural milkweed stands.

The Study Organism: *Danaus plexippus*

The monarch butterfly, *Danaus plexippus* L., and one of its host species, common milkweed, *Asclepias syriaca* L., were selected for this study because they are abundant and charismatic butterflies whose conservation fate has captured the public's interest. The monarch is easily recognized both during the adult stage and as a caterpillar (Wagner, 2005). This familiarity was an added benefit of this species because it facilitated the recruitment of volunteer citizen scientists in this project. Monarchs are specialists on milkweeds in the genus *Asclepias* and use most of the species present in North America (Oberhauser and Solensky, 2004). *Asclepias syriaca* is an acceptable host to monarchs, is found commonly throughout Pennsylvania and the East, and is presumed to be the principal host plant of monarchs in the region (Malcolm, et al., 1989). The large leaves and straight stalks of milkweed ramets make them easy to locate and identify in the field, and also facilitate searches for monarch eggs. Using common milkweed as an experimental host plant was also desirable

because it is relatively easy to propagate and manipulate at useful sizes compared to many woody butterfly host plants.

Little is known about monarch flight patterns during the breeding season, but anecdotal observations suggest that they are highly mobile, and capable of locating isolated patches of their host plants (Wagner, 2005). Patches of milkweed that were planted for this study were thus likely to have been encountered by monarchs, even if such patches were rejected as oviposition sites.

Monarchs are renowned for their round trip migration, an exceptionally rare phenomenon among insects. Despite the wealth of attention afforded monarchs as study organisms, they remain in the ‘not evaluated’ classification according to the IUCN red list of threatened and endangered species (IUCN, 2011). North American migrating populations of monarchs face a number of threats that could place them at risk of extinction. Logging within Mexican overwintering sites leaves migratory populations of monarchs vulnerable to high mortality during winter storms; recently a single storm was estimated to kill greater than 80% of overwintering monarchs in the large Conejos colony northwest of Mexico City (Brower et al., 2004). Monarchs may also suffer non-target effects from Bt corn, when genetically modified pollen settles on milkweed leaves and is ingested by larvae (Lang and Otto, 2010; Losey, et al., 1999). Monarchs are parasitized by an introduced species of Tachinidae, and have demonstrated a long-term shift in sex ratios toward a male-dominated population, possibly the result of differential mortality caused by a protozoan parasite (Davis and Rendon-Salinas, 2010). Adults are killed by the introduced Chinese Mantid *Tenodera sinensis* Saussure (Orthoptera: Mantidae), which hides among flowers and may ambush dozens of butterflies that visit for nectar (B. Cutting, personal observation).

This large mantid is the only insect that I regularly saw consuming adult monarchs. Hundreds of thousands of flying monarchs are struck by traffic during the fall migration (McKenna et al., 2011) while larvae are killed in untold numbers when fields and roadsides are routinely mowed during the summer months. Increasing threats to monarchs and population estimates trending towards decline underscore the importance of providing ample habitat in breeding regions, and sending robust populations of monarchs to their vulnerable overwintering locations every autumn. Determining whether butterfly gardens are useful for restoring monarch habitat is an important step in identifying the best ways to conserve this species, and will provide some indication as to whether gardens are a viable tool for restoring habitat for other species.

Chapter 2

METHODS

Site Selection

To compare how the habitat matrix surrounding host plants affects monarch butterfly populations I established 60 study plots in which I planted common milkweed (*Asclepias syriaca*). The 60 sites consisted of two treatments: 40 ‘natural’ treatment sites, and 20 ‘garden’ treatment sites. Of the 40 ‘natural’ sites, 20 were planted within 10 m of existing patches of *A. syriaca*, while 20 sites were planted in locations where they were isolated from other milkweeds by distance of 10 m or more. This distinction between ‘isolated’ and ‘milkweed present’ was to ensure that any observed trends were due to site location in the larger scale landscape, rather than proximity to other host plants. As no difference was detected between these sites, data from all natural sites were pooled for analysis. These 40 natural sites were assumed to be the experimental control.

The natural sites (40) (Figure 1) were selected in meadow areas at Longwood Gardens, and Cartmel retirement community both in Kennet Square, Pennsylvania. Areas on these properties were identified using satellite images on Google Earth software, and later scouted on the ground. These sites were chosen for their distance from managed landscapes, and similarity of sun exposure. I planted milkweed at these sites regardless of whether other milkweed was already present. This was to ensure that plants in the garden and natural treatments were of the same provenance.

Twenty ‘garden’ sites were established in areas where landscapes were under human management (Figure 2). The surrounding matrix at these sites consisted mostly of mowed cool-season Eurasian turf grasses and exotic ornamental shrubs. 2 of these sites were placed on the property of the Kendal/Crosslands retirement community, and 18 were established within the yards of homeowners who volunteered for the project. Volunteers had been previously recruited for the project by word of mouth, door-to-door visits in suitable neighborhoods, and with brochures left in the local library. All of the managed sites were less than 4 miles from Longwood Gardens.

Site Establishment

Asclepias syriaca seeds of Pennsylvania provenance were purchased from Ernst Conservation Seeds (www.ernstseeds.com). The seeds were cold-wet stratified to break dormancy. In early March of 2009, common milkweed seeds were wrapped in moist paper towels and placed into sealed petri dishes. The dishes were placed in a refrigerator at 38° F for three weeks, after which they were stored at room temperature as seeds germinated (adapted from recommendations from Susan Cook-Patton, Cornell University, personal communication, 2009). As individual seeds began to germinate they were removed from the paper towels and potted in flats of pro-mix growing media. This method provided poor germination rates and was labor intensive, so a different stratification method was adopted in 2010. Seeds were washed in a 5% bleach solution to prevent disease, and were placed on top of flats of moist sphagnum moss with a thin layer of sphagnum spread over top of the seeds (Wallace Pill and John Frett, personal communications). The flats were covered with

plastic wrap to prevent desiccation and placed in a refrigerator at 40° F. After one week, a refrigerator malfunction raised the temperature to above 65° F over a weekend, and many of the seeds germinated. These seeds were then potted in promix. Seedlings were grown in the greenhouse on warming mats and were repotted into 6" standard pots when roots began growing out of the drainage holes in pots. Heavy damage from thrips stunted the growth of some plants; therefore, all plants were treated with horticultural soap and the systemic insecticide Conserve™ (Spinosad) to control populations of thrips. Naive plants in the field are disproportionately vulnerable to herbivory (Susan Cook-Patton, Cornell University, personal communication 2009); therefore, plants were moved to a semi-protected outdoor location to harden off after the local frost-free date of May 10. Milkweed plants were transplanted to field sites in late May and early June. Seedlings had not been chemically treated for at least 5 weeks before placement in field sites.

Sites were prepared by using a string trimmer to remove all existing vegetation above ground level. Twenty milkweed plants were planted at each site, and hardwood mulch was used to slow the growth of other plants within sites. Each site consisted of a circular plot approximately 1 meter in diameter with milkweed plants spaced evenly within. An exception to that shape was made at two managed garden sites where volunteers requested that sites be located in a comparable area in an existing garden bed. Where possible, the same plants were used in the second year of the study. If 20 ramets did not regrow in the second year, new plants were added to the site to bring the total number of ramets to 20. In 2010 plants were watered weekly if no natural rain events were expected, and plants that were lost were replaced when possible.

Project 1: Oviposition Attractiveness

To determine if milkweed plants in a managed landscape are as attractive to adult monarch butterflies for oviposition as plants in a natural setting, all plants were regularly and thoroughly searched for monarch eggs and larvae. Encountered eggs and larvae were removed to ensure that they were not counted multiple times. Searching began as soon as adult monarchs were observed locally (7 July 2009 and 6 July 2010), and continued until early September when oviposition rates fell off. Because plants at some sites died or had depressed growth due to deer herbivory, the number of plants at each site was recorded at the time of egg search. Not all lost plants were replaced, due to constraints on time and the number of replacement plants available. Monitoring was discontinued at a given site if it had fewer than four healthy plants remaining. In 2010 many sites were lost early in the summer. Monitoring was halted in July while young plants were added to plots but was resumed August 20th after the added plants were well established. For consistency of comparisons, data from 2009 and 2010 were compared between August 20th, and September 3rd. Between these dates, there were four observations per site in 2009, and six per site in 2010. Data from these observations were from searches on half of the plants in a site, as the other half of the plants were used for the survival experiment during this time period.

Data Analysis: Oviposition rates were non-normal because particular sites often had no oviposition on given visits. Therefore, I used the non-parametric Kruskal-Wallis test ($\alpha = .05$) to compare oviposition in garden and natural sites.

Project 2: Quantifying Larval Survivorship

Data collection for Project 2 began in the third week of August when monarchs had reached high regional population numbers as determined by relative frequency of encounters with eggs and flying adults. Half of the plants in each plot were used for an artificial oviposition experiment in which one 1st instar larva was placed on each plant. Most of the larvae were not encountered again, and this experiment was abandoned. The second group of plants in each site was used to quantify survival at natural oviposition densities (as opposed to the artificial density placed on the first group of plants). In 2009 plants were initially searched, all eggs were circled with marker on the opposite side of the leaf from the egg to avoid influencing larval behavior, and all present larvae were recorded. On subsequent visits all eggs that had been added were circled and recorded, and total numbers of larvae and old eggs at a site were recorded. In 2010, data were collected similarly; however, each ramet was treated as a separate data entry, and the estimated developmental stage of each larva was also recorded. This allowed me to better follow the development of larvae on each plant, whereas in 2009 data was only recorded on the site level. I calculated sub-adult mortality by measuring mortality of all eggs and larvae. I further subdivided the sub-adults into the component cohorts to determine which age class has the largest impact on sub-adult survival.

Data Analysis: The larval placement experiment failed and was not analyzed. To compare larval survival at natural oviposition densities in both treatments I used a

Kaplan-Meier procedure for staggered entry of animals, and a log-rank test ($\alpha = .05$) to check for statistical differences between the two treatments (Pollock et al. 1989).



Figure 1. Locations of natural sites. The blue shaded area is the Longwood Gardens property in Kennett Square, PA. Orange ‘C’ sites and Green ‘MP’ sites are natural sites planted in meadows. The MP sites are within 5 meters of existing stands of *A. syriaca*. Blue ‘M’ sites are gardens planted in heavily managed landscapes.

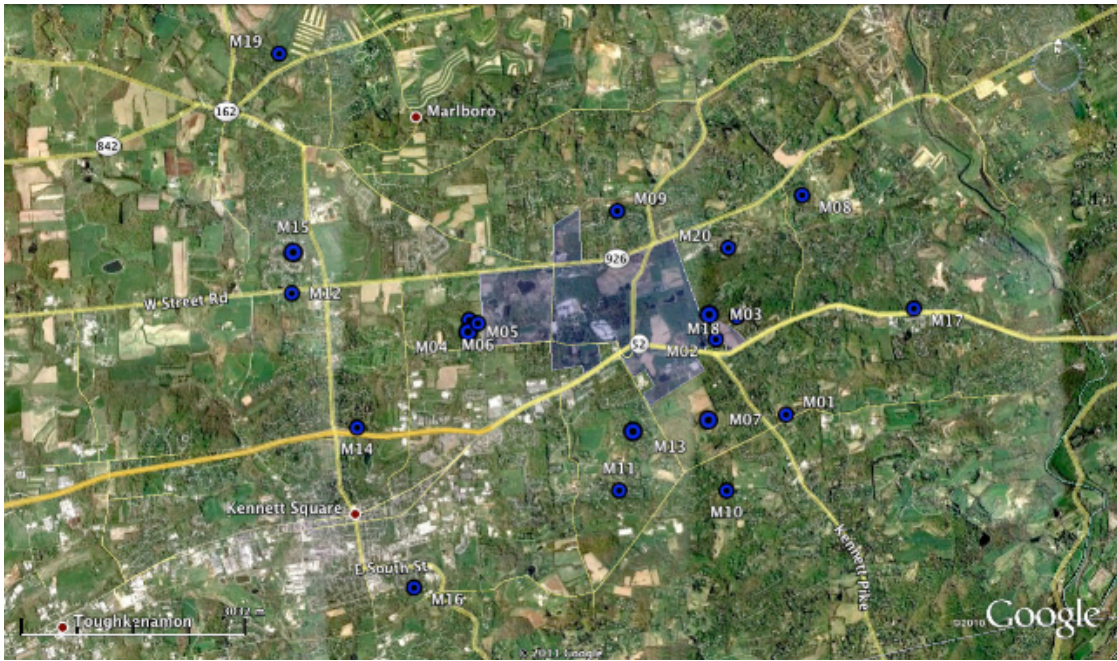


Figure 2. Locations of garden sites. The blue shaded area is the Longwood Gardens property. Blue ‘M’ sites are gardens planted in heavily managed landscapes.

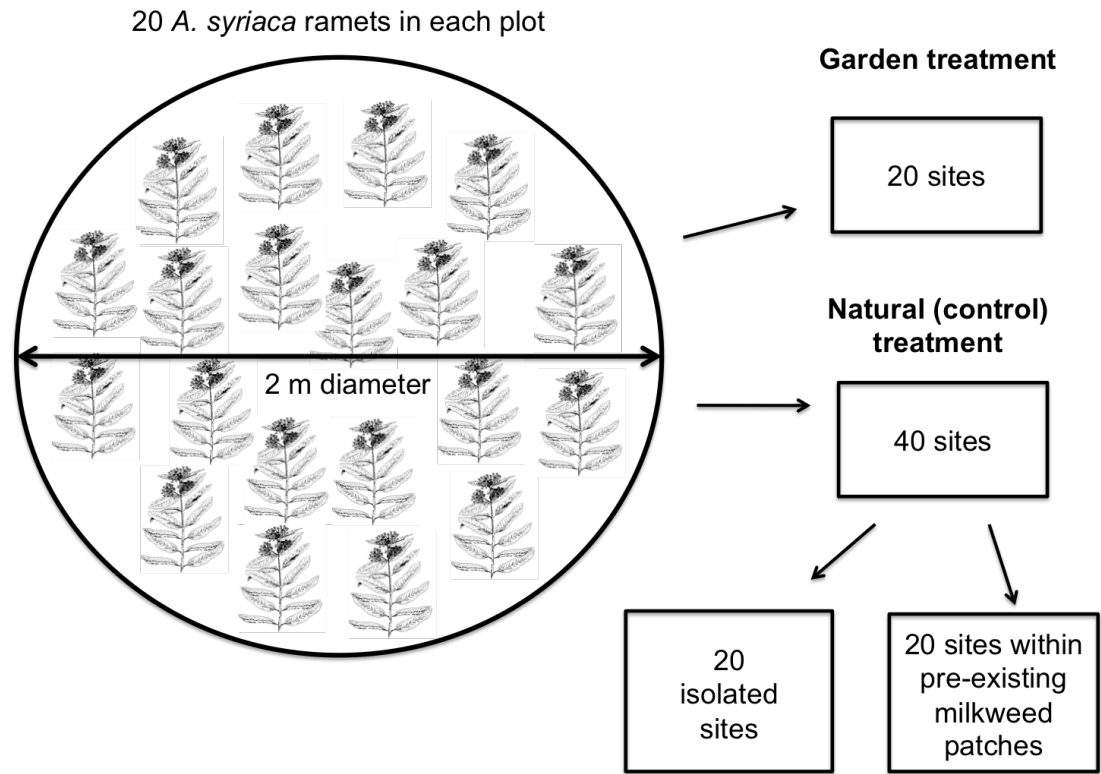


Figure 3. Layout of each individual plot, and division of 60 sites between 2 treatments.

Chapter 3

RESULTS

In the oviposition experiment in 2009 there was no difference between the plots that were planted in ‘isolated’ areas or ‘milkweed present’ areas in the natural treatment (Kruskal-Wallis: $H = 0.041$, d.f. = 1, $p = 0.84$); therefore, for all further analysis the data for all sites in this treatment were pooled. By late August, when the larval survival experiment was initiated, many plants in natural sites had been lost to deer herbivory (see discussion). Thus, the average number of plants in the garden sites was greater than in natural sites (2009 average plants per garden site = 18.13, average plants per natural site = 15.13; T-test: $t = 3.171$, d.f. = 44, $P = 0.003$). Oviposition data during the survival experiment revealed a significant correlation between the number of milkweed ramets in a site and the number of eggs laid there ($R^2 = 0.117$, d.f. 151, $P < .001$); accordingly, oviposition values at each site were adjusted for the number of ramets present in both years of the study and are reported as number of eggs per plant.

In both years oviposition was significantly higher in garden sites than it was in natural sites (Table 1). In 2009 garden sites received an average of 0.509 ± 0.096 (SE) eggs per ramet, while natural sites received only 0.266 ± 0.044 (SE) eggs per ramet (Kruskal-Wallis: $H = 7.759$, d.f. = 1, $P = 0.005$). In 2010 the same pattern was observed, with garden sites having more than 6 times as many eggs as natural sites (0.421 ± 0.085 (SE) and 0.068 ± 0.022 (SE) respectively (Kruskal-Wallis: $H =$

25.567, d.f. = 1, $P < 0.001$). Average oviposition on each visit in 2009 and 2010 is shown in figure 3 and figure 5 respectively.

I found no difference in cumulative sub-adult survival in garden sites and natural sites (Table 2). In 2009 I tracked the survival of 252 eggs and 119 larvae. The combined cumulative survival of eggs and caterpillars in gardens at natural oviposition levels was 6.9%, while in natural areas it was 11.4% (Kaplan-Meier: $\chi^2 = 2.813$, $P = 0.093$). In 2010 394 eggs and 141 larvae were tracked. Garden survival was 8.7% and natural areas 3.9% (Kaplan-Meier: $\chi^2 = 1.689$, $P = 0.194$). Survival curves for 2009 and 2010 are presented in figures 4 and 6. When separated into cohorts of the egg stage and larval stage, there were differences in survival between gardens and natural areas, but no consistent pattern emerged (Table 2). Gardens supported significantly better larval survival in 2009, and significantly better egg survival in 2010 when compared to natural sites. Natural sites supported significantly better egg survival in 2009.

Table 1. Monarch oviposition in natural and garden sites in 2009 and 2010. The mean number of eggs laid per ramet at each site within a treatment is presented. Statistical interval = SE. ** indicates difference at $P < .01$, *** $P < .001$

	2009		2010	
	Garden	Natural	Garden	Natural
Mean eggs/ramet	0.509 ± 0.096 **	0.266 ± 0.044	0.421 ± 0.085	0.068 ± 0.022 ***

Table 2. Cumulative survival of monarchs in natural and garden sites in 2009 and 2010. Cumulative survival is shown for eggs, larvae, and all sub-adult monarchs present, regardless of life stage. Statistical interval = 95% confidence interval. n is the sum of all at risk individuals in each treatment throughout the study period. * indicates a difference at $P < .05$, ** $P < .01$

	2009		2010	
	Garden	Natural	Garden	Natural
Sub-adult Survival	0.0690 ± 0.0089 $n = 717$	0.1136 ± 0.0271 $n = 265$	0.0872 ± 0.0144 $n = 783$	0.0391 ± 0.0172 $n = 134$
	ns		ns	
Egg Survival	0.0204 ± 0.0033 $n = 518$	0.1276 ± 0.0477 $n = 166$	0.1560 ± 0.0314 $n = 615$	0.0445 ± 0.0220 $n = 104$
	*		*	
Larval Survival	0.2208 ± 0.0453 $n = 199$	0.1029 ± 0.0318 $n = 99$	0.0065 ± 0.0018 $n = 168$	0.0128 ± 0.0124 $n = 30$
	*		ns	

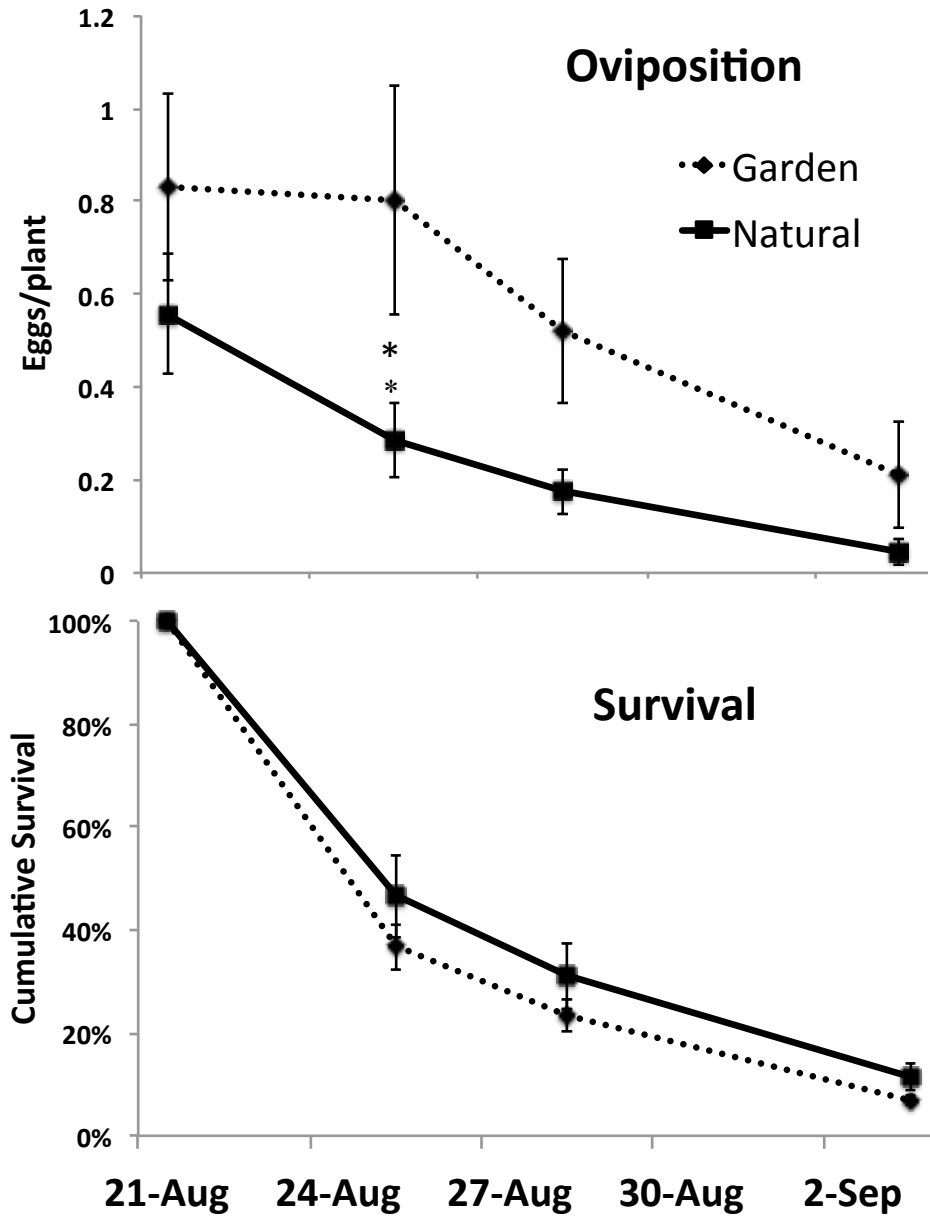


Figure 4. Oviposition (mean \pm standard error) and survival (mean \pm 95% confidence intervals) of *Danaus plexippus* in 2009. * indicates $P < 0.05$ when comparing garden and natural sites.

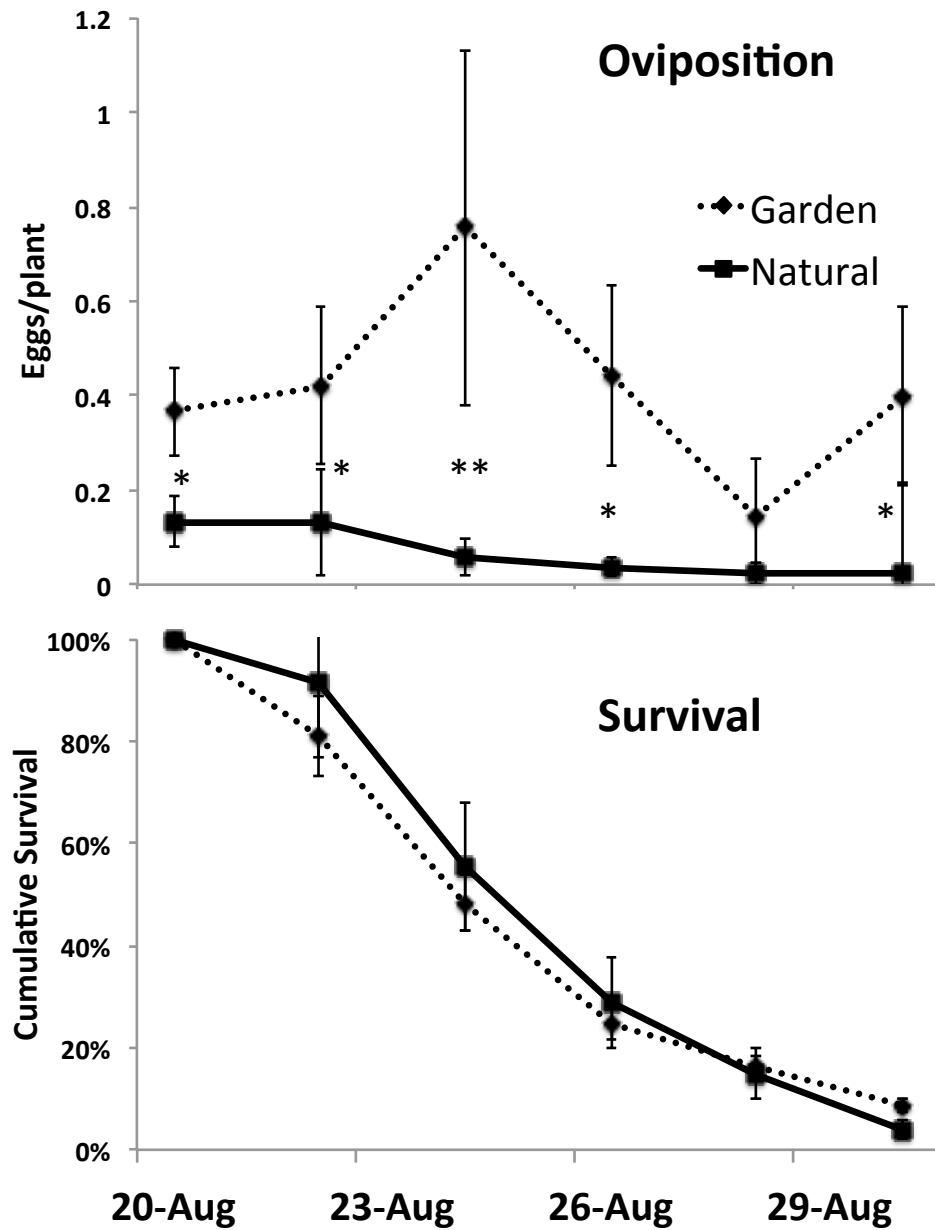


Figure 5. Oviposition (mean \pm standard error) and survival (mean \pm 95% confidence intervals) of *Danaus plexippus* in 2010. * indicates $p < 0.05$, ** indicates $p < 0.005$ when comparing garden and natural sites.

Chapter 4

DISCUSSION

This study demonstrates that host plants in managed garden settings are preferred sites for oviposition by female monarch butterflies. Furthermore, no cumulative sub-adult survival difference was detected between natural and garden sites; in some years, egg and larval survival was greatest in gardens, while in other years, egg survival was greater in natural areas. These findings indicate that gardens with monarch host plants that are managed with similar methods to those used in this study are most likely not ecological traps and may be net producers of butterflies. Survival differences between gardens and natural areas are not consistent from year to year, but gardens with milkweed regularly attract greater monarch oviposition. Planting milkweed within a managed landscape matrix is recommended as a strategy for supporting populations of monarchs and other organisms that depend on these butterflies for food.

What determines host selection for monarchs?

Oviposition preference in Lepidoptera is influenced by many selection pressures (Thompson and Pellmyr, 1991). Monarchs have different needs in different life stages, and ovipositing monarch females must strike a balance between choices that benefit their offspring and/or themselves; that is, a balance between optimal oviposition and optimal foraging (Janz, et al., 2005; Scheirs and De Bruyn, 2002;

Thompson, 1988). A landscape that provides for the needs of both larval and adult life stages should be good quality habitat that is preferred for oviposition.

Monarch oviposition on *A. syriaca* was consistently higher in managed gardens than in unmanaged natural areas. The differences I observed in oviposition between years may have been due to extreme differences in the weather that occurred between years, as well as to differences in numbers of plants monitored in different years (see Study Limitations). 2009 was much cooler, with more rain than 2010. The total growing degree-days (base 50) on August 1 was 1376 in 2009, and 2098 in 2010. Despite such differences in weather between years, monarch females laid more eggs per plant in gardens than in natural areas in both years of the study.

The monarch's preference for egg laying in gardens contrasts with the response of *B. philenor*, which was found to oviposit infrequently in California garden settings (Levy and Connor, 2004). The differences between these species may be a function of differences in host plant size and as well as behavioral differences between monarchs and pipevine swallowtails. Levy and Connor (2004) found that plant size dictates oviposition preference in pipevine swallowtails, with egg density (eggs/m² foliage/week) greater on larger plants. Pipevine swallowtails lay their eggs in clusters, and larvae feed gregariously. Larvae are at risk of defoliating small plants, and ovipositing females exhibit behavior that indicates that they sense the biomass of a potential host before accepting it as an oviposition site (Levy and Connor, 2004). There is evidence that pipevine of substantial size supports higher rates of *B. philenor* survival than plants that are rejected, underscoring the swallowtail's need for large host plants (Thompson and Pellmyr, 1991). In contrast, monarch egg densities do not vary with plant size (Cohen and Brower, 1982). Monarchs do not feed gregariously,

and ovipositing females visually recognize and avoid eggs of other monarchs (Thompson and Pellmyr, 1991). In this study, oviposition patterns relative to plant size followed patterns found in pipevine swallowtail by Levy and Connor (2004); milkweed ramets in gardens were generally taller than corresponding plants in natural areas while their garden plants were smaller than natural plants.

Monarch oviposition in this study could have been driven by the position of milkweed plants in the landscape. Monarchs have been observed to oviposit most frequently on milkweed plants that are isolated (Wagner, 2005). In garden sites where milkweed clumps are more isolated from other milkweeds than in natural areas, I observed individual ovipositing females return to a particular site repeatedly, laying eggs each time and not leaving the vicinity of the plot for 10 minutes or more. Such repeated use of isolated plants could be driven by selection for improved larval survival (Zalucki and Kitching, 1982), or simply by the increased likelihood of revisiting an isolated plant when chemical cues in the landscape are not complicated by volatiles or oviposition opportunities from other milkweed plants.

Oviposition choices could also be influenced by the foraging needs of gravid females. Optimal foraging theory predicts that monarch females should lay eggs preferentially on plants in close proximity to nectar sources (Kamil et al., 1987). Such a preference has been demonstrated in *Manduca quinquemaculata* (Sphingidae) (Karbon, 1997), *Euphydryas chalcedona* (Nymphalidae) (Murphy et al. 1984), *Polyommatus icarus* (Lycaenidae) (Janz et al., 2005), and *Vanessa cardui* (Nymphalidae) (Janz, 2005). In my study the availability of nectar at study sites was not measured; however, personal observations suggest that nectar availability was not a strong factor influencing oviposition attractiveness. Nectar resources in natural

areas varied temporally, while garden sites varied greatly between sites in the number of flowering plants present. Garden sites that had the most nectar resources available (presumably those with *Buddleja davidii* present) were not reliably the same sites that had the highest oviposition. Proximity to other nectar sources may be a minor factor for monarchs since milkweeds themselves are a good nectar source for at least the early part of the breeding season. Nectar resources may be more important during fall migration when monarch adults accumulate lipid reserves to sustain them through their long flight to Mexico and the subsequent winter (Brower et al., 2006).

Monarch Larval Survival

The crux of determining if gardens are ecological traps is whether an egg in a garden has the same or better chance of survival as it would if it were laid in a natural area. I did not detect differences in sub-adult monarch survival between garden sites and natural sites; however, I did find differences in egg and larval survival in some years. It is possible that sub-adult differences exist that were not detected because of the number of sites that had been lost over the course of the study (See Study Limitations). Survival rates in this study were within the range of other published studies that found survival of 3% (Zalucki and Kitching, 1982), 4% (Cohen and Brower, 1982), 18% (Oberhauser and Solensky, 2004) and 24% (Zalucki et al., 2001). The highest rate of survival I recorded was near 11%. Detection of differences at such low survival rates would likely have required many more replicates than were available in this study.

Survival of monarch eggs and caterpillars is subject to complex tri-trophic interactions (Singer et al. 2004). The cardenolides that monarchs sequester from their

milkweed hosts provide protection from predation but retard development, leaving caterpillars exposed to enemies for longer time periods; especially high concentrations of cardenolides or latex can be lethal to monarchs (Zalucki et al., 2001). Cardenolide concentrations differ among milkweed species, populations within species, and individual plants within single populations (Agrawal, 2005; Ladner and Altizer, 2005; Malcolm et al., 1989). Studies have found varying results when testing whether monarch survival is directly related to cardenolide concentrations in host plants (Cohen and Brower, 1982; de Roode et al., 2008; Zalucki et al., 2001).

In natural sites I observed monarch larvae being consumed by spiders and predatory bugs (Pentatomidae). I did not see these predators in gardens, but did observe ants in gardens removing monarch eggs from leaves and carrying them away. I also reared parasitoid tachinid flies from monarch larvae from both garden sites and natural sites. Moreover, I encountered adult monarchs being consumed by Chinese mantids, predominantly in natural sites. While I did not attempt to measure adult survival, such information could be useful in elaborating the population dynamics of Lepidoptera in gardens.

Study Limitations

It is difficult to definitively identify habitats that are population sinks, and more challenging still to identify ecological traps. Ideally, doing so would require a long-term study over a broad geographical area (Dias, 1996). A mark – recapture study to directly monitor population trends would be resource intensive, and probably fruitless for measuring local populations in the case of the highly mobile monarch.

Nevertheless, looking at recruitment and survival in gardens enabled some insight into the population dynamics of this system.

The design of my study attempted to isolate some of the factors that might influence monarch habitat use. Specifically, milkweed was planted in natural areas in an effort to ensure that plants in both treatments had similar phenology. Studying similar plants was to have allowed inferences about the effect of landscape matrix while controlling for plant chemistry. In practice, establishment of plants in natural areas was slower than in gardens, and the phenology and chemistry may have been more dissimilar than it would have been had existing milkweed plants been used exclusively.

Several environmental factors complicated and compromised the study. Deer, an unexpected complication given the toxicity of milkweed, destroyed a large number of sites. Exclusion fences were attempted but proved to be inadequate barriers. This along with heavy insect herbivore pressure in natural areas may have been a result of using greenhouse-grown plants that may have had lower than normal concentrations of inducible defense chemicals. Differences in weather between the study years were extreme; 2009 was an unusually cold and wet summer, while 2010 was unusually hot and dry. This impacted both plant establishment and permanence, as well as monarch base population levels and survival. The estimated overwintering population of monarchs between the two years of the study was the lowest on record (Rendon-Salinas, 2011). These certainly were not typical years for monarchs; accordingly these findings should be interpreted conservatively.

Recommendations

The ecological processes that support life on earth are failing as natural areas are directly and indirectly degraded or destroyed by human activity. Less than five percent of the land area in the U.S. remains relatively pristine and functional habitat patches are no longer large enough to sustain pre-settlement levels of biodiversity (Rosenzweig, 2003). By destroying habitat, we have accrued an ‘extinction debt;’ species temporarily persist after their habitat has been compromised but they will disappear in time (Tilman et al. 1994). This species loss could destabilize the ecosystems that we depend on for the production of ecosystem services and thus our own survival (Ehrlich and Ehrlich, 1981; Hassan, 2005), but it may be avoidable if humans can restore functional habitat where we live, work and farm. Opportunity for such restoration exists in residential areas where landscape designs have been based on the decorative value of plants rather than plant function (Tallamy et al., Submitted). By encouraging homeowners to implement management strategies based on research, mitigation of species loss is possible.

Despite the aforementioned complications, results of this study indicate that butterfly gardens could be an effective way to restore habitat for monarchs, other Lepidoptera, and possibly other insect herbivores and their natural enemy complexes as well. If effective, butterfly gardens offer an easy first step to ecosystem restoration. Lepidoptera are a good food source for other animals and butterfly and moth diversity can be a good indicator of ecosystem health (Blair and Launer, 1997). Gardens are relatively easy and inexpensive to plant and maintain and are already appealing to many homeowners. Fortunately, many butterfly species appear to be more sensitive to

habitat quality than to fragmentation; therefore, planting isolated gardens may be a worthy conservation strategy (Levy and Connor, 2004; Wood and Pullin, 2002).

Further research is needed to solidify understanding of how residential gardens work for conservation of monarchs and other species. These studies must look at population dynamics in garden settings, rather than simply adult abundance as has been the case with some previous work (Konvicka and Kadlec, 2011; Mathew and Anto, 2007; Matteson and Langellotto, 2011). Future research could focus on other specialists on easily manipulated herbaceous plants, such as the red admiral and comma butterflies on nettle, the curve-lined owlet on greenbrier, and the pink shaded fern moth on ferns. Meanwhile, as a conservative approach, gardeners should be encouraged to manage habitat in ways that mimic natural habitat and provide complex and diverse landscapes.

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