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PATCH-SCALE MOVEMENT DYNAMICS IN THE IOWA GRASSLAND BUTTERFLIES *SPEYERIA CYBELE* AND *MEGISTO CYMELA* (LEPIDOPTERA: NYMPHALIDAE)

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ABSTRACT

An understanding of the movement dynamics of invertebrates can be critical to their conservation, especially when managing relatively small, isolated habitats. Most studies of butterfly movement have focused on metapopulation dynamics at relatively large spatial scales, and the results from these studies may not translate well for patchy populations within a single nature preserve. In this work we use individual mark and recapture (IMR) methods to follow the movements of two species of butterfly, *Megisto cymela* (Cramer) and *Speyeria cybele* F. (Lepidoptera: Nymphalidae) within a 240 hectare forest and grassland preserve in central Iowa, USA. Significant redistribution was seen in both species, with 55.7% of *S. cybele* and 31.1% of *M. cymela* undergoing interpatch movement. Median movement rates during the study were 105 m/day for *S. cybele* and 38 m/day for *M. cymela*, with the top decile moving at a rate of over five times these values. This movement did not appear to be random. *S. cybele* exhibited directed movement towards patches with high nectaring potential, although not all such patches were selected. *M. cymela* aggregated in particular prairie patches, especially those with high edge to area ratios, although the reason for aggregation is not clear.

The Iowa landscape has undergone more significant land-use changes than that of perhaps any other state in the United States (Smith 1998). Native tallgrass prairie and savanna ecosystems have been diminished in extent and connectivity, to the point that remnants and newly planted prairie restorations are largely isolated fragments of relatively small size (Rosburg 2001). In such fragmented systems, local extinction rates are likely to be high for insect species if populations are: (i) confined to a spatially limited area; (ii) characterized by small size or; (iii) exposed to localized but potentially frequent disturbances such as prescribed burning (Hammond and McCorkle 1983, Warren 1992, Thomas and Hanski 1997, Thomas 2000). Because connectivity among patches is a critical factor influencing species' distribution among remnant and restored habitat patches, the success with which grassland restorations re-accumulate insect species may in some cases be more a function of landscape context than other commonly used measures of habitat suitability such as habitat area or precise floral assemblage (Packard and Ross 1997, Gutiérrez and Thomas 1999). Some insect species are unwilling to cross hostile matrix, while others are of limited vagility, leading to colonization failure and population aggregation (With and Crist 1995, Schultz and Crone 2001). In highly fragmented landscapes such as the Iowa Tallgrass prairie, interpatch distance often occurs at the scale of 10 km or more, resulting in significant isolation of habitat fragments and potentially exceeding the modal dispersal distance of many grassland insects (Thomas and Hanski 1997). Under these circumstances, within-system dynamics of

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patchy populations (sensu Thomas and Harrison 1992) (on the scale of ½-2 km) becomes the major factor in management and post-disturbance recovery for non-vagile species.

Unfortunately, this type of information is not well-known, especially for butterfly communities in the American Midwest. While there is good large-scale data on some charismatic butterfly species such as *Euphydryas editha bayensis* Sternitzky (Lepidoptera: Nymphalidae) (Harrison 1989) and *Speyeria idalia* Drury (Lepidoptera: Nymphalidae) (Ries and Debinski 2001), pest species (Jones 1977, Root and Kareiva 1984), high altitude species (Matter et al. 2003, Auckland et al. 2004) and European species (Thomas et al. 1992, Thomas and Hanski 1997, Gilbert and Raworth 2005), data that can be used to manage patchy populations in tallgrass prairie regions is lacking (Panzer 2002).

As in many ecosystems, tallgrass floral communities often require burning or other disturbance for their restoration in order to reduce encroachment by native and exotic nonprairie species (Shelford and Winterringer 1959, Leach and Givnish 1996, Wilson and Stubbendieck 1997). Since most remaining prairie habitats are small and fragmented, there is concern that destructive management may have highly deleterious effects upon invertebrate populations (Schlict and Orwig 1998, Swengel 2001). While there is evidence that insect communities may recover after restricted (i.e., partial) burns through local recolonization, even this can be incomplete and populations may suffer depression in the face of repeated disturbance (Panzer 2002, Tooker and Hanks 2004). Because most prairie preserves are managed with fire by splitting them into sub-units and burning at that scale, movement among patches within preserves may be as important as movement among prairies within a landscape (Bestelmeyer et al. 2003).

The goal of this paper is to study the movement patterns of two common butterflies in a tallgrass prairie preserve in central Iowa. In particular, we look at distances traveled and emigration fraction (Hill et al. 1996, Thomas and Kunin 1999) of particular habitat patches. We predicted that the highly vagile *Speyeria cybele* F. (Lepidoptera: Nymphalidae) would move easily between patches, especially as nectaring opportunities shifted throughout the study period (Schneider et al. 2003), thus exhibiting high emigration fraction and large travel distances. On the other hand we predicted that the energetically limited *Megisto cymela* (Cramer) (Lepidoptera: Nymphalidae), whose host plants were common throughout the study site, would exhibit dramatically lower emigration rates and lower travel distances (Auckland et al. 2004). At the same time, because *M. cymela* is an edge associate and may be more tolerant of flying through shady habitat, we expect the matrix to be more permeable to it than to *S. cybele*.

MATERIALS AND METHODS

Study Species. We worked with two species in this study that were chosen for their significant differences in body size, perceived vagility, and predilection for nectaring; both species are relatively common in mesic Tallgrass prairie vegetation in the Midwestern USA (Richard and Heitzman 1996). The first was *S. cybele*, a vagile, non-migratory butterfly, common in Iowa grasslands. In the caterpillar stage, *S. cybele* feeds upon various species of *Viola* (Robinson et al. 2002). As an adult, *S. cybele* actively nectars on a variety of prairie forbs, especially species of *Echinacea* (Asteraceae), *Asclepias* (Ascelepiadaceae), and *Eupatorium* (Asteraceae) (Scott 1986). Adults are ecologically comparable to *S. idalia* (e.g., females aestivate, both species actively nectar on similar species, both are about the same body size), a species of conservation concern in Iowa that is undergoing active reintroduction in other prairies in the state (Shepherd and Debinski 2005).

We also worked with *M. cymela*. Unlike *S. cybele*, *M. cymela* is a fairly weak flyer, whose dispersal ability might be constrained by limited adult feeding.

Adults may feed on some easily accessible food sources (tree sap, fungi, aphid honeydew secretions, and so on), and have occasionally been observed visiting flowers (Scott 1986, Iftner et al 1992), but the majority, if not all, of *M. cymela*'s energy is accumulated in the larval stage (Allen 1997). While *M. cymela* is single-brooded in Iowa, two flight peaks may be occasionally observed due to delayed eclosion of some individuals (Glassberg 1999), or short-term aestivation (Allen 1997). *M. cymela* is an edge associate but not a forest-dwelling butterfly. Iftner et al. (1992) describe the habitat associations of *M. cymela* as "forest margins, brushy meadow, and fields", and Richard and Heitzman (1996) describe it as a species of open woodlands and brushy grasslands. Opler and Krizek (1984) list its host plants as various grasses not found in the forest interior, including *Dactylis glomerata* L. (Poaceae). (Species nomenclature follows Voss 1972, 1985, 1996). Because the canopy cover in the forest was 70-90%, regions between prairie patches were considered interhabitat forest matrix, although forest edge and roadways would be considered habitat.

Site Characteristics. We worked at the Kuehn Conservation Area, a 260 ha tallgrass prairie preserve in southwestern Dallas County, Iowa (41°31'17"N; 94°7'17"W). This region is bordered by the Raccoon River, a private forested area to the east, and a steep woodland ridge system to the west, both serve to contain grassland butterflies largely within the preserve valley (Fig. 1). Kuehn Conservation Area is characterized by six small (0.5-9 ha) prairie openings (Table 1) surrounded by forested ridges dominated by *Quercus alba* L. (Fagaceae),

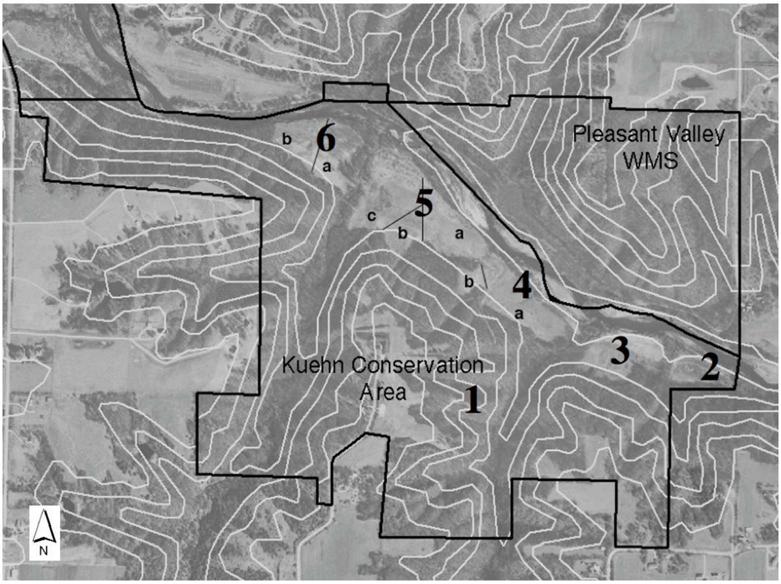


Figure 1: Arial photo of study site with prairies numbered 1-6 (see Methods and Table 1). Contour lines are 10-foot intervals from the United States Geological Survey's 7.5 minute quadrat (distance scale: 2.5 cm ≈ 250 m). All research was conducted within the boundaries of the Kuehn Conservation Area, largely within the valley visible in the center of the figure. The Pleasant Valley WMS is a forested site, dominated by hardwoods (*Quercus* spp. and *Carya* spp.). To the south and west are agricultural lands. Toward the northwest is a wilderness management area consisting of planted forage grasses and *Phragmites australis*.

Table 1. Characteristics of prairie patches. Perimeter to area ratio (P/A Ratio) is the ratio of forest edge to grassland area.

Prairie	**Patch Area (Ha)†**	**P/A Ratio (m/Ha)†**	**Dominant Vegetation‡**
1	0.5	0.071	*Andropogon gerardii, Amorpha canescens, Dalea purpurea., Echinacea pallida*
2	1.1	0.046	*Phalaris arundinacea, Asclepias syrica, Echinacea pallida, Populus deltoides* (saplings)
3	2.91	0.032	*Phalaris arundinacea, Andropogon gerardii, Rubus* spp., *Echinacea pallida*
4	4.14	0.028	*Andropogon gerardii, Sorghastrum nuttans, Ratibida pinnata, Echinacea pallida*
5	8.41	0.018	*Andropogon gerardii, Rubus* spp., *Echinaceae pallida, Phalaris arundinacea*
6	3.96	0.026	*Andropogon gerardii, Helianthus* spp., *Asclepias syrica, Echinaceae pallida*

† Estimates obtained from 2002 digital aerial photos analyzed using ArcView GIS (version 3.2)

‡ From Summerville (unpublished data)

Carya ovata (Miller) K. Koch (Juglandaceae), and *Ulmus* spp. (Ulmaceae). Each of the prairie patches is dominated by grasses (Poaceae), mostly *Andropogon gerardii* Vitman, *Sorghastrum nutans* (L.) Nash, and in more mesic depressions *Phalaris arundinacea* L. Dominant forbs consist of *Echinacea pallida* (Nutt.) Nutt. (Asteraceae*)*, *Ratibida pinnata* (Vent.) Barnhart (*Asteraceae*), *Asclepias syriaca* L. (Asclepidaceae*)*. A variety of other forbs (primarily Asteraceae, Lamiaceae, and Fabaceae) are also frequently encountered throughout the preserve. Prairies 3-6 tended to slope gently downward towards the river, the northeastern regions wetter and generally dominated by *Phragmites australis* (Cav.) Steudel (Poaceae). A region to the west of prairie 1 was actively used for park activities, so was managed as a mix of mown turf grasses and areas of prairie forbs and grasses. Some study species were observed in this area.

This site was optimal for our study because it exhibits natural features of fragmentation and contains the prairie-woodland mosaic typical of Iowa, Missouri, and southern Illinois. This region is deeply bisected by forested habitat (Rosburg 2001), which may affect thermoregulation by individuals attempting to move long distances through a relatively "cooler" habitat type (Daily 1996, Saarinen 2002). The prairie openings at the study site are separated by varying distances through woodlands (70-90% canopy cover in most areas), making this an ideal area to obtain data regarding movement through a heterogeneous landscape, and between habitat patches. The longest measurable distance for travel in our study (a movement from the northwestern edge of Prairie 6 to the southeastern edge of Prairie 2) would have been just over 3 km.

Field Techniques. We used individual mark and recapture (IMR) techniques to obtain data on the large-scale movement of individual butterflies. IMR, where specimens are captured, marked, and then recaptured at some later date to determine characteristics of their movement, provides detailed spatio-temporal information on the individual level which can be directly translated into behaviorally-based models (Odendaal et al 1988, Turchin 1998). GPS was used to determine the location of capture and release and times were recorded for each.

In order to reduce handling stress through multiple recaptures on a given day, and to increase capture efficiency, netted butterflies were immediately transferred to a numbered glassine envelope that was placed within a portable cooler for a period of up to three hours (although periods of 15-60 minutes were more common). Care was taken to avoid damaging wings and legs during transfer. Butterflies were stored with wings in the closed position to reduce stress and unnecessary movement. After capture efficiency decreased markedly at a given site (indicating a high capture fraction), all butterflies were marked and released, and the site was not resampled until a subsequent date. Sites were revisited every 3-5 days depending upon weather conditions. Unique marks were applied with a permanent marker to the underside of the wings according to well-established techniques (Ehrlich and Davidson 1960, Kearns and Inouye 1993, Horner-Devine et al. 2003, Winter 2003). In most cases the marks were easily interpreted upon recapture but occasionally the loss of wing fragments where marks could have been would lead to ambiguous readings. When this occurred, attempts were made to use other information (such as sex, extent of wing damage, and other captures on the same day) to uniquely identify individuals. If this could not be done, the recapture data was not used in subsequent analyses, although the individual was recorded as a recapture.

When capturing, we attempted to walk in a regular pattern throughout the prairie openings. We had one to four researchers working in a patch at a time and when we had more researchers in a patch we also spent time sampling in the forest within about 25 m of the edge. We also sampled along a mown path to the southwest of Prairie 5 and a gravel road to the southwest of Prairie 4. On a few occasions we encountered an individual while outside of the active sampling region. These individuals were also captured and marked.

As shown in Fig. 1, prairie fragments were given a number (1-6), Prairie 1 being a small, isolated prairie in the southern range of the park, 2-6 moving from the southeast to northwest. All prairies were isolated from the others by forest matrix except the two largest prairies: 4 and 5. Although these prairies were connected, the corridor region was relatively small and Prairie 4 sloped uphill away from the corridor, such that the two appeared more distinct at the site than in the photographs. For the less vagile *M. cymela*, the large prairies 4, 5, and 6 were further subdivided according to landscape features (abrupt change in forest edge direction or significant change in slope) also shown in Fig. 1. Prairie 6 is the only prairie where there was no obvious feature to distinguish regions. It was simply split roughly in half.

In order to investigate behavior on a finer scale, we also followed individual butterflies for a period of twenty minutes each, or until the individual was lost, as happened occasionally. We were careful to avoid casting shadows upon the butterflies or otherwise disturbing their behavior. We set marker flags to indicate points of resting between flights, waiting until the individual had risen again to avoid causing premature flight. This process was easier for *M. cymela* than *S. cybela*, because it was very difficult to follow the latter quickly enough to keep it in sight while at the same time not disturbing it. Hence information on these observations will only be reported for *M. cymela*. Occasionally, *M. cymela* would exhibit apparent avoidance behavior where it would spiral rapidly into the forest canopy. As this behavior often appeared to be a response to disturbance from the researchers, we halted tracking at this point. See Schtickzelle and Baguette (2003) for a more complete description of this technique.

Data Analysis. To estimate the total population within the study area, we used the Jolly-Seber method of daily population estimation (Southwood 1978, Blower et al. 1981). This method allowed for the accurate estimation of population size at various times even under conditions of: 1) movement of individuals between habitat patches outside of the study area; 2) emergence and death of new individuals; and 3) unequal sampling effort in any given region on a particular day and similarly unequal time between sampling events.

Given the small populations in individual prairies or prairie fragments, as well as the relatively small number of recaptures within the prairie of initial capture, we did not use the Jolly-Seber method to calculate these population sizes as errors would be large. In this case, we were interested only in relative (rather than absolute) population sizes. Assuming that emergence and death rates were similar throughout the study area, we can determine the fraction of the total population residing in a given patch by calculating a modified Lincoln Index for each patch. There, $P_i = n_i^2 / m_i$, where P_i is the relative population in patch i, n_i is the total number of captures in that patch, and m_i is the number of recaptures of marked individuals in patch i originating from that patch before a given date (Blower et al 1981). We used this estimate to determine the fraction of butterflies in a given prairie patch and then combined this with the Jolly-Seber estimate of the total population to produce population estimates for each patch. Sensitivity values were calculated as the change in the population estimate per patch that would result if one more or one fewer butterflies were recaptured. Most, but not all, of the population estimates were fairly insensitive to small changes in the number of recaptures (the median sensitivity is about 7%). This amount of change led to a difference of about 0.8% when estimating the relative fraction of butterflies within a given patch.

All of our linear regressions and statistical comparisons were made using PC SAS for Windows v 9.1 Service Pack 2 (SAS Institute, 2006). Confidence levels of 95% or greater were considered statistically significant.

RESULTS

We captured 402 individuals of *S. cybele* and 883 individuals of *M. cymela* from June – August 2004. Recapture rates for each species were roughly 20% (Table 2). Of recaptures, 44.3% of *S. cybele* and 68.9% of *M. cymela* were observed within the same prairie as release. If we consider the scale of subprairies for the smaller *M. cymela*, 39.3% of recaptures occurred in the same subprairie as release. There was no observed difference in movement distance between males and females for either species (*S. cybele*: Mann-Whitney, $z = -0.76$, 70 cases, $P = 0.45$; *M. cymela*: $z = -0.52$, 120 cases, $P = 0.60$), or in movement rates (*S. cybele*: $z = -0.9$, $P = 0.37$; *M. cymela*: $z = -0.077$, $P = 0.94$), so data for males and females were combined in subsequent analyses except where noted. The median movement rate (total distance between captures/time between captures) for *S. cybele* was 105 m/day and 38 m/day for *M. cymela* (Table 2). Although both species exhibited a large range of distances traveled (Fig. 2), the movement rate per day was generally more compact (Fig. 3). Both species exhibited large tails in the latter measure representing highly vagile individuals.

Table 2. Capture, population, and movement statistics observed for *M. cymela* and *S. cybele* at Kuehn Conservation Area. Emigration fraction is calculated as the number of individuals captured in a different prairie than the one in which they were marked, divided by the total number of captures.

	M. cymela	***S. cybele***
Number of captures	883	402
Fraction recaptures (%)	20.7	19.7
Mean/longest period between recaptures (days)	5/16	6/25
First and last sampling dates	June 11-Jul 28	June 11-August 6
Number of sampling dates	19	23
Emigration Fraction E	57/183 (31.1%)	44/79 (55.7 %)
Estimated population	509 (+/- 265)	213 (+/- 136)
Median movement rate (m/day); 10th–90th percentile	38; 6–198	105; 13–775

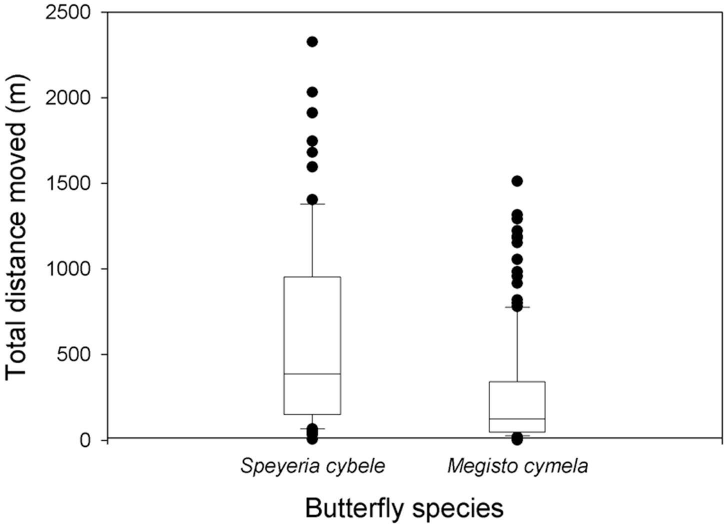


Figure 2: Box and whisker plot of total movement distances (in meters) for recaptured individuals of both species.

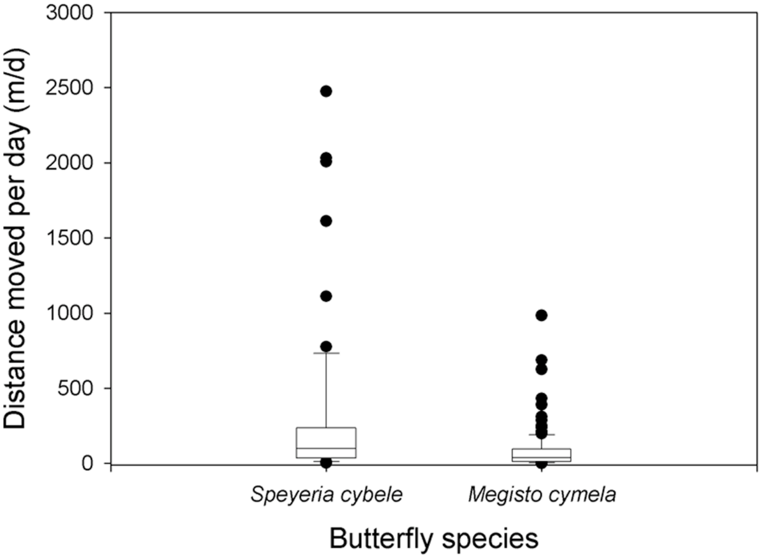


Figure 3: Box and whisker plot of movement rate (in meters per day) for recaptured individuals of both species.

Population estimates for *S. cybele* varied with patch size and ranged from 7 to 54 individuals (Table 3). *S. cybele* population sizes were marginally correlated with prairie size using a simple linear regression model (SAS Institute, 2006) (patch size parameter estimate = 5.01, $P = 0.0577$, $r^2 = 0.64$), with the highest population in the largest prairie, prairie 5, and the smallest in the half-hectare prairie 1. *S. cybele* had the most captures in prairie 2 and the southeast segments of prairies 4 and 5 (Fig. 4). These sites all had abundant *Asclepias sullivantii* A. Gray, *Cirsium arvense* (L.) Scop. (Asteraceae), and other nectar sources, although prairie 2 had a high cover of shrub species as well, including *Cornus* spp.(Cornaceae) and *Salix* spp (Salicaceae). The northwest region of prairie 6 had a large population of *A. syriaca*, but few individuals were ever observed in that area. Although prairie 1 had nectaring opportunities and a few individuals were captured there, during most of our visits there were no *S. cybele* in this prairie. Although significant search time was spent in the northeastern regions of the prairies, very few individuals of either species were found there. The dominance of *P. australis* in these regions left little nectaring opportunity for *S. cybele*, and few suitable egg-laying sites for either species.

We observed a fair amount of interpatch movement for *S. cybele* (Fig. 5a). Prairies 3-6 all exchanged individuals, while individuals were observed to move into prairie 2 only from 3 and 4. Of 8 individuals marked in prairie 1, none were recaptured later, and no marked individuals were recaptured in prairie 1, indicating that most of the interhabitat exchange with prairie 1 was probably with the unsampled area to the west of prairie 1. The largest amount of interaction was between prairies 4 and 5, not surprising because individuals could move between these prairies without entering inter-habitat matrix. If we calculate the per capita emigration (*E*) of various patches (the number of butterflies recaptured in a different prairie from where they were marked, divided by the total number of recaptures from that prairie, from Hill, et al. (1996), we find almost no emigration from prairie 2 (9%; 1/11 individuals). All other prairies had 45% or greater *E*. Very few *S. cybele* were seen in prairie 2 early in the season of study but as time passed the population increased dramatically. Given that this growing population included marked individuals from prairies 3 and 4, it seems likely that much of this population increase was due to immigration from elsewhere (e.g., Fig. 5a). Possible explanations for this movement are: nectaring opportunities were high in this prairie; it may have been too small to support a large larval population, or: eggs might have been destroyed during spring flooding. In either event, butterflies were clearly able to move through the matrix to find this habitat, although we cannot say whether they dispersed again to lay eggs.

Population estimates for *M. cymela* ranged from 4 to 93 individuals (Table 4). *M. cymela* populations were not correlated with patch area ($P = 0.24$) but the highest population estimates were in prairies 1 and 5b. Of 31 individuals marked in 5b, none were recaptured there, while 7 were recaptured in other prairies, perhaps indicating that this patch functioned more as a corridor than as habitat for a stable population. Nearly all individuals were captured along

Table 3. Population estimates for Speyeria cybele observed within each prairie patch at Kuehn Conservation Area. Where the population estimate is based upon a single recapture, the upper bound is recorded as NA.

Prairie #	**1**	**2**	**3**	**4**	**5**	**6**
Area (ha)	0.5	1.1	2.91	4.14	8.41	3.96
Population	7	28	41	53	54	30
Sensitivity	4/NA	26/30	36/48	52/55	52/55	25/38

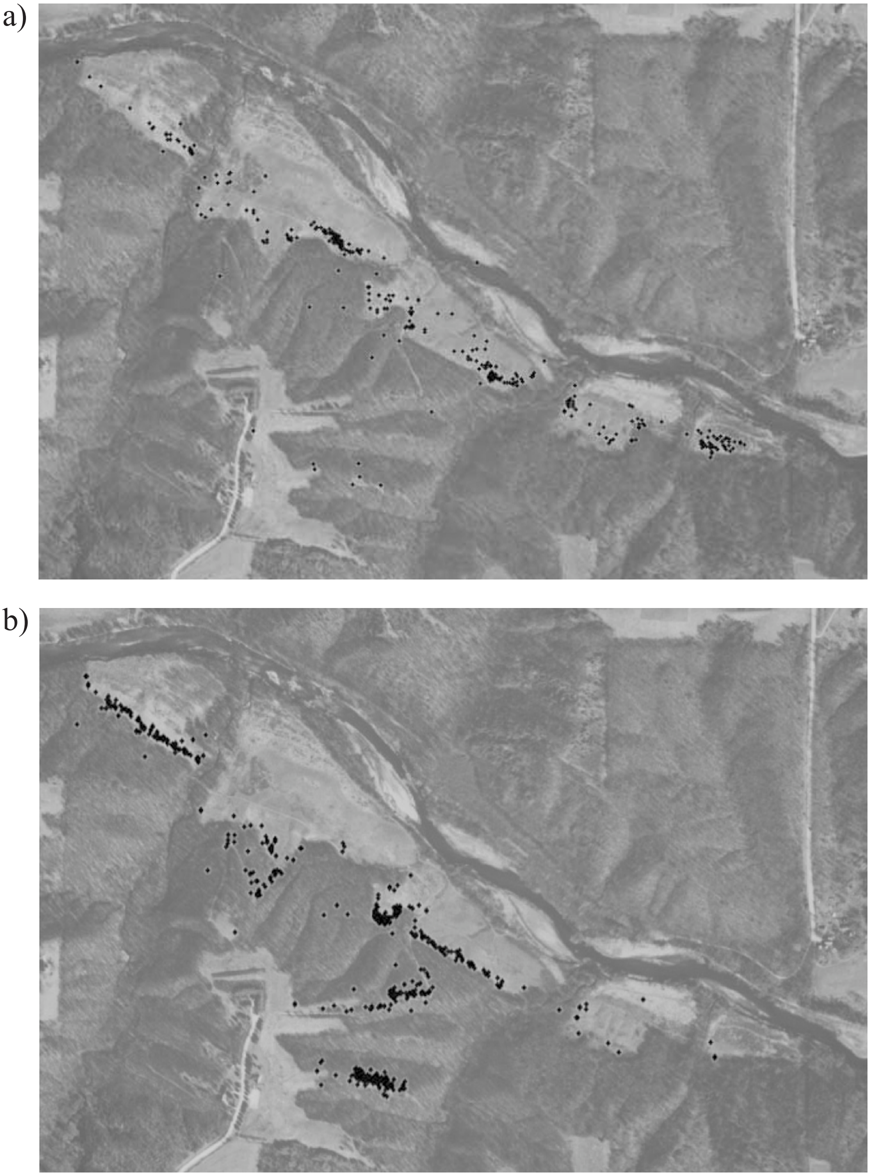
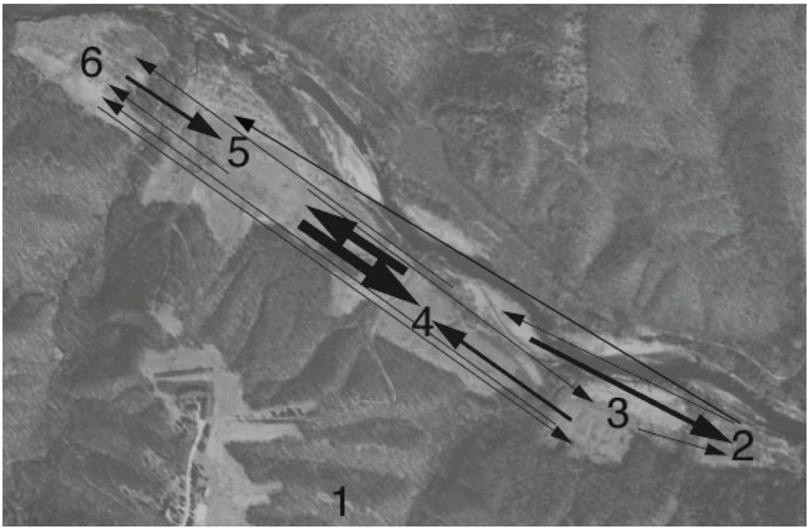


Figure 4: Location of butterfly captures throughout study: a) captures of *S. cybele*. Numerous captures were made in regions of prairies 2, 4, and 5 where nectaring opportunities were high. Very few butterflies were captured in prairie 1 or the western part of 6, although numerous nectaring opportunities existed in these regions as well. Few butterflies were captured in the regions sloping toward the river, even though these sites were visited frequently by researchers; b) captures of *M. cymela*. Nearly all captures were made along the forest edge or within forest matrix. Numerous captures were made in prairie 1, and very few in prairies 2 or 3 (compared with *S. cybele*).

a)



b)

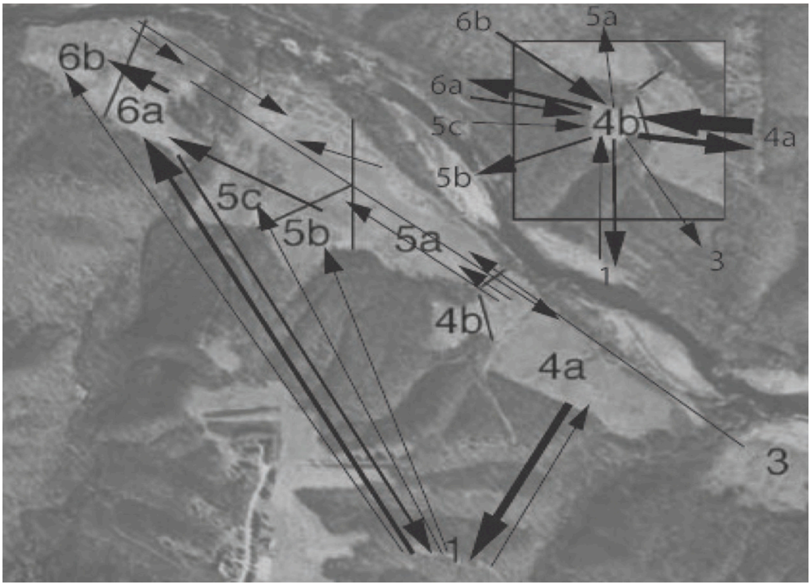


Figure 5: Movement of *S. cybele* (a) and *M. cymela* (b) within the study site. Arrow thickness indicates relative numbers of butterflies observed moving between prairies. In b, subprairie 4b has been separated and added as an inset due to the number of movements in and out of this subprairie patch. The small numbers around this inset indicate which prairies the movement is occurring between but do not indicate actual positions of prairies or subprairies.

Table 4. Population estimates for *M. cymela* in each subprairie patch. GR stands for the long gravel road that moves upslope between prairies 4a and 1. Where a population estimate is impossible, it is recorded as NA. Where a population estimate is based upon a single recapture, the upper bound is recorded as NA.

Prairie #	**1**	**2**	**3**	**4a**	**4b**	**5a**	**5b**	**5c**	**6a**	**6b**	**GR**
Population	93	NA	15	43	50	5	82	4	36	53	71
Sensitivity	91/96	NA	8/NA	41/44	49/51	3/10	54/163	3/6	35/37	44/66	67/76

the southwestern forest edge (Fig. 4b), along the gravel road connecting the visitor's center with subprairie 4a, and in a mown, steeply graded pathway to the southwest of prairies 5b and 5c. We found almost no *M. cymela* in prairie 2 and very few in prairie 3. Prairie 5b started out as a highly populated site in the early spring but became depleted as the season continued. Conversely, as the study progressed, 4b changed from a site with few capture opportunities to one of the two sites with the least amount of time between captures for *M. cymela* (the other being prairie 1). Population density was negatively correlated with patch size ($P = 0.034$) but this effect appears to have been due largely to the very high density in prairie 1 (over twice that of the next-highest density found in prairie 4b). If prairie 1 is left out of the regression, the relationship becomes insignificant ($P = 0.15$).

We find that emigration (E) was lowest in prairie subpatches 6a (31%), 1 (29%), and 4b (25%), indicating that these patches tended to retain individuals. All other subpatches had E above 4a's, which was 59%. In the case of *M. cymela*, there was no obvious reason for the retention within these sites, in terms of abundance of egg-laying sites, shape factor index (sensu Forman 1995), or patch area. Using a linear model, however, for the relationship between butterfly density and the perimeter to area ratio (in meters per hectare), we find that density is positively correlated to perimeter to area ratio, with a slope of 31.8 individuals/ha per m/ha ($P = 0.002$), and an insignificant intercept (-5.8). This suggests that *M. cymela* may seek out, or not exit, prairies dominated by edge habitat, or that preferential movement along edges increases capture frequency.

Megisto cymela were never observed deep in open prairie. Of the 39 individuals for which we followed fine-scale movement and mapped routes traversed, one moved 18 m away from trees and into open prairie before turning back toward the trees, and no others ever moved more than 6 m from the forest edge. The one that ventured the farthest into the prairie may have been exceptional, because it had been following a single row of trees fairly far from the forest edge, and may have been searching for more suitable habitat. On the other hand, numerous individuals were followed into the forest. Movement tended to be along the habitat edge, with 62% (18/29) of those individuals that were tracked at a clearly definable habitat edge having the major axis of their movement along this edge, while only 21% (6/29) moved away from the edge (either into or out of the forest), and 17% (5/29) exhibited no overall bulk movement. This indicates that for *M. cymela*, the presence of edge habitat between larger habitat regions may be useful to encourage population exchange.

DISCUSSION

Our work indicates that *S. cybele* and *M. cymela* exhibit significant movement during the course of a season, with individuals of both species moving between some of the most distant patches in our study site. *S. cybele* is able to cross small amounts of forested matrix habitat in search of nectar sources and tends to aggregate in these areas. As the nectar sources change, or if larval and adult food sources are not locally congruent, we would expect to see net movement of the type observed (Schneider et al. 2003, Auckland et al. 2004, Dennis 2004). In the case of *M. cymela*, the movement is more surprising. As adults are not active feeders, one might expect them to have high patch residence times and remain near emergence sites. While the movement rates recorded in Table 2 may include downward biases due to the nature and scope of the study (mostly related to the fact that highly vagile individuals may leave the limited study area; see Cook et al. 2001, for a discussion and methodological suggestions), it is clear that important redistribution does occur between prairie segments. *M. cymela* was able to cross at least the half-kilometer forested region between prairies 1 and 4, and probably crossed much larger forested regions in moving between prairies 1 and 6. We did not observe marked *S. cybele* crossing more than a few hundred meters of forested area, but this was probably due to the dearth of these captured in the most distant prairie (prairie 1). We did observe some individuals flying into the upper canopy or above it, often as an avoidance behavior. If this is common, it might limit the shade constraint on this species. Numerous individuals were also spotted flying along the gravel pathways and other thin corridors connecting the large grassy area near prairie 1 with the prairies that were part of our study, although these individuals were difficult to capture as they were rarely observed resting in these areas, indicating that *S. cybele* can certainly cross larger expanses of matrix than we observed here. Small pathways may aid this movement as edge effects appear to be important according to Ovaskainen (2004).

The observation that the emigration fraction for *S. cybele* was as low as 10% from prairie 2, and that for *M. cymela* prairie fragments often have emigration fractions on the order of 30%, indicates that prairie management techniques such as burning are likely to destroy the majority of the individuals produced on that patch. *S. cybele* overwinters as unfed 1st instar larvae and *M. cymela* overwinters at the base of grass stems or in the duff as 4th instar larvae (Scott 1986), so fire is likely to result in nearly 100% kill fractions. These kill levels might be tolerable to land managers if: (i) local demes are large and produce at least 25% of their population as emigrants, and; (ii) females indeed move as far as males (Panzer 2003).

Our results indicate that *S. cybele* in the conservation area probably acts as a single population. Only 55% (39/71) of individual recaptures occurred in the same prairie as initial capture and release, indicating that the barriers within the conservation area do not appear to isolate individual subpopulations. The story with *M. cymela* is more complex. If we look at the level of distinct prairie patches separated by inter-habitat matrix or height gradients (i.e. those numbered in Figure 1), 70% of individual recaptures occurred in the same prairie as initial capture and release. This indicates that within the site *M. cymela* may be acting more as a metapopulation, along the continuum between a single population and entirely isolated ones, (Dover 1996, Thomas and Kunin, 1999). It is interesting to note that the two most densely populated patches in our study (1 and 4b) appeared to exhibit a fairly large amount of immigration from most other patches in the study, even though prairie 1 was distant from the others. Both 1 and 4b had small emigration fractions.

Table 5 provides parameters for distance decay curves (frequency of observations versus distance traveled) obtained for both species with a least-squares fit of the negative exponential, as well as a standardized major axis regression for the power function (PROC GENMOD, SAS Institute 2006). These functions were both fit to the inverse cumulative proportion of movement distance per day (Hill et al. 1996). Data are given for males (M), females (F), and both sexes combined. For *S. cybele*, the negative exponential has a higher r^2 than the power function, with values ranging from 0.78 (F) to 0.89 (M) for the negative exponential, and 0.66 (F) to 0.80 (M) for the power function. Hill et al. (1996)

Table 5. Parameter values for least-squares fit of negative exponential and the reduced major axis fit of a power function to the inverse cumulative probability values of movement distances. In the Sex column, C stands for “combined”.

	Bin Size (meters)	**Sex**	$I = e^{-kD}$			$I = CD^{-n}$	
			k	r^2	C	n	r^2
S. cybele	400	M	8.35x10-4	0.891	18.7	0.823	0.801
		F	4.37x10-4	0.779	2.53	0-Jan	0.657
		C	9.11x10-4	0.866	30	0-Jan	0.738
M. cymele	100						
		M	0.00291	0.839	17.5	1.02	0.946
		F	0.00183	0.688	4.66	0.751	0.813
		C	0.00341	0.904	22.2	1.12	0.971

have suggested that the power function may more accurately predict long-distance colonization for some species, and would indicate that perhaps 1.2% of *S. cybele* might move distances of 5 km or more, while the negative exponential would indicate that about 1.1% would move this distance. For *M. cymela*, both models have fairly good fits, with $r^2 = 0.904$ the negative exponential (males and females combined) and 0.971 for the power function. For both species, the fitted parameters for females result in larger movement distances than for males but the differences were not significant (see above). Similar results, with males moving farther or no significant difference between the sexes, have been reported for butterflies elsewhere (Nieminen 1996, Brommer et al. 1999, Norberg et al. 2002). It is possible that this observation is an artifact of the study scale and that particularly vagile males, for example, were less likely to be resampled as they left the study site.

The power function model would suggest that about 0.16% of *M. cymela* would move distances of 5 km or more while the negative exponential indicates that fewer than 1×10^{-7} would move this far. In either case, the probability of colonization of a distant habitat patch becomes vanishingly small in a state such as Iowa because the likelihood of encountering another habitat patch in a random walk across the landscape is remote.

Thus, our work, coupled with the frequent observation of individuals moving along the gravel road and smaller mowed pathways within the forest, suggests that connectivity will need to be increased in order to improve interactions between isolated populations of similar butterflies in Iowa.

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