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Butterfly responses to habitat edges in the highly fragmented prairies of Central Iowa

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Summary

1. The behaviour of two butterfly species, a habitat specialist (*Speyeria idalia*) and a habitat generalist (*Danaus plexippus*), was tracked at four prairie edges to determine the extent to which edges act as a barrier to emigration. The four edge types studied were crop, road, field and treeline. The edges differed in structure ranging from high-contrast (treeline) to low-contrast (field).

2. *S. idalia*, the habitat specialist, responded strongly to all edges, even those with low structural contrast. However, *S. idalia*'s response was strongly affected by conspecific density at crop and field edges; individuals were less likely to exit from high density plots. *S. idalia* responded to edges both by turning to avoid crossing them, and returning to the plot if they had crossed.

3. *D. plexippus* responded strongly only to treeline edges. Wind direction and time of year were important factors influencing behaviour at edges for this species. Conspecific density was not a significant factor affecting their behaviour. *D. plexippus* responded to edges by not crossing them, but rarely returned once they had crossed.

4. In highly fragmented landscapes, such as the one in which this study occurred, butterflies which show little or no response to edges may exhibit high emigration rates because of the high probability of encountering an edge in small habitat patches. Butterflies may respond strongly to even subtle habitat boundaries, but those responses may be modified by the edge structure, local environment or other conditions. Therefore, modifying edge structure may be a way to influence emigration rates, making it a useful tool for conservation.

Key-words: edge permeability, habitat fragmentation, lepidoptera, tracking study.

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Introduction

The movement of individuals between subpopulations is a critical factor in the population dynamics of organisms with fragmented distributions (Levins 1969; Taylor *et al.* 1993; Ims & Yoccoz 1997). This issue has recently gained considerable practical importance because remaining natural habitat has become increasingly fragmented by human activity. Populations occupying these fragmented landscapes are generally assumed to be more isolated and vulnerable to the stochastic processes that may cause local extinctions (MacArthur & Wilson 1967). Movement between habitat patches can 'rescue' populations from local extinction (Brown &

Kodric-Brown 1977) and reduce inbreeding depression (Spieth 1974). Despite the obvious importance of interpatch movement, we know very little about how readily most animals move through heterogeneous landscapes (Ims & Yoccoz 1997). One reason is the difficulty of gathering the field data necessary to estimate movement parameters and measuring rare, but important, long-distance migration events (Higgins & Richardson 1999).

One solution that has been used to gain insight into complex, difficult-to-measure processes is to break that process into parts and study each step separately. Our study focuses on the first step of interpatch movement: leaving a patch. Emigration rates are determined by the probability of occurrence of two events: (1) encountering the edge of a habitat patch and (2) crossing that edge once it is encountered (Stamps, Buechner & Krishnan 1987). Encountering an edge may be influenced both by the amount of edge relative to total patch area and the movement patterns of an individual within that patch. Although mobility clearly varies widely

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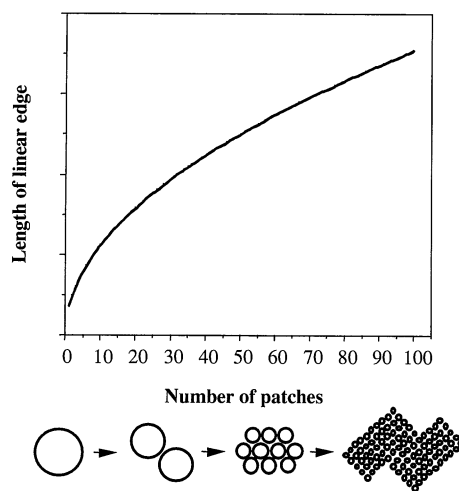


Fig. 1. Graphic representation of the increase in edge (measured as a two-dimensional attribute of a habitat patch) as a patch is divided into an increasing number of smaller, circular patches while holding area constant (reprinted, with permission, from Sisk & Margules 1993).

between species and even between individuals within a species, it is probably true for all species that, as the edge to interior ratio increases with increasing fragmentation (Fig. 1), the probability of encountering an edge will also increase.

The component of emigration that is much less easily understood and has not been widely studied is what occurs when an individual actually encounters an edge. There are several factors, both internal and external, that can influence whether or not an individual crosses an edge or remains within the habitat patch. Intrinsic factors may inhibit dispersal (Ehrlich 1961), and these factors may include genetic dispersal cues and an individual's expectation of fitness within the patch (for reviews of adaptive reasons for dispersal, see Johnson & Gaines 1990; Stenseth & Lidicker 1992). External factors, which have received much less study, include the structure of the edge (which includes abruptness and degree of contrast), the immediate local environment at the point of edge encounter, the quality of the habitat as a whole and the type and quality of the bordering habitat. Stamps *et al.* (1987) define the probability that an individual crosses an edge it has encountered as 'edge permeability'. However, individuals may not perceive an edge as a barrier to movement, or may not 'choose' to stay within a patch until they sample the habitat on the other side. Therefore, not only must the permeability of an edge be determined, but also the probability that an individual will continue on its path rather than return to the focal patch (thus becoming a true emigrant).

Few studies have examined specifically how animals respond when they encounter an edge, and most have focused on high contrast edges, such as a field bordered by a woodlot (see below). These studies have shown generally that individuals tend to avoid crossing into very different habitat types. Several tracking studies

have shown that individuals are more likely to leave a patch through corridors of similar habitat (Johnsson & Adkisson 1985; Sutcliffe & Thomas 1996; Machtans, Villard & Hannon 1997; Haddad 1999). However, all these studies used fields bordered by woodlands. Fry & Robson (1994) studied movement across less distinct boundaries and showed that butterflies were more likely to cross a field edge when the edge vegetation height was low. Thomas (1982) found a staryrid butterfly reluctant to cross from its breeding habitat in unimproved grassland into a bordering sown grass pasture. In a mark-release study, Kuussaari, Nieminen & Hanski (1996) found higher emigration rates from patches surrounded by more open habitat. Among these studies, there was little focus on how responses vary within and among species. Of the studies mentioned above, only Kuussaari *et al.* (1996) examined how emigration is influenced by other local factors and Haddad (1999) was the only investigator to collect data on more than one species. Identifying the factors that are most likely to influence the permeability of edges across a range of species and edge types is crucial in order to build a general framework of how edges affect populations.

In this study, we tracked the movement of two butterfly species with very different life-history characteristics at four prairie edge types in central Iowa. Individuals can respond to edges either by not crossing them (i.e. turning or stopping) or, having crossed into a new habitat type, individuals may reverse course and return to the patch. Variation in crossing and return behaviour can be used to determine which factors most influence edge response. Our objectives were to:

1. determine the edge permeability and return rates at four different prairie edge types;
2. measure how responses are affected by wind, conspecific density, flower abundance and time of year; and
3. compare the responses of two butterfly species with different habitat affinities.

STUDY SYSTEM: BUTTERFLIES IN PRAIRIES

Prairie is considered to be one of the most endangered ecosystems in the United States (Smith 1981). Tall-grass prairie is the most drastically affected with a decline in total area estimated between 82 and 99%, more than any other major ecosystem in North America (Samson & Knopf 1994). Iowa has been one of the most severely affected states, with less than 0.01% of the original tallgrass prairie remaining (Samson & Knopf 1994). Most prairie fragments in central Iowa are less than 4 ha and are often separated from the next closest prairie by several kilometres. A survey of 26 prairies in central Iowa showed that 50% of the total perimeter of prairie edges consisted of row crops and had a road or treeline as an intersecting boundary feature 38% of the time (Leslie Ries, unpublished data). Other common adjacent land types included old fields, pasture and woodland.

Table 1. Description of each prairie used in the study and the number of individuals of each species tracked at each site

Prairie	Edge type (no. plots)	Size (ha)	Adjacent land	<i>D. plexippus</i> tracked	<i>S. idalia</i> tracked
Anders I ^{1,2}	Field (3)	8	Bromefield	52	12
Anders II ^{1,2}	Crop (3)	8	Soybeans	42	6
Doolittle	Treeline (3)	4	Corn	70	9
Harker	Treeline (2)	2	Corn	49	49
Kalsow	Road (3)	256	Corn	43	11
Kalsow	Crop (3)	256	Corn/Soy	59	51
Kish-Ke-Kosh	Field (2)	7	Lawn	24	0
Kurtz ²	Road (3)	32	Corn	16	0
Liska-Stanek	Road (2)	16	Corn	19	64
Liska-Stanek	Crop (3)	16	Corn	16	83
Moeckley	Field (3)	16	Pasture	46	185

¹Ander's property contains two 8-ha prairies.²Reconstructed prairie.

The two butterfly species used in this study were chosen because they vary greatly in their life history characteristics and are sufficiently abundant to make rigorous comparisons of their behaviour. Regal fritillaries (*Speyeria idalia* Drury) are restricted to grasslands in the central and eastern United States and are declining throughout their range due to loss of habitat (Hammond & McCorkle 1983). In Iowa, *S. idalia* is generally restricted to native prairie where their host plants, prairie or bird's foot violet (*Viola pedatifida* Don and *V. pedata* L.), are found. A 1995 survey of 52 Iowa prairies revealed only 11 sites that had individuals present (Debinski & Kelly 1998). *S. idalia* is listed as a species of special concern in Iowa; however, Schlicht & Orwig (1998) suggested that its status in Iowa be elevated to threatened. *S. idalia* is non-migratory and individuals generally stay within the same local area throughout their lifetime (Scott 1986; Nagel, Nightengale & Dankert 1991), although some adults have been known to move long distances (Opler & Wright 1999). The monarch (*Danaus plexippus* L.), on the other hand, is widespread in North America and found throughout much of the world (Scott 1986). Adults found in Iowa overwinter in Mexico and, over several generations, move north as far as southern Canada before returning to Mexico. Their host plants include several species of milkweed (Asclepiadaceae) which are found commonly in Iowa both in and outside of prairies.

Materials and methods

STUDY SITES

Based on the most common adjacent land and boundary characteristics of central Iowa prairies, four edge types were chosen for study: row crops with no intersecting boundary feature (CROP), row crops with a treeline between the crops and prairie (TREELINE), row crops with a gravel road between the crops and prairie (ROAD) and non-prairie grassland, such as old fields or pasture, with no intersecting boundary feature (FIELD). Native prairies in central Iowa were targeted

for study, but two reconstructed prairies were included to increase the number of study sites. Our goal was to establish three plots each in three prairies for a total of nine study plots for each edge type. However, due to the limited number of larger prairie remnants in central Iowa, some sites contained only two plots. In addition, plots with treeline boundaries were established in only two prairies. Descriptions of each study site are in Table 1.

PLOT SET-UP AND SURVEY PROTOCOL

Plots were located inside prairies with one edge of the plot contiguous with the edge of the prairie (Fig. 2). Plots were placed randomly along the edge, subject to the restriction that they were at least 30 m from a corner and fully contained the appropriate edge type. Sites were eliminated if wetland habitat covered more than 25% of the area selected or if they were adjacent to another plot. Treeline plots were additionally restricted to contain no gaps in the treeline. Plots were 40 × 40 m and were marked using flags which were implanted in 1.2 m bamboo poles so they could be seen over the top of the vegetation. Flags were placed at 20 m intervals within the plot and they allowed butterfly positions to be approximated within one of the 16 10 × 10 m quadrats (Fig. 2).

All surveys were conducted between 1000 and 1900 h on sunny days. A survey was conducted by searching each of the 16 10 × 10 m quadrats within each plot for 2 min. Searches were suspended while tracking individuals and recording data. Quadrats were surveyed in random order, with a different set of random numbers chosen for each survey. Surveys were conducted until all 16 quadrats were completed or while weather and light conditions remained conducive to butterfly activity (i.e. sunny with low wind). Unfortunately, the sex of neither species could be identified consistently in flight, so no data on sex were collected. If an individual was spotted, it was tracked until it left the plot or remained perched for 5 min, at which time the track was abandoned. Individuals that left the plot were followed until they were at least 10 m beyond the plot. If they returned to the plot before exceeding

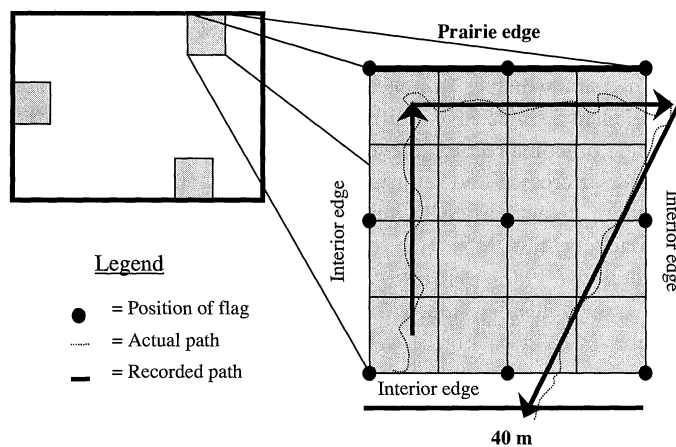


Fig. 2. Plot placement and survey design. Study plots were placed within prairies with one edge of the plot contiguous with the edge of the prairie. Each plot had 16 10×10 m quadrats. Butterfly positions within the plot were located using nine flags positioned at 20-m intervals. A representation of how an actual flight path would be recorded during a survey is shown.

the 10 m buffer, tracking continued. A 10-m buffer was used because there was often a barrier, such as a ditch or a barbed wire fence, separating the prairie from the adjoining habitats, so observations could only be made accurately for a short distance. An individual was considered to have exited the plot only when it left and did not return. Tracks were recorded so that small variations in flight direction were ignored (Fig. 2). Although this 'smoothing' of tracks was by necessity somewhat subjective, the subsequent analysis of movement was performed only on coarse-scale movements and therefore was not sensitive to the loss of this fine-scale information. Butterfly tracks were recorded for *S. idalia* and *D. plexippus*. All *S. idalia* present were tracked, but only the first 10 *D. plexippus* spotted in each survey were tracked. This approach was taken to avoid spending excessive amounts of time recording *D. plexippus* tracks because this species is often very abundant. Care was taken to avoid tracking the same individual twice during the survey, although there is no way to ensure this never happened. All plots were surveyed two or three times, with an average of 15 days separating surveys at the same plot to ensure a new group of individuals was being tracked.

In order to ascertain how movement was affected by local conditions, information on several factors was collected including wind direction, speed and flower abundance. To collect data on any one of these factors in great detail would have been prohibitively time-consuming. We therefore collected measurements that would allow us to look for coarse-scale effects, yet would not dominate our time spent in the field. Fluorescent flagging tape was attached to each pole in the survey plot, which allowed an estimation of the strength and direction of the wind to be recorded after each butterfly was tracked. This was accomplished by recording the approximate angle between the flagging tape and the pole as well as the direction the tape was blowing. In addition, a wind metre (Wind Wizard, model 281) was used to obtain average wind speeds for

each survey day. Wind speed estimates were taken at breast height. For surveys where the wind ranged between 0 and 8 kph, the wind was classified as either still or low. On days when there was a consistent wind reaching 8–12 kph with gusts to 24 kph, wind was classified as low when the flagging tape was within 60° of the pole (approximately 2–8 kph based on comparisons with the wind speed indicator) or high when the flagging tape was greater than 60° from the pole (> 8 kph based on comparisons to the wind speed indicator). No surveys were carried out on days with average wind speeds greater than 12 kph because butterflies rarely flew under those conditions.

For each quadrat, an order of magnitude estimate was made of the total number of flowers in bloom. Using this information, each plot was categorized as having low, medium or high flower abundances which translated to an average quadrat abundance of approximately tens, hundreds or thousands of flowers, respectively. Eighty per cent of the flower surveys were conducted within 2 weeks of the butterfly survey and the remaining surveys were all completed within a month. At this scale of measurement flower abundance remained fairly constant from week to week, so the lag time in flower surveys would rarely have an impact on the flower abundance category that was assigned for each survey completed.

DATA ANALYSIS

Responses at the prairie edge were compared to responses at the three interior 'edges' of the plot (see Fig. 2). Because the three interior plot 'edges' were not true edges, they acted as a reference so that behaviour at the true edge could be compared to movements within the plot. Responses measured included which edge the individual used to exit the plot (exits were recorded when an individual crossed the edge and did not return), whether an individual on an intercept course with the edge crossed or avoided it (recorded

separately at 0, 10, 20 and 30 m from the edge), and whether an individual that had crossed the edge returned immediately to the plot. Individuals that approached a single edge multiple times had only the ultimate outcome recorded (eventually crossed, never crossed, or crossed and returned). Edge permeability estimates, defined as the proportion of individuals approaching the edge that subsequently cross it (Stamps *et al.* 1987), were also calculated for each edge type. Individuals that approached within 10 m of the interior 'edges' (see Fig. 2) were used for these estimates so that the data were comparable to the estimates at the true prairie edge. Edge approaches were divided into 10 m sections at increasing distance from the edge.

A chi-square goodness-of-fit test was used to determine if individuals exited from the plot by crossing the prairie edge less frequently than expected if movements were random. Expectations of random frequencies for exit direction were based on the fact that each edge constituted 25% of the total perimeter of the plot. A chi-square test was also used to determine whether individuals avoided crossing prairie edges more frequently than the three interior 'edges' of the plot and at what distance from the edge responses were significantly different from behaviour at the interior 'edges'.

A stepwise logistic regression (SAS 1990) was used to model the influence of the edge (prairie vs. interior), edge type (crop, treeline, road, field), wind direction (with or against butterfly path), wind strength (low or high), conspecific density, flower abundance (low, medium, high) and week (1–10, modelled as a continuous variable) on the probability that an individual that approached an edge would (1) cross vs. not cross, and (2) return vs. not return (only if the individual had crossed). All factors, including interactions between density and each edge type as well as interactions between wind speed and direction, were entered into the logistic model. A significance level of 0.1 was used for both entry and retention in the model so any trends could be considered, even if they did not meet the standard 0.05 significance criteria. An index of density was estimated by calculating the mean number of individuals tracked during each of the 16 2-min surveys. In the event that tracking *D. plexippus* was cut off after 10 individuals (this occurred in 19 of 68 surveys), the density value was an underestimate. Density indices calculated applied only to each individual plot and not to the prairie as a whole.

For the purposes of logistic regression, no distinction was made between the three interior edges. However, a single butterfly may have approached each of the plot's four edges several times during the course of a single survey. In order to ensure the independence of points used in the logistic regression, only the response to the first edge each butterfly approached was used in the analysis. While this 'first approach' method allowed a rigorous comparison between behaviour at the true prairie edge with the interior 'edges', nearly one-third of the approaches towards the actual prairie edge were

dropped from the analysis. Because behaviour at the prairie edge was the focus of our study a second, similar analysis was performed exclusively on the approaches towards the prairie edge. This second 'prairie edge' analysis allowed all data on behaviour at the true prairie edge to be retained.

Results

A total of 72 surveys where either *S. idalia* or *D. plexippus* were recorded were completed between June 21 and August 31, 1997. Table 1 shows the number of individuals of each species tracked at each prairie. A total of 470 *S. idalia* were tracked during 43 surveys; 436 *D. plexippus* were tracked during 68 surveys.

EXIT DIRECTION

Of the 433 *S. idalia* that were tracked until they left the plot, only 42 individuals exited by crossing the prairie edge. A chi-square goodness-of-fit test showed that exit directions differed significantly from random at treeline, crop and field edges with a strong bias towards individuals remaining in the prairie (Fig. 3a). The strongest response was seen at the treeline edge where only 4% of individuals exited the plot by crossing the prairie edge ($\chi^2 = 12.41$, d.f. = 3, $P < 0.001$). Exits at road edges did not differ significantly from random ($\chi^2 = 0.667$, d.f. = 3, $P = 0.95$). Of 412 *D. plexippus* tracked, 85 exited the plot by crossing the prairie edge. Exit directions differed significantly from random only at the treeline edge ($\chi^2 = 13.13$, d.f. = 3, $P < 0.001$; Fig. 3b).

EDGE PERMEABILITY AND DISTANCE OF RESPONSE (TURNING BEHAVIOUR)

Boundaries were less permeable to *S. idalia* than to *D. plexippus* (Table 2). Both species had the lowest permeability estimates at treeline edges, although the estimate was about three times higher for *D. plexippus* compared to *S. idalia*. *S. idalia* showed a stronger response at crop and field edges compared to road edges. *D. plexippus* showed similar responses at road, field and crop edge types. These estimates were only slightly lower than the estimate at the interior 'edges', which are used as a reference to compare responses at true edges to movements within the prairie. Interior 'edges' had the highest permeability estimates and were similar for both species (Table 2).

Figure 4 shows the proportion of individuals that avoided crossing each edge type as distance from the edge increased. Individuals that did not turn at 0 m subsequently crossed the edge. At all four edge types, *S. idalia* avoided crossing the edge more frequently compared to the interior edges between 0 and 9 m from the edge ($P < 0.001$) and 10–19 m from the edge ($P < 0.001$). After 20 m, however, no significant differences were found in turning frequencies among the five edge types. *D. plexippus* turned more frequently within

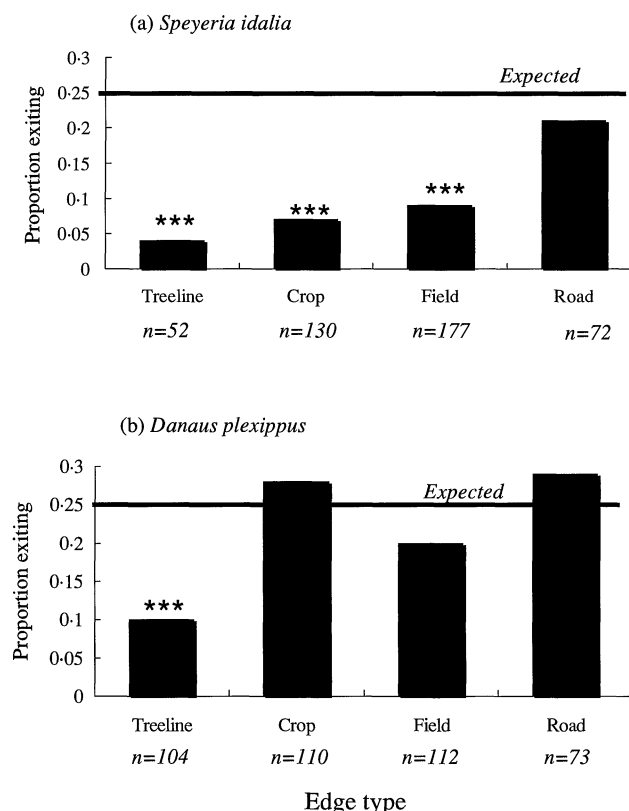


Fig. 3. Proportion of *S. idalia* (a) and *D. plexippus* (b) leaving the plot by crossing the prairie edge. Values less than 25% indicate a bias against crossing the edge because the prairie edge constitutes 25% of the perimeter of the plot. Differences between expected and observed values were tested using a chi-square goodness-of-fit test (***) $P < 0.001$.

Table 2. Estimates of edge permeability for *S. idalia* and *D. plexippus* for each edge type including interior edges. Edge permeability is defined by Stamps *et al.* (1987) to be the proportion of individuals approaching an edge that cross. The 95% confidence interval range (one-sided) is indicated in parentheses

Edge type	<i>Speyeria idalia</i>	<i>Danaus plexippus</i>
Treeline	0.08 (0.10)	0.24 (0.13)
Crop	0.29 (0.11)	0.64 (0.13)
Field	0.25 (0.09)	0.50 (0.14)
Road	0.43 (0.15)	0.68 (0.16)
Interior	0.70 (0.05)	0.75 (0.05)

10 m from the edge ($P < 0.001$) at only the treeline edges. The 20–29 m distance also showed a significant difference between edge types ($P < 0.05$); however, this result should be interpreted with caution due to the fact that this response class had a small sample size resulting in expected values less than five.

RETURN BEHAVIOUR

S. idalia that crossed the prairie edge returned more frequently than those that crossed the interior 'edges', and the strongest responses occurred at the crop and field edges (Fig. 5a). *D. plexippus* uniformly showed a low return rate; less than 10% of the individuals returned to the prairie after crossing the edge at all edge types

(Fig. 5b). For both *S. idalia* and *D. plexippus*, only about 2% of the individuals who crossed the interior edges returned to the plot. Treeline edges were excluded from this analysis because individuals that crossed the treeline could no longer be seen. Due to the extremely low number of individuals that returned after crossing the edge, the expected number of individuals returning to the plot was less than one. Therefore, chi-square analyses were not possible.

LOGISTIC REGRESSION – *S. IDALIA*

For *S. idalia*, the factors of week and edge type were strongly correlated. This was not due to allocation of effort, but to pulses in butterfly abundances in certain prairies. For that reason, week was excluded as a factor from this analysis. *S. idalia* has no known trends in seasonal movements (Scott 1986) and no trend in movement with respect to week was evident in our data, so it is unlikely that including week is critical for this analysis. *S. idalia* was found only in prairies where flower abundances were generally high; of all the surveys, only two plots out of 43 were categorized as low. Therefore, low and medium flower categories were combined and flower abundances were scored as either medium or high. One survey that had a markedly higher proportion of individuals crossing the edge compared to other surveys with similar conspecific densities was identified as an outlier (circled in Fig. 6b,c) and excluded from

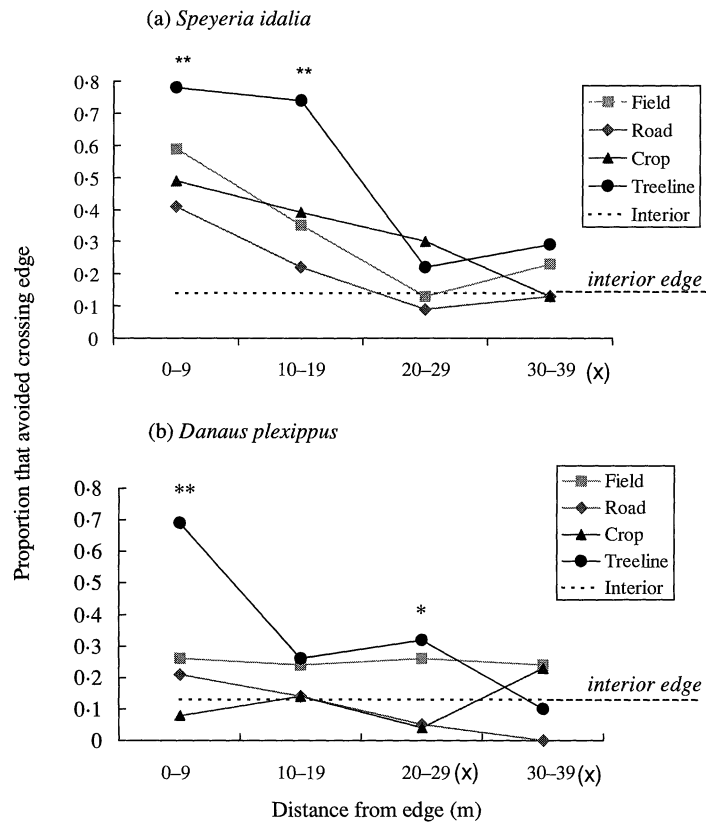


Fig. 4. Proportion of *S. idalia* (a) and *D. plexippus* (b) turning to avoid crossing the edge as distance from the edge increases. The proportion of individuals that turned to avoid crossing the interior edges is also shown. Each distance category was tested for differences in proportion avoiding crossing the edge between edge types using a chi-square goodness-of-fit test (** $P < 0.001$, * $P < 0.05$). Distances with low expected values are marked with an (x) and therefore the significance test should be interpreted with caution.

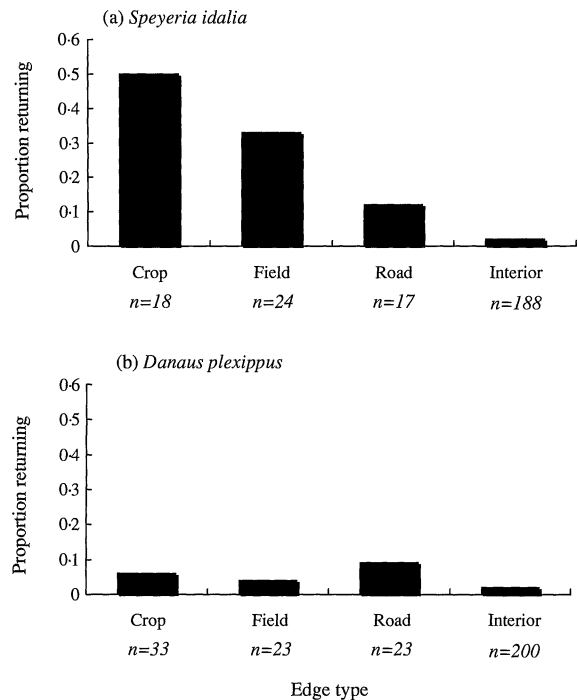


Fig. 5. Proportion of *S. idalia* (a) and *D. plexippus* (b) that returned to the plot after crossing the prairie edge. The treeline edge type was excluded because, once individuals crossed the edge, they could no longer be seen.

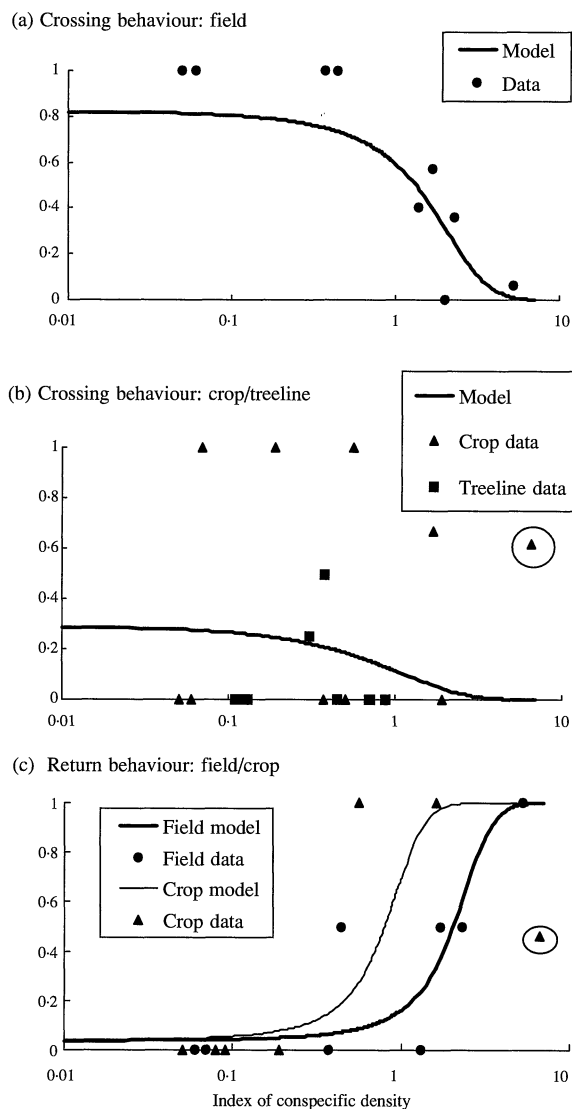


Fig. 6. For *S. idalia*, the probability that an individual approaching a field edge (a) or a crop or treeline edge (b) will cross the edge, and the probability that an individual who has crossed a field or crop edge will return to the plot (c) as conspecific density increases. Density values are based on the number of individuals observed in a two minute period. Lines represent estimated probabilities based on parameters generated by a logistic model (Tables 3 and 4). Points represent the observed proportion of individuals crossing the prairie edge during one survey. Results are shown for an analysis performed only on behaviour at true prairie edges. An outlier excluded from the analysis is circled (b,c).

the logistic regression. This point represents the only survey completed during the entire summer where there were high, sustained winds (up to 15 kph) blowing directly towards the prairie edge. However, it should be noted that even during that survey, only seven of 50 (14%) individuals tracked exited the plot by crossing the prairie edge. When this outlier was included in the analysis, similar results were obtained, but crop edges did not show a density effect. The parameter estimates of factors selected by the stepwise process are summarized in Tables 3 and 4 and Fig. 6.

S. idalia was less likely to cross prairie edges as compared to interior 'edges', especially as conspecific density increased (Table 3). This pattern was strongest at field edges (Fig. 6a) and weaker at crop and treeline edges where the overall probability of crossing was much lower (Fig. 6b). It is important to note that

density values varied widely *within* some prairies and the response to conspecific density was seen within these prairies. Results from the two analyses ('first approach' and 'prairie edge') were similar, except for at road edges which showed an opposite trend under the two different analyses (Table 3). This result may be due to the fact that there were no surveys done at road sites with high densities comparable to the other three edge types. The highest density value for road plots was 1.3 individuals seen every 2 min, whereas the highest values for field and crop plots were 5.3 and 6.6, respectively. Wind was a factor only in the model that included interior edges and flower abundance was never included in the model (Table 3). The analysis including all prairie edge approaches showed that the probability of return increased with increasing conspecific density ($P < 0.01$) and was higher at crop edges than at other kinds of

Table 3. Factors selected by the stepwise logistic procedure as affecting crossing behaviour for *Speyeria idalia* and *Danaus plexippus*. Results are shown for (1) an analysis where the first edge approached was used, and (2) when only approaches towards the prairie edge were included. Standard errors are in parentheses; d.f. = 1 for all parameter estimates. Significance level required for entry and retention in the model was 0.1. Edge interactions signify this factor was only significant when an individual was approaching the prairie edge as opposed to an interior edge. Graphical representations of major results are shown in Fig. 7 (* $P < 0.10$, ** $P < 0.05$, *** $P < 0.001$)

Factors chosen	<i>Speyeria idalia</i>		<i>Danaus plexippus</i>	
	First approach parameter (SE)	Prairie edge parameter (SE)	First approach parameter (SE)	Prairie edge parameter (SE)
Intercept	0.21 (0.16)	-0.90 (0.36)**	0.61 (0.42)	-1.71 (0.68)**
Prairie edge	NS	—	NS	—
Density (at prairie and interior edges)	-0.13 (0.06)**	—	NS	—
Density \times prairie edge	-0.83 (0.23)***	-1.15 (0.28)***	NS	NS
Density \times road edge	-3.04 (1.17)**	1.74 (0.50)***	NS	NS
Density \times crop edge	-1.28 (0.41)*	NS	NS	NS
Field edge	0.90 (0.55)*	2.43 (0.56)***	NS	NS
Treeline edge	-2.44 (1.05)**	NS	-2.44 (0.77)**	-0.94 (0.45)**
Wind blowing towards approach edge	0.49 (0.22)**	NS	1.01 (0.23)***	0.74 (0.38)
Week†	—	—	NS	0.29 (0.10)**
Flower abundance‡	NS	NS	-0.29 (0.17)*	NS
Concordance	65.7%	78.0%	52.7%	70.0%
Pearson goodness-of-fit	$P = 0.0001$ (d.f. = 90)	$P = 0.001$ (d.f. = 43)	$P = 0.34$ (d.f. = 140)	$P = 0.28$ (d.f. = 66)

†Week values range from 1 to 10.

‡Flower abundance values are 1 (low), 2 (med), 3 (hi).

—Not included in regression model.

Table 4. Factors selected by the stepwise logistic procedure as affecting return behaviour for *Speyeria idalia*. Results are shown for (1) an analysis where the first edge crossed was used and (2) when only returns after crossing the prairie edge were included. Standard errors are in parentheses; d.f. = 1 for all parameter estimates. Significance level required for entry and retention was 0.1. Edge notations signify this factor was only significant when an individual was approaching the prairie edge as opposed to an interior edge. Graphical representations of major results are shown in Fig. 7 (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$)

Factors chosen	<i>Speyeria idalia</i>	
	All edges parameter (SE)	Prairie edge parameter (SE)
Intercept	-2.56 (0.21)***	-3.27 (0.98)**
Density (at prairie edge)	NS	1.61 (0.62)**
Crop edge	NS	2.50 (1.23)*
Concordance	Not calculated ¹	79.3%
Pearson goodness-of-fit	$P = 0.01$ (d.f. = 83)	$P = 0.39$ (d.f. = 16)

¹Due to the fact that no factors were significant.

edges at lower butterfly densities ($P < 0.05$; Table 4, Fig. 6c).

LOGISTIC REGRESSION: *D. PLEXIPPUS*

D. plexippus only avoided crossing treeline edges ($P < 0.001$; Table 3, Fig. 7). When all edges were considered, higher flower abundances decreased crossing ($P < 0.05$); however, when only approaches toward the prairie edge were analysed, flower abundance dropped out of the model, and week became a significant factor ($P < 0.01$) with the probability of crossing increasing as the summer progressed (Fig. 7). Both analysis methods showed that wind blowing towards the edge of approach increased crossing (Table 3, Fig. 7). An analysis of return behaviour was not possible because too few individuals returned to the plot (Fig. 5).

Discussion

Our results show that habitat edges can act as a barrier to movement, even when the adjacent habitats are structurally similar. However, other environmental factors played a dominant role in modifying edge response. *S. idalia* responded strongly to field edges, but only when conspecific densities were high (Fig. 6a,c). Surprisingly, at high densities, the response of *S. idalia* to field edges, structurally a very subtle edge, was comparable to treeline edges, an extremely high contrast edge type (Fig. 6a,b).

We have also demonstrated that, along with the probability of crossing an edge, return behaviour is an important factor that should be considered when measuring responses to edges. For *S. idalia*, the combination of both avoiding crossing an edge (Fig. 4a)

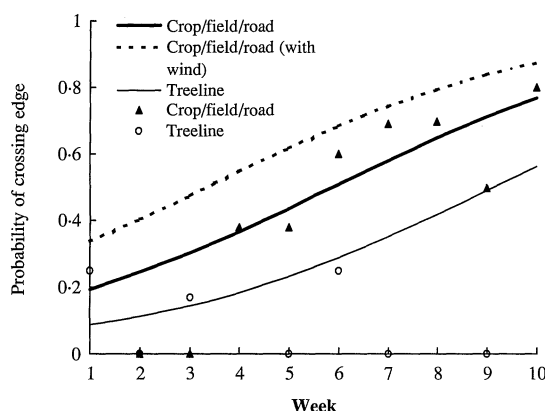


Fig. 7. For *Danaus plexippus*, the probability that an individual will cross the prairie edge as summer progresses. Lines represent estimated probabilities based on parameters generated by a logistic model (Table 3). Points represent the observed proportion of individuals crossing the edge during each week. The increased probability of crossing when wind is blowing towards the prairie edge is shown for crop, field and road edges, although the same increase is estimated for treeline edges.

and returning to the plot after crossing (Fig. 5a) was responsible for the overall pattern in exit direction observed (Fig. 3a). In contrast, the pattern of exit direction for *D. plexippus* (Fig. 3b) was caused solely by avoiding crossing an edge (Fig. 4b) rather than returning to the plot after crossing (Fig. 5b). This indicates that *S. idalia* may be responding to the quality of bordering habitat, whereas *D. plexippus* does not. Butterflies have been shown to return to patches from a distance of 100 m (Conradt *et al.* 2000); therefore, we probably underestimated the number of butterflies which returned to the prairie after crossing. However, the differences observed in return behaviour likely reflect the general tendency of each species to return to the patch.

With the exception of *S. idalia* at treeline edges, all permeability estimates were above 0.10, and ranged from 0.24 to 0.68 at the prairie edge (Table 2). According to Stamps *et al.* (1987), when permeability estimates are greater than 0.10 the size and shape of the patch are the most important factors determining emigration rates. Therefore, in this system emigration rates are most influenced by the probability of encountering an edge, which is likely to be high considering that most prairies are small (ranging from 1 to 10 ha). In Iowa therefore emigration rates are likely to be high. Although increased movement between habitat patches is considered to mitigate many of the problems associated with isolation (Brown & Kodric-Brown 1977), in the severely fragmented Iowa landscape increased dispersal may have an overall negative effect resulting from a drain on the local population (Thomas *et al.* 1998; Thomas & Hanski 1999) and a very low probability of finding a new patch. Therefore, modifying edge structure to reduce dispersal may become an important management option.

Our results demonstrate that two species with different life history characteristics responded to very different factors. *S. idalia* showed a stronger overall response to edges than *D. plexippus*, which may not be surprising considering the host plant of *S. idalia* is restricted to prairies and *D. plexippus* is a long-distance migrant. However, the results of this study cannot be used to make generalizations regarding the response of habitat specialists to edges because data on only one habitat specialist were collected. One reason *S. idalia* was chosen for study was because, despite its regional rarity, it is often locally abundant. There are several other prairie specialist butterflies resident in Iowa (Schlicht & Orwig 1998), yet most of these species are found only in low densities, if at all. It may be that most prairie butterflies *do not* respond strongly to edges, and therefore consistently have low or zero densities in small prairie remnants while *S. idalia*, having a strong edge response, often maintains high densities where it occurs. To test this idea, surveys are necessary in much larger prairies where several prairie specialists persist.

S. idalia showed significant responses only within 20 m of the edge (Fig. 4a), *D. plexippus* within 10 m of the edge (Fig. 4b). This is consistent with the results of a tracking study done in South Carolina that showed three species of butterflies responded to a wooded edge only when within 16 m (Haddad 1999) and may reflect a general response range for butterflies. This range of response may also be an indicator of the extent to which 'edge effect' extends into a habitat, providing one method of estimating 'core' habitat area (Laurence & Yensen 1991).

RESPONSE OF *S. IDALIA* TO CONSPECIFIC DENSITY

S. idalia formed high-density aggregations within prairies. Individuals within these aggregations were less likely to cross the edge and were more likely to return to the prairie if they did cross compared to individuals outside of aggregations (Fig. 6). Many other insect species have been shown to form such aggregations (Turchin 1989) including aphids, beetles and caterpillar, as well as several species of butterflies. Reduction of migration from high density aggregations has also been noted for other species of butterfly (Brussard, Ehrlich & Singer 1974; Kuussaari *et al.* 1998).

The effect of density on emigration rate has important implications for conservation. If *S. idalia* are more likely to emigrate from low-density patches, population growth rates may decline with declining population levels, an example of the 'Allee effect' (Allee 1931). If this is the case, stochastic events causing populations to decrease may be exacerbated by higher emigration rates. In addition, re-establishing a population after extinction may also be less likely because initial population levels are likely to be low. Although higher emigration rates at lower densities have been documented in other butterfly populations (Gilbert & Singer 1973;

Brussard *et al.* 1974; Brown & Ehrlich 1980; Kuussaari *et al.* 1998), our results show that this phenomenon also occurs *within* a single patch where there is variation in densities within that patch.

The density effect on edge response may also have implications for corridor use. In this system, roadside prairies have often been suggested as possible corridors between prairie remnants (Ries, Debinski & Wieland 2001). Corridors of habitat between patches have been proposed to reduce isolation in fragmented systems, but have remained controversial due to a lack of empirical evidence supporting their use (Rosenberg, Noon & Meslow 1997). If data on corridor use are lacking, edge reflectance has been suggested to be a predictor for targeting species likely to respond to corridors as a management tool (Soulé & Gilpin 1991; Schultz 1998; Haddad 1999). By those criteria, our results superficially indicate that *S. idalia* would be an ideal candidate for this type of management; overall, we found a strong reflective bias at edges (Fig. 4a). However, the fact that at low densities individuals showed a reduced response to edges may mean that *S. idalia* movement may *not* be directed by corridors because densities in corridors are likely to be low. However, managers could take advantage of the fact that certain edge types, such as treelines, tend to elicit a stronger response.

S. idalia did not appear to respond to road edges as barriers to movement (Fig. 4a), and the logistic regression showed mixed results to increases in density (Table 3). However, this may be explained by the fact that no plots near roads exhibited high densities relative to other edge types. The fact that surveys performed at road edges had relatively low densities may in itself explain the lack of response to road edges (Fig. 3a). Alternatively, individuals may be responding to some unknown factor in the local environment near roads, such as differences in temperature or the reflective nature of roads. Further study is necessary to establish if *S. idalia* truly has a differing response to road edges or if this was a spurious result.

THE INFLUENCE OF THE LOCAL ENVIRONMENT ON EDGE CROSSING AND RETURNS

Wind influenced the movement of *D. plexippus* much more so than *S. idalia*. In general, however, we avoided doing surveys on excessively windy days, and it was clear from observations that at higher wind speeds (above 10 kph), butterfly movement was affected to some degree. However, as wind increased *S. idalia* activity decreased, suggesting that individuals often dealt with wind by not flying. Therefore, it seems unlikely that wind exerts an important influence on *S. idalia* emigration rates. Wind exerted a much greater influence on the movement direction of *D. plexippus*; individuals were more likely to cross any edge of the plot (prairie or interior) when the wind was blowing

towards it (Fig. 7). However, this may be indicative of the weak response of *D. plexippus* to prairie edges rather than a lesser ability of *D. plexippus* to control their flight direction with respect to the wind.

In this study, we used flower abundance as a surrogate for nectar abundance. High flower abundance decreased the probability that *D. plexippus* would cross all edge types when data using 'first approaches' were used (Table 3). However, flower abundance dropped out of the model when only behaviour at the true prairie edge was considered. This may be due to individuals turning more frequently within prairies (thus flying along a more convoluted path), without affecting responses to the true prairie edge. *S. idalia* did not show a significant response to flower abundance (Tables 3, 4). However, this result should not be used to draw general conclusions regarding the sensitivity of *S. idalia* to flower abundance. In this study, *S. idalia* were only found in the highest quality prairies where flower abundances were generally high. Nectar therefore may not have been a limiting resource for *S. idalia* in this case. In addition, coarse scale measurements of flower abundance may be a poor surrogate for nectar availability (Schultz & Dlugosch 1999).

D. plexippus were more likely to cross plot edges (prairie edges as well as interior) towards the end of the summer (Fig. 7), which coincides with their southward fall migration (Scott 1986). Haddad (1997) showed that during migratory periods, some butterflies are less likely to be deflected from their path, and this may have occurred in this case.

Conclusions

In contrast to earlier studies (Fry & Robson 1994; Kuussaari *et al.* 1996), we found that individuals can show strong responses to even subtle differences in vegetation structure. However, our results indicate that the responses of butterflies to prairie edges are highly variable, and dependent on the species, edge characteristics and the local environment experienced by an individual. Our results indicated that edge permeability may be the most important factor determining emigration rates in central Iowa, due to high edge permeability rates and the small size of individual prairies found there. However, the factors that influenced edge permeability were very different for *S. idalia* and *D. plexippus*, as was the range of their responses. The extent of this variability suggests that when estimating movement parameters, species specific responses and the influence of local conditions should be considered. It is clear from our results that in order to build a general framework of how landscape affects movement, responses of several species in a variety of environments needs to be measured. Even though our study only measured very small-scale movements, we suggest that edge structure can have important implications for population dynamics through its impact on emigration rates.

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