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Research article

Edge avoidance and movement of the butterfly *Parnassius smintheus* in matrix and non-matrix habitat

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Abstract

We experimentally examined edge effects and movement patterns of the butterfly *Parnassius smintheus* in two habitat types, its preferred meadow habitat, and intervening forest matrix habitat. We followed the movement of 46 butterflies released at either 5 or 20m from a forest edge in either forest or meadow habitat. In contrast to theoretical predictions, we found that butterflies flew less frequently, shorter distances, and at lower rates in matrix habitat than they did in meadow habitat. Distance from the edge had little effect on these aspects of movement. Flight was strongly influenced by light levels with butterflies flying more readily at higher light levels. Light levels were higher in meadows than in forest explaining much of the difference in movement patterns. Turning angles showed that butterflies flying in meadow habitat avoided forest edges and that this effect extended nearly 25 m into meadows. Analysis of net displacement from the forest edge reinforced this result and showed that there may be attraction to the meadow for butterflies flying within forest.

Introduction

The dispersal of individuals is a fundamental process in population ecology affecting local and regional population dynamics (Connor et al. 1983; Pulliam 1988; Thomas et al. 1996; Hanski 1999). In spatial systems, studies generally relate dispersal among populations to geographic factors such as the distance between populations and the size of habitat patches (e.g., Hanski 1994; Matter 1996, 1997; Moilanen and Niemenen 2002). This approach may neglect other potentially important factors (Tischendorf and Fahrig 2000; Crone et al. 2001). One factor affecting dispersal is the type of habitat through which organisms disperse (Pither and Taylor 1998; Haddad 1999; Roland et al. 2000; Ricketts 2001). Habitats may differ in their permeability to dispersing individuals. Thus the effective isolation of populations may depend on both the type and amount of habitat through which organisms move (Kuussaari et al. 1996).

Habitats may differ in the ability with which organisms move through them (viscosity). For example, translocation studies have found differences in the ability of organisms to move through different habitats (Pither and Taylor 1998; Jonsen et al. 2001; Gobeil and Villard 2002). Habitat may also be a barrier to dispersal if organisms avoid particular habitats or the conditions prevalent in certain habitats. Examples of this are the avoidance of open areas by small mammals (Lima and Dill 1990; Matter et al. 1996), the reluctance of certain bird species to cross water or open areas (Belisle and Desrochers 2002), and the avoidance of low light environments by some butterflies (Brdar 2000; Ide 2002). Edge effects or edge avoidance often occur where habitats meet (Ries and Debinski 2001; Schtickzelle and Baguette 2003). Organisms may respond to negative or positive conditions in one habitat, tending to keep them from crossing habitat borders.

Because their natural history and taxonomy is relatively well known from both popular and scientific pursuit, butterflies have emerged as an important model group for ecological and evolutionary study (Ehrlich 2003). Nowhere is this more evident than in the study of spatial population dynamics. Despite the attention given to butterflies, their spatial population dynamics, and dispersal, few studies have investigated the effects of habitat on their dispersal.

(Roland et al. 2000 and Matter et al. 2004) have shown that the dispersal of the butterfly *Parnassius smintheus* Doubleday is affected by habitat type. Using mark-recapture methods within 21 alpine meadows, they found that forest habitat was approximately twice as resistant to dispersal of the butterfly as was non-forested habitat. This result contrasts with theoretical expectations predicting that organisms should move quickly through habitat low in resources (Turchin 1991). The mechanism by which forest inhibits the dispersal of *P. smintheus* has not been not directly investigated and may elucidate why this species deviates from theory. Potentially butterflies do not enter forested habitat and disperse to isolated meadows by a convoluted route through open habitat. Alternatively, butterflies may move through or over forest with difficulty or less frequency. Here, we examine the mechanisms by which forest isolates populations of *P. smintheus*. We experimentally compare movement patterns within forest and meadow habitat and investigate the role that forest edge may play as a barrier to movement. Understanding the mechanisms responsible for differences in movement between different habitats should lead to better generalizations and predictions concerning the dispersal, population dynamics, and conservation of species.

Methods

Natural history and study site

Parnassius smintheus is abundant within sub-alpine meadows in the Rocky Mountains, although congeners are threatened in Europe (Vä;isä;nen and Somerma 1985; Kuras et al. 2000). The butterflies' host plant, *Sedum lanceolatum* Torr., occurs in gravelly sites above tree-line (Fownes and Roland 2002). *Parnassius smintheus* is univoltine with a flight period from mid-July to September in our study area (Roland et al. 2000). Adult males are generally more apparent than the relatively sedentary females. Nonetheless, estimated dispersal distances are equal between the sexes (Roland et al. 2000). Butterflies nectar-feed on species with yellow flowers such as *S. lanceolatum, Potentilla fruticosa*, and *Solidago multiradiata* which are prevalent within the meadows (Matter and Roland 2002).

Experiments were conducted in six meadows located above tree-line (~2100m) along Jumpingpound Ridge, Alberta, Canada (51°57′N, 114°54′W, Figure 1). Meadows are comprised of grasses, sedges, and wildflowers including *Sedum lanceolatum* and are bordered by forest consisting of *Pinus contorta*, *Abies lasiocarpa*, and *Picea engelmannii*.

Experimental design

To examine movement patterns of *P. smintheus* and the effects of the forest edge, a single butterfly was released at either 5 or 20m from the forest edge (release distance) in either forest or meadow habitat. We chose larger meadows and sites with well defined forest edges to conduct trials (Figure1). One trial was conducted per butterfly and each site was used for only one trial, although the same meadows were used for multiple trials. Butterflies were released onto vegetation at ground level. After release, we followed butterflies from a distance to avoid disturbing them while recording their movement behavior, either flying or crawling (it is not uncommon for *P. smintheus*, especially females, to move by crawling), and the time between alightings. At each stopping point, we took a light intensity reading (EXTECH^{tm} light meter) immediately after the butterfly left and placed a flag at the point. Each butterfly was followed until either we lost sight of it or one hour had elapsed. After each trial, we measured the distance and bearing between moves, and the distance and bearing from each point to the closest forest edge. All butterflies used for trials were male and were used shortly after capture (< 1 hr). These butterflies were netted by hand, generally from the meadow in which they would be used, and kept in the net at ambient temperature until use. Trials were conducted on days suitable for mark-recapture, i.e., sunny and not too windy. Weather conditions did vary non-systematically

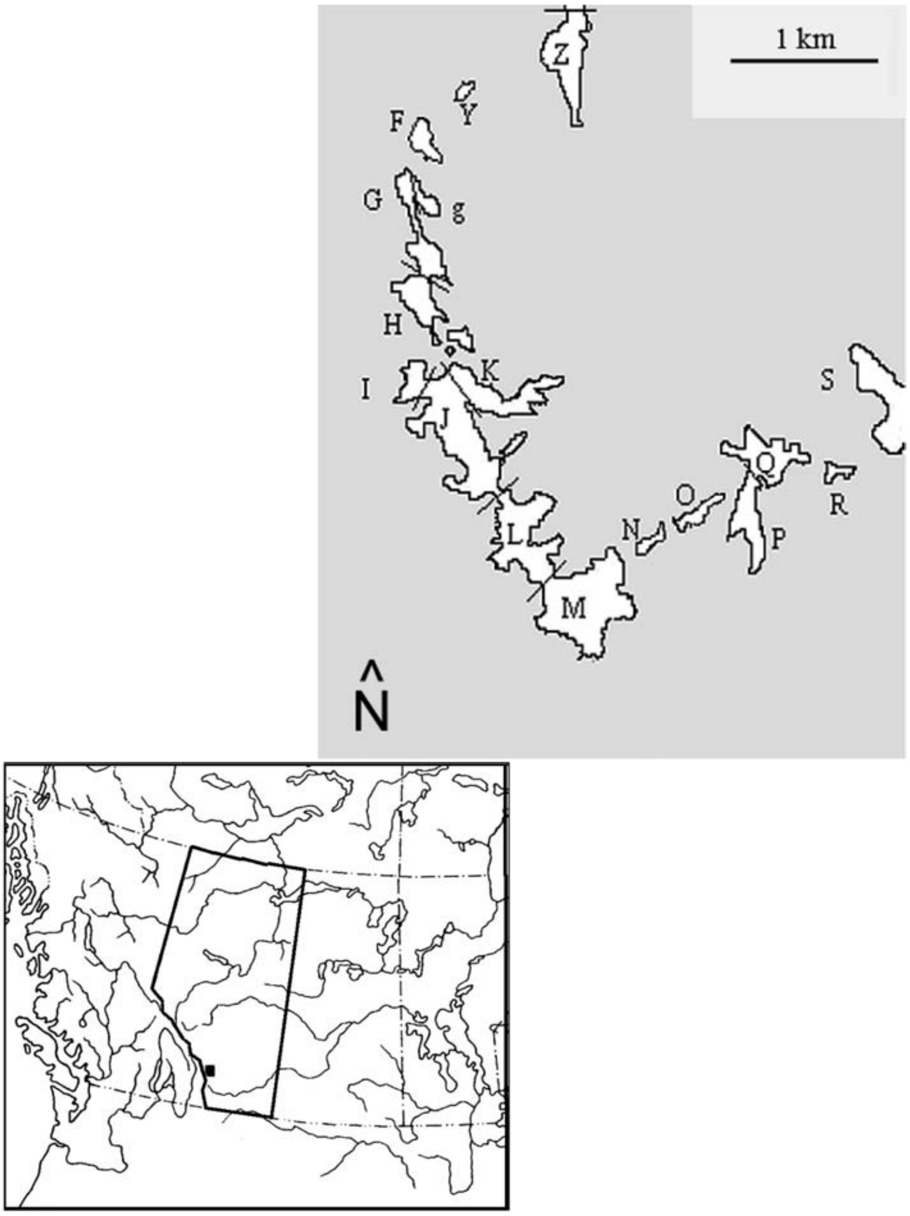

Figure 1. A depiction of the study site, alpine meadows along Jumpingpound Ridge. Meadows are in white, forested habitat in gray. Trials were conducted in meadows F, G, L, O, S, and Z. The inset shows the geographical location of the study site within the province of Alberta, Canada.

between and within trials which may affect movement (Merckx et al. 2003), however quantitative meteorological conditions (other than light intensity) were not collected. We conducted 12 replicates of each combination, totaling 48 trials using 48 different butterflies; however, two trials were excluded from analysis because the butterflies were judged to have damaged wings. Trials were conducted on ten dates from July 23 through August 19, 2002.

Data analysis

To compare movement patterns between habitats and distances from the edge, we examined the number of flights, total distance moved by flight and/or crawling (the sum of each step length), rate of movement (total distance moved/total observation time), and mean flight distance (total distance moved by flying/number of flights) for butterflies released at each location. For these analyses, habitat and release distance were considered as factors, each with two levels and we only considered data from the habitat type in which a butterfly was released. As number of flights consists of counts, it was analyzed using a generalized linear model with a Poisson error term. Total distance moved, rate of movement, and mean flight distance were analyzed using general linear models with normal error. Because the number of flights and total distance moved may be influenced by the length of observation, observation time was included as a covariate in the analysis of these two variables. The independent variables – release distance, habitat, and their interaction, were entered into all models sequentially. All dependent variables for the general linear model failed to meet Levine's test for equality of variance, necessitating transformation. After cubic-root transformation all variables met the assumption of equality of variance ($p < 0.05$).

To examine the effect of light levels on flight, we used logistic regression. For each alighting point (including the point of release) we examined whether a butterfly flew from there or did not (crawled or did not move) relative to the light intensity at that point. We also considered if the propensity to fly varied between habitats or with distance from the edge for reasons that may not be related to light intensity, so we included habitat type (forest or meadow) at each point as a dichotomous independent variable and distance from the edge (note this is the measured distance to the nearest forest edge from each alighting point, not the fixed release distance) as a continuous independent variable in the analysis. Because multiple observations of each butterfly were made within a trial for this analysis, the individual butterfly was also included as an independent variable in the model. Independent variables were entered into the model in a stepwise manner, first examining the effects of individuals followed by light, habitat, and distance from the edge.

To determine the effects of the forest edge on movement, we first identified whether a movement was toward or away from a forest edge. We used a 180° detection radius. Any movement was considered toward the edge if it fell on a bearing ± 90° of the bearing to the nearest forest edge. (n.b. we also examined a 90° detection radius and found similar results, not presented). We constructed a logistic regression with the effects of individuals and distance from the edge as independent variables. We expected that if there is edge avoidance, it would diminish with distance from the forest edge. Because movements were tallied as either toward the edge or away from the edge, our expectation for the logistic model also implies more 'attraction' to the forest edge at increasing distance, where rather we might expect no effect of the edge at a distance. We tested this assumption directly, by fitting models with an effect of individuals and an interaction between distance from the forest edge and a dummy variable. The dummy variable coded for whether a distance was 'near' or 'far' from the edge, and was scored as either 1 for near (including an effect of distance from the edge) or 0 for far (no effect of distance from the edge). Thus, these models tested whether there was repulsion close to the forest edge and no effect, rather than attraction to the edge, farther from the forest edge. Because the choice of cut points for 'near' and 'far' distances was arbitrary, we examined all possible combinations. We analyzed butterflies released in meadow or forest separately as effects of the edge would be expected to differ for each habitat.

To further evaluate edge effects, we also measured net displacement toward or away from the forest edge following release. For this analysis we subtracted the distance from the edge at the last observation point from the initial distance from the edge (point of release). Thus, if a butterfly crossed the forest edge from either forest or meadow it would have a negative value for net displacement. Net displacement was analyzed in the same manner as for total distance moved, however there was no need to transform the data.

Results

Parnassius smintheus made significantly more flights in meadow habitat than in forested habitat after accounting for observation time (Figure 2A). There was no significant main effect of release distance from the edge, however there was a significant interaction between habitat type and release distance. The greatest number of flights occurred 20m into the meadow and the fewest occurred 20m into the forest. The total distance moved by butterflies, by both flight and crawling, was also significantly greater in meadows than in forest (Figure 2B). In general, distances moved by crawling were

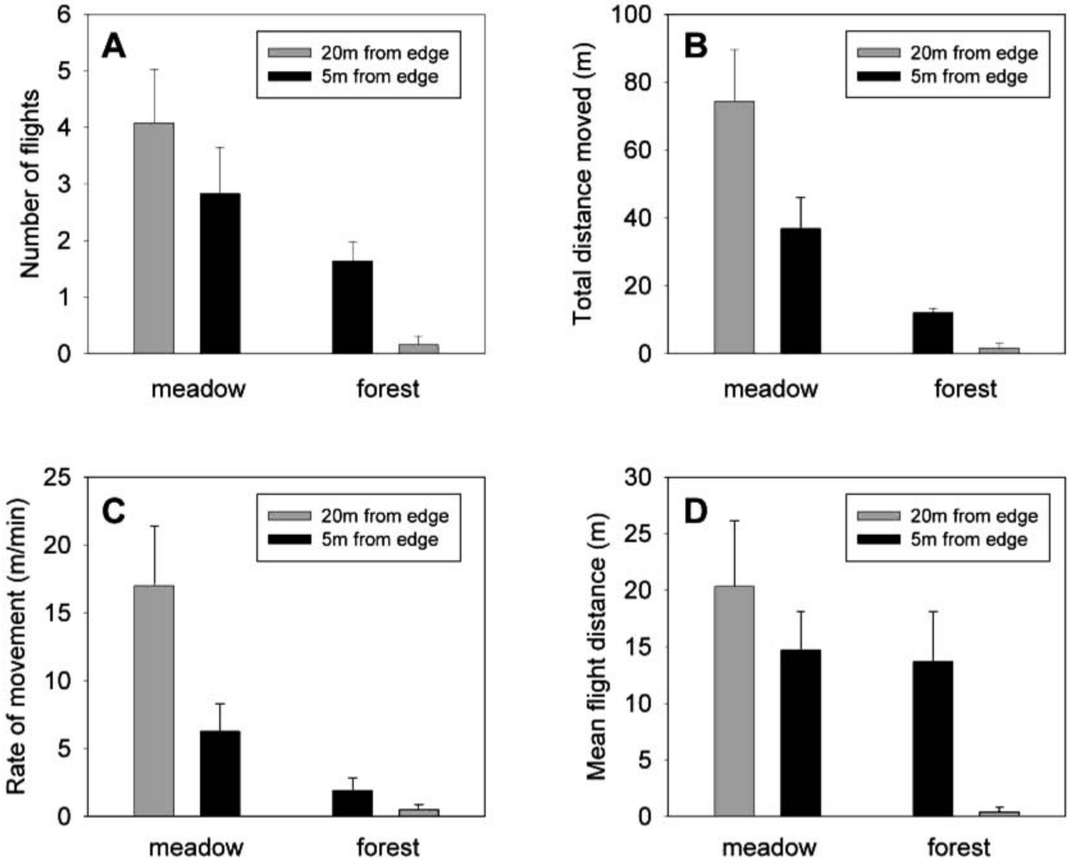

Figure 2. A comparison of the number of flights (A), total distance moved (B), movement rate (C) and mean flight distance (D) of *P. smintheus* released in meadow or forest habitat, 5 or 20 m from a forest edge. For the number of moves there was a significant effect of observation time ($\chi^2 = 46.50$, df = 1, $p < 0.01$), habitat ($\chi^2 = 20.10$, df = 1, $p < 0.01$) and the interaction between habitat and release distance ($\chi^2 = 8.90$, df = 1; $p < 0.01$), but no main effect of release distance ($\chi^2 = 0.98$, df = 1; $p = 0.32$). For total distance moved, after accounting for observation time ($F_{1,40} = 16.03$; $p < 0.01$) there was a significant effect of habitat ($F_{1,40} = 16.65$; $p < 0.01$), but no effect of release distance ($F_{1,40} = 0.66$; $p = 0.42$) or interaction ($F_{1,40} = 1.48$; $p = 0.23$). For the rate of movement there was a significant effect of habitat ($F_{1,41} = 21.46$; $p < 0.01$) and a significant interaction ($F_{1,41} = 7.61$; $p = 0.01$), but no main effect of release distance ($F_{1,41} = 0.01$; $p = 0.97$). For mean flight distance there was a significant effect of habitat ($F_{1,41} = 13.73$; $p < 0.01$), release distance ($F_{1,41} = 6.70$; $p = 0.01$), and a significant interaction ($F_{1,41} = 10.77$; $p < 0.01$). Analyses of total distance moved, rate of movement, and mean flight distance were conducted using cubic-root transformed data. Means shown are untransformed˘ standard errors.

short (< 2m). There was no significant main effect of release distance or interaction between release distance and habitat type.

The rate of movement was significantly greater in meadow habitat than in forest (Figure 2C). The greatest rates were seen 20m from the edge into the meadow and the lowest 20m into the forest, producing a significant interaction, but no main effect of release distance on the rate of movement. Mean flight distance was significantly farther in meadow than in forest. Flights were farther 5m from the forest edge than 20m from the edge, and there was a significant interaction between release distance and habitat type on mean flight distance (Figure 2D).

Because our measurements may simply reflect an effect of the propensity to fly in different habitats or at different release distances from a forest edge (see effects of light on flight below), we also conducted these analyses restricting the data to only those butterflies that flew at least once. After accounting for observation time ($\chi^2 = 3.66$; df = 1; $p = 0.06$), the number of flights by butterflies that flew at least once was significantly greater in meadow (4.37 ± 0.65, ± SE) than in forest (1.67 ± 0.28; $\chi^2 = 17.57$; df = 1; $p < 0.01$), but there was no main effect of release distance ($\chi^2 = 0.60$; df = 1; $p = 0.44$) or an interaction between release distance and habitat ($\chi^2 = 1.67$; df = 1; $p = 0.20$). The total distance moved by these butterflies, after accounting for observation time ($F_{1,25} = 0.25$; $p = 0.63$), was significantly greater ($F_{1,25} = 20.28$; $p < 0.01$) in meadow (67.97 ± 9.48 m) than in forest (12.77 ± 2.74 m), but there was no main effect of release distance ($F_{1,25} = 2.28$; $p = 0.14$) or any interaction between release distance and habitat type ($F_{1,25} = 3.77$; $p = 0.06$). The rate of movement by butterflies that flew was also significantly greater in meadow than in forest (14.25 ± 1.98 versus 2.50 ± 3.26 m/min, for forest and meadow respectively, $F_{1,26} = 12.54$; $p < 0.01$, analysis of square-root transformed data), but again there was no main effect of release distance from the edge ($F_{1,26} = 3.71$; $p = 0.07$) or interaction ($F_{1,26} = 1.74$, $p = 0.20$). Similarly, mean flight distance was greater in meadow than in forest (21.37 ± 3.21 vs 8.80 ± 5.30 m, $F_{1,26} = 4.13$; $p = 0.05$), but there was no main effect of release distance ($F_{1,26} = 0.23$; $p = 0.64$) or any interaction ($F_{1,26} = 2.45$; $p = 0.13$).

Effects of light, habitat and distance from the edge on flight

Light intensity at each alighting point had a strong effect on the flight of *P. smintheus. Parnassius smintheus* flew more often as light intensity increased. After accounting for effects of individuals ($\chi^2 = 95.30$; df = 42; $p < 0.01$) and light intensity ($\chi^2 = 23.62$; df = 1; $p < 0.01$) flight was not affected by habitat type ($\chi^2 = 1.02$; df = 1; $p = 0.31$) but increased with increasing distance from the forest edge ($\chi^2 = 8.21$; df = 1; $p < 0.05$). Light intensity was significantly lower in forested habitat than in meadows (295.3 ± 56.1 versus 805.0 ± 26.0 lx, $F_{1,146} = 11.82$; $p < 0.01$). Light intensity did not vary directly with distance from the forest edge ($F_{1,146} = 1.21$; $p = 0.27$), but there was an interaction between habitat and distance with light levels tending to be lower farther from the edge in forest and slightly higher farther from the edge in meadow habitat ($F_{1,146} = 4.33$; $p = 0.04$).

Effects of forest edge

Butterflies flying in meadow habitat flew away from the forest edge slightly more than an expected 50% of the time (33/57 flights). Assuming no effect of individuals or distance from the edge, there was no avoidance of the edge ($\chi^2 = 1.42$; df = 1; $p = 0.23$). However, after accounting for individual differences and distance from the forest edge, there was a clear pattern of edge avoidance that decreased with increasing distance from the edge (Figure 3). These results also indicate that there may be some attraction to the forest edge at a distance from the edge. No model using the interaction between distance and a dummy variable coding for whether that distance was 'near' or 'far' explained more deviance than did the model using distance alone. The residual deviance for the model using individuals and distance was 35.24 while the best models using individuals and an interaction (with the cut point for the dummy variable at 25m) had a residual deviance of 41.35.

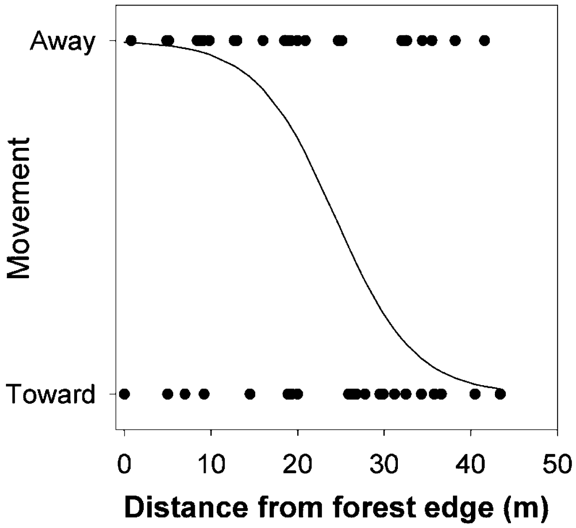

Figure 3. Forest edge avoidance by *P. smintheus* in meadow habitat. There was a significant effect of individual ($\chi^2 = 27.21$, df = 15, $p < 0.01$) and distance from the forest edge ($\chi^2 = 15.14$, df = 1, $p < 0.01$) on whether a butterfly flew toward or away from a forest edge.

An examination of turning angles for butterflies flying in the forest provided little evidence for attractiveness of the edge. Twelve of an expected 15 out of 30 movements were toward the edge ($\chi^2 = 1.20$; df = 1; $p = 0.27$). After accounting for individual effects, we found no effect of distance from the edge on edge avoidance or attraction (Individuals: $\chi^2 = 10.23$; df = 12; $p < 0.01$; distance from edge: $\chi^2 = 0.48$, df = 1, $p = 0.49$). However, after accounting for observation time ($F_{1,25} = 0.24$; $p = 0.63$) the net displacement of butterflies (initial distance – final distance from the forest edge) showed a repulsion from the edge for butterflies flying in meadow and an attraction to the meadow for butterflies in forest ($F_{1,25} = 5.84$; $p = 0.02$). The net displacement of butterflies was away from the edge in meadow habitat (13.50 ± 4.88m) and toward the edge in forest habitat (-11.53 ± 4.01). There was no effect of release distance ($F_{1,25} = 1.64$; $p = 0.21$) or an interaction between habitat and distance ($F_{1,25} = 0.12$; $p = 0.73$) on net displacement. Butterflies released in forest moved into meadow habitat more frequently (5/11) than butterflies released in meadow habitat moved into forest (2/18, $G_{adj} = 4.13$; df = 1; $p < 0.05$).

Discussion

Forest habitat affects the movement of *Parnassius smintheus* in two ways. First, forest habitat adjacent to meadow creates an edge effect – butterflies tend to move away from forest edges. Second, movement is quantitatively different within forest habitat than it is within meadows. Butterflies flew less often and for shorter distances in the forest than they did in the meadows. These two results are in agreement with the population-level findings of (Roland et al. 2000) and the individual-level findings of (Matter et al. 2004). In their analyses of mark recapture data of *P. smintheus*, they found that the distance composed of forest between two meadows reduced the number of movements between meadow pairs to a much greater degree than did that of open meadow habitat. In addition to a distance effect, (Roland et al. 2000) found that whether two meadows were separated by forest or not had an additional effect on the number of movements, and interpreted this result as edge effect, which we also see here.

Our results concerning total distance moved and the number of flights should be interpreted cautiously. Both of these measures are affected by our ability to follow butterflies which is more difficult in forest than in meadow. However, we see the same inhibitory effects of forest habitat on movement for the rate of movement and mean flight distance, which are not subject to this problem, indicating that these results are robust. One particular assumption of our experimental design does deserve attention. By releasing butterflies at ground level in forest we are not suggesting that these butterflies regularly encounter such conditions, rather we are trying to demonstrate why they avoid such conditions. *Parnassius smintheus* are almost never found in forested habitat, likely because it is not bright enough. In fact, most movement across forested habitat probably occurs above the canopy, although these butterflies rarely fly at that altitude. By releasing butterflies in forest after capture, in comparison to their encountering forest when flying at normal body temperature, potentially we are exaggerating differences between the habitats. We assessed this potential problem by examining the time it took until the first flight among habitats and release distances. We found that it took approximately 5 min longer for butterflies to ‘heat up’ in forest versus meadow, although the difference was not significant ($F_{1,26} = 0.26$, $p = 0.61$). In addition there was no main effect of release distance or an interaction between release distance and habitat ($p > 0.22$). It should be noted that our power for detecting differences between habitats was low, 0.08, thus we cannot rule out some bias. However the magnitude of this bias appears to be minimal.

Our results also indicate significant variation among individuals in their response to habitat. These effects may reflect individual differences in movement; however, since trials were not repeated at each location, individual differences cannot be disentangled from location effects. Our results are contradictory for an attraction of the forest edge for butterflies flying in forest. The logistic regression examining movement toward or away from the edge shows no attraction to the edge, while analysis of displacement shows a strong attraction toward the edge and meadow. The lack of effect for the angle of movement is likely due to the nature of light at the edge. In general, the brightest path back to the meadow from the forest may not be a straight line to the edge as our analysis assumes. Thus, if butterflies flying in forest are responding to light, movement toward the meadow may not follow a straight line to the edge.

Much of the difference in movement between the two habitat types is due to differences in light levels. Forest habitat has a much lower light intensity than does meadow habitat. Light levels also tend to decrease moving into the forest. *Parnassius smintheus* flew much more readily when light levels were high.

Our results have many implications for the spatial population ecology and conservation of *P. smintheus* and other butterflies that are habitat specialists. At our site, encroaching forest following a large fire in 1938 has reduced the size of meadows along Jumpingpound Ridge by over 78% (Roland et al. 2000). Rising treeline directly reduces habitat area, and may reduce the area of meadows used by butterflies through edge effects. Given the parameter values from the logistic regression examining edge avoidance, we estimate 98% of movements to be away from the edge at a distance of 5m, decreasing to 50% away from the edge at a distance of 23.8m. Assuming a conservative acceptance angle of 3° (Land 1997; Rutowski et al. 2001), *P. smintheus* at a distance of 23.8m, should be able to discern objects as small as 1.3m (Land 1997), well under the height and length of a forest edge. Thus, there appears to be no physiological limit to butterflies detecting an edge from such a distance. Given the distance at which butterflies begin to avoid forest edges, meadows may have to be nearly 50m wide to incur no edge effects. Although the large meadows where we conducted experiments are much larger than this limit, several of our meadows are small enough to be subject to an edge effect throughout. It should be noted that this edge effect is not strongly related to light levels. Obviously, very close to a forest edge light levels may be low depending on aspect and time of day. However, there was only a marginal trend for light levels to increase within meadows with increasing distance from the edge ($F_{1,110} = 3.64$, $p=0.06$). Furthermore, predicted light levels at the edge (733 lx) are well above levels where flight is impeded.

In addition to reducing meadow area, rising treeline will also isolate populations within the meadows. Because *P. smintheus* tends to avoid forest edges and moves much less easily within forest, meadows surrounded by forest will produce fewer emigrants and receive fewer immigrants than meadows without forested boundaries, other factors being equal. Reduced movement among populations alters the genetic structure of *P. smintheus*(Keyghobadi et al. 1999) and may affect local and spatial population dynamics and persistence.

Many studies have shown edge effects and edge avoidance for a variety of taxa (Kuussarri et al. 1996; Haddad 1999; Brdar 2000, Pryke and Samways 2001; Ricketts 2001; Ries and Debinski 2001; Schultz and Crone 2001), although such effects are by no means universal across species or boundary types (Bowne et al. 1999; Brdar 2000; Pryke and Samways 2001; Ries and Debinski 2001; Ricketts 2001). Few studies have directly shown movement patterns that differ in different habitats (see Turchin 1991). (Pryke and Samways 2001) through direct observation showed that movement rates of several butterflies were greater in open strips of corridor connecting grasslands than in open grassland habitats. More often, the effects of habitat types on movement, or lack thereof, have been inferred from census data (Moilanen and Hanski 1998; Haddad 1999; Roland et al. 2000; Ricketts 2001, Matter et al. 2004). Through mark recapture (Hein et al. 2003) showed that the movement of the bush cricket, *Platycleis albopunctata*, differs between suitable habitat and two (but not a third) types of matrix habitat. In contrast to our study, they found that the mean daily movement distances of crickets was farther in non-habitat than in suitable habitat – a result which is consistent with foraging theory (Turchin 1991). The main difference between our results and those of (Turchin 1991 and Hein et al. 2003) is that in our case the matrix habitat affects the ability of *P. smintheus* to disperse. *Parnassius smintheus* cannot not fly well in forest matrix habitat due to lower light levels. Thus, the expectation of a higher rate of movement through non habitat due to foraging considerations is likely dependent on the organism's ability to move through particular types of habitat.

Although evidence for specific effects of different habitat types on dispersal is now emerging, such effects have often been presupposed. Organisms moving through different habitats at different rates or with different success is the theoretical basis for habitat corridors (Simberloff et al. 1992) and part of the reasoning for protective hedgerows around crop fields (Racette et al. 1992). Understanding how organisms move through and respond to different landscape elements is highly important in fragmented habitats, where the effective isolation of populations may not simply be a function of distance but a combination of distance and habitat types.

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