Factors that determine distribution of butterflies within complex prairie habitats at Pierce Cedar Creek Institute, Barry County, MI.

Zach Mills and James Dunn

Summer 2009

Abstract. Spatial distribution of native lepidopteron species was examined in correlation with various environmental components of restored prairie habitats in Barry County, Michigan. We examined the influence of host and nectaring plant species as well as micro-altitude on distribution. By using mark-recapture methods we assessed individual movement patterns in relationship with environmental quality. By assessing the relative altitude of capture locations, we determined that breeding populations of butterflies, specifically *Euphydryas phaeton* (Baltimore Checkerspot), prefer to aggregate in areas higher in elevation than the surrounding environment. From this we can deduce that areas of high vegetative quality (e.g., host and nectaring plant densities) are not predictive of high butterfly concentration and that micro-relief of sites (e.g. hilltops) is more important. In addition butterfly species were catalogued and capture data were used in the development of approximate flight periods.

INTRODUCTION

Butterflies (Lepidoptera) are a diverse taxa that use grassland vegetation for foraging and mating. The movement of individual species most influenced by encounters with host plant species (ovipostional) and nectar producing plant species (foraging) (Thomas and Singer 1987, Matter et al. 2003). Other features, such as man-made structures (roads, buildings) and areas of prominent vegetation have been associated with movement and distribution of insect species (Ehrlich and Wheye 1986, Scott 1986, Alcock 1987).

Female distribution is affected by two distinct factors: host plants and nectar producing plants. Therefore, they aggregate in concentrated areas of these resources (Odenedaal et al. 1989). Males are attracted to areas of high female density, suggesting high male densities in areas of high host and nectar producing plant species. However, male harassment often results in females avoiding such areas (Odenedaal et al. 1989), causing variation in male and female distribution.

An insect’s perception of habitat quality is dictated by the frequency in which they encounter host plant species (Thomas and Singer 1987). Increasing abundance of nectar flowers directly increases emigration but likely has no affect on immigration (Matter et al. 2003). Thus, a diverse selection of nectar producing and host plant species attracts a more diverse group of foragers who are less likely to leave such a site. Therefore, high species richness in such locations is indicative of high ecological function (Tillman and Downing 1994). A decrease in concentration of host and nectar producing patches will force butterflies to abandon a habitat patch. (Crone and Shultz 2003)

Environmental features important for survival and reproduction are important in insect habitat selection but are often difficult to define (Sharp et al. 1974). Habitat suitability is based upon the presence of obvious plants. Those species with limited movement must often accept the host species present in their vicinities regardless of their preference (Thomas and Singer 1987, Dunn 2008). Distribution of plant resources is critical in both population structures and distribution (Sharp et al 1974). Even if butterflies have a high preference for particular landscape features, there is still a stochastic component in movement and distribution (Crone and Schultz 2003).

Butterflies and other insects frequently aggregate on distinct topographical features (hilltops) to facilitate mate location (Shields 1967, Scott 1974, Alcock 1987). Males in these locations are thought to have higher success than other areas (Ehrlich and Wheye 1986). There is little evidence to support this phenomenon, but it is likely that hilltopping behavior is closely associated with the law of energy conservation (Shields 1967, Scott 1974, Alcock 1987, Ehrlich and Wheye 1986).

In butterfly species, both sexes will travel considerable distances to reach mating sites. Males tend to remain in sites favorable for mating, whereas females will likely relocate. In diurnal Lepidoptera (butterflies), two mate-locating behaviors are utilized (Scott 1975):

1) Perching is a behavior in which males rests, usually at topographical or vegetation sites. Males wait to investigate passing objects and possible breeding females.

2) Patrolling is a behavior in which males continuously fly to seek out potential mates.

Butterflies restrict their flight activities to areas of high ecological function that maintain the environmental features necessary for their survival and reproduction (Sharp et al. 1974). The factors that dictate flight activities (distribution and dispersal) are of key ecological interest as effective movement is detrimental to species preservation. Distribution and dispersal amongst a species genetically link isolated metapopulations throughout complex habitats (Cowley et al. 2000, Wilson and Thomas 2002). By monitoring the factors that influence movement, prairie restoration projects will be able to assess species health and prevent genetic isolation (Pollard and Yates 1993, Dunn et al. 2006, Koperski 2007).

Prairies and grassland communities are rare in the Great Lakes region (Dunn et al. 2006). Most remaining patches of prairie vegetation are second growth with only a small percentage of the remaining prairies having never been cultivated (Chapman and Crispin 1984). These few remaining remnants are isolated from other patches, which likely impact the population dynamics of those organisms which inhabit them. Therefore, to maintain high ecological function, species must have access ideal environmental components within patch boundaries.

We examined the significance of several environmental variables on inter-patch distribution in various prairie dwelling Lepidoptera species. Concentrated populations of breeding Lepidoptera species were sampled to predict preferences of these variables in regards to distribution. Our objectives for this study were:

- Assess the progress of the Pierce Cedar Creek restoration project by sampling Lepidoptera taxa.
- Assess the significance of distribution factors that influence movement in isolated prairie habitats.
- Analyze the importance of topographical features in butterfly distribution in correlation with vegetative quality.

METHODS

Study Area & Butterfly Survey

Butterfly populations were sampled in four distinct restored grassland prairie locations at Pierce Cedar Creek Institute, Barry County, MI, from June 10th-June 20th 2009 and July 14th 2009-July 24th 2009. The four sites were in various stages of restoration and will be referred to as Field 1 (Southeast Yellow Prairie), Field 2 (Southwest Orange Prairie), Field 3 (Northwest Orange Prairie) and Field 4 (North Red Prairie). Fields were sampled using sweep netting techniques with a soft Bio Quip butterfly net through the plant canopy along evenly spaced transects.

Piece Cedar Creek Institute is located on 661 acres and maintains once fallow farm fields that have been restored into traditional prairie habitats. The restored prairies, which have undergone a series of burning, mowing, and planting, consisted of: *Andropogen geradii* (Big bluestem), *Schizachyrium scoparium* (Little Bluestem), *Sorghastrum nutans* (Indian grass), *Elymus Canadensis* (Canadian wild-rye), *Asclepias tuberose* (Butterfly Weed), *Rudbeckia hirta* (Black-eyed Susan), *Rudbeckia pinnata* (Grey-headed coneflower) and other prairie grasses and wildflowers.

Transects were established every 25 paces (1 pace = 1 meter) throughout each prairie along which any visible butterfly would be sampled. Any butterfly observed but not collected was not recorded. Lepidoptera species were identified using Peterson Field Guides Eastern Butterflies (Opler and Malik 1992) and Michigan Butterflies and Skippers (Nielsen MSU 1999), in addition to professional resources and preserved specimens maintained by Pierce Cedar Creek Institute. Mark-recapture methods (MRR) (Sheppard and Bishop 1973, Dunn 2008) were used to assign a unique 1 letter/2 Digit tag number to individual butterflies. MRR techniques require the wing to be folded and marked on the outer bottom-edge of the hind wing with permanent marking-pen (Sharpie) [developed by Ehrlich and Davidson (1960) and refined by Dunn 2008]. Individuals were immediately recorded according to species, sex, quality and location with a Thales MobileMapper Pro GPS. Quality was assigned to each individual by a scale of 1 (high quality wing condition), 2 (moderate wing condition) and 3 (poor wing condition). After marking and recording individuals were immediately released. Recaptured individuals were recorded in a separate spreadsheet and were assigned a different attribute in the GPS device.

Vegetation Analysis

Four equal distant transects were established within each study site. They were systematically placed evenly within each prairie using a MobileMapper Pro GPS and MobileMapper Office Software. Along these transects, stratified sampling was used to establish vegetation plots. To establish plots along each transect, we would walk 25 paces and generate a random number. This random number would be used to identify a unique place in which a 1 meter x 1 meter quadrat would be established (Figure 13).

Within each unique vegetation quadrat, vegetation was both qualitatively and quantitatively assessed. The entire plot was observed for % coverage (both total and grass coverage), blooming flowers present, nectaring species present, and host species present. The concentrations of nectaring plants and host plants were then assigned a qualitative rank based on their density within a plot; 1 (heavy concentration), 2 (Moderate concentration) 3 (infrequent concentration). Individual plot locations were recorded via a GPS device to be refereed back to with seasonal vegetation development (Figure 14). One-way analysis of variance tests were used to test for significance of vegetation and topographical analysis on butterfly distributions using Stastistix 9.0.

Spatial Distribution

Data collected with the Thales MobileMapper GPS was analyzed using MobileMapper Office and ArcGis software. Spatial distribution was examined for each study site using habitat layers provided by Pierce Cedar Creek Institute. Digital elevation models and topographic sequence models were used to assess the butterfly elevation distribution.

Before butterfly sampling commenced, the perimeter of each study site was plotted to approximate the bounds of each prairie. The perimeters of biologically significant areas (i.e. hilltop, isolate deciduous clusters, lowland marshes) were plotted as separate entities within the larger habitats to allow for further investigation of habitat variation. Spatial data were extracted from ArcGis and compounded using Microsoft Excel. Spatial distribution statistics were analyzed using ArcGis, S.P.S.S 14.0 and Statistix 9.0.

Sampling sites were assessed based upon a spatial grid. The ArcGis grid allowed individual cells to be evaluated based upon vegetation quality, elevation, and capture density. By ranking each cell according to the elevation of the area and the quality of the vegetation present, distribution preferences could be predicted based upon capture success. Vegetation quality was based upon plots within a grid while elevation was based upon the Barry County digital elevation model. These data allowed investigation of the importance of vegetation (host vs. nectaring species) and elevation in butterfly distribution (Figure 15).

RESULTS

We successfully captured and tagged 311 butterflies from June 10-June 20 2009, and 174 butterflies from July 14 – July 24 2009. We recaptured 23 individuals (7.96%) in the first capture period and 16 individuals (10.1%) in the second capture period. From June 10-June 20 we identified 17 Lepidoptera species and from July 14-July 24 we identified 9 Lepidoptera species. Each period was dominated by an individual species, *Euphydryas phaeton* in June (55.9% of all captures) and *Colias philodice* in July (49.4% of all captures). All sites had considerable variation in capture success in June (Prairie 1 = 60.5%, Prairie 2 = 21.7%, Prairie 3 = 10.7%, Prairie 4 = 6.9%) and July (Prairie 1 = 22.6%, Prairie 2 = 20.7%, Prairie 3 = 9.8%, Prairie 4 = 47.0%) (Table 1). Species identified also varied from June to July, with high species variation occurring in July (Figure 1 and 12)

Individual study plots varied with capture successes. Prairie 1 had high capture success of *Euphydryas phaeton* in June (130) whereas Field 4 had high capture success of *Colias philodice* in July (64). We also see variation in species diversity success amongst each study site in June (Prairie 1 = 8 , Prairie 2 = 10 , Prairie 3 = 5 , Prairie 4 = 7) and July (Prairie 1 = 6, Prairie 2 = 4 , Prairie 3 = 4 , Prairie 4 = 6) (table 1). We also see variation in the vegetation analysis from June to July in host species, nectar producing species, percent cover, and flowers present (Table 2, Table 3). No significant fluctuations were noted in Prairie 4.

Distribution was location dependent. There was no trend for elevation preference for all fields, but Prairie 1 had the highest capture success at high elevation (Figure 3) in June. In July, capture success was high at high elevation in Prairie 2 (Figure 3). We also see more success with male captures in Prairie 1 in June as well as in Prairie 2 in July. No other study location showed a strong propensity toward capture success at high elevation (Figure 4). Females in Prairie 1 did aggregated at high elevations in June, but this wasn't recorded at any other time (Figure 5). We did not observe any significance in female elevation preference in correlation with their wing quality (Figure 6).

Butterfly capture success was not influenced by flower densities. No obvious trends were present to suggest any preference for areas with higher blooming flower concentrations in correlation with capture success. This is consistent for both capture periods (June and July) (Figure 7).

Butterfly capture success was not influenced by host plant ovipositional species. No obvious trends were present to suggest any preference for areas with higher ovipositional sites had any influence on the distribution of species ($p>0.005$). This is consistent with both capture periods (June and July) (Figure 8).

Butterfly captures success was not influenced by the percent ground coverage. There was no significance in capture success ($P>0.005$) in correlation to the percent vegetation coverage within randomly sampled quadrats. This is consistent for both capture periods (June and July) (Figure 9).

Butterfly capture success was significantly influenced by nectar producing plant concentrations. In June, we noticed butterflies distributing more heavily in areas with high host plant densities ($P<0.05$). In July, we noted trends to suggest a preference for areas maintaining high concentrations of nectar producing plants, but did evidence was inconclusive ($p<0.1$) (Figure 10).

Euphydryas phaeton showed a strong preference for areas of high elevations, with 50.5% of captures occurring at high elevation, 34.1% occurring at a median elevation, and 15.3% occurring at low elevation (June 10 – June 20 200). *Colias philodice* showed no preference for elevation in their distribution, with 29.5% of captures occurring at high elevation, 30.2% occurring at a median elevation, and 36.4 occurring at a low elevation (Figures 11 and 12).

DISCUSSION

Various environmental features are associated with butterfly movement patterns and distribution (Sharp et al. 1974, Luoto et al. 2001, Scott 1974). These features are often based upon the surrounding vegetation; however this is not always the case (Shields 196, Scott 1974). Other features, such as manmade structures (e.g., roads, building) and hilltops can influence the distribution more than vegetation, particularly in densely concentrated breeding insect populations.

We did not gather conclusive evidence to suggest that butterfly distribution is based solely upon elevation. However, our data does suggest that elevation can play an important role in distribution in relationship to the location. Pierce Cedar Creek Institute's rigorous restoration project has developed contrasting prairies that have independent influence on distribution. In areas with high vegetation quality (Prairie 2), we expected to see more sporadic dispersal as individuals have access to various resources, both for foraging and reproduction (Matter et al. 2003, Thomas and Singer 1987, Sharp et al. 1974). However, in areas of intermediate vegetation quality (Fields 1 and 3), we expect to see distribution patterns congregated to areas of high vegetative quality or areas maintaining useful environmental features (Matter et al. 2003, Ehrlich and Wheye 1986) Areas of low vegetation quality, both foraging and reproduction (Prairie 4), have high concentrations of generalist butterflies (*Colias philodice*) and clusters of diversity and high concentrations of butterflies in isolated areas of high quality vegetation.

Our data suggests that butterflies favor nectar producing plants for foraging purposes when considering other vegetation features (host species, ground cover, flowers). This is likely due to high caloric output during breeding periods and the energy requirements to replaces this output that nectar provides. Our capture success in areas of high foraging sites indicates that butterflies consistently favor foraging locations when distributing through a heterogeneous landscape.

Generalist butterfly distribution throughout a complex landscape is more sporadic and less dependent on environmental features, as noticed in *Colias philodice*. This is because generalists are able to exploit a more diverse range of resources (Thomas and Singer 1987). Specialists, however, have more predictable dispersal as they can only exploit a select amount of resources, as seen in *Euphydras phaeton.* We expect specialist species to congregate in areas of high ecological function (Matter et al. 2003). In the absence of high quality vegetation, we expect to see species utilizing other environmental features that facilitate overall survival and reproduction, such as elevation.

There are many explanations why environmental features maintain appeal to insects, most of which relate to energy conservation. By aggregating in areas of high elevation, butterflies are able utilize thermoregulation when foraging and locating mates (Shields 1967, Scott 1974, Alcock 1987). Thermoregulation allows minimal energy expenditure for males while patrolling for females as they are able to fly aloft thermal currents. By congregating in areas of high elevation, butterflies may be able to maintain higher internal temperatures by utilizing both warm air thermals and immediate ultraviolet rays from the sun. We notice that in the absence of high quality vegetation, butterflies are more likely to utilize environmental features that encourage energy conservation (Shields 1967). This behavior is energetically efficient as butterflies not maintaining access to resources that fuel caloric expenditures must store energy when possible.

Acknowledgments:

Thank you so much to my amazing summer assistance: Chantel Caldwell, Melissa Bobowski, Brian Wilder, Kevin Wilder, and PCCI Staff.

Special thanks to Pierce Cedar Creek Institute, Matt Dykstra, Dr. Shaily Menon, Dr. Erik Nordman, Aaron Ashbrook, Derek Loutzenhiser, Dr. James Dunn for their invaluable assistance in the field and during analysis.

* Any further publications will be submitted to Pierce Cedar Creek Institute.

Table I. Capture success of identified Lepidopteron species in four study plots: Southeast Prairie (Prairie 1), Southwest Orange Prairie (Prairie 2), Northwest Orange Prairie (Praire 3) and North Red Prairie (Prairie 4). Capture periods were recorded in two periods: June 10- June 20 2009, and July 14th – July 24th 2009.

Prairie (June 10 – June 20 2009)	**1**	**2**	**3**	**4**
Euphydryas phaeton (Baltimore Checkerspot)	130	27	9	8
Vanessa virginiensis (American Painted Lady)	0	1	0	0
Lycaena phlaeas (American Copper)	0	0	1	0
Papilio polyxenes (Black Swallowtail)	0	1	0	0
Lycaena hyllus (Bronze Copper)	1	0	0	0
Pieris rapae (Cabbage White)	3	0	18	0
Colias philodice (Clouded Sulphur)	0	1	0	5
Papilio cresphontes (Giant Swallotail)	2	0	0	0
Speyeria Cybele (Great Spangled Fritillary)	0	2	0	2
Danaus plexippus (Monarch)	1	2	0	0
Colias eurytheme (Orange Sulpur)	0	0	0	1
Vanessa cardui (Painted Lady)	0	1	0	0
Phyciodes tharos (Pearl Crescent)	3	0	2	1
Polygonia interrogationis (Question Mark)	0	0	0	1
Limenitis arthemis (Red Spotted Purple)	0	1	0	0
Chlosyne nycteis (Silvery Checkerspot)	22	13	0	0
Megisto cymela (Little Wood Satyr)	13	14	1	2
Total Individuals	175	63	31	20

Prairie (July 14 – July 24 2009)	**1**	**2**	**3**	**4**
Euphydryas phaeton (Baltimore Checkerspot)	0	1	7	1
Vanessa virginiensis (American Painted Lady)	0	0	0	1
Lycaena phlaeas (American Copper)	1	0	0	0
Colias philodice (Clouded Sulphur)	6	16	0	64
Cupido comyntas (Eastern Tailed Blue)	3	0	0	0
Speyeria Cybele (Great Spangled Fritillary)	7	4	6	3
Danaus plexippus (Monarch)	0	0	0	1
Colias eurytheme (Orange Sulpur)	1	0	1	7
Megisto cymela (Wood Nymph)	19	13	2	0
Total Individuals	**37**	**34**	**16**	**77**

Table II. Vegetation analysis of study plots from June 10 – June 20 2009 within spatial grids in each prairie. Vegetation was observed for flowers, percent overall coverage (% Coverage), host species, nectaring species, elevation rank (per study plot), capture success, and recapture success.

Field	***Grid***	***Flowers***	***% Coverage***	***Host Species***	***Nectaring Species***	***Elevation Rank***	***Captures***	***Recaptures***
1	1	25	91	7	2	5	11	3
1	2	173	92	10	6	1	8	1
1	3	0	97	2	6	6	3	0
1	4	44	94	5	4	2	1	1
1	5	15	100	4	5	7	6	0
1	6	46	97	6	10	3	3	0
1	7	74	92	3	7	4	5	0
2	1	39	78	2	11	4	20	1
2	2	57	85	2	12	1	32	5
2	3	77	80	4	14	2	18	3
3	1	20	98	1	8	4	6	1
3	2	26	86	4	5	3	7	1
3	3	2	86	1	6	2	11	0
3	4	13	71	1	4	1	3	0
4	1	7	75	1	7	1	0	0
4	2	0	75	0	6	8	1	0
4	3	0	64	0	8	5	0	0
4	4	1	90	1	6	2	2	0
4	5	0	63	0	8	7	0	0
4	6	0	97	0	5	6	0	0
4	7	1	84	3	7	4	9	1
4	8	0	49	2	5	9	0	0
4	9	0	71	0	7	10	3	0
4	10	0	50	0	11	3	2	0
4	11	0	76	1	11	11	2	0

Table III. Vegetation analysis of study plots from July 14 – July 24 2009 within spatial grids in each prairie. Vegetation was observed for flowers, percent overall coverage (% Coverage), host species, nectaring species, elevation rank (per study plot), capture success, and recapture success.

Field	**Grid**	**Flowers**	**% Covg**	**Host Species**	**Nectaring Species**	**Elevation Rank**	**Captures**	**Recaptures**
1	1	45	86	3	2	5	3	0
1	2	8	91	2	5	1	9	0
1	3	30	93	5	5	6	1	0
1	4	32	96	4	5	2	5	0
1	5	35	95	2	3	7	0	0
1	6	31	94	0	8	3	3	0
1	7	95	92	2	5	4	1	0
2	1	39	82	3	11	4	6	0
2	2	25	84	3	11	1	0	1
2	3	37	82	3	12	2	8	0
2	4	24	92	5	4	3	0	0
3	1	18	98	1	6	4	4	1
3	2	56	96	1	7	3	7	0
3	3	68	77	3	7	2	6	0
3	4	114	100	1	4	1	1	0
4	1	7	75	1	7	1	0	0
4	2	0	75	0	6	8	8	1
4	3	0	64	0	8	5	1	0
4	4	1	90	1	6	2	2	1
4	5	0	63	0	8	7	6	1
4	6	0	97	0	5	6	5	1
4	7	1	84	3	7	4	10	1
4	8	0	49	2	5	9	8	2
4	9	0	71	0	7	10	6	0
4	10	0	50	0	11	3	3	0
4	11	0	76	1	11	11	2	1

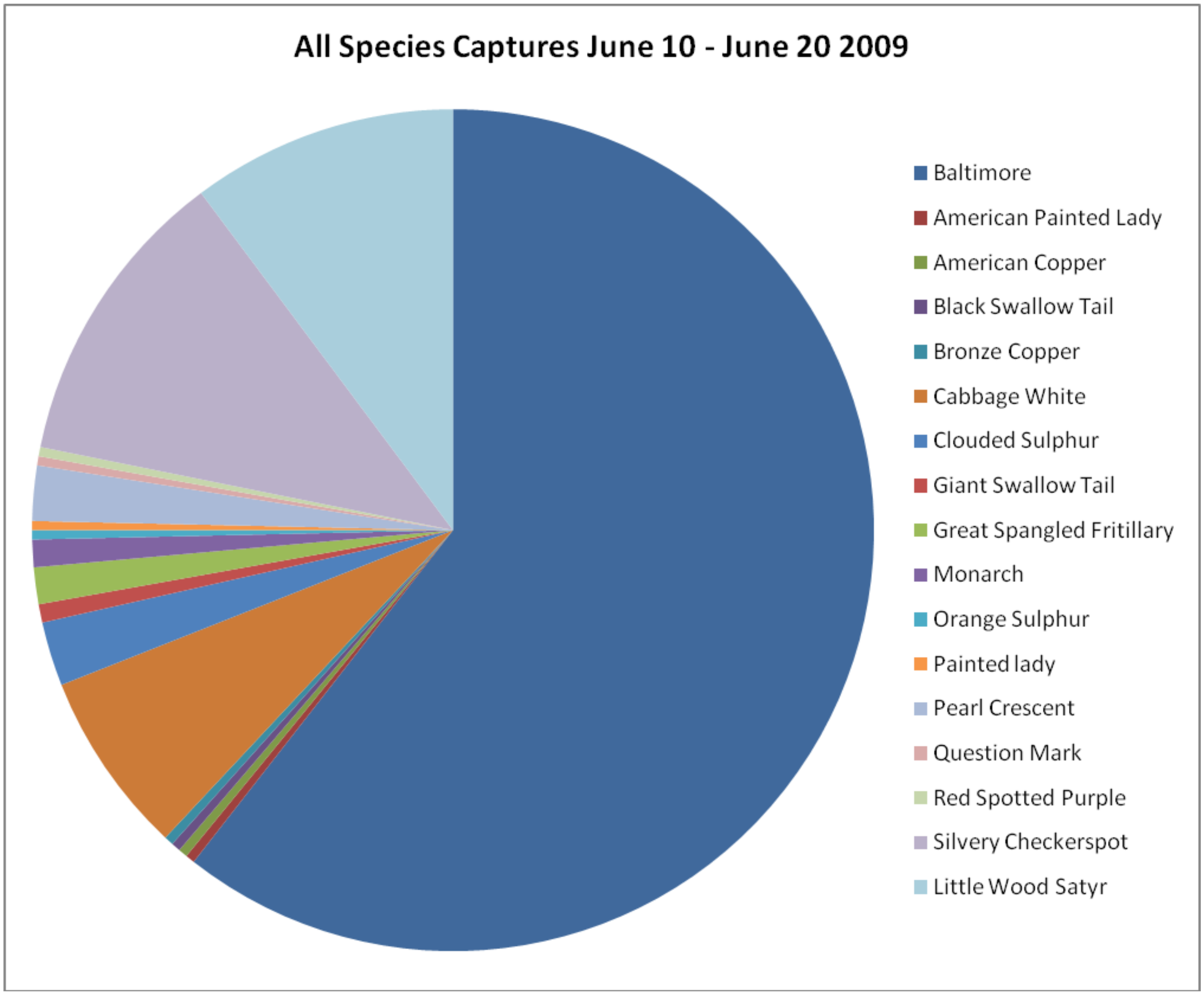


Figure 1. Percent of species captured in correlation with total captures for all prairies June 10 – June 20 2009.

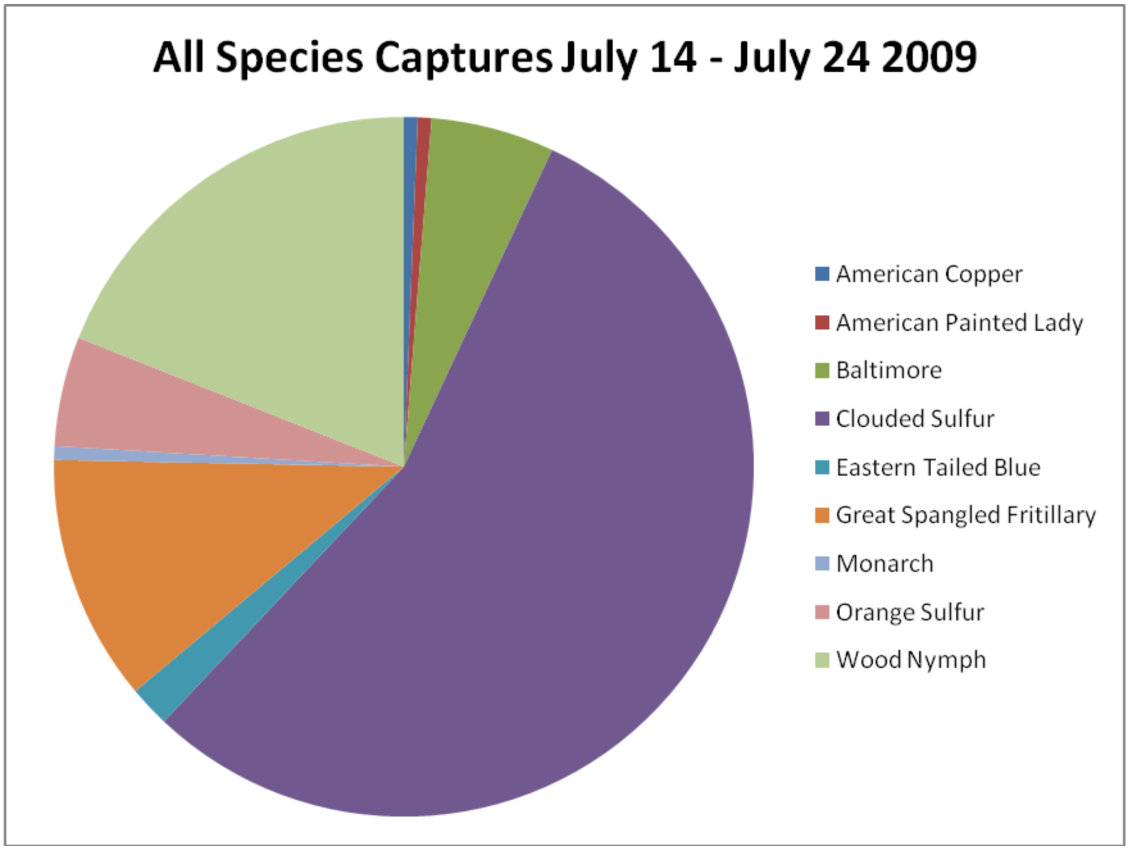
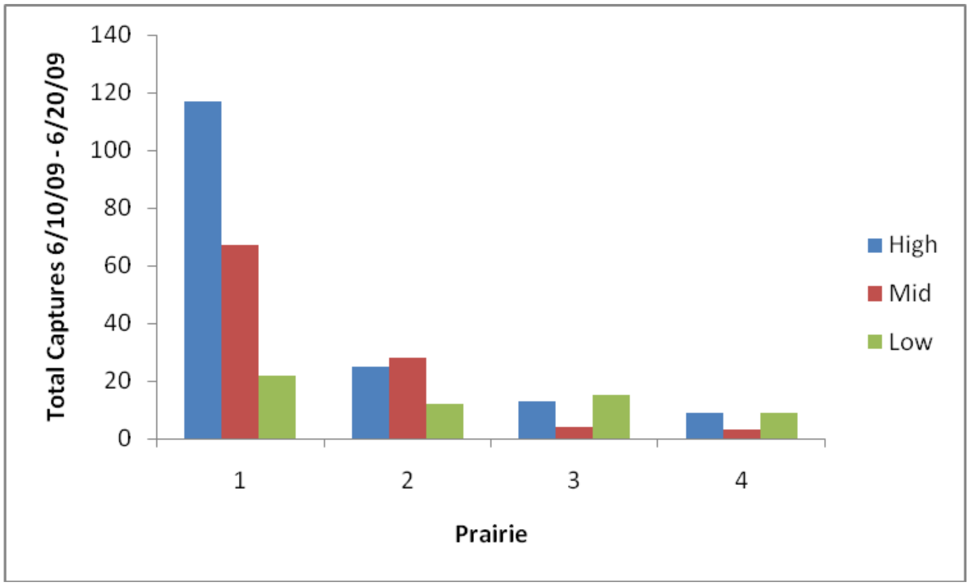


Figure 2. Percent of species captured in correlation with total captures for all prairies July 14 – July 24 2009.



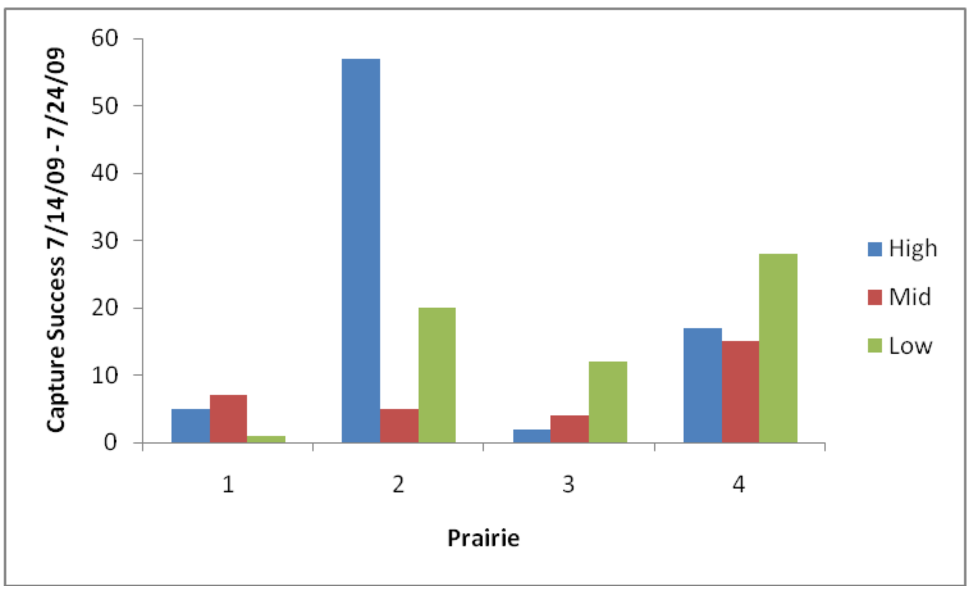
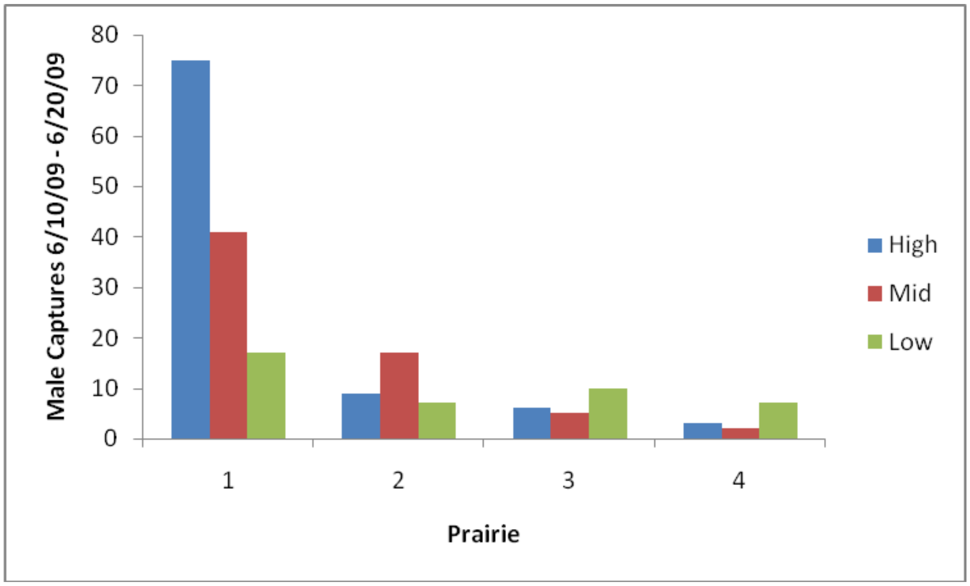


Figure 3. Capture success at elevation ranks high, middle, and low for both capture periods. Recorded for all species and both sexes.



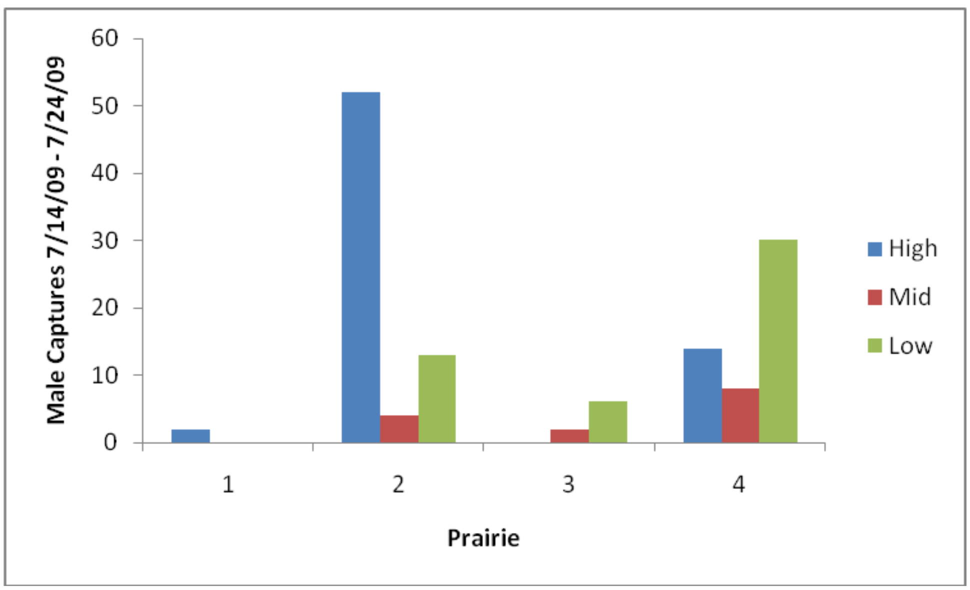
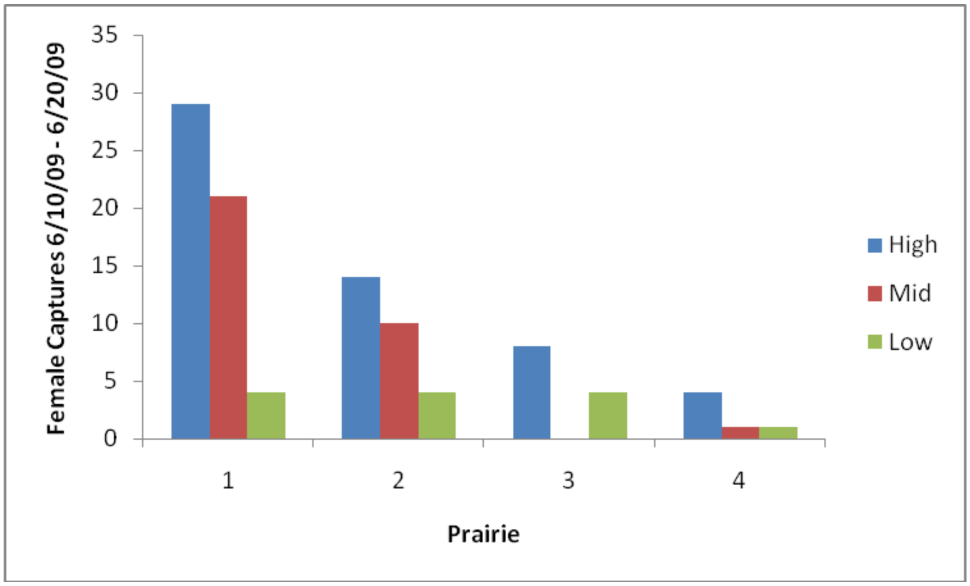


Figure 4. Male capture success at elevation ranks high, middle, and low for both capture periods. Recorded for all species



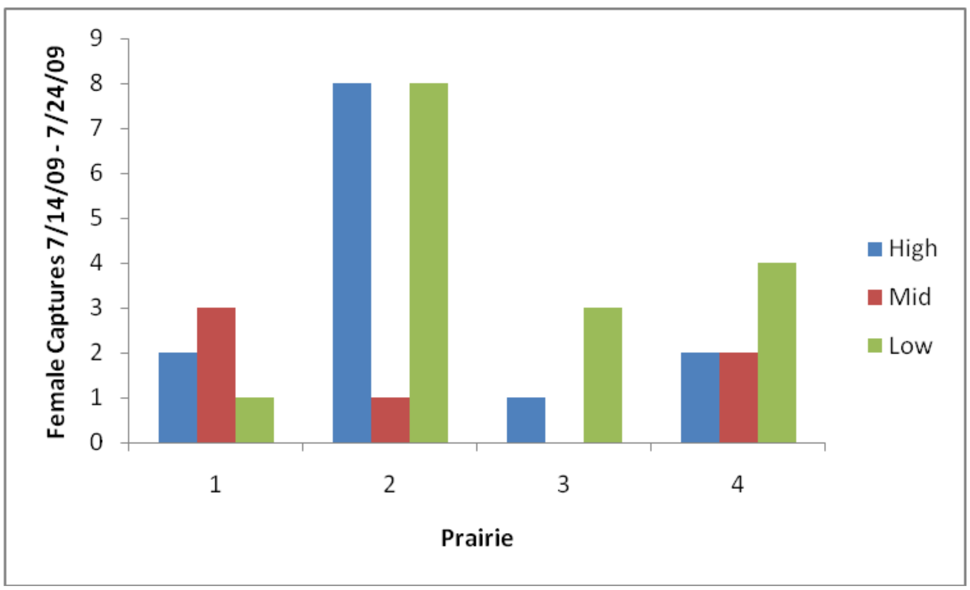
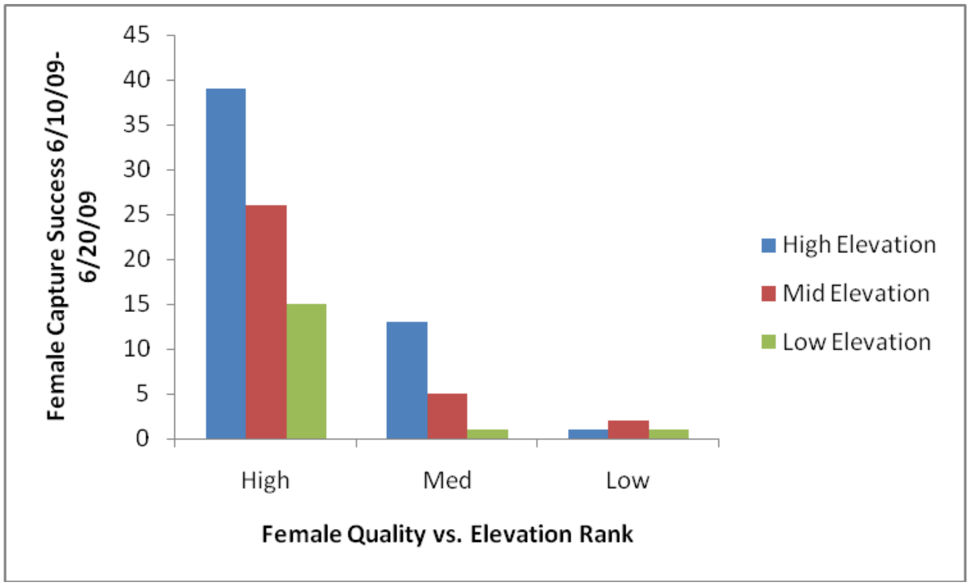


Figure 5. Female capture success at elevation ranks high, middle, and low for both capture periods. Recorded for all species.



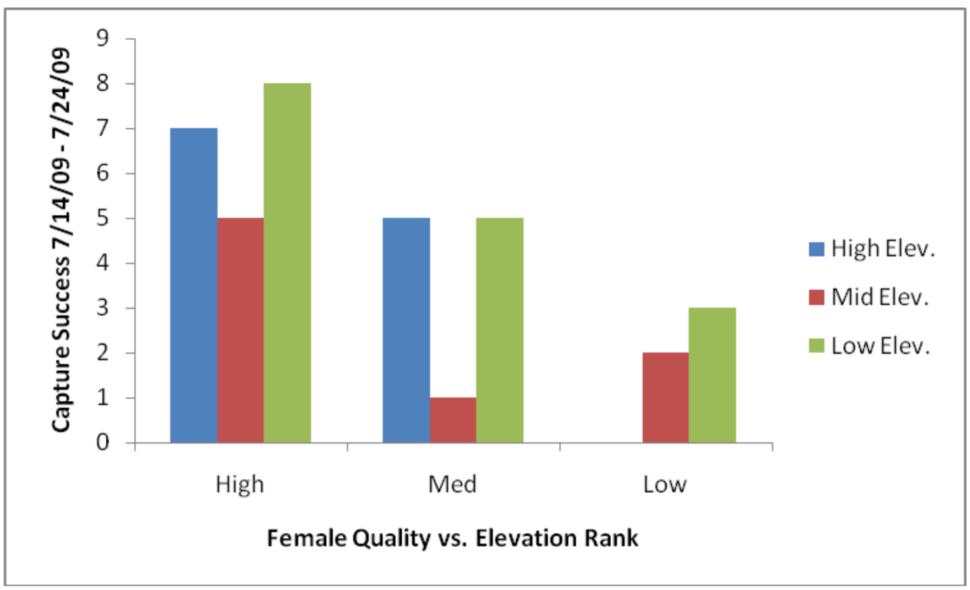
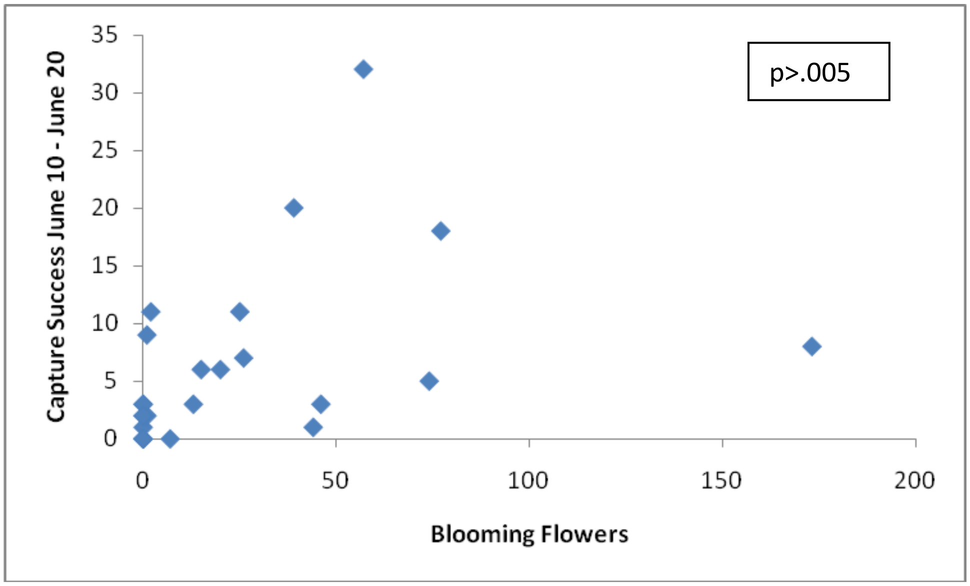


Figure 6. Female capture success at elevation ranks high, middle, and low, in correlation to female wing quality for both capture periods. Recorded for all species.



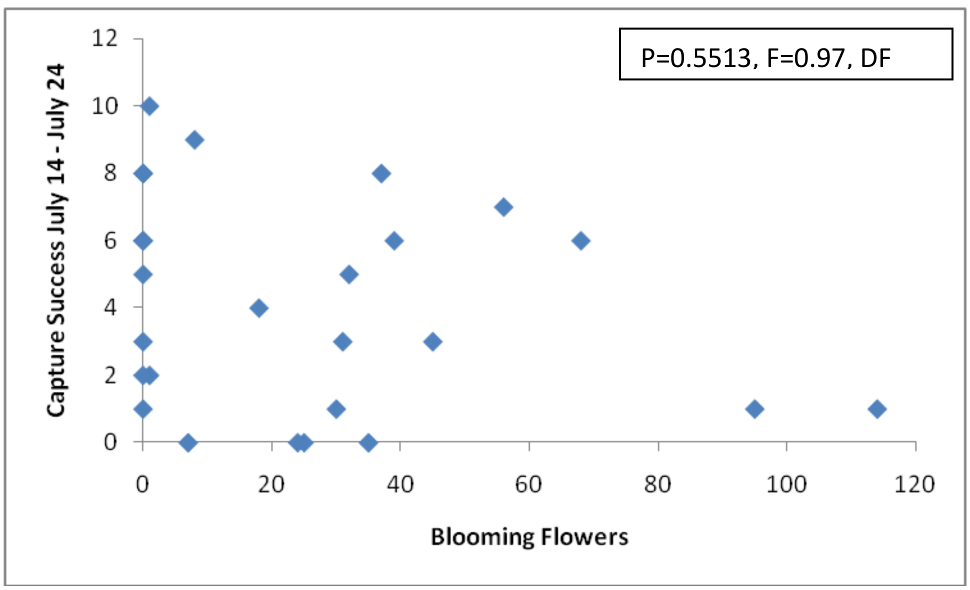
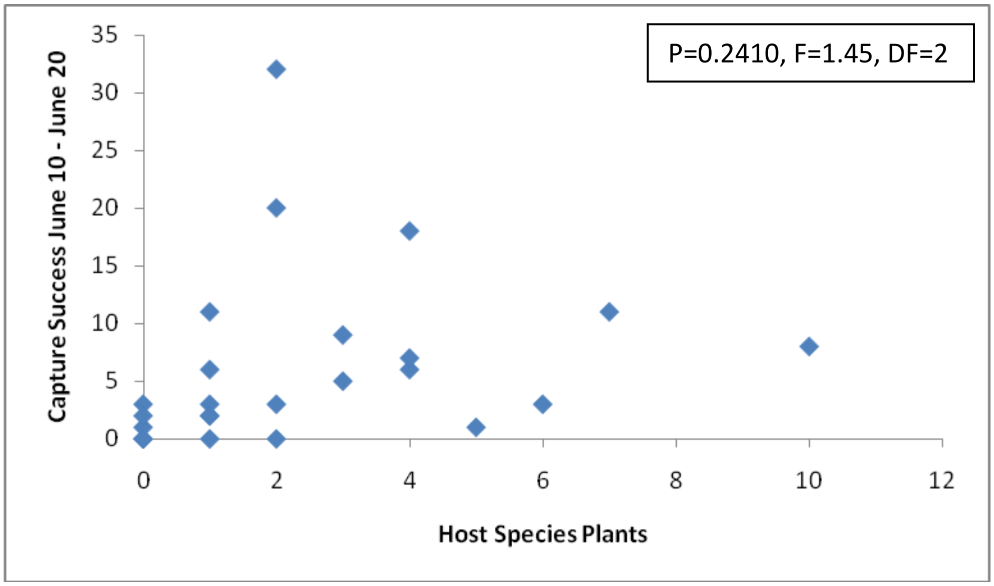


Figure 7. Butterfly capture success for all species in correlation to blooming flowers observed in each vegetation plot. Recorded for males and females in both capture periods.



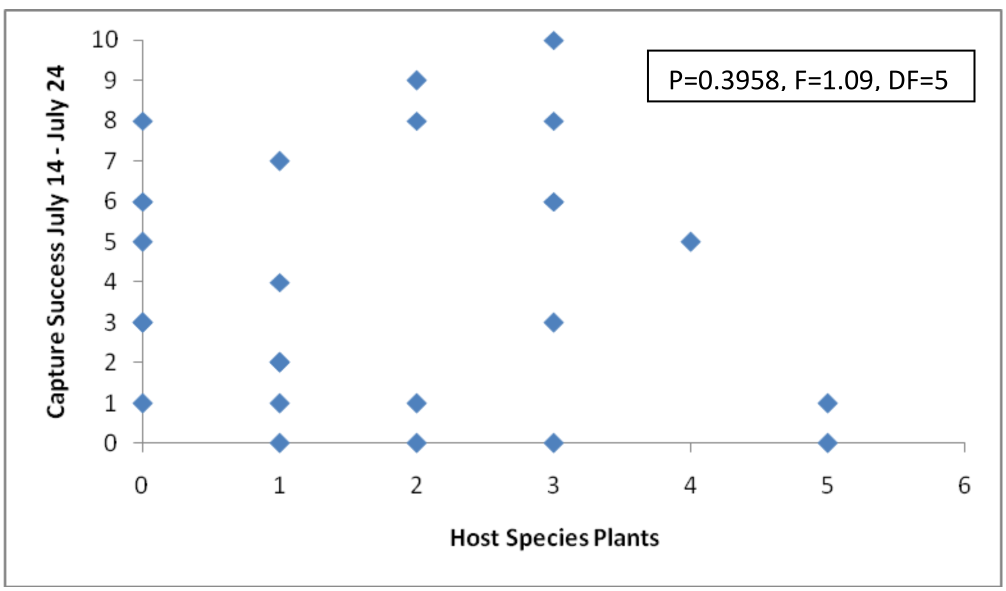
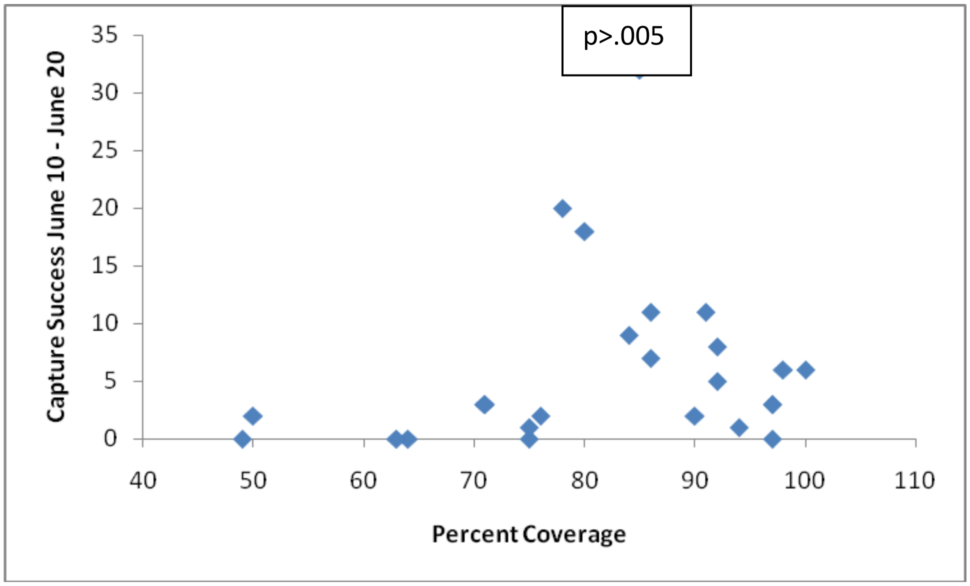


Figure 8. Butterfly capture success for all species in correlation to host plant species observed in each vegetation plot. Recorded for males and females in both capture periods.



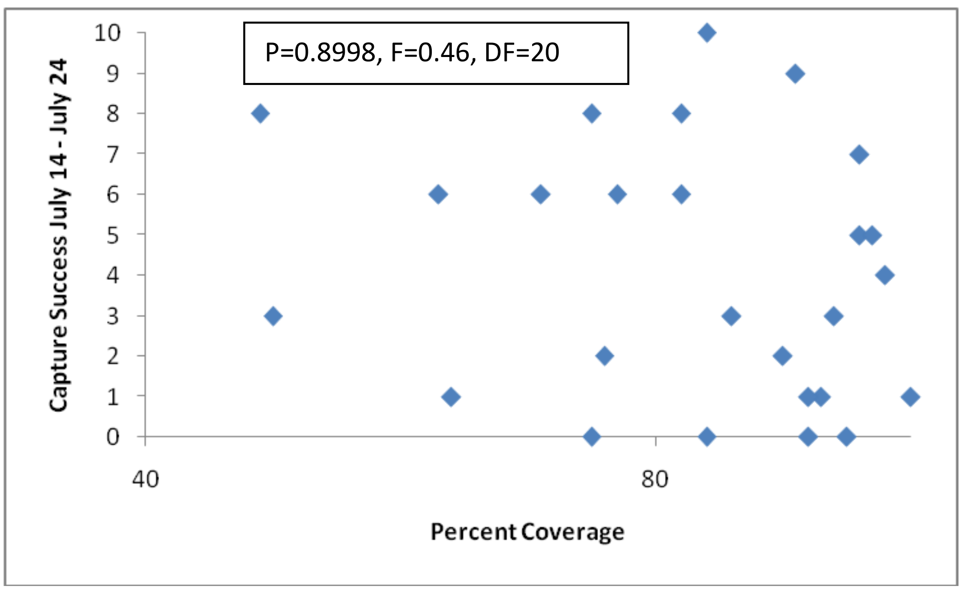
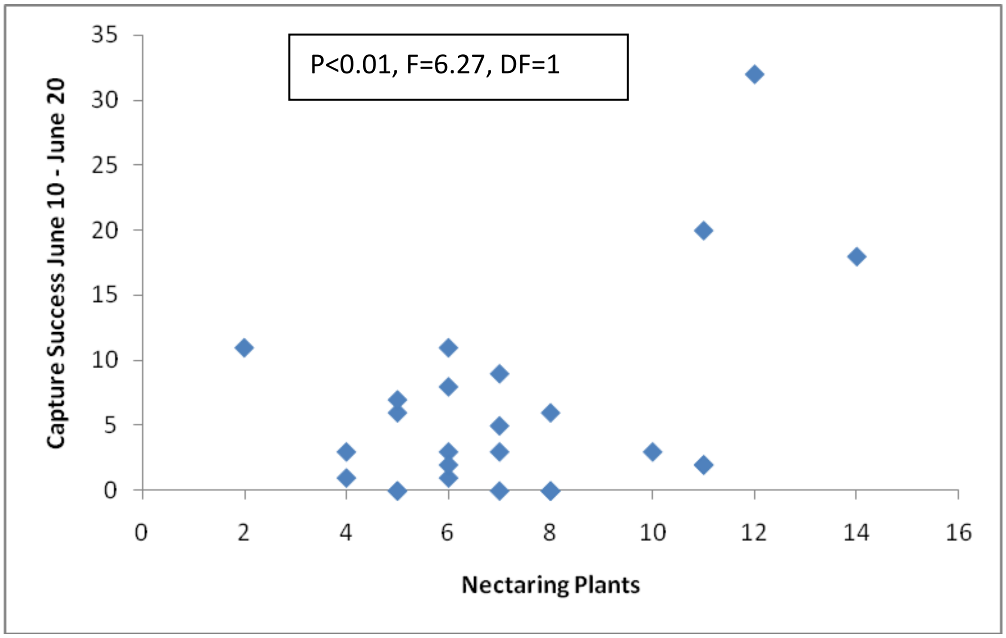


Figure 9. Butterfly capture success for all species in correlation to percent coverage observed in each vegetation plot. Recorded for males and females in both capture periods.



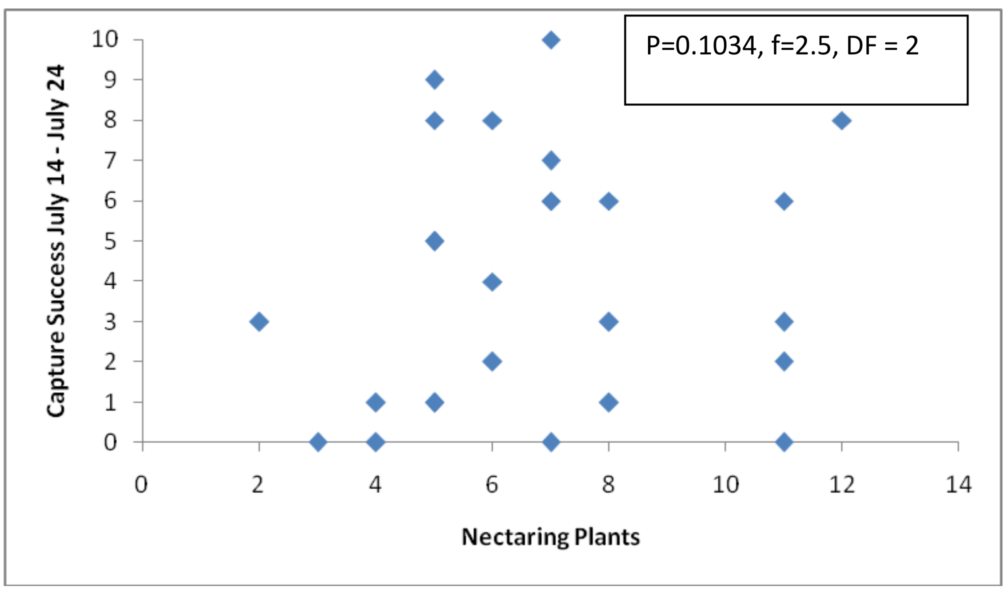


Figure 10. Butterfly capture success for all species in correlation to nectaring species observed in each vegetation plot. Recorded for males and females in both capture periods.

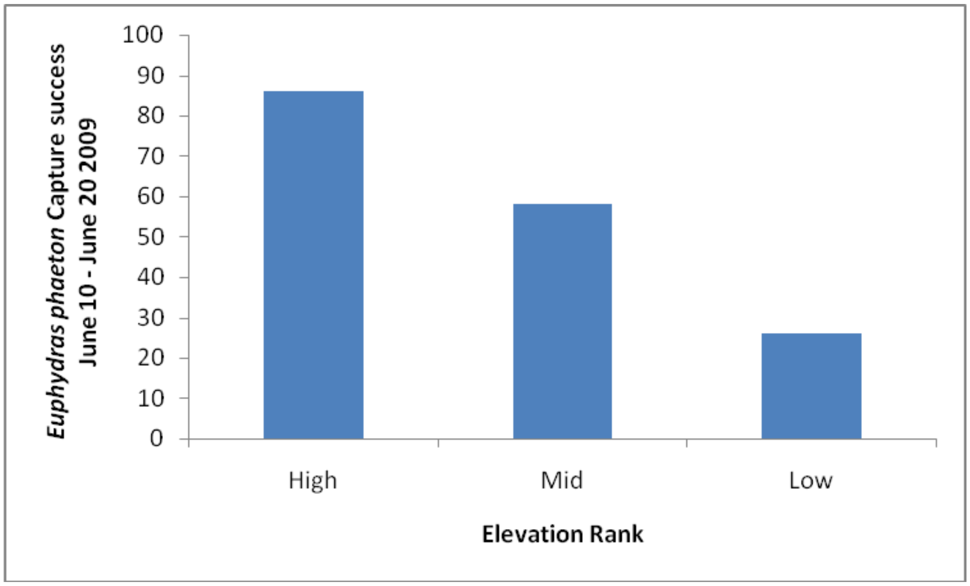


Figure 11. *Euphydras phaeton* capture success as high, mid, and low elevations for all study sites from June 10 – June 20 2009.

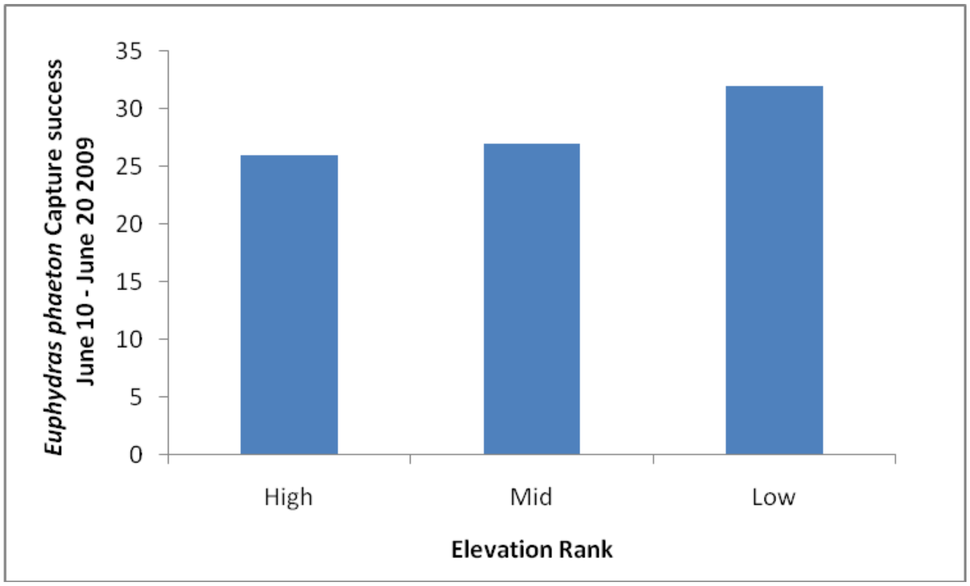


Figure 12. *Colias philodice* capture success as high, mid, and low elevation for all study sites from July 14 – July 24 2009.

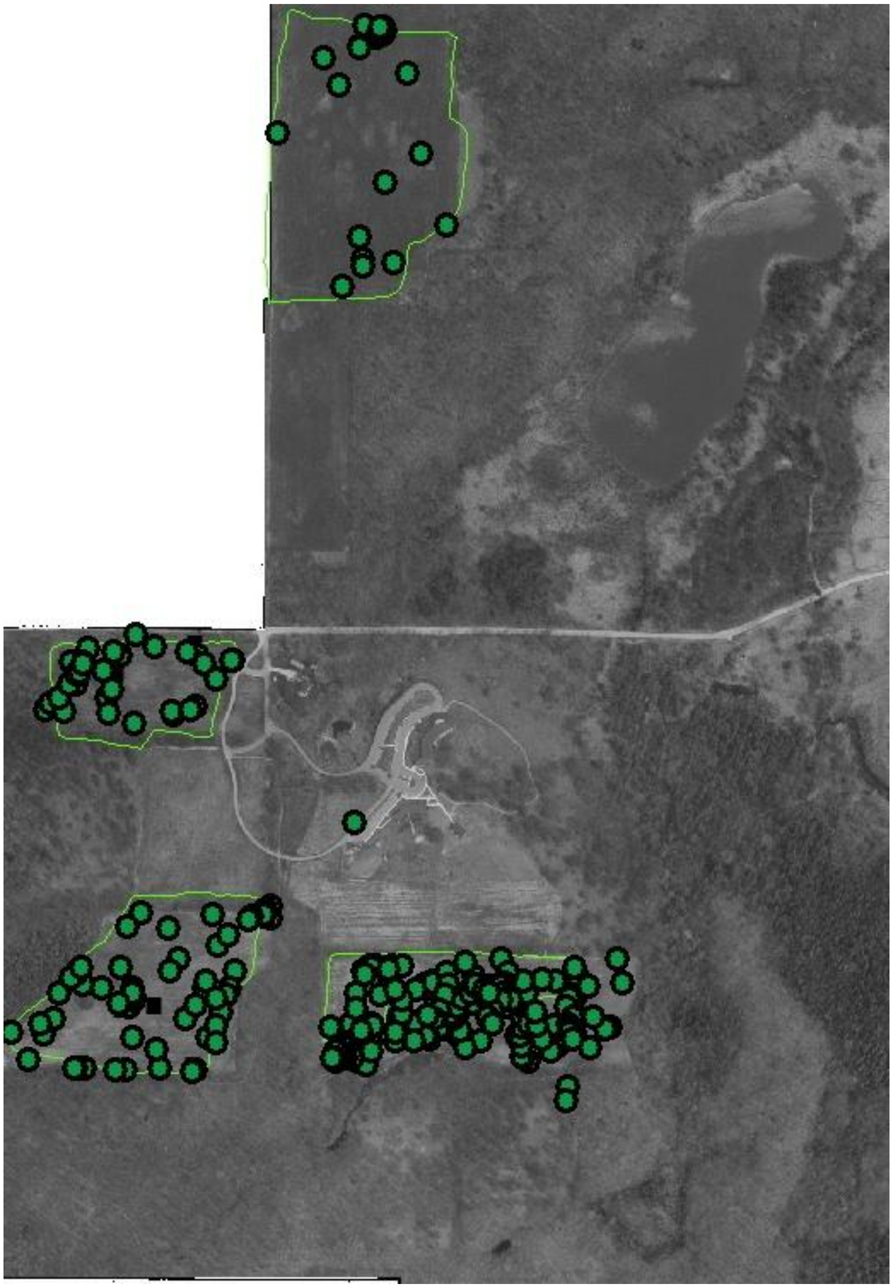


Figure 13. Prairie locations outlines with unique butterflies identified as individual attributes. Spatial distribution analyzed using ArcGIS.

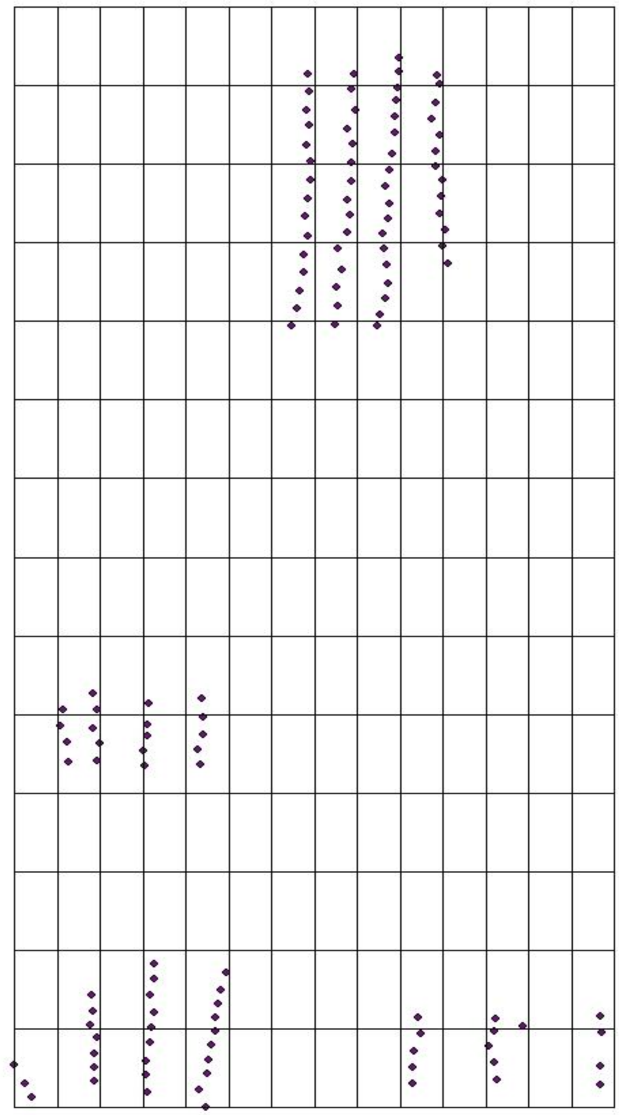


Figure14. Spatial distributions of vegetation plots. Plots within each cell were used to obtain vegetation quality data.

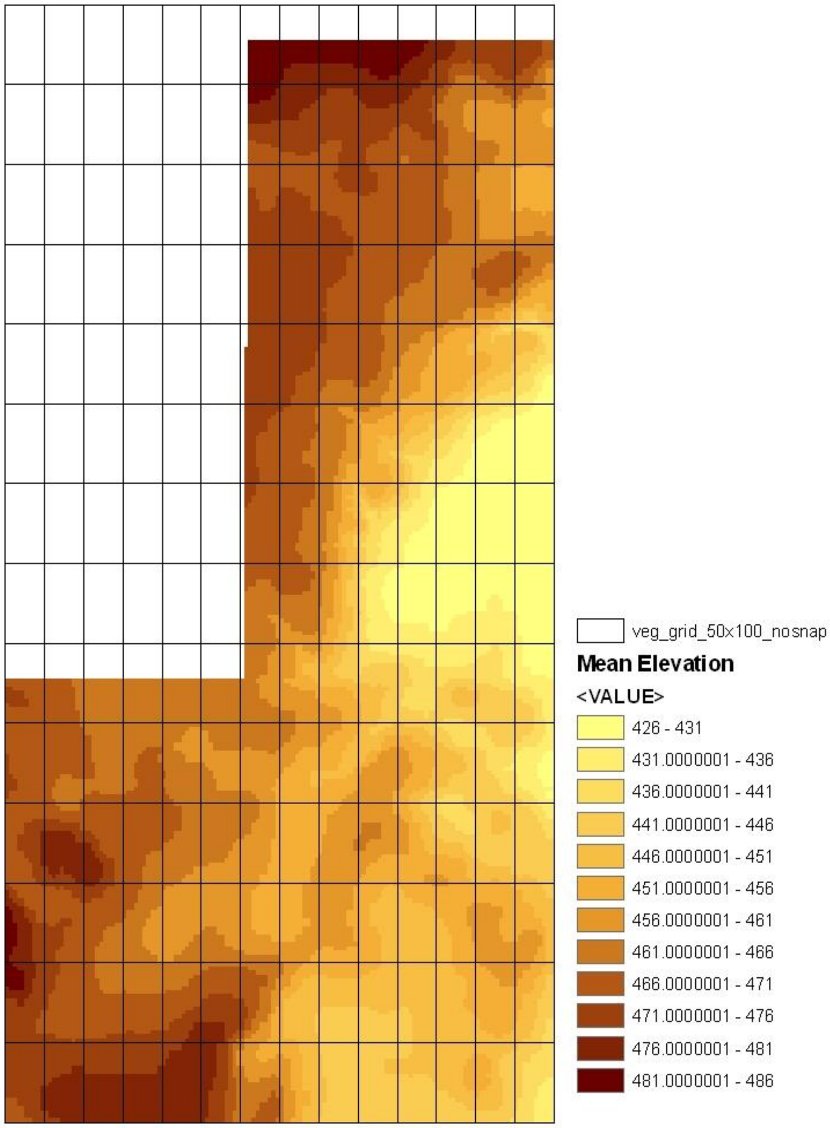


Figure 15. Digital elevation model assigned to study area using ArcGis. This shows elevation variation between individual cells in study plots.

Literature Cited

Cowley MJR, Wilson RJ, Leoncortes JL, Gutierrez D, Bulman CR, Thomas CD 2000. Habitat based statistical models for predicting the spatial distribution of butterflies and day-flying moths in a fragmented landscape. Journal of Applied Ecology. 37: 60-72.

Daubenmire R. 1959. A canopy-coverage method of vegetational analysis. NorthWest Science. 33:43-64.

Dunn JP, Hereau HA, and AJ Klomp. 2006. Diversity of Cicadellidae and Cercopidea (Hemiptera) on sand prairies of Newaygo County Michigan. The Great Lakes Entomol. 39: 113-122.

Dunn JP. 2008. Investigations of adult dispersal, habitat quality analysis, and the development of monitoring techniques for the Karner blue butterfly within the Muskegon Recovery Unit. Final Report – Wildlife Division, Michigan Department of Natural Resources. 40 pages.

Ehrlich PR and SE Davidson. 1960. Techniques for capture-recapture studies of Lepidoptera populations. J. Lepidopterist's Society. 14: 227-229.

Ehrlich PR and Wheye D 1986. "Nonadaptive" hilltopping behavior in male checkerspot butterflies (*Euphydras editha).* American Naturalist 127: 477-483.

Fleishman E, Ray C, Sjogren-Gulve P, Boggs CL and DD Murphy. 2002. Assessing the roles of patch quality, area, and isolation in predicting metapopulation dynamics. Conservation Biology. 16: 706-716.

Hanski I. 1999. Metapopulation Ecology. Oxford University Press. 313 pp.

Harrison S and AD Taylor. 1997. Empirical evidence for metapopulation dynamics. Pages 27-42 in I Hanski and ME Gilpin, editors. Metapopulation biology: ecology, genetics and evolution. Academic Press.

Koperski C. 2007. Insect diversity in old field and newly restored prairies at Pierce

Cedar Creek Institute, Barry County, Michigan. PCCI - URGE Final Report .

Luoto M, Kuussaari M, Rita H, Salminen J, and Bonsforff TV 2001. Determinants of distribution and abundance in the clouded Apollo butterfly: a landscape ecological approach. Ecography. 24:601-617

Matter SF. 2003. The effects of isolation, habitat area and resources on the abundance, density and movement of the butterfly Parnassius smintheus. The American Midland Naturalist. 150: 26-36.

Odendaal FJ, Turchin P, and Stermitx FR 1989. Influence of host-plant density and male harassment on the distribution of female *Euphdryas anicia (Nymphalidae)*. Oecologia. 78: 283-288

Pollard E and TJ Yates. 1993. Monitoring Butterflies for Ecology and Conservation. Chapman and Hall. 274 pp.

Ricketts TH. 2001. The matrix matters: effective isolation in fragmented landscapes. The American Naturalist. 158: 87-99.

Roland JR, Keychobadi N, and Fownes S. 2000. Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. Ecological Society of America. 81 (6): 1642-1653

Scott, JA 1974. Mate locating of butterflies. American Midland Naturalist. 91: 103-117.

Sharp MA, Parks DR, and Ehrlich PR 1974. Plant resources and butterfly habitat selection. Ecology. 55: 870-875.

Shields, O 1967. Hilltopping. J.Res.Lepid. 6:69-178

Sheppard PM and JA Bishop. 1973. The study of populations of Lepidoptera by capture-recapture methods. J. Res. Lepid.12:135-144.

Thomas CD and MC Singer.1987. Variations in host preference affects on movement patterns within a butterfly population. Ecological Society of America. 68: 1262- 1267.

Thomas CD. 2000. Dispersal and extinction in fragmented landscapes. Proc. Royal Soc. London. 267:139-146.