Effect of landscape structure on the movement behaviour of a specialized goldenrod beetle, *Trirhabda borealis*

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Abstract: We hypothesize that the ability of an organism to move through a landscape is determined by the interaction between its movement behaviour and the landscape structure. In contrast, models predicting spatial distribution, local population stability, or metapopulation stability typically assume that movement ability is independent of landscape structure. These model predictions will be invalid if the assumption of constant movement ability is incorrect. To assess the influence of landscape structure on movement behaviour (and therefore movement ability), we tracked individual goldenrod beetles (*Trirhabda borealis*) through microlandscapes composed of three patch types (goldenrod, cut vegetation, and cut vegetation containing camouflage netting to a height of 50 cm) that differed in terms of available food resources and structural complexity. In goldenrod patches, beetles moved infrequently in brief bursts of slow meandering movements. In cut patches, beetles moved frequently in sustained bursts of slow directed movements. In netting patches, beetles moved frequently in brief bursts of fast meandering movements. Using mark–release experiments, we determined that *T. borealis* did not detect goldenrod from afar or respond to edge type. Since *T. borealis* movement behaviour differed between patch types, its movement ability must depend on landscape structure. If this general result applies to other species, it implies that predictions of local population and metapopulation responses to landscape alteration could be erroneous. Effects of landscape alteration on movement behaviour should be incorporated into models of population response to landscape alteration.

Résumé : Nous posons en hypothèse que la capacité d'un organisme de se déplacer dans un paysage est déterminée par l'interaction entre son comportement de déplacement et la structure du paysage. En revanche, les modèles qui prédisent la répartition dans l'espace, la stabilité des populations locales ou de la métapopulation assument ordinairement au départ que la capacité à se déplacer est indépendante de la structure du paysage. Les prédictions de ces modèles seront invalides si la capacité constante de se déplacer ne se réalise pas. Pour évaluer l'influence de la structure du paysage sur le comportement de déplacement (et, par conséquent, la capacité de se déplacer), nous avons suivi des coléoptères *Trirhabda borealis* dans des micro-paysages composés de trois types de parcelles de végétation (verge d'or, végétation coupée, végétation coupée contenant du grillage de camouflage jusqu'à 50 cm de hauteur), différant par leurs ressources alimentaires et par la complexité de leur structure. Dans les parcelles de verges d'or, les coléoptères se déplacent rarement, par séquences brèves de mouvements lents et sinueux. Dans les parcelles ou la végétation a été coupée, les insectes se déplacent fréquemment, par séquences brèves de mouvements lents et dirigés. Dans les parcelles avec grillage, les coléoptères se déplacent souvent, par séquences brèves de mouvements rapides et sinueux. Les expériences de marquage–lâchage indiquent que *T. borealis* ne détecte pas la verge d'or de loin et ne réagit pas au type de bordure. Puisque le comportement de déplacement de *T. borealis* diffère d'une parcelle à l'autre, sa capacité de déplacement doit donc dépendre de la structure du paysage. Si ce résultat général s'applique à d'autres espèces, cela veut dire que, dans les populations locales et dans la métapopulation, les prédictions des réactions à des modifications du paysage peuvent être erronées. Les effets de modifications du paysage sur le comportement de déplacement doivent donc être intégrés aux modèles de réactions des populations aux modifications du paysage.

[Traduit par la Rédaction]

Introduction

The ability of organisms to move within and through landscapes determines, at least in part, the spatial distribution of the population and the likelihood of moving between populations (Fahrig and Merriam 1994). Population distribution can have important ecological effects. Species interactions such as predation, parasitism, competition, and herbivory can be facilitated or impeded by aggregation of individuals within and movements between local habitat patches (Harri-

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son and Thomas 1991; Roland and Taylor 1997; Sakai and Noon 1997). In predator–prey systems, local population stability may depend on patch-to-patch movements (Huffaker 1958; Kareiva 1987). Furthermore, long-distance movements between isolated populations may be necessary to maintain a regional metapopulation (Hanski and Gilpin 1997). Predictions of local distributions within a habitat mosaic, local population dynamics, or persistence of a regional metapopulation all depend on understanding the movement ability of the species. Movement ability is often viewed strictly as an organism trait, uninfluenced by landscape structure (e.g., Buechner 1987; Liu et al. 1995; Lindenmayer and Possingham 1996; Schumaker 1996). We, along with others (Knaapen et al. 1992; Taylor et al. 1993; Wiens 1997), hypothesize that it may not be appropriate to view dispersal ability solely as an organism trait. Instead, the interaction between landscape structure and an organism's movement behaviour will dictate the organism's movement ability. This distinction is important when considering organisms in landscapes undergoing anthropogenic alteration. If dispersal ability depends on landscape structure, changing as the landscape changes, predictions of local distributions and their ecological consequences, and predictions of regional metapopulation persistence, will be invalid. The purpose of this paper is to test the idea that alteration of landscape structure affects movement behaviour (and therefore dispersal ability) of a particular organism.

Patch type can influence within-patch movement through three main mechanisms: (*i*) presence or absence of various resources, (*ii*) physical limitations placed on movement by the internal structural complexity of the patch, and (*iii*) risk of injury or death. Patches high in resources (primarily food) can elicit movement behaviour aimed at remaining in the desirable patch, and patches low in resources should have the opposite effect and elicit behaviour aimed at allowing quick movement through the undesirable patch (Jones 1977; Kareiva 1982; Zalucki and Kitching 1982; Root and Kareiva 1984; Lawrence 1988; Visser 1988; Wallin and Ekbom 1988; Odendaal et al. 1989; Charrier et al. 1997). Patches high in structural complexity (e.g., high number of stems per unit area or high plant complexity) might interfere with organism movements, and patches low in structural complexity should have the opposite effect and not interfere with organism movements (Yang 2000). Patches where there is a high risk of injury or death (e.g., high physiological stresses or high predation pressure) can demand movement behaviour aimed at minimizing risk (Rijnsdorp 1980; Taylor and Merriam 1995; Jonsen and Taylor 2000). In the case of predation, organisms may have to balance moving quickly through a high-risk area against being cautious enough (e.g., moving slowly, less frequently) to avoid being preyed upon (Zollner and Lima 1999). Patches may also influence movement outside their own borders. Distant patches, particularly resource patches, can influence movement behaviour. For example, many herbivorous insects use sensory cues to detect host plants from a distance (e.g., Moericke et al. 1975; Saxena and Saxena 1975; Smith 1976; McKibbin et al. 1977; Ralph 1977; Hamilton et al. 1978; Rausher 1981; Visser 1988; but for counter examples see Dethier 1959; Price 1976; Cappuccino and Kareiva 1985; Fahrig and Paloheimo 1987), and detection of distant resource patches can elicit movement

Fig. 1. The three patch types, goldenrod patches (*a*), cut patches with camouflage netting suspended to a height of 50 cm (*b*), and cut patches (*c*), arranged according to the food resources and structural complexity each represents for individual goldenrod beetles, *Trirhabda borealis*.
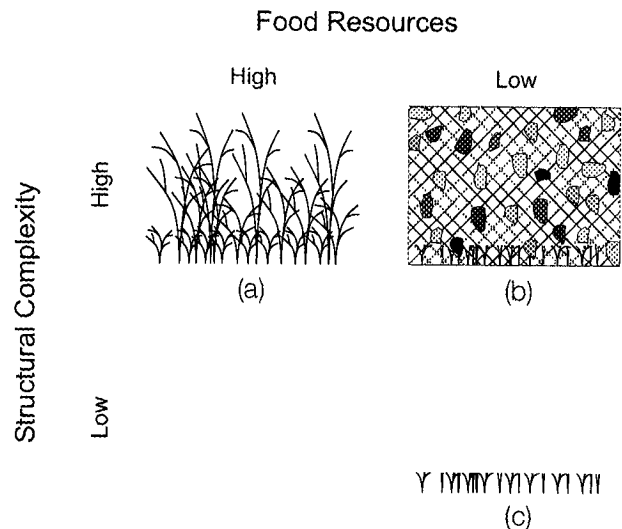
behaviour aimed at encountering the patch. Finally, patch edges may play a particularly important role in modifying movement in heterogeneous landscapes. To respond to an edge, an organism must detect the edge and decide which of the two neighbouring patches is desirable.

In this paper we report on a series of field experiments investigating the influence of different patch and edge types on the local movement behaviour of adult goldenrod beetles (*Trirhabda borealis*). *Trirhabda borealis* is a relatively large (length around 1 cm) native leaf-feeding goldenrod (*Solidago* spp.) specialist, occasionally feeding on asters (*Aster* spp.) during both the larval and adult life stages (Messina and Root 1980; Messina 1982*a*). *Trirhabda borealis* and a congeneric, *Trirhabda virgata*, often dominate the goldenrod herbivorous fauna in upper New York State (Messina and Root 1980; Root and Cappuccino 1992), and *T. borealis* was the dominant goldenrod herbivore at our study site (personal observation). Adults eclose in late June and then spend roughly 2 weeks in a preovipositional dispersal phase (Messina 1982*b*), during which long-distance flights (hundreds of metres) are common (Herzig 1995), until females become gravid, rendering them incapable of sustained flight. From this point on, movement in both sexes is primarily by walking (Messina 1982*b*), although they occasionally make short descending flights from the tops of plants (personal observation). Adults avoid predation by dropping from the plant into the litter and are also distasteful to vertebrates (Messina 1982*c*).

Movements were studied in microlandscapes (sensu Wiens and Milne 1989) containing three patch types (goldenrod, cut vegetation, and cut vegetation containing camouflage netting to a height of 50 cm) that differed in levels of food resources and structural complexity (Fig. 1). Goldenrod patches were relatively high in both food resources and structural complexity, owing to the stems and leaves of the plants. Netting patches had high structural complexity because of the suspended camouflage netting but low food resources because

of the lack of goldenrod plants. Finally, cut patches were low in both food resources (no goldenrod) and structural complexity (only stubble).

We predicted that *T. borealis* in goldenrod patches (high structural complexity, high food availability) would have a low propensity to move, and, when moving, individuals would move slowly (via short step-lengths) and trace out tortuous paths because of turning frequently. Beetles in the cut patches (low structural complexity, low food availability) would have a high propensity to move, and, when moving, individuals would move quickly (via long step-lengths) and trace out relatively straight paths because of turning infrequently. Finally, beetles in the netting patches (high structural complexity, low food availability) would have an intermediate propensity to move (owing to a conflict between the need for high mobility because of a lack of food and the physical constraint due to the structure of the camouflage netting) and, when moving, individuals would move more quickly than in goldenrod patches but not as quickly as in cut patches and would trace out somewhat tortuous paths (because of turning more frequently than in the cut patches but not turning as much as in goldenrod, since the individual needs to move through the netting patch to find food).

We also needed to consider any long-distance effects of goldenrod patches on movement behaviour. If *T. borealis* can detect goldenrod from afar, then neighbouring goldenrod patches might influence movement behaviour in non-goldenrod patches so that they move toward the goldenrod patch. We assessed the ability of *T. borealis* to detect goldenrod plants from a distance.

We also considered the influence of patch edges on movements of *T. borealis* across those edges. For *T. borealis* we predicted a high probability of moving into, and a low probability of moving out of, goldenrod patches. Since a goldenrod–cut edge has higher contrast, and is more conspicuous, than a goldenrod–netting edge, the probability of leaving a goldenrod patch for a cut patch should be lower than that of leaving a goldenrod patch for a netting patch. The converse should also hold; that is, there should be a higher probability of crossing from a cut patch into a goldenrod patch than of crossing from a netting patch into a goldenrod patch. Additionally, beetles might favour netting patches over cut patches, owing to the higher structural complexity used for predator defence, and have a higher probability of crossing from a cut patch into a netting patch than the reverse.

Methods

Field methods

Field experiments were performed in an abandoned farm field 6 km south of Ottawa, Ontario, Canada. The vegetation consisted primarily of goldenrod, grasses, purple vetch (*Vicia americana*), raspberries (*Rubus* spp.), and milkweed (*Asclepias syriaca*) with some scattered shrubs (primarily willows, *Salix* spp.) and young planted spruce (*Picea* spp.). Sixteen 5 by 5 m microlandscapes were constructed at four sites (four microlandscapes per site). Microlandscapes consisted of three patch types: (1) goldenrod (4% cover), (2) netting (10 or 30% cover), and (3) cut (remainder of landscape). In the cut patches, vegetation was kept to a height of 2 cm or less. The
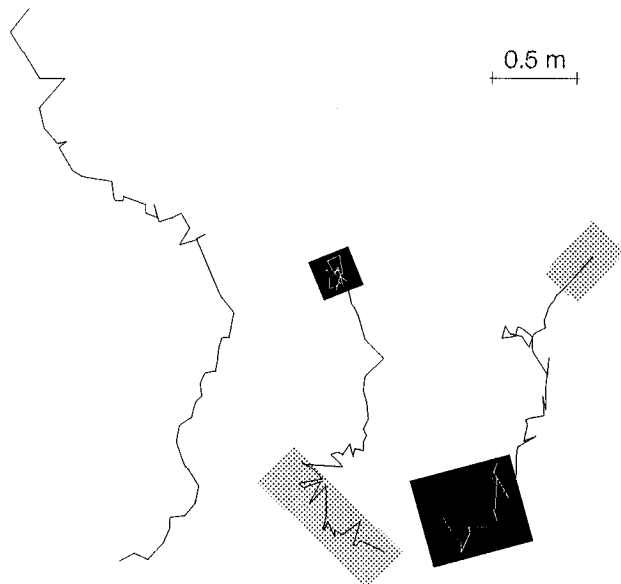
netting patches were essentially cut patches containing camouflage netting. Netting was strung so that the top of the netting was suspended approximately 50 cm above the ground. As the netting was 1–1.3 m wide, this created a vertical panel of suspended netting (emulating the structure of standing vegetation) with the rest of the netting piled on the ground (emulating the structure of plant litter and ground-cover vegetation). Each cluster of microlandscapes at a site was surrounded by 8 sticky traps (32 in all). Sticky traps were 1 m² in area and were mounted vertically with the bottom of the trap 2 m above the ground (Messina 1982*b*). Both faces of the trap (facing into and away from the cluster of microlandscapes) were sticky. Traps were monitored from July to September 1995 and checked every 2–3 days. Individual *T. borealis* were removed when captured and the traps were replaced when saturated with other insects. The sticky traps were no longer intercepting flying *T. borealis* individuals by the third week of July 1995, indicating the cessation of preovipositional dispersal flights (Messina 1982*b*).

We tracked individuals to determine their movement behaviour between 27 July and 6 September, 1995. Fifteen minutes to 2 h before observations began, we captured individual *T. borealis* from the surrounding vegetation using a sweep net. Beetles were held in a shaded container with fresh goldenrod leaves. Individuals were marked with a single dab of Liquid Paper on one elytron, ensuring that the elytra were not glued shut, which made it easier to spot the cryptically coloured beetles against the background vegetation. After preparation, individuals were released in a randomly assigned patch type and landscape and allowed to wander for 5 min, to allow any effects of handling on movement behaviour to diminish, and were then tracked either until they were lost or for 49.5 min. All tracking was performed between 10:00 a.m. and 4:00 p.m. on calm days. Movement trails were marked with numbered surveyor's flags, which were placed in the ground every 30 s. To avoid disturbing or herding the beetles the surveyor's flags were displaced 10 cm in a constant direction that minimized the chance of shadows cast by the tracker falling on and disturbing the beetle (Turchin et al. 1991). The coordinates of the resulting path were mapped using triangulation with a measuring tape from a fixed baseline of known length (Turchin et al. 1991). During tracking, the beetle's activity (walking, resting, flying, or feeding) and patch type were recorded. Over the tracking season, 30 individuals were captured, processed, and tracked.

In a separate set of experiments we used an L-shaped arena constructed of polypropylene sheet to assess the ability of individual *T. borealis* to detect goldenrod plants from a distance. One arm of the arena contained a potted goldenrod plant and the other arm was empty. Goldenrod plants were dug up from the surrounding field and consisted of 15–20 ramets, each between 1 and 1.5 m tall. The goldenrod plant was in a pot that was set flush with the ground at three different distances from the intersection of the two arms of the arena. Between 31 and 33 marked individuals were released in the intersection of the two arms of the arena, and once individuals had moved into one arm or the other, they were removed and scored as having moved toward or moved away from the goldenrod.

We also assessed the response of *T. borealis* to patch edges. We released between 22 and 30 marked individuals

Fig. 2. Typical movement trails of three individual *T. borealis*. All trails were traversed during 50 min of tracking and three patch types were traversed: goldenrod (solid area); camouflage netting (shaded area); and cut (open area). Note that the three trails are from different landscapes and have been arranged for clarity of presentation.

Fig. 3. Components of a *T. borealis* movement trail. The broken line represents the trail traced by the beetle. Open circles represent the points that were marked on the trail, with the numbers indicating how long the individual spent at that spot (the number of 30-s time steps). Thus, this path segment would consist of a bout of mobility that lasted for two time steps, a bout of immobility lasting nine time steps, and a bout of mobility lasting three time steps. The dotted line indicates how the turning angle (θ) is determined.
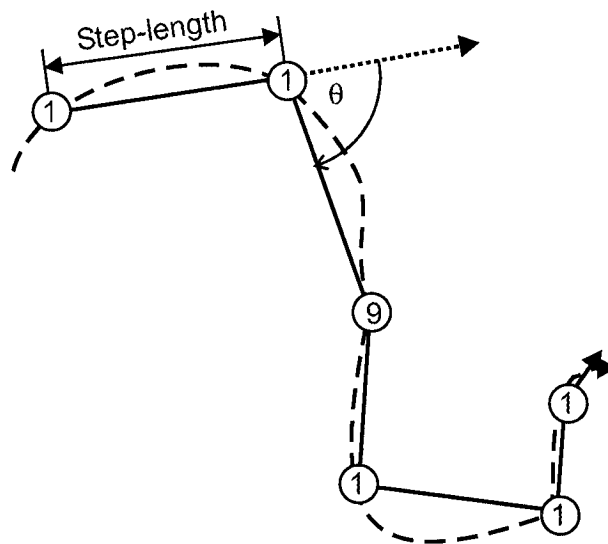
within a patch of one type but within 2 cm of an edge with another patch type and then allowed them to move freely. Once an individual had moved 10 cm away from the edge (either back into the original patch or into the neighbouring patch), it was recaptured and scored as having either crossed or not crossed the edge. This experiment was performed for all combinations of patch types.

Data analysis of movement trails

Our analysis of the tracking data had two goals: (1) to compare composite measures of movement ability in the three patch types, using path segments as the measure of replication, and (2) to summarize and compare distributions of movement parameters in the three patch types, using time steps as the unit of replication. Since some individuals crossed into different patch types during tracking (Fig. 2), it was necessary to break each individual trail into segments (of one or more steps) that were entirely in one of the three patch types before analyzing the influence of patch type on movement (Turchin 1998). Each movement trail comprised one or more path segments, each consisting of a series of coordinates describing the path of an individual beetle as it moved through a specific patch type. These path segments allowed us to determine composite measures of movement behaviour that could be compared across the three patch types: displacement (straight-line distance between start- and end-points of the path segment), duration, and displacement rate (displacement divided by duration). For the composite measures of movement, path segments were the level of replication. Patch comparisons were made using a Kruskal–Wallis test for a difference in medians due to the skewed nature of the data.

We described movement behaviour within each patch type in terms of the propensity to move (usually measured as the

probability of moving in a given, fixed amount of time, but see below), the step-length of a movement (measured as displacement per mobile time step), and the turning angle (the angle between the new direction of movement and the previous direction) (Kareiva and Shigesada 1983; Turchin et al. 1991). We found the probability of moving to be inappropriate for describing the propensity of *T. borealis* to move, owing to temporal autocorrelation (see Results). Instead, we used the duration of bouts of mobility (i.e., the number of consecutive time steps an individual displaced horizontally) and immobility (i.e., the number of consecutive time steps an individual was not detected to have displaced horizontally) as a measure of the propensity to move. The general approach to this analysis was to (*i*) test whether it was valid to pool the different path segments in the same patch type (i.e., individual path segments within a patch type were not significantly different) (Cain 1989), (*ii*) test whether the multiple data points composing each path segment were statistically independent to allow for correct statistical analysis (Turchin 1998), and (*iii*) describe the movement parameter.

We assessed whether path segments in the same patch type could be pooled by comparing the means and variances of the movement parameters (duration of bouts of mobility or immobility, step-length, turning angle; Fig. 3) for each path segment. For duration of bouts of mobility and immobility and step-lengths, means were compared using Scheffé's test and variances using Bartlett's test (Zar 1996). Turning angles are circular data and must be analyzed accordingly; for these, it was possible to compare the distributions directly using a nonparametric technique, the *r*-sample extension of the two-sample uniform scores test, estimating the significance of the test statistic using a randomization approach

(Fisher 1993). In the randomization, the observed turning angles were randomly assigned to path segments (maintaining the observed number of turning angles per path segment) and the test statistic was calculated. This procedure was repeated 1000 times, generating the distribution of the test statistic under the hypothesis of random assortment of turning angles (i.e., all path segments are the same). The test statistic from the actual data could then be compared with the randomly generated distribution to estimate p.

To check that the series of data points making up a path segment were statistically independent, we tested for temporal autocorrelation using a runs test for movement probabilities (Zar 1996) and examined the autocorrelation function (ACF) of the other movement parameters (Diggle 1990). Runs tests or ACFs had to be determined for each path segment separately. Since turning angles are circular data, turning-angle ACFs were determined following Fisher (1993). Temporal autocorrelations were calculated for time lags up to a quarter of the observations in a path segment to a maximum of 10. This restricted the construction of ACFs to path segments that were tracked for 4.5 min or longer to ensure a long enough time series for the lagged correlations to be meaningful. We then summarized the tests of temporal autocorrelation for a particular movement parameter across all the path segments in a patch type to ensure that all of the data points for a particular movement parameter were statistically independent. This was done by calculating either a weighted-mean normal deviate of the number of runs from the expected number of runs under randomness (runs tests) or a weighted-mean correlation coefficient at each time lag (ACF) using meta-analytic techniques (Rosenthal 1994).

With heterogeneity between path segments and temporal autocorrelation within segments ruled out, we quantified the different movement parameters. The distributions of duration of bouts of mobility and immobility were compared using a survival analysis, since some of the durations were censored; that is, we stopped timing them before the event was actually over, since it extended past the 49.5-min observation period. In such a case, a survival analysis allows all of the data to be used and accounts for the censored data (Fox 1993). Differences in step-length distributions in the different patch types were investigated using ANOVA on log-transformed step-lengths. Mean turning angles in each of the patch types were assessed using 95% confidence intervals (Batschelet 1981), and the fit of either a uniform or von Mises (unimodal) distribution was assessed using the appropriate tests described in Batschelet (1981).

Goodness-of-fit tests were used to evaluate the null hypothesis that individual *T. borealis* did not detect, and therefore move toward, goldenrod plants from a distance (i.e., a 50% chance of moving toward and away from goldenrod). Similarly, goodness-of-fit tests were used to test if *T. borealis* individuals crossed any of the patch edges more or less frequently than would be expected under the null hypothesis of no response to the edge (i.e., a 50% chance of crossing and not crossing the edge).

Results

We caught and followed 30 beetles. Only 3 of the 30 beetles were lost during tracking; they were tracked for 33.5,

36, and 36.5 min. Despite the release of equal numbers of individuals in each of the three patch types, the patch types within which the beetles were first tracked were not completely equal (37% in goldenrod, 30% in netting, and 33% in cut). Also, the beetles spent more time in some patch types than in others (43% of all time steps in goldenrod, 18% in netting, and 39% in cut). During tracking, individuals spent most of their time resting (approximately 70% of the time across all patches; Table 1). Feeding behaviour was only observed in 3.8% of time steps (8.8% in goldenrod). When individuals were moving, flying was rare (flying was observed in only 3% of all nonresting time steps; Table 1). Only 74% of the walking and flying time steps resulted in detectable horizontal displacement, indicating that not all movements were treated as a mobile time step.

The 30 trails were subdivided into 47 path segments, each occurring in a single patch type. The duration of the path segments was highly skewed and, based on a Kruskal–Wallis test for a difference in medians, was significantly different among patch types ($\chi^2_{[2]} = 10.3, p = 0.0058$), primarily because of shorter periods spent in the netting patches (Fig. 4b). Measured displacements (straight-line distance between start- and end-points of the path segment) were marginally different between patch types ($\chi^2_{[2]} = 4.86, p = 0.088$), primarily because of shorter displacements in goldenrod patches (Fig. 4a). Combining the two measures into a displacement rate indicated no difference among the patch types ($\chi^2_{[2]} = 2.783, p = 0.2486$; Fig. 4c).

Duration of bouts of mobility and immobility

For many of the path segments, runs tests (Zar 1996) revealed that mobile and immobile time steps were nonrandomly ordered. Furthermore, combining the results of the runs tests for all the path segments within the cut and netting patches indicated that in general, mobile and immobile time steps were significantly nonrandomly ordered (weighted-mean normal deviate ± 95% confidence interval: cut, 3.40 ± 0.06; netting, 2.31 ± 0.09). This temporal autocorrelation in mobile and immobile time steps indicates that the probability of moving in a time step was inappropriate for summarizing the propensity of an individual to move. Instead, we investigated the duration of bouts of mobility or immobility.

Within each patch type, mean duration for bouts of both mobility and immobility was not significantly different among path segments (Scheffé's post-hoc comparisons). Variability in the duration of bouts of both mobility and immobility was significantly different among path segments in cut patches (Bartlett's tests: $B_c = 36.6$ (where B_c has a χ^2 distribution (Zar 1996)), df = 13, $p = 0.0005$, and $B_c = 35.1$, df = 17, $p = 0.0006$, for mobility and immobility, respectively). For the other patch types, variability in the duration of bouts of mobility (goldenrod: $B_c = 13.1$, df = 9, $p = 0.16$; netting: $B_c = 14.4$, df = 11, $p = 0.21$) or immobility (goldenrod: $B_c = 9.88$, df = 11, $p = 0.54$; netting: $B_c = 15.2$, df = 12, $p = 0.23$) was not significantly different. There was no evidence of temporal autocorrelation in the duration of bouts of either mobility or immobility in any of the patch types (all 95% confidence intervals around weighted-mean temporal autocorrelation at all time lags contained 0). In all patch types, individual *T. borealis* persisted in bouts of immobility longer than in bouts of mobility (Fig. 5). Based on a survival analysis,

Table 1. Summary of observed *T. borealis* activity for all 30 individuals, shown as the number of 30-s time steps in which an activity was observed, for separate patch types and for all observations combined.

Patch type	Resting	Flying	Walking	Displacement	Eating
Goldenrod	1000 (80.8)	17 (1.4)	220 (17.8)	131 (10.6)	109 (8.8)
Netting	314 (60.4)	3 (0.6)	203 (39.0)	133 (25.6)	na
Cut	703 (62.3)	3 (0.3)	422 (37.4)	381 (33.8)	na
All patches	2017 (69.9)	23 (0.8)	845 (29.3)	645 (22.4)	109 (3.8)

Note: Each time step was scored as being predominantly resting, flying, or walking. The detection of horizontal displacement and the number of time steps during which eating was observed are also tabulated. Values in parentheses are percentages; na, not applicable.

there were significant differences in the duration of bouts of both mobility and immobility among the different patch types (mobile: $\chi^2_{[2]} = 7.65$, $p = 0.025$; immobile: $\chi^2_{[2]} = 25.5$, $p < 0.0001$). Bouts of mobility lasted longer in cut patches than in the other two patch types, while bouts of immobility lasted longer in goldenrod patches than in the other two patch types.

Step-lengths

Within each patch type, mean step-lengths were not significantly different among path segments (Scheffé's post-hoc comparisons on log-transformed data). For both the goldenrod and cut patches, variances of log-transformed step-lengths were not significantly different among path segments (goldenrod: $B_c = 8.50$, df = 11, $p = 0.81$; cut: $B_c = 16.9$, df = 18, $p = 0.53$). The variances of step-lengths in the netting patches were significantly different among path segments ($B_c = 29.5$, df = 14, $p = 0.009$), but removal of three path segments with extremely low variances left the remaining path segments indistinguishable ($B_c = 9.55$, df = 11, $p = 0.57$). For all patch types and all time lags, except for a time lag of 2 min in the cut patch, the weighted-mean temporal autocorrelations for step-lengths were not significant (all 95% confidence intervals contained 0). Step-lengths were highly skewed in all three patch types (Fig. 6), and mean step-lengths were significantly different (ANOVA on log-transformed step-lengths: $F_{[2,632]} = 8.55$, $p = 0.0001$, $n = 635$). Surprisingly, step-lengths in the cut patch were significantly shorter than in the netting patches, and step-lengths in the goldenrod patches were indistinguishable from those in the other two patch types.

Turning angles

In cut patches, turning-angle distributions differed significantly among path segments ($W_r = 62.0$, $p = 0.001$, based on a randomization test with 1000 draws), but removal of two straighter path segments removed this effect ($W_r = 40.8$, $p = 0.115$). In goldenrod patches, turning-angle distributions differed significantly among path segments ($W_r = 43.1$, $p = 0.004$), but removal of a straighter path segment removed this effect ($W_r = 18.1$, $p = 0.841$). In netting patches there were no significant differences in turning-angle distributions among path segments ($W_r = 38.0$, $p = 0.085$). For all patch types and all time lags, the weighted-mean temporal autocorrelations for turning angles were not significant (all 95% confidence intervals contained 0). For all patch types, the mean turning angle was not significantly different from 0°, based on 95% confidence intervals, indicating that the

Fig. 4. Box–whisker plots of path-segment displacements (*a*), duration of path segments (*b*), and path-segment displacement rates (*c*) in the three different patch types: cut (*n* = 18), goldenrod (*n* = 17), and netting (*n* = 12). Whiskers indicate the ranges, boxes indicate the interquartile ranges, and horizontal lines indicate the median values.
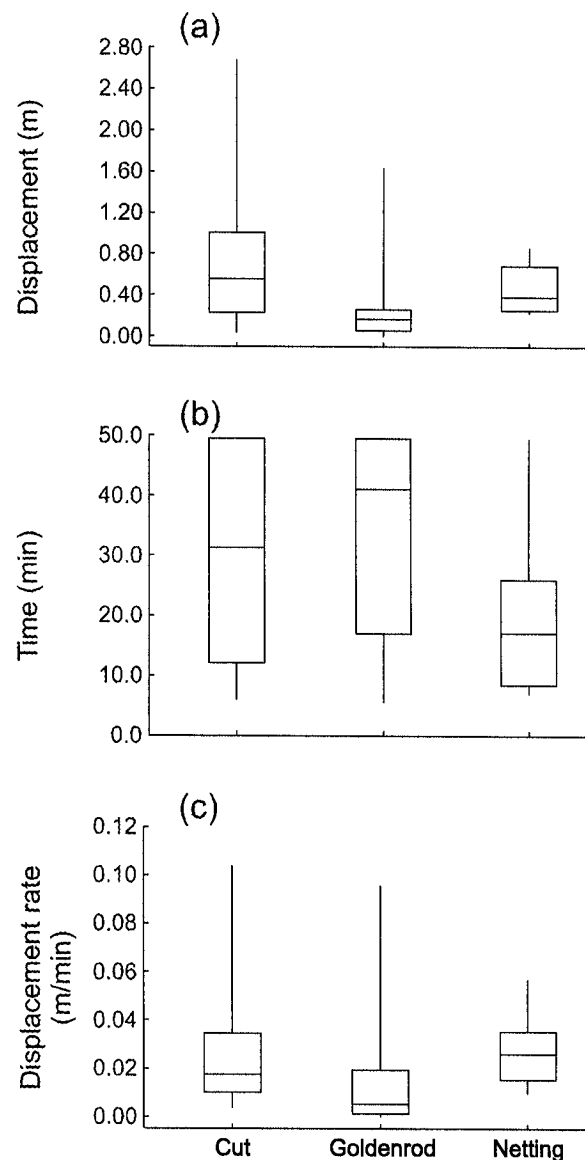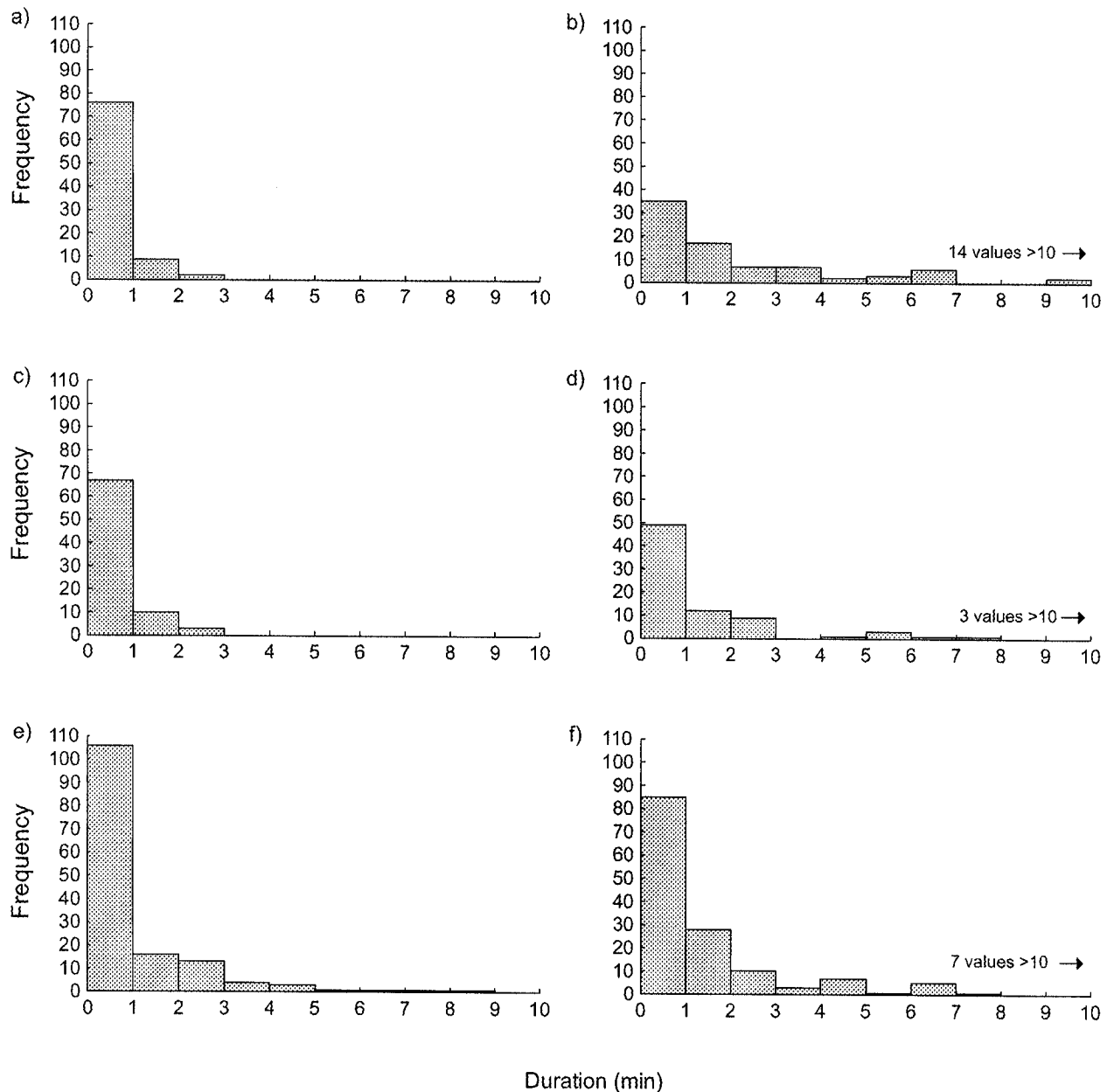
Fig. 5. Distributions of the durations of either bouts of mobility (left-hand panels) or bouts of immobility (right-hand panels) for *T. borealis* in goldenrod (*a* and *b*), netting (*c* and *d*), and cut patches (*e* and *f*).


Duration (min)

beetles did not favour either left or right turns. Turning angles in the goldenrod patches were uniformly distributed both with ($V = 1.06, p > 0.15$; Fig. 7) and without ($V = 1.45, p > 0.15$; Fig. 7) the path segment that was different from the rest. Turning angles in the netting patch were also uniformly distributed ($V = 1.53, p > 0.15$; Fig. 7). Turning angles in the cut patch were not uniformly distributed ($V = 3.05, p < 0.01$, for all path segments and $V = 2.09, p < 0.01$, with the two different path segments removed) but were described by a von Mises distribution with a mean turning angle of 0° ($K = 0.42, U^2 = 0.04, 0.25 < p \leq 0.5$ for all path segments and $K = 0.25, U^2 = 0.12, 0.05 < p \leq 0.1$ with the two different

path segments removed; Fig. 7). A von Mises distribution is unimodal (Batschelet 1981; Fisher 1993), so this indicates that the turning angles in the cut patches were concentrated in the forward direction, which would produce more directed, less tortuous movement than a uniform distribution.

Detection of goldenrod from afar and edge-crossing behaviour

We did not detect a response of *T. borealis* to distant goldenrod plants. The only significant response to the goldenrod plant during the releases in the arena occurred at 0.5 m and was away from the goldenrod (Table 2). Also, we did not

Fig. 6. Distributions of observed step-lengths for *T. borealis* in goldenrod (*a*), netting (*b*), and cut patches (*c*).
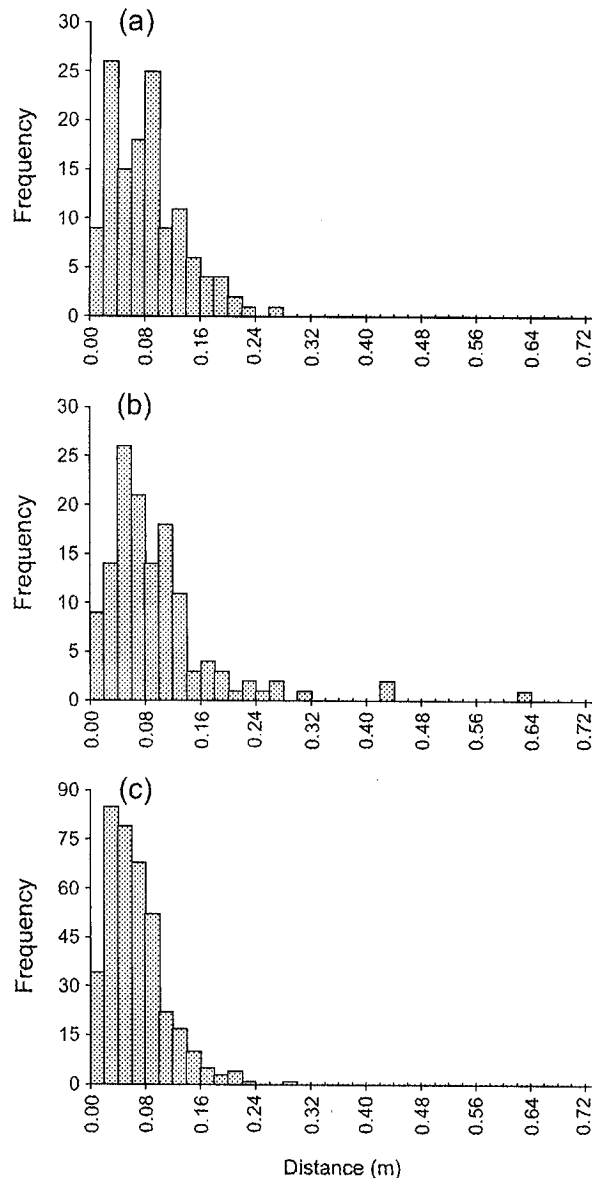
detect *T. borealis* responses to edges. There were no significant differences between the number of individuals moving into the neighbouring patch and the number remaining in the original patch (Table 3).

Discussion

A typical individual *T. borealis* in a goldenrod patch hardly moves, and when it does, movements are brief, relatively slow, and meandering (Fig. 2). The long bouts of immobility could be due to time spent feeding or processing a meal. However, feeding was only observed during 10% of the immobile time steps (*n* = 1106) and seems unlikely to have been solely responsible for the duration of the bouts of immobility in goldenrod. Another possibility is an adaptive

response to decrease the amount of movement in order to remain in the food-plant patch. The tortuous paths in the goldenrod patches will also tend to maintain contact with the food patch. In some predatory (Kareiva and Odell 1987) and herbivorous (Root and Kareiva 1984; Visser 1988) insects, frequent turning maintains contact with resources.

A typical individual *T. borealis* in a cut patch sustains relatively slow, directed movements (Fig. 2). The sustained bouts of mobility seem to be an attempt to move out of the cut patch; without food on hand, the beetles cannot afford to sit still. Tracing straight paths also seems to be a good strategy for crossing an adverse patch quickly. We expected *T. borealis* to move quickly (long step-lengths) in the cut patch. Other species do this in response to nonhost plants (Bach 1980; Turchin 1987; Elmstrom et al. 1988), predators, or unfavourable locations (Rijnsdorp 1980; Taylor and Merriam 1995; Charrier et al. 1997). But for *T. borealis*, step-lengths were significantly shorter in the cut patches. This apparent inconsistency may have been in response to the risk, or perceived risk, of predation. *Trirhabda borealis* evade predation by dropping off the plants into the litter, where they are camouflaged (Messina 1982*c*). Since cut patches lack vertical structure from which to drop, individual *T. borealis* may face an increased risk of predation. Without their natural defence system in place, individuals may move slowly and cautiously, both to avoid detection and to allow them to detect predators early (Zollner and Lima 1999). However, this explanation is highly speculative, as we have only observed a single predation event, when a beetle wandered onto a spider web. Most of the natural enemies of *T. borealis* prey upon the larvae, and adults are known to be distasteful to vertebrates (Messina 1982*c*).

A typical individual *T. borealis* in a netting patch has many brief bursts of fast meandering movements (Fig. 2). Bouts of mobility were similar in duration in netting and goldenrod patches, suggesting that the absence of food does not necessarily cause individuals to sustain longer bouts of mobility. However, bouts of immobility were shorter in the netting patches than in the goldenrod patches, suggesting that the beetles may respond to a lack of food by spending less time not moving. Furthermore, the structural complexity of both the netting and goldenrod patches could play an important role in limiting the duration of bouts of mobility by interfering with horizontal displacement. If beetles were spending much of their movement time moving up and down structures, some of the time steps would result in no detectable displacement. These no-displacement time steps would break up the run of mobile time steps, thereby shortening the bouts of mobility. In fact in many time steps the beetles were observed to be actively walking but were only moving up and down stems (10% of immobile time steps in goldenrod) or strands of camouflage netting (19% of immobile time steps in netting). Netting patches caused beetles to trace tortuous paths by inducing more frequent turning with more extreme turn angles. Since we also saw this behaviour in goldenrod patches, this suggests that the proximate cause of increased turning is actually the structural complexity of a patch. The structural complexity of the netting patches could also be thought of as a resource, since *T. borealis* require the vertical structure for their antipredator defences. This could

Fig. 7. Turning-angle distributions for *T. borealis* in goldenrod (*a*), goldenrod but with the significantly straighter path segment removed (*b*), netting (*c*), cut (*d*), and cut but with the two significantly straighter path segments removed (*e*) (see the text). The solid lines are fitted distributions (either uniform or von Mises). The forward direction is indicated by 0°. These are wrapped distributions and we have shown two full revolutions (as suggested by Fisher 1993), so each histogram represents twice the sample size.
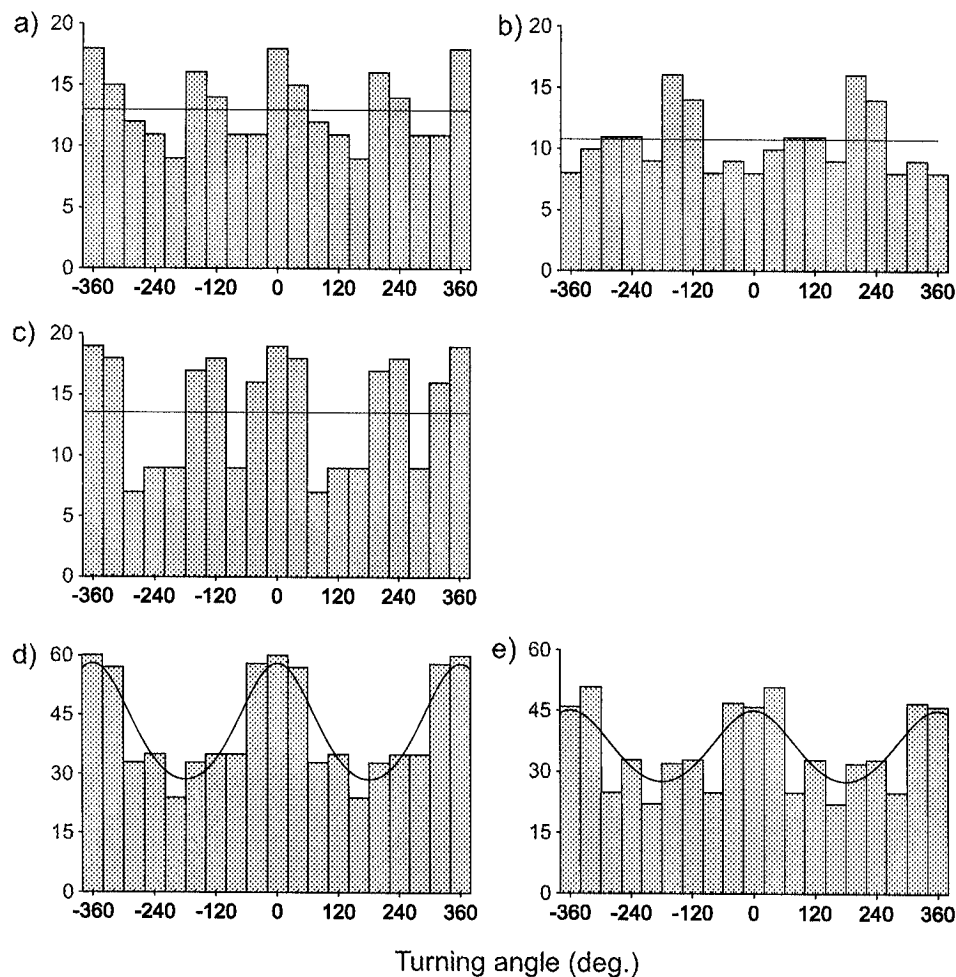

Turning angle (deg.)

Table 2. Numbers of individual *T. borealis* that were released at three different distances and either detected or did not detect a goldenrod plant.

Distance (m)	No. released	Detected plant	Did not detect plant	χ^2	p
0.05	31	15	16	0.032	0.858
0.50	33	10	23	5.121	0.024
1.00	33	17	16	0.030	0.863

Note: Chi-squared values and their associated p values were calculated for the null hypothesis that the beetles did not detect the goldenrod from a distance.

Table 3. Numbers of *T. borealis* released that either remained in the release patch or crossed an edge into a different patch.

From patch type	Into patch type	No. released	No. remaining	No. crossing	χ^2	p
G	N	24	14	10	1.08	0.30
	C	26	16	10	1.39	0.24
N	G	22	10	12	0.18	0.67
	C	30	12	18	1.20	0.27
C	G	29	11	18	1.69	0.19
	N	25	10	15	1.00	0.32

Note: G, goldenrod; N, netting; C, cut. Chi-squared values and their associated p values were calculated for the null hypothesis that the beetles did not respond to the edge.

explain why beetles moved more quickly (longer step-length) through the netting patches: they perceived a lower risk of predation yet needed to move to find food.

Netting patches are low in food availability, like the cut patches, yet high in structural complexity, like the goldenrod patches, allowing us to tease apart whether *T. borealis* movement behaviour was a response to the food or to the structure

in a goldenrod patch. Movement in netting patches produced long displacements similar to those in the cut patches, suggesting that long overall displacements are a response to lack of food. Netting patches were also unique in terms of

path segments having shorter durations, indicating that beetles were leaving netting patches more quickly than either the goldenrod or the cut patches. This was due to the longer displacements moving individuals out of the netting patches more quickly than out of the goldenrod patches. Such long displacements in the cut patches did not reduce the duration of path segments because the cut patches were dominant in the microlandscapes, making it more difficult to move out of a cut patch. Despite displacements being similar to those in cut patches, movement behaviour in the netting patches was more similar to that in the goldenrod patches than to that in the cut patches, except that bouts of immobility were shorter in netting patches than in goldenrod patches. This suggests that almost all of the movement behaviour observed in goldenrod patches was in response to the structural complexity of the patch, not to the presence of a food resource, since the same behaviour was observed in the netting patches, which had structure but no food. The one exception, duration of bouts of immobility, which were longer in goldenrod patches and shorter in netting patches, seemed to be a response to the presence/absence of food.

Some other herbivorous insects can detect their host plant from afar (e.g., Moericke et al. 1975; Saxena and Saxena 1975; Smith 1976; McKibbin et al. 1977; Ralph 1977; Hamilton et al. 1978; Rausher 1981; Visser 1988) and (or) respond to patch edges in such a way as to remain on host plants or in host-plant patches (Jones 1977; Lawrence 1982). We did not observe these responses in *T. borealis* individuals. In fact, the beetles seemed oblivious to nearby goldenrod patches and patch edges. There is probably only strong selection to remain in a host-plant patch for species that are either relatively sedentary, and thus unlikely to move into another host-plant patch after leaving a patch (e.g., Dethier 1959), or historically associated with a rare, and therefore difficult to find, plant species (e.g., Tabashnik 1980; Lawrence 1982). Since goldenrod patches are locally common, there is no need for the beetles to either remain in or quickly move into a goldenrod patch, as the chances of running into another one are good. Also, despite having a reduced ability to move after preovipositional dispersal flights, *T. borealis* are still vagile enough to move easily between goldenrod patches within a field.

These results demonstrate that patch type influences *T. borealis* movement behaviour. This suggests that for *T. borealis*, and most likely for other organisms, dispersal ability is not a constant species trait but depends on landscape structure. Therefore, attempts to predict population responses to landscape change that do not link dispersal ability and landscape structure will lead to erroneous conclusions, with potentially disastrous results for the population. To make population predictions that link dispersal ability and landscape structure will require knowledge about differences in movement behaviour in different patch types in a landscape. We suggest that modelling approaches to predicting population responses to landscape change should use landscape connectivity in place of dispersal ability. Landscape connectivity is the landscape property that results from the interaction between landscape structure and movement behaviour (Merriam 1984) and is "the degree to which the landscape facilitates or impedes movement among resource patches"

(Taylor et al. 1993). As long as the measure of landscape connectivity accurately reflects the impact of landscape structure on movement behaviour, then models incorporating landscape connectivity instead of organism dispersal ability should be better able to predict population responses to landscape change.

Acknowledgements

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