

**Keeping up with the Karners: habitat, population growth and
persistence of a local federally endangered species**

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Complex and multi-stakeholder models for land and species conservation often produce varying opinions on management strategies, especially when developed to accommodate mixed, and sometimes-incompatible land usage. Management can be further complicated by legislation meant to preserve endangered species, producing varying methods of quantifying population viability through time and space. However, even in areas with minimal development, species distribution will be intrinsically varied. Qualitative differences in habitat patches create distinct and often dissimilar differences in population structure between subpopulations, which is crucial to understanding theories such as risk spreading, the “rescue effect”, and the effects of local extinctions and colonizations, as strategies to maintain species persistence (Possingham et. al., 1994).

To inform management, conservation scientists must understand the host of variables influencing endangered species population fluctuations and persistence. To date, two population models have risen to the forefront of insect population monitoring and theory; the habitat-based paradigm and the metapopulation paradigm (Gutiérrez et. al., 1999). The habitat-based method of analysis is based on findings that populations are often lost after degradation or alteration to habitats, which was observed dramatically in the case of many butterfly species that were lost even after subtle environmental changes (Gutiérrez et. al., 1999). Sufficient access to a necessary quality and quantity of resources for larvae and adults, appropriate microclimatic conditions, and synchrony between host plant and insect are substantial factors influencing population persistence in habitat-focused analysis. The metapopulation paradigm, in contrast, is based on a model of assessing a population in a fragmented landscape where local populations are connected by migration, with populated patches varying through space and time based on local extinction and colonization events (Bravo et. al, 2007).

Both habitat and metapopulation analysis are important in predicting long term survival and designing management plans. To fully understand the a species’ population dynamics and create an effective management plan that facilitates long-term viability, both temporal and spatial fluctuations in habitat degradation, as well as corresponding population estimates must be examined to predict future persistence (Vulleumier et. al., 2007).

To address these ideas we examined the federally endangered Karner Blue Butterfly. In the case of the Karner Blue, research is often focused on availability of the only larval food source, Wild Blue Lupine (Grundel and Pavlovic, 2007). However, narrow assessments of populations based on host plant availability overlook many other aspects of colonization and prevalence, including connectivity between patches, and the likelihood of occupation in surrounding patches (Grundel and Pavlovic, 2007). Furthermore, studies have shown that the range of the Karner Blue Butterfly is considerably restricted compared to its host plant, suggesting significant influence of other variables in ensuring long-term population stability (Grundel et. al., 1998).

Though much research has been conducted about the Karner blue as a species, the driver of temporal variation among the populations is unclear (pers.comm Zimmerman). For example, the largest Karner Blue population in the Glacial Lake Albany Recovery Unit was the Saratoga Airport, which at one point contained 10,000 butterflies (U.S Fish and Wildlife Service, 2003), however, this population was severely reduced and may now be on the order of 100s without an apparent cause (pers.comm Zimmerman), necessitating further study to understand long term populations fluctuations.

In an attempt to grasp these long-term population fluctuations, we analyzed the distance sampling data collected by The Nature Conservancy and the NY – Department of Environmental

Conservation from the 2006-2011 to determine predictive factors of temporal variation in population size. These factors include habitat quality indicators such as lupine abundance, patch size, and shade frequency, density dependence and the interactions between several habitat quality indicators. From these analyses, we can track the population fluctuations in conjunction with habitat composition and quality to gain a broader understanding of the host of variables influencing the population dynamics of the Karner Blue Butterfly

The Focal Species

The Karner blue butterfly, *Lycaeides melissa samuelis* Nabokov (Lepidoptera: Lycaenidae) is a federally endangered butterfly occurring in Minnesota, Wisconsin, Indiana, New York, New Hampshire and Ohio (U.S Fish and Wildlife, 2003). The historic Karner blue habitat once spanned into a number of other states and sections of Ontario. Due to habitat loss, many habitats were eliminated (U.S Fish and Wildlife, 2003). The Karner blue subsists in remnant oak and pine savanna or barrens ecosystems consisting of sandy soils and Wild Blue Lupine, *Lupinus perennis* (Fabaceae), (U.S Fish and Wildlife, 2003) which were historically maintained by fire (Guiney et al., 2010).

The Karner blue is bivoltine, completing two life cycles (generations) a year (U.S Fish and Wildlife, 2003). The larvae hatch from overwintered eggs in late April or early May and begin feeding on the lupine the sole larval food species (Guiney et al., 2010; U.S Fish and Wildlife, 2003). The larvae mature through four instars over approximately three to four weeks and pupate in late May or early June (U.S Fish and Wildlife, 2003). The butterflies from the first brood (hereafter “Spring”) fly late May to late June, with an average adult lifespan of four to five days, though some have been observed to live as long as three weeks (U.S Fish and Wildlife Service, 2003). The second (Summer) brood hatches within five to ten days after oviposition, and are typically flying from mid July to late August (Swengel, 1996; U.S Fish and Wildlife Service, 2003), though weather conditions may delay the flight period (U.S Fish and Wildlife Service, 2003). The summer brood population is typically two to three times larger than the spring brood (U.S Fish and Wildlife, 2003).

The dispersal of the Karner blue is not well understood. Within sites, movement is believed to average less than 200 meters (U.S Fish and Wildlife, 2003). The Karner may move between suitable sites 1000 meters apart, often through unsuitable habitat (U.S Fish and Wildlife, 2003). As a result, the inter-population distance most likely to support recolonization of metapopulations is no greater than 2 kilometers (U.S Fish and Wildlife, 2003).

As of 2003, 41 ant species were recorded tending to larvae (across the range) (Swengel, 1996; U.S Fish and Wildlife Service, 2003). The ants tend to be opportunistic which may have habitat management implications; the ant species that is present in the habitat may develop a mutualism with the larvae, however, protection and restoration techniques may be too varied adversely affecting the success of the butterflies (Swengel, 1996; U.S Fish and Wildlife, 2003).

The Focal Habitat

The Karner blue butterfly was first described in the Albany area of New York State (U.S Fish and Wildlife Service, 2003). Today, the Karner blue populations occur in the Glacial Lake Albany Recovery Unit, which encompasses the Albany Pine Bush and the Saratoga Sandplains Recovery Unit (U.S Fish and Wildlife Service, 2003). In 2010, 24 of 83 historic Karner blue sites were monitored (Zimmerman et al., 2010). Nine monitoring sites are part of the Wilton Wildlife Preserve and Park (WWPP). In 1996, a 1.1 acre parcel of land supporting a Karner blue

population was auctioned by the County of Saratoga and purchased by the Town of Wilton (History of Organization). Wilton allocated 3000 acres for a butterfly preserve and recreation area, ultimately creating Wilton Wildlife Preserve and Park (Wilton Wildlife Preserve and Park, 2011). The Nature Conservancy and New York Department of Environmental Conservation have been conducting Karner blue monitoring and habitat restoration in the Wilton site since the 1980s (Wilton Wildlife Preserve and Park, 2011). The area is also protected habitat other species, including the Blandings Turtle, Spadefoot toad, and Hognose snake.

The data we utilized to address our research goals was collected at the following sites: CSN, CSS, ERN, ERS, ERR, ERSP, FX12, FX3, JKD, ODG, OPD (Figure 1). These sites are actively managed using techniques such as mowing, tree and stump removal, planting of nectar plants and lupine, and localized use of herbicide. Controlled burning is not used at this time. The Nature Conservancy and NY-DEC assesses the quality of each habitat based on a number of factors: habitat size, lupine density, lupine stems, nectar density, overstory frequency, shade frequency and grass frequency (Bried et al. 2005).

Methods and Results

I. Population Growth: contrasting observed and expected

Based on field and data observations, we expected the population growth between the spring and summer broods to be larger than between the summer and spring brood of the following year.

Methods: From 2005-2011 the Karner blue habitat patches were monitored using a distance sampling technique for the spring (late May-mid June) and summer (early July - late July) broods. The monitor walked transects and recorded observed butterflies perpendicularly from the transect (Zimmerman et al., 2010). This technique generates an observed population number for each transect and patch, which is used to generate total population estimates. From these estimates we calculated two different lambda (λ) or population growth values: summer (population growth between spring brood and summer brood) and winter (population growth of summer brood to next spring brood). We conducted a paired t-Test of ln-transformed λ to assess variation in population growth between these two generations. We used the population estimates and λ to generate 20 random population models for each site. To create each model, we started with the earliest population estimate for that site. From there, we multiplied this number by either a λ value randomly drawn from the pool of values (from all sites) for the appropriate season. Based on a ranking system of the models we assessed site performance. We ranked the observed model out of twenty-one (one observed model plus twenty random models for each site) twenty-one being the least performing, one being the best performing.

Results: Due to inconsistencies in the data only five of the sites had λ values for both the summer and winter time-steps. There was no data collected for the 2008 season, which prevented calculations of population change between the 2007 summer brood and 2008 spring brood. The ln transformed mean winter λ was 1.652 (SD = 1.01), and the summer λ was 2.187 (SD = 0.94). There was no statistically significant variation in growth between the summer λ and winter λ values (ln transformed values; paired t-Test; $t = -1.146$, $df = 4$, $n = 5,5$, $p = 0.158$).

The average site ranking was 12.9/21, which is modestly lower than the mean ranking expected by chance (10.5). Performance at one site was much better than expected (FX3; rank = 3/21; Figure 3) and at ERR the observed populations were lower than all 20 random population projections (Figure 2).

II. Population change as a function of population size

We expect the population to be density dependent because as individuals increase, resources become increasingly limited. This will ultimately cause population growth to slow until resources are no longer limiting.

Methods: The incidence of density dependent variation in λ was analyzed by linear regression, using ln-transformed λ . We performed one linear regression based on all winter and summer λ values, as well as a linear regression for winter and summer λ s individually. In both cases, we used ln-transformed values.

Results: Across all time-space combinations, population growth rates were greatest for small populations, and decreased as population sizes increased (Table 1). We see a similar relationship between these factors when the two time steps are separated (Figure 4). For both summer and winter λ s there is a trend towards negative population growth as population increases (Table 1).

III. Population size as a function of patch proximity

We expected a positive correlation between patch proximity and population change. ODP, the most isolated site, is still 2km from its farthest neighbor. Previous research suggests the Karners have a maximal recolonization distance of 2km, and these sites are within that distance.

Methods: Using ArcGIS10, we obtained the distance between each pairwise combination of sites. We identified proximity as the distance to the nearest neighboring site and calculated aggregate proximity as the sum of the inverse of these distances for each site. The coefficient of variation of λ was calculated based on summer λ values from 2009 and 2010 for CSN, CSS, ERR, ERSP and ODG (as these sites had the same available data). We used linear regression to assess the relationship between coefficient of variation in population change and site proximity.

Results: ERSP was found to be a greatly influencing outlier and was eliminated from the analysis. No relationship exists between site proximity and $CV\lambda$ of the four sites analyzed (proximity = $0.01 CV\lambda + .04$, $R^2 = .004$)

IV. Population change as a function of habitat characteristics.

We predicted the overperforming sites would be larger in size, have high nectar density, shade frequency, overstory frequency, lupine abundance, lupine stems, and low grass frequency.

Methods: From the density dependence linear model we categorized each site as either underperforming or over performing by calculating the residuals of the linear regression of all winter and summer λ values; if the observed λ was higher than we expected based on population size, the site was described as over performing. If the observed λ was lower than expected the site was underperforming (Table 2). We compared each of these habitat quality indicators with population growth in each site by linear regression. Additionally, We compared the habitat quality indicators, individually, between the over and underperforming sites using t-Tests assuming unequal variances (habitat size and lupine abundance) or t-Tests assuming equal variances (nectar density, shade frequency, overstory frequency, lupine density, and grass frequency) (Table 3).

Results: As the number of butterflies per lupine stem increases the growth rate of the population is reduced (Table 1). The regressions indicated no relationship of lupine density to λ , significant and positive relationships between λ and grass frequency, nectar plant density, shade frequency between overstory, and a significant negative relationship between λ and habitat size (Table 1). Over performing sites were larger than underperforming sites ($5.41\text{ha} \pm 1.92$ and $1.75\text{ha} \pm 0.20$, respectively) contained greater nectar ($81.6\% \pm 13.5\%$ and $68.4\% \pm 14.5\%$, expressed as percent quartiles), and higher lupine abundance ($12.1e^5 \pm 19.9e^5$ and $11.8e^5 \pm 2.0e^5$, respectively, expressed as lupine density * habitat size). The over-performing sites also were also more heterogeneous with regard to shade ($38.6\% \pm 22.1\%$ and $13.1\% \pm 15.8\%$, percent transects $>30\%$ shade) and overstory cover (0.26 ± 0.13 and 0.11 ± 0.11 , percent habitat with canopy >2 m in height).

V. Creating a parsimonious model to predict population change over time

Our original maximal model included shade frequency, nectar density, patch size, nectar abundance, lupine density, grass frequency, population size, lupine abundance and crosses between population size x nectar abundance, and lupine abundance and shade frequency. We expected a pattern between lupine abundance and shade frequency to be related based on observed effects of shade on lupine quality.

Methods: We used Stepwise Regression to assess the relative importance of these habitat quality indicators as predictors of λ (ln transformed). The Stepwise Regression began with an original maximal model that included all of the aforementioned habitat quality indicators and interaction terms between lupine abundance and shade frequency and nectar abundance and population size. We eliminated non-significant terms ($p > 0.05$) until the model only included statistically significant independent variables.

Results: Lupine density, lupine abundance, shade frequency and the interaction between shade frequency and lupine abundance were found to be significant predictors of the rate of population change ($F=2.97$, $df = 4, 18$, $p = 0.048$, $R^2 = 0.397$). We

Discussion

Population fluctuation between broods

Significant variation in population between seasonal broods is common within Karner Blue Butterfly meta-populations. Previous studies have found up to four times as many adults in the summer brood, compared to the spring brood (Schweitzer 1994), which is consistent with brood variation observed at the Wilton sites. Even though spring broods are often smaller due to expected overwintering egg mortality, failure of larvae to find lupine in the spring, and enhanced oviposition of first-flight females (U.S. Fish and Wildlife, 2003), spring and summer growth rates are easily affected by numerous outside variables, producing unpredictable changes in λ across spring and summer broods. Although our results suggest no significant difference in winter (summer to next spring brood) and summer (spring to summer brood) λ across all sites, this conclusion may not be indicative of the Sandplain's true seasonal variation. Data gaps in 2008 only allowed for the calculation of 5 winter lambdas, and 20 summer lambdas, possibly

misrepresenting the significance of the winter lambdas by magnifying the observed results. Even though our results did not significantly illuminate variations between spring and summer populations based on λ , we do see variation between the mean summer and winter λ (ln-transformed) that align with expected results (0.71 and 0.35, respectively). A larger and more long-term sample size, with equal number of winter and summer λ replicates, may yield a significant pattern.

Population density dependence

Our results indicate that the Karner Blue Butterfly population at the Wilton sites is modestly density dependent (Figure 4). We found a trend of density dependence in both the pooled data (including both summer and winter λ) and when summer and winter λ were separated. It is interesting to note that the dramatic difference in the fit of the models for the summer and winter λ alone (Figure 4), a probable effect of sample size variation. These findings are consistent with other studies conducted in this region, particularly at ERSP and the Saratoga Airport (not included in our analysis). Density dependence was seen for summer λ at ERSP, but not for winter λ (Pickens, 2007). Because our analysis only included five winter λ values, we would expect the strength of the model to decline as sample size increased due to variability among the sites and the influence of other factors in the habitat on population fluctuation. High densities of Karner Blue Butterflies can potentially strengthen meta-population persistence by decreasing issues associated with mate selection, low dispersal rates, and population fluctuations due to disease or external variables (Baguette and Schtickzelle, 2003). However, high density can also increase likelihood of mortality from disease or specialized predators (Baguette and Schtickzelle, 2003). Similarly, other studies emphasize that both large and small population sizes can influence population size fluctuation. The Allee Effect influences particularly small Karner populations because it reduces oviposition rate and limits dispersal and recolonization rates (Fuller, 2008).

Patch proximity and fluctuating population size

Although there is limited research devoted to Karner dispersal, there are relevant findings that suggests low and short movement usually restricted to less than 200 meters and maximal recolonization distance of 2km (U.S. Fish and Wildlife, 2003). While our study was particularly limited due to small sample size, ours were within 2 km of each other. Our findings were consistent with the Karner's limited dispersal abilities, however, dispersal could occur at this distance but did not in this population. Site proximity demonstrated no correlation to λ , implying the low likelihood of Karners moving between sites. The Karners' short lifespan (5 days), further limits potential between-site movement, especially in sites with high resource availability and favorable landscape composition. Furthermore, despite an overall lack of study regarding Karner dispersal behavior, anecdotal evidence points to the potential impact of geographic, vegetational, and human-constructed barriers (U.S. Fish and Wildlife, 2003). Due to the heterogeneous varied nature of WWPP, any of these factors could limit Karner movement, further weakening proximity's relationship on λ . Our examination of proximity only included four sites. A longer term data set would enable more sites to be considered and would potentially illuminate more subtle trends in proximity.

Influence of habitat composition on population fluctuation

This study does not attribute variation in population size to proximity and only a small degree of the variation can be accounted for by density dependence. While density dependence within populations has been shown to fluctuate from brood to brood and site to site, habitat quality accounts for much of the variation. Without consideration of resource density (Moilanen, 1999), habitat area and population size do not adequately explain population persistence and growth.

Our results indicate that shade and overstory frequency have a positive effect on population growth as represented by λ . This relationship may be due to the preferred location of different life stages of the butterfly (U.S Fish and Wildlife, 2003). Shaded areas are preferred oviposition sites for females (Grundel, 1998). Additionally, the over performing sites showed a higher degree of both shade and overstory, suggesting increased population success in more heavily shaded landscapes. However, this effect is varied across restoration areas, both within the Wilton area and across state lines, which indicates that does not drive population fluctuation exclusively (Grundel, 2007).

A variety of habitats are ideal for the persistence of Karner through the entirety of its life cycle. Larval feeding and oviposition occur at higher rates in relatively closed habitats, whereas mating and adult feeding occur in open habitats (U.S Fish and Wildlife, 2003). In the Saratoga Sandplains, the Edie Road sites are mostly underperforming (the highest ranked site fared 11/21) and have relatively low shade cover and overstory. The homogenous habitat may be adversely affecting population growth compared to other sites such as the Fox sites which have nearly 4x the overstory frequency in addition to open habitat areas (observed) and are categorized as overperforming sites for all years sampled.

Additionally, sites with greater density of nectar plants that can nourish adult Karners had higher growth rates than expected (based on population size) and generally higher population growth rates in absolute terms. Although the organizations that manage these sites regard nectar abundance as the “least worrisome” habitat variable (Bried, 2009), access to nectar-providing plants can be meaningful to other butterfly species. For example the Imperial Common Blue butterfly (also of the Lycaenidae family) lays three times more eggs when nectar is abundant, and females may leave an area without sufficient nectar resources even if host plant resources are adequate (Schultz and Dlugosch 1999). Though certain species of nectar plants are preferred, the Karner is believed to be an opportunistic nectar feeder because they utilize the nectar species most widely available in the habitat (U.S. Fish and Wildlife, 2003).

Multi-factor interactions

Though we examine a number of factors such as lupine abundance, nectar density and shade, none of these factors accounted for the variation in population size by themselves. The relationship between shade and lupine and the life stages of the butterfly may be driving population fluctuation. The degree of shade may not be what is preferable, but rather the influence of shade on other habitat features. Shaded areas contain varied levels of lupine density

and the interaction between the two vary across the landscape. The influence of shade in medium abundance areas was most pronounced; within medium lupine abundance areas with low shade the effect on lambda is minimal, whereas in high degree of shade we see the population growth is greater (Figure 6). This relationship may be because areas that are more shaded fostered larger lupine leaves, which are preferred for oviposition (Grundel, 1998). In addition, the nutrient content of the plants is higher in these shaded areas (Grundel, 1998). However, too much or too little shade will influence the ability of the lupine to grow at all. Additional relationships between other habitat features may also have similar effects on population change. For example, though Wilton Wildlife Preserve and Park is not nectar limited, the amount of shade may have similar effects on the quality and quantity of the adult food source.

Recommendations

Wilton Wildlife Preserve and Park must balance competing interests and financial constraints while pursuing the long-term viability of an endangered species. An optimal strategy for a highly significant recovery unit such as Wilton Wildlife would minimize human interference and incorporate management practices to perpetuate all significant habitat characteristics, but such a management-intensive and exclusionary vision for Wilton Wildlife is both incompatible with the Park's mission and the budget limitations of The Nature Conservancy and the New York Department of Environmental Conservation. The Karner Blue Butterfly habitat at Wilton Wildlife Preserve and Park is also a recreation area frequented by butterfly enthusiasts, hikers and bikers, and as such, must expect at least minimal disturbance, specifically to females during oviposition. Previous management efforts have focused on the preservation of Blue Lupine (*Lupinus perennis*) (United States Fish and Wildlife, 2003). Although preservation of lupine has obvious consequences for the population growth, our results demonstrate that maintaining and growing subpopulations also requires a more combination of habitat variables (see also Pickens and Root 2008). No one variable can be deemed *the* predictor of population growth and decline, and it is clear that population viability rests on the maintenance of several variables in order to foster a habitat suitable for feeding, mating and oviposition. While we did not explicitly test lupine quality as an indicator of population growth, the statistical significance of shade, which other studies have shown to be correlated to larger lupine plants and higher nutrient content, would suggest that the quality of lupine may outweigh abundance in establishing a successful population.

If, herbaceous plant density is positively correlated to Karner density, management should shift from traditional activities such as controlled burning, and consider broader habitat factors than simply lupine abundance. Further studies assessing the significance of herbaceous cover to Karner population growth and the identification of specific plants that positively affect lupine abundance and quality would further bolster our findings and thus inform management for more consistent and successful implementation. Although the traditional emphasis on lupine abundance as the key factor in habitat management made for straightforward and directed management, sustainable populations cannot be maintained by simply ensuring the availability of a single resource. Ecosystem-based management that emphasizes the interplay between many habitat variables and attempts to completely recreate whole habitats, rather than encourage a

single habitat variable presents a more complete and consistent paradigm for establishing stable Karner populations.

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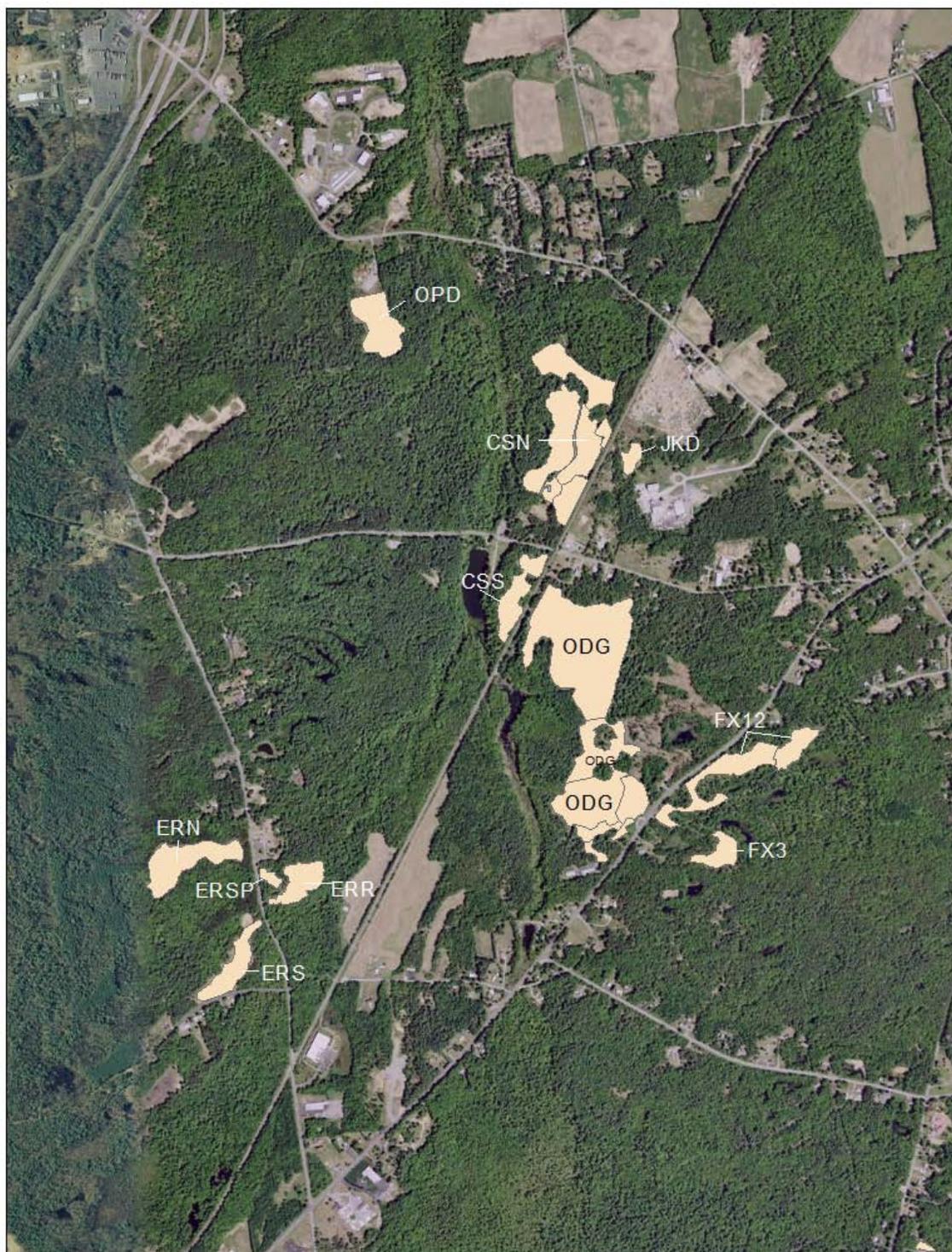


Figure 1 The distance monitoring sites used for distance sampling from 2006-2011.

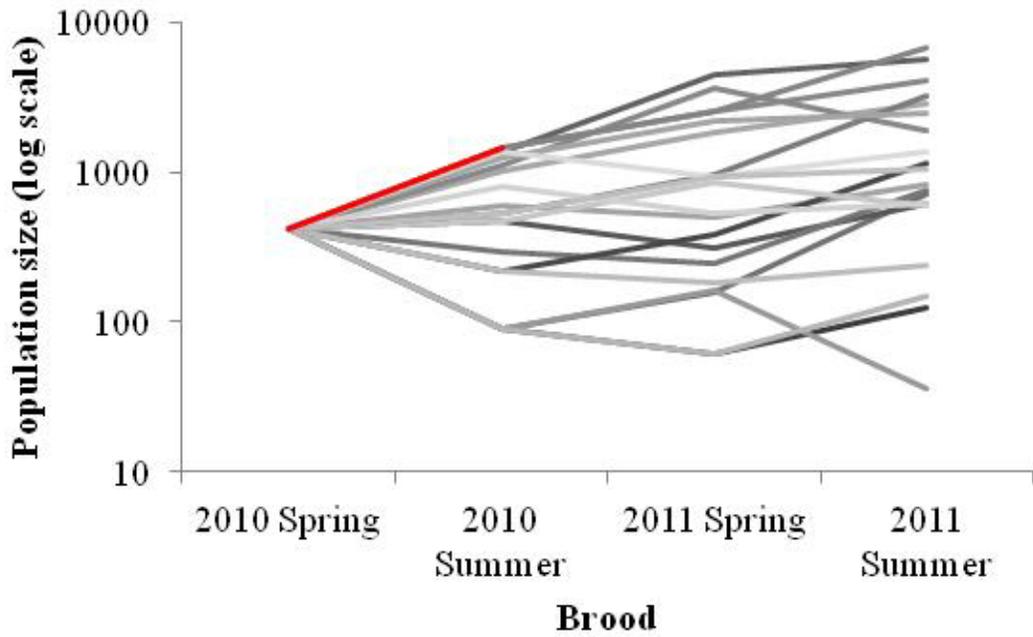


Figure 2 Twenty random populations models (in grey) based on observed population size (in red) at FX3. The observed population trend is performing at or above what is expected from the model projections.

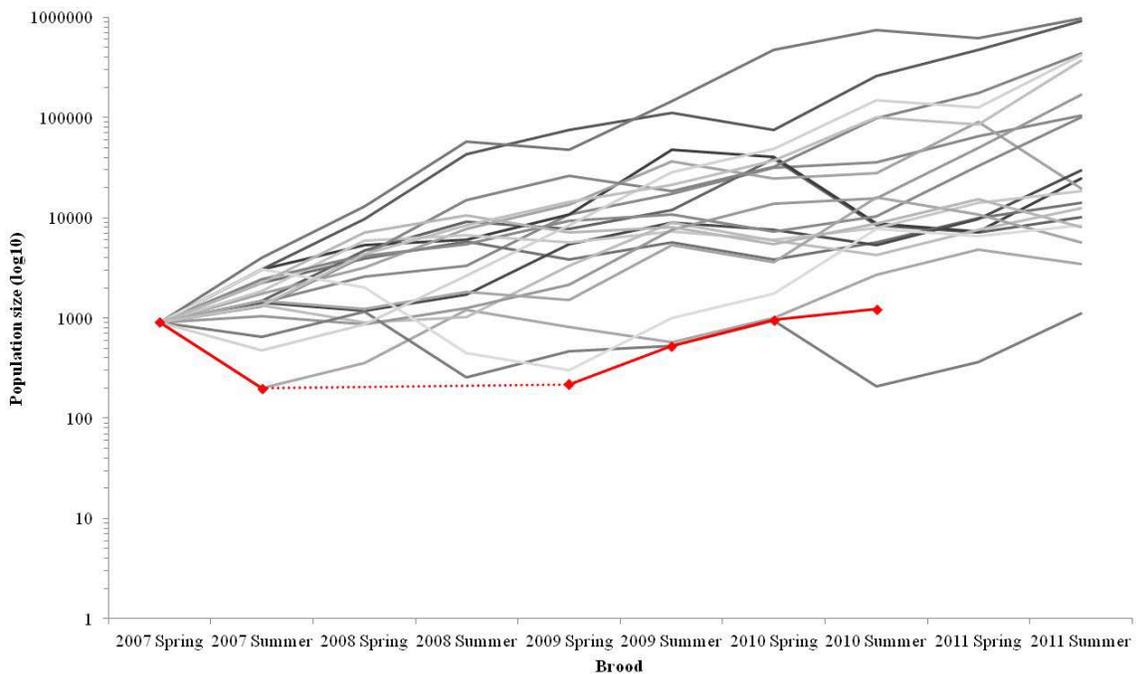


Figure 3 Twenty random populations models (in grey) based on observed population size (in red) at ERR. Missing data from 2008 is indicated by the dotted line. The observed population trend is underperforming compared to model projections.

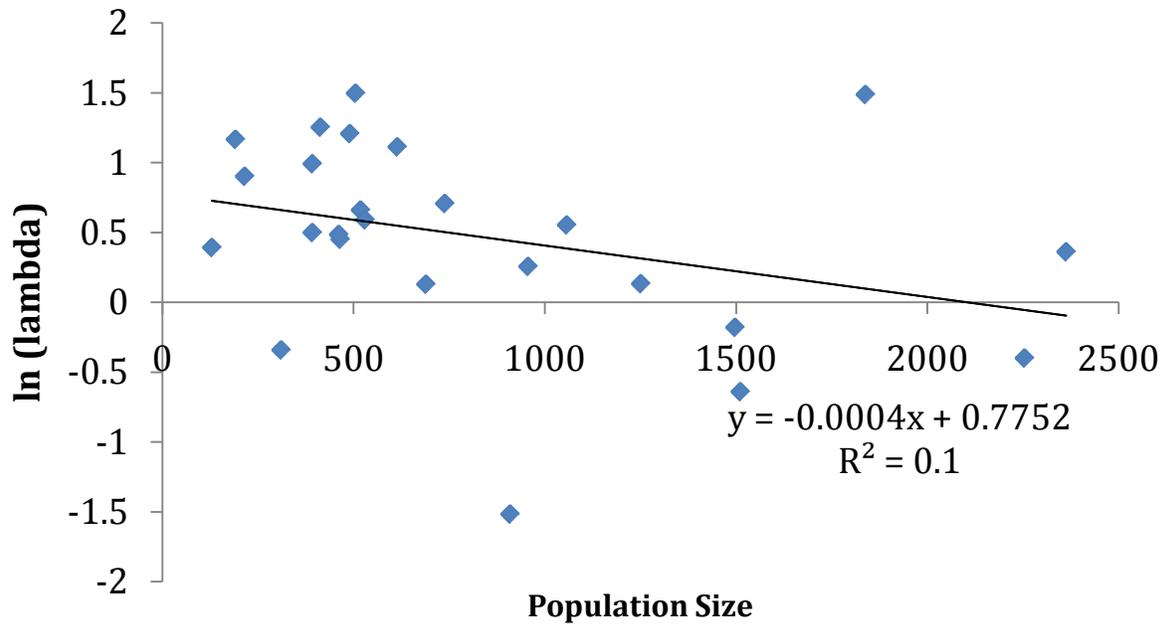


Figure 4 Population size influence on population change for pooled summer and winter lambda

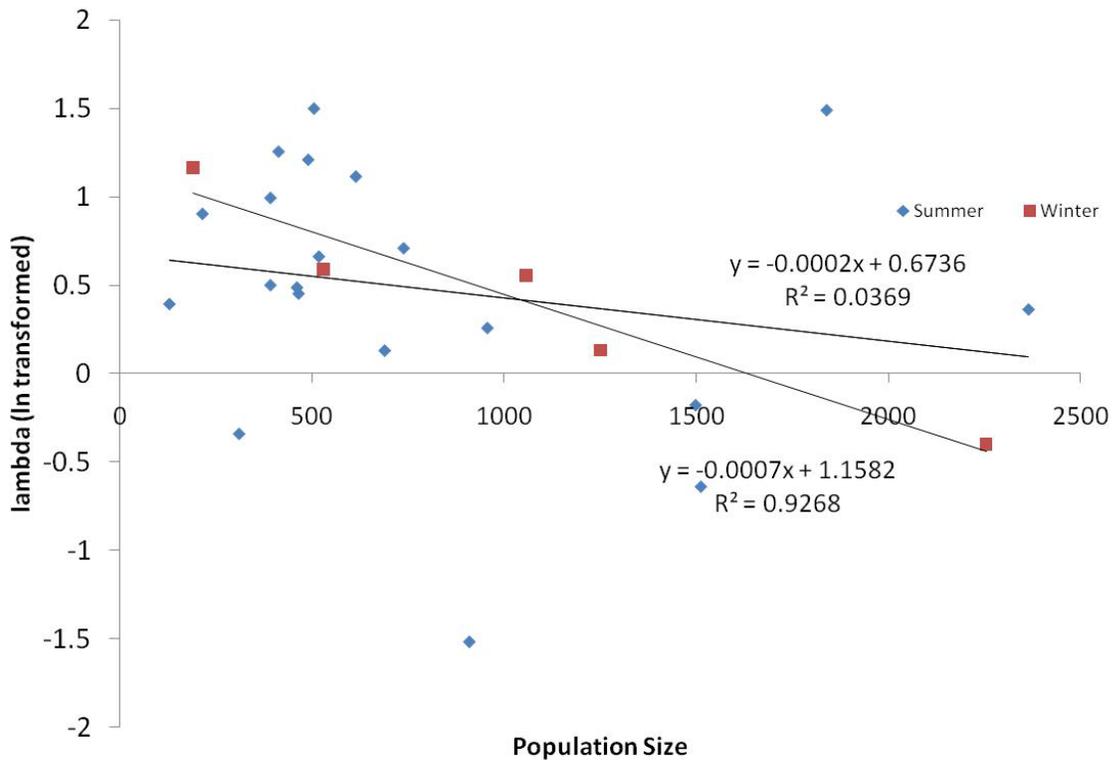


Figure 5 Population size influence on population change varies between Summer and Winter time-steps across the metapopulation.

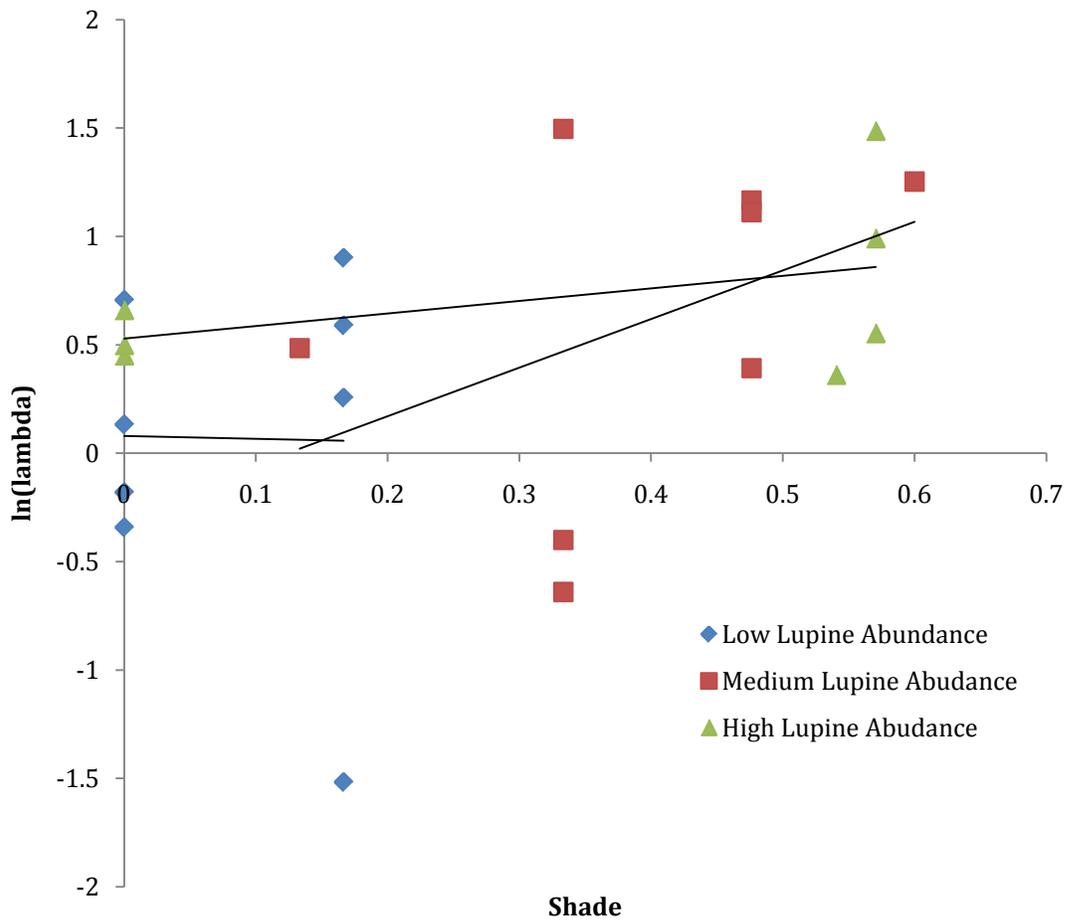


Figure 6 Influence of shade within three lupine abundance categories on population fluctuation. Low (9000-12000), Medium (26000-94000), High (110000-450000) as measured in stems per transect.

Table 1 Linear Regression Summary of Habitat Indicators

Test	Variable 1	Variable 2	Equation	F Stat	R²
Linear Regression	Grass Frequency	Lambda	$y = 1.99x + 1.38$	0.076	0.0034
Linear Regression	Lupine Abundance	Lambda	$y = 3.31^{-8} + 0.46$	0.108	0.005
Linear Regression	Lupine Density	Lambda	$y = 1.3^{-6} + 0.40$	0.125	0.0006
Linear Regression	Nectar Density	Lambda	$y = 1.04x - 0.33$	1.09	0.0462
Linear Regression	Shade Frequency	Lambda	$y = 1.08x + 0.168$	2.93	0.117
Linear Regression	Overstory	Lambda	$y = 1.91x + 0.08$	3.83	0.148
Linear Regression	Habitat Size	Lambda	$y = 0.008x + 0.45$	0.076	0.003

Table 2 Categorization of performance based on site.

Site	Year	Performance	Site	Year	Performance
CSN	2009	over	CSN	2007	under
CSS	2009	over	CSN	2010	under
CSS	2010	over	CSN	2010	under
ERR	2009	over	CSS	2009	under
ERSP	2009	over	ERN	2010	under
ERSP	2009	over	ERS	2010	under
FX1+2	2010	over	ERR	2009	under
FX3	2010	over	ERR	2010	under
ODG	2009	over	ERR	2007	under
ODG	2009	over	ERSP	2010	under
ODG	2010	over	JNK	2010	under
OPD	2010	over			

Table 3 T-Tests of habitat variables based on performance

Test	Variable 1	Variable 2	Mean Over performing sites	Mean Under performing sites	n	DF	p Value	t Stat
Two-Sample Assuming Unequal Variances	Habitat Size	Lambda	5.411626	1.750738	12,11	11	0.0425	1.8924
Two-Sample Assuming Equal Variances	Nectar Density	Lambda	0.816835	0.683844	12, 11	21	0.0169	2.2707
Two-Sample Assuming Equal Variances	Shade Frequency	Lambda	0.386468	0.131169	12,11	21	0.0023	3.1545
Two-Sample Assuming Equal Variances	Overstory	Lambda	0.265971	0.10868	12,11	21	0.0033	3.0028
Two-Sample Assuming Equal Variances	Lupine Density	Lambda	45915.35	26229.25	12,11	21	0.1371	1.1225
Two-Sample Assuming Unequal Variances	Lupine Abundance	Lambda	1210594.2	118356.6	12,11	11	0.0427	1.8899
Two-Sample Assuming Equal Variances	Grass Frequency	Lambda	0.410416	0.223053	12,11	21	0.0161	2.2920

