Forest Habitat Reduces the Flight of Pontia occidentalis (Reakirt) (Lepidoptera: Pieridae) Relative to Alpine Meadow Habitat

Authors: Matter, Stephen F., Gargano, Corey, Kim, Kenneth I., and Wick, Anne

Source: The Journal of the Lepidopterists' Society, 70(2) : 108-113

Published By: The Lepidopterists' Society

URL: https://doi.org/10.18473/lepi.70i2.a5

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/The-Journal-of-the-Lepidopterists'-Society on 07 Jun 2025
Terms of Use: https://complete.bioone.org/terms-of-use

Journal of the Lepidopterists' Society
70(2), 2016, 108–113

FOREST HABITAT REDUCES THE FLIGHT OF *PONTIA OCCIDENTALIS* (REAKIRT) (LEPIDOPTERA: PIERIDAE) RELATIVE TO ALPINE MEADOW HABITAT

STEPHEN F. MATTER
Department of Biological Sciences, University of Cincinnati, Cincinnati, OH 45221-0006 USA and
Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9 Canada email: mattersf@uc.edu

COREY GARGANO
Environmental Studies Program, University of Cincinnati, Cincinnati, OH 45221-0006 USA email: corey.gargano@gmail.com

KENNETH I. KIM
Department of Biology, Truman State University, Kirksville, MO 63501 USA email: kimki@uci.edu

AND

ANNE WICK
Department of Biological Sciences, University of Cincinnati, Cincinnati, OH 45221-0006 USA email: Wickak@gmail.com

ABSTRACT. We compared the movement of *Pontia occidentalis* in forest and meadow habitat. We hypothesized that flight distances and overall movement would be greater in forested habitat than in meadow habitat. This hypothesis was based on forging theory predicting that organisms should spend less time in areas where resources are scarce than where they are abundant. Because this species is a generalist in its use of open habitat and regularly encounters forest when dispersing and hilltopping, we also hypothesized that forested habitat would not impose a physiological limitation on their flight. To test this hypothesis we released 68 butterflies in either forest or alpine meadow habitat and followed their movement. Contrary to our hypothesis, the total distance moved, mean flight distance, and rate of flight were all lower in forest relative to meadow habitat. Forest habitat did not exert an edge effect for *Pontia occidentalis* flying in meadow habitat. Contrary to our second hypothesis, differences in movement appeared to be due to differences in the light levels between forest and meadow habitat. *Pontia occidentalis* flew more often and farther distances with increasing light intensity, which was greater in meadow habitat than in forest. Overall, the results indicate that forest may impede the movement of *Pontia occidentalis*, despite it regularly encountering it. The results also indicate that structural and physiological limitations on movement imposed by different habitats may preclude optimal responses to resources.

Additional key words: dispersal, ecotone, light intensity, matrix, migration

The movement of organisms is a fundamental feature of life, affecting processes from foraging, to spatial population dynamics, to speciation (Fretwell & Lucas 1970, Roland & Matter 2007, Claramunt et al. 2012). Many insect species exist in relatively heterogeneous environments and regularly encounter different habitat types, which may affect their movement (Pither & Taylor 1998, Ross et al. 2005, Dover & Settle 2009). Thus, the presence of different types of habitat in a landscape has the potential to affect a range of ecological and evolutionary processes.

Understanding movement in different habitats has been approached from different perspectives. According to foraging (Zollner & Lima 1999) and mating (Gilroy & Lockwood 2012) theory, organisms should minimize time in habitats where resources are lacking. Thus, rates of movement and distances moved are predicted to be greater in habitat that contains few or no resources than in habitats containing an abundance of resources or mates (Turchin 1991, Merckx et al. 2003). From a physiological perspective, different habitats may impose a variety of constraints on dispersal ability. Many ectotherms, and butterflies in particular, rely on the external environment to raise their body temperature to levels where movement or flight are possible. Thus, differences in temperature, light, and the physical structure of different habitats can affect the ability to move as well as movement distances and rates (Merckx et al. 2003, Ross et al. 2005, Dover & Settle, 2009, Schultz et al. 2012).

The effects of habitat type on dispersal have been evaluated most frequently for specialist species using distinct habitats within spatial population networks, where habitat patches are imbedded in an inhospitable matrix. In these studies, the implicit assumption is that habitat patches contain resources and matrix habitat does not (Dennis et al. 2013); dispersal is then compared between or among different habitat types

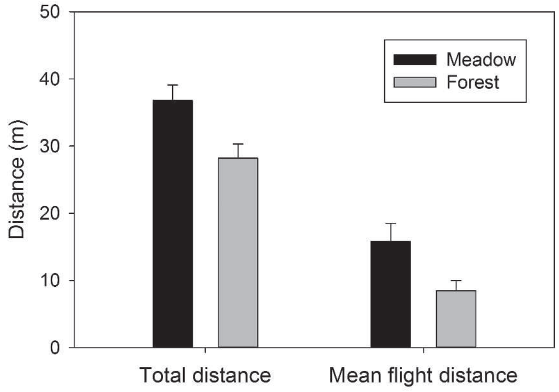

FIG. 1. Total distance moved and mean flight distance of *Pontia occidentalis* in forest and meadow habitat. Error bars represent one standard error. The means shown for total distance moved are adjusted for differences in observation time.

(Dover & Settle 2009). Possibly due to the ability to assess habitat and non-habitat for specialist species (but see Dennis et al. 2013), the effect of different types of habitat on the dispersal of generalist species has received less attention than specialists. For generalists, we might expect more similar movement among different types of habitat because different habitats are more likely to contain resources, albeit at different abundance and quality (Dennis et al. 2013). Similarly from a physiological perspective, generalists likely have to contend with a wider range of environmental conditions. Thus, the dispersal of generalists may not vary as greatly among habitats as for specialists.

Here, we compare the movement of the Western White, *Pontia occidentalis*, between alpine meadow and forested habitat. We were particularly interested in whether forest affects its flight because previous research at the same location has shown that forest habitat greatly reduces the flight and dispersal of the alpine specialist *Parnassius smintheus* Doubleday among meadow habitats (Matter & Roland 2003) largely through a reduction in light levels in forest (Ross et al. 2005). Forest encroachment at this site has reduced non-forested habitat by over 75% over the last 75 years (van Ee et al. 2015). Thus, if forest reduces dispersal among alpine meadows it may reduce persistence in this habitat in addition to any effects from habitat loss.

Based on foraging theory, we predicted that movement distances and rates of *Pontia occidentalis* would be greater in forested than in meadow habitat because resources are very low to non-existent in forested habitat. Additionally, because of *Pontia occidentalis*' generalist nature and regularly encountering forested habitat, we predicted that it would not experience limitation in flight due to lower light levels in forest.

MATERIALS AND METHODS

Study site and species. Experiments were conducted during July and August (2003–05 and 2007–08) in meadows above treeline (~2100 m) on Jumpingpound Ridge, Alberta, Canada (51°57'N, 114°54'W, see Matter et al. (2009) for a depiction of the study site). Vegetation within the meadows consists of grasses, sedges, and wildflowers. Meadows are bordered by forest consisting of *Abies lasiocarpa* (Hook.), *Picea engelmannii* Parry ex Engelm., and *Pinus contorta* Dougl. ex. Loud. (Pinaceae).

Pontia occidentalis (Reakirt) (Lepidoptera: Pieridae) inhabits a variety of open habitats in western North America from alpine meadows, to prairies, to grassy roadsides (Guppy & Shepard 2001). It ranges from Alaska to northern New Mexico. In Alberta, there is one to possibly three generations per year (Bird et al. 1995). Many species of Brassicaceae are host plants (Bird et al. 1995, Guppy & Shepard 2001) and a wide variety of nectar flowers are used in these meadows (Ezzedidne & Matter 2008). Because this butterfly exploits patchily distributed resources, it likely encounters a variety of habitat types and range of environmental conditions. In addition, these butterflies often traverse forested habitat to hilltop and feed on nectar in alpine meadows. At our site, *Pontia occidentalis* is an irruptive species. In most years they are present in moderate numbers, but in 2003 they were extremely numerous with many individuals presumably arriving from lower elevations.

Experimental design. Butterflies were netted by hand and kept at ambient temperature until use (< 1 hr). One trial was conducted per butterfly at independent sites with well-defined forest edges. At each site a butterfly was released onto vegetation at ground level from 5–20 m from a forest edge in either forest or meadow habitat. Butterflies were then observed for up to one hour, or until we lost sight of the butterfly. We placed a marking flag at each alighting point just after the butterfly left and took a reading of light intensity (lux/100) using a portable light meter (Extec). After each trial, we measured the distance and bearing between alighting points and the distance and bearing from each point to the closest forest edge by hand using a meter tape and compass. These data allowed us to evaluate movement in each habitat as well as any edge effects.

All trials were conducted on days suitable for mark-recapture, i.e., sunny and not too windy. Being in an alpine environment, however, weather conditions did

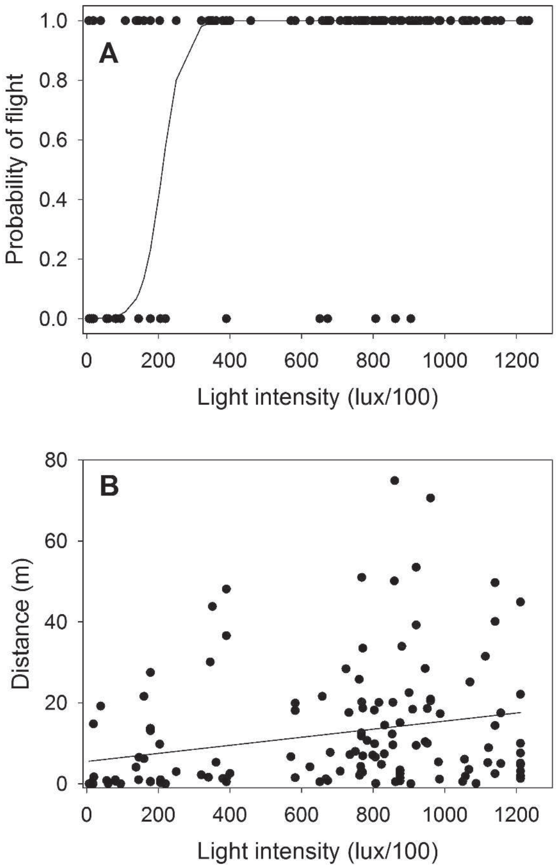

FIG. 2. Effects of light levels on the flight of *Pontia occidentalis*. The top panel (**A**) shows the probability of flight versus crawling or not moving relative to light intensity in lux divided by 100 (the units in which it was measured). The fitted line is the predicted logistic response not accounting for random effects variation among individuals (N=45). The bottom panel (**B**) shows the distance moved by *Pontia occidentalis* relative to light levels (mixed model fixed effect slope and intercept: $\beta = 0.014 \pm 0.004$, t = 3.40, P = 0.08; $\beta_0 = 4.088 \pm 2.365$). The plotted line does not account for differences among individuals. The model explained significant deviance in distance moved relative to a null containing only the mean and random effect of individuals ($\chi2 = 18.17$, df = 3, $P < 0.01$). Random effects variation due to individuals was low (1.11×10^{-4}, SD = 0.011). Several trials could not be used because light levels were not measured for individual movements.

vary within and among trials. Meteorological conditions (wind speed, temperature) which can affect movement (Merckx et al. 2003) were collected at the start of most, but not all trials. Trials were conducted under wind speeds ranging from 0.0 to 14.2 km/h and temperatures from 10.7° to 30.6° C. We conducted a total of 68 trials (34 each in forest and meadow habitat).

Statistical analyses. To evaluate movement in forest and meadow habitat, we examined the number of flights, total distance moved by flight and/or crawling (the sum of the distance between each alighting point), rate of flight (total distance moved by flight/total observation time), and mean flight distance (total distance moved by flying/number of flights) for butterflies released in each habitat. For these analyses forest or meadow was considered a fixed effect. Number of flights consists of counts, thus it was analyzed using a generalized linear model with a quasipoisson error term to account for overdispersion. Total distance moved, rate of flight, 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 variables.

We used logistic regression to examine the effect of light levels on flight. At 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. Because multiple observations of each butterfly were made within a trial for this analysis, the individual butterfly was included as a random effect in the model. We used a similar analysis, but with normal errors, to examine whether the distance that a butterfly moved varied with light intensity.

To determine whether forest exerts an edge effect, we first classified movements toward or away from a forest edge. We first used a 90° arc; any movement was considered toward the edge if it fell on a bearing ± 45° of the bearing to the nearest forest edge. Because this angle was arbitrary, we also examined a broader 180° arc. For each arc, we constructed a logistic regression with individual as a random effect and distance from the forest edge as an independent variable. We expected that if there is an edge effect, it would diminish with increasing distance from the forest edge. However, movements were tallied as either toward the edge or away from the edge. Thus, the expectation for a logistic model implies "attraction" to the forest edge at increasing distance, where in contrast, we expect no effect of the edge at greater distance. We evaluated this expectation by fitting models with 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 with the interaction tested whether there was repulsion close to the forest edge and no effect, rather than an attraction to the edge farther from the forest edge. Because the choice of how to define near and far distances from treeline was arbitrary, we used a range of distances in 5

Table 1. Analysis of edge effects induced by forest habitat for *P. occidentalis* flying in alpine meadows. Results from mixed logistic models are shown assuming a 90° or 180° arc determining whether movements were towards or away from forest expecting that if there is an edge effect it should diminish with increasing distance from the forest edge. A dummy variable coded (1 = near, 0 = far) whether a distance was near or far from a forest edge. The interaction between distance and the dummy variable tested whether there would be repulsion near a forest edge and no effect far from the edge (rather than attraction). For each analysis individual butterflies were considered a random effect.

90° arc				180° arc		
	Estimate(SE)	Z	P	Estimate(SE)	Z	P
>5m "far"						
Intercept	2.12(0.76)	2.80	<0.01	1.40(0.62)	2.26	0.02
Distance	-0.01(0.02)	-0.12	0.91	-0.07(0.02)	-2.85	<0.01
Dummy	-0.14(1.27)	-0.11	0.91	0.14(1.10)	0.13	0.90
Interaction	-0.10(0.25)	-0.38	0.70	-0.23(0.22)	-1.03	0.30
>10m "far"						
Intercept	1.90(0.89)	2.14	0.03	1.09(0.75)	1.45	0.15
Distance	0.01(0.03)	0.10	0.92	-0.06(0.03)	-2.12	0.03
Dummy	-0.42(1.27)	-0.33	0.74	-0.27(1.07)	-0.26	0.80
Interaction	0.07(0.17)	0.43	0.67	0.03(0.13)	0.25	0.80
>15m "far"						
Intercept	2.67(1.02)	2.60	0.01	1.18(0.83)	1.41	0.16
Distance	-0.02(0.03)	-0.53	0.60	-0.06(0.03)	-2.05	0.04
Dummy	-0.50(1.28)	-0.39	0.70	-0.30(1.04)	-0.28	0.77
Interaction	-0.07(0.12)	-0.57	0.57	0.02(0.10)	0.20	0.84
>20m "far"						
Intercept	5.35(1.77)	3.02	<0.01	1.58(1.29)	1.22	0.22
Distance	-0.07(0.04)	-1.85	0.06	-0.07(0.04)	-1.75	0.08
Dummy	-3.50(1.79)	-2.00	0.05	-0.58(1.37)	-0.42	0.67
Interaction	0.06(0.06)	0.91	0.36	0.01(0.05)	0.22	0.83

m intervals encompassing the distance from treeline where we observed butterflies. We tested the interaction using each near and far setting in separate models.

All analyses were conducted using the program R version 3.0.2 (R Core Development Team, 2013).

Results

We were able to follow individual butterflies for a mean of 25.8 ± 2.8 (S.E.) min. Only three butterflies crossed habitat boundaries; two moved into forest from meadow and one moved from forest into meadow.

Contrary to our hypothesis, the movement of *Pontia occidentalis* was reduced in forest habitat relative to meadow habitat (Fig. 1); its total distance moved was significantly farther in meadow than in forest habitat ($F_{1,65}$ = 8.00, P < 0.01) after accounting for the effects of observation time ($F_{1,66}$ = 8.81, P < 0.01). Its mean flight distance was also greater in meadow than in forest ($F_{1,66}$ = 8.16, P < 0.01) as was its rate of flight (8.5 ± 1.8 vs. 1.0 ± 0.4 m/min.; $F_{1,66}$ = 15.59, P < 0.01). *Pontia occidentalis* also tended to initiate more flights in meadow (3.4 ± 0.5) than in forest habitat (1.4 ± 0.8), although the difference was not significant ($F_{1,65}$ = 2.82, P = 0.09) after accounting for the marginal effect of observation time ($F_{1,66}$ = 3.60, P = 0.06).

The flight of *Pontia occidentalis* was affected by light intensity (Fig. 2). They flew more often when light levels were high than under low light intensity (β = 0.036 ± 0.018, Z = 2.00, P = 0.04; β_0 = -7.627 ± 3.524). The overall model explained significant variation in whether a butterfly flew or not (χ^2 = 48.849, df = 3, P < 0.01); variation attributable to mean differences among individuals was minimal (2.4×10^{-3} , SD = 0.05). Flight distance also increased with increasing light intensity (Fig. 2). Not surprisingly, light levels in meadow habitat were greater than in forested habitat (771900 ± 47600 vs. 421500 ± 48300 lux; t = 6.33, separate variance df = 125.6, P < 0.01).

There was little evidence that *Pontia occidentalis* avoided forest habitat though edge effects. These butterflies were equally likely to move towards or away from forest at any distance based on the more conservative 90° arc (Table 1). Using a 180° arc, we found that *Pontia occidentalis* tended to move away from forest near the edge and towards forest father from the edge as indicated by the significant effect of distance. However, the interaction between distance from the edge and the dummy variable was not significant, implying that there is attraction towards forest when far from an edge, but not repulsion from forest when close to the edge.

DISCUSSION

Our hypothesis that the movement distances and rates of *Pontia occidentalis* would be greater in forest than in meadow habitat was not supported; its movement was reduced in forest habitat relative to alpine meadow habitat. That *Pontia occidentalis* does not move as far or fast in forest habitat, is inconsistent with the hypothesis that movement should be greater in habitats with low resources than in habitats with abundant resources (Zollner & Lima 1999). Our hypothesis that the light environment would not affect the movement *Pontia occidentalis* was somewhat equivocal. Low light intensity may reduce the flight of butterflies adapted to high light environments such as alpine meadows, but we predicted that the generalist nature of *Pontia occidentalis* would allow it to fly in lower light such as that experienced in forested habitat. Dispersal by *Pontia occidentalis* was affected by ambient light intensity. Under high light conditions *Pontia occidentalis* flew almost exclusively and the distance moved increased with increasing light intensity; however, its flight was not particularly limited by low light levels. Thus, shadier forest habitat may not place physiological limits on the flight of *Pontia occidentalis*. That is, there may be enough ambient sunlight to allow them to warm their flight muscles, but they tended to fly less often when light levels were low limiting their ability to respond optimally to available resources, i.e., moving quickly through the low resources in forest habitat. Our results show that movement can differ among habitat types even for generalist insect species regularly encountering these different types of habitat.

The reduced flight in forest relative to alpine meadow for *Pontia occidentalis* was somewhat similar to that seen for the alpine specialist butterfly *Parnassius smintheus* (Ross et al. 2005). For male *P. smintheus* flight was reduced in forest relative to open meadow habitat and the propensity for this butterfly to fly decreased dramatically with light intensity, much more so than for *Pontia occidentalis*. For *P. smintheus* there also was a strong edge effect; however, this was not seen for *Pontia occidentalis*. For both of these species, forest may be a barrier to flight by limiting light, particularly if the butterfly alights in forested habitat. Forest habitat has been shown to reduce the between population dispersal of *P. smintheus* affecting its population growth (Roland & Matter 2007) and genetic structure (Keyghobadi et al. 2005, Caplins et al. 2014). Despite the effects seen for flight, it seems less likely that forest habitat will have similar effects at the population level for *Pontia occidentalis*. First, it is unlikely that individual meadows contain semi-independent populations of *Pontia occidentalis* due to the influx of hilltopping butterflies from lower elevations, particularly during warm, dry summers. Second, *P. smintheus*, like many alpine specialists, generally does not fly high above the ground (Ross et al. 2005). In contrast, *Pontia occidentalis* often flies high above the ground and may simply fly over forested habitat, avoiding shading and any structural effects, but potentially at a cost of encountering buffeting winds avoided by low flying species in alpine regions (Matter, personal observation).

Numerous studies now have shown that dispersal is a function of habitat type (e.g., Pither & Taylor 1998, Haddad 1999, Jonsen et al. 2001) and many studies have been conducted in habitats that differ in resources. These studies generally have found results that are consistent with foraging theory, i.e., that dispersal distances are longer and more directed where resources are lacking. Such dispersal results in less time spent in resource poor habitat than in areas where resources are abundant (Haynes & Cronin 2006, Schtickzelle et al. 2007, Kuefler et al. 2010). However, a growing number of studies indicate that structural differences in habitat can affect dispersal, sometimes with larger effects than resources (Ross et al. 2005, Schultz et al. 2012).

The results of this study indicate that dispersal can vary among habitat types even for the generalist *Pontia occidentalis* which regularly encounters a variety of habitat types. Environmental differences among habitats potentially impose physiological or behavioral constraints, such as the propensity to fly, which may preclude appropriate response based on foraging theory.

ACKNOWLEDGEMENTS

This research was supported by NSF grants DEB 0918929 and 0326957 to S.F. Matter and an NSERC Discovery grant to Jens Roland. We thank two reviewers for comments that improved the manuscript.

LITERATURE CITED

CAPLINS, S.A., K. J. GILBERT, C. CIOTIR, J. ROLAND, S. F. MATTER & N. KEYGHOBADI. 2014 Landscape structure and the genetic effects of a population collapse. Proc. R. Soc. B 281: 1796-1798.

CLARAMUNT, S., E. P. DERRYBERRY, J. V. REMSEN JR. & R. T. BRUMFIELD. 2012. High dispersal ability inhibits speciation in a continental radiation of passerine birds. Proc. R. Soc. B 279: 1567–1574.

BIRD, C. D., G. J. HILCHIE, N. G. KONDELA, E. M.PIKE & F.A.H. SPERLING. 1995. Alberta butterflies. The Provincial Museum of Alberta, Edmonton. 349 pp.

DOVER, J. & J. SETTELE. 2009. The influences of landscape structure on butterfly distribution and movement: a review. J. Insect Conserv. 13: 3-27.

EZZEDDINE, M. & S. F. MATTER. 2008. Nectar flower use and electivity by butterflies in sub-alpine meadows. J. Lep. Soc. 62: 138-142.

FRETWELL, S. D. & H. L. LUCAS. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. Acta Biotheor. 19: 16-36.

GILROY J. J. & J. L. LOCKWOOD. 2012. Mate-finding as an overlooked critical determinant of dispersal variation in sexually-reproducing animals. PLoS ONE 7: e38091 doi:10.1371/journal.pone.0038091

GUPPY, C. & J. SHEPARD. 2001. Butterflies of British Columbia. University of British Columbia Press, Vancouver. 414 pp.

HADDAD, N. M. 1999. Corridor use predicted from behaviors at habitat boundaries. Am. Nat. 153: 215–227.

HAYNES, K. J. & J. T. CRONIN. 2006. Interpatch movement and edge effects: the role of behavioral responses to the landscape matrix. Oikos 113: 43–54.

KEYGHOBADI, N., J. ROLAND, S. F. MATTER & C. STROBECK. 2005. Among- and within-patch components of genetic diversity respond at different rates to habitat fragmentation: an empirical demonstration. Proc. R. Soc. B 272: 553-560.

KUEFLER, D., B. HUDGENS, N. M. HADDAD, W. F. MORRIS & N. THURGATE. 2010. The conflicting role of matrix habitats as conduits and barriers for dispersal. Ecology 91: 944–950.

MATTER, S.F., M. EZZEDDINE, E. DUERMIT, J. MASHBURN, R. HAMILTON, T. LUCAS & J. ROLAND. 2009. Interactions between habitat quality and connectivity affect immigration but not abundance or population growth of the butterfly, *Parnassius smintheus*. Oikos 118: 1461-1470.

MERCKX, T., H. VAN DYCK, B. KARLSSON O. LEIMAR. 2003. The evolution of movements and behaviour at boundaries in different landscapes: a common arena experiment with butterflies. Proc. R. Soc. B 270: 1815–1821.

PITHER, J. & P. D. TAYLOR. 1998. An experimental assessment of landscape connectivity. Oikos 83: 166-174.

R CORE TEAM. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

ROLAND, J. & S. F. MATTER. 2007. Encroaching forests decouple alpine butterfly population dynamics. PNAS 104: 13702-13704.

ROSS, J. A., S. F. MATTER & J. ROLAND. 2005. Edge avoidance and movement of the butterfly *Parnassius smintheus* in matrix and non-matrix habitat. Land. Ecol. 20: 127-135.

SCHTICKZELLE, N., A. JOIRIS, H. VAN DYCK & M. BAGUETTE. 2007. Quantitative analysis of changes in movement behaviour within and outside habitat in a specialist butterfly. BMC Evo. Bio. 7: doi:10.1186/1471-2148-7-4.

SCHULTZ, C.B., A. M. A. FRANCO & E. E. CRONE. 2012. Response of butterflies to structural and resource boundaries. J. Anim. Ecol. 81: 724-734.

TURCHIN, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. Ecology 72: 1253–1266.

VAN EE, J., M. WESTBROOK, S. YADAV, J. ROLAND & S.F. MATTER. 2015. Predicting the effects of forest encroachment for *Sedum lanceolatum* and *Rhodiola integrifolia* at a subalpine ecotone. In Press, Alp. Bot. DOI:10.1007/s00035-015-0148-0.

ZOLLNER, P. A. & S. L. LIMA. 1999. Search strategies for landscape-level inter-patch movements. Ecology 80: 1019–1030.

Submitted for publication 11 June 2015; revised and accepted 11 September 2015.