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ORIGINAL PAPER

Modeling caterpillar movement to guide habitat enhancement for *Speyeria zerene hippolyta*, the Oregon silverspot butterfly

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Abstract Studies of at-risk species are likely to have greater conservation impact if they: involve managers in question formulation, set specific management or restoration goals, and are based on detailed knowledge of species' resource needs. These ideas guided our investigation of the foraging behavior of larvae of a US federally threatened butterfly, the Oregon silverspot (*Speyeria zerene hippolyta*), with the goal of making management recommendations for habitat restoration. *S. z. hippolyta* larvae feed exclusively on *Viola adunca* and must consume multiple individuals to pupate successfully. Larvae forage at random through meadow vegetation to locate host plants. Observations of larvae foraging under field conditions revealed that larger, older larvae move more rapidly and turn less acutely than smaller, younger larvae; the consequence of these developmental differences is that younger larvae tend to remain in one place while older larvae tend to range more widely, presumably in search of new host plants. Results from a simulation model initialized with these data suggested that a host plant density of at least four *V. adunca* plants/m^2 (depending on predation intensity to which larvae are exposed) is required in order for 4th instar larvae to have a 10 % chance of survival to pupation. These findings are being used to guide a violet restoration program for this sensitive species.

Keywords Caterpillar · Conservation · Habitat management · Host-finding · Lepidoptera · Restoration

Introduction

The last 20 years have seen an explosion of studies of the relationships between habitat spatial structure and animal species occurrence, abundance, and diversity, driven in large part by the well-documented connection between human-caused landscape alteration and the decline of biodiversity (Andren 1994; Laurance et al. 2002; Fahrig 2003; Lindenmayer and Fischer 2006). However, these studies have not always had as great an impact on the management of sensitive species and habitats as we might wish (Milner-Gulland et al. 2009; Arlettaz et al. 2010; Cabin et al. 2010; Milner-Gulland et al. 2012). There are many reasons for the variable impact of conservation-oriented research. First, for a study to usefully guide conservation practice, it is important to ask the right questions. Here, collaboration between scientists and land managers can promote studies that are both rigorously-designed and that answer questions that are relevant to management (Campbell 2007; Milner-Gulland et al. 2012; Thorpe and Stanley 2011). Secondly, in the case of habitat restoration or improvement, goal-setting is key to determining the success of a project (Oates 1995; Miller and Hobbs 2007). However, identifying habitat improvement goals can be difficult, because detailed information about a site's historical state is often unavailable (Thorpe and Stanley 2011). Finally, basic information about how organisms use/respond to habitat elements is often lacking (New et al. 1995; Pollard and Eversham 1995; Miller and Hobbs 2007; New 2007; Settele and Kühn 2009; Thomas et al. 2009; Henry and Schultz 2013), making it difficult to know what specific aspects of the habitat to restore or manage.

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We have tried to address all three of these criteria in this study of *Speyeria zerene hippolyta* (W.H. Edwards 1879), the Oregon silverspot butterfly. This USA federally-threatened Nymphalid species is considered a "representative case study" of butterfly conservation efforts in North America (New et al. 1995). It is found in saltspray meadows along the Pacific Northwest coast, where larvae feed exclusively on *Viola adunca*, the common blue violet. These meadows, which are highly threatened by agriculture and development (New et al. 1995), represent a relatively short-lived stage in the successional sequence leading to coastal forest. *S. z. hippolyta,* thought to have once ranged widely along the coast of Oregon, southern Washington, and northern California USA (U. S. Fish and Wildlife Service 2001), is currently restricted to five small populations (U. S. Fish and Wildlife Service 2001; Crone et al. 2007). Our study took place at Cascade Head, along the Oregon coast, a preserve owned and managed by The Nature Conservancy, where one of the extant populations of *S. z. hippolyta* is found.

There is increasing recognition that the quality of the larval habitat is one of the most important factors determining long-term dynamics of many butterfly populations (Thomas et al. 2011). Larval habitat quality might be expected to be particularly important for *S. z. hippolyta*, which overwinter as first instar larvae and begin foraging for host plants as *V. adunca* emerge in the spring (U. S. Fish and Wildlife Service 2001). Over the several months that elapse between emergence and pupation, larvae progress through six instars and increase their weight by three orders of magnitude (Bierzychudek, unpublished data). To accomplish this growth, a larva must locate and consume multiple host individuals (Bierzychudek, unpublished data).

Silverspot larvae lack the ability to orient toward a distant host (Bierzychudek et al. 2009). Foraging larvae move randomly through their habitat while searching for new hosts; to distinguish a host plant from non-host species, *S. z. hippolyta* larvae must physically contact the plant (Bierzychudek et al. 2009). This search strategy likely evolved under conditions of relatively high host density. However, at Cascade Head, the density of the silverspot's host plant, *V. adunca*, has declined dramatically over the last 20 years (P. Bierzychudek, unpublished data), in concert with both successional change and invasion of the habitat by non-native grasses (U. S. Fish and Wildlife Service 2001). Its search strategy may no longer be optimal under these changed conditions.

Active habitat management for the silverspot, which has been taking place since 1990, has concentrated on reversing observed declines in larval habitat quality (New et al. 1995). Early efforts were focused on restoring the early-successional character of the habitat through interventions like controlled burning (New et al. 1995; Opler 1995). More recently, managers have turned their attention to direct enhancement of the density of *Viola adunca*. The objective of our study was to determine the optimal density and spatial distribution of host plants for these habitat enhancement efforts.

To answer this question we developed a simulation model of individual larvae moving through landscapes with varying host plant densities and spatial distributions. To parameterize the model we used data from field observations of larval movement. The model predicted how larval host finding success might vary under these different conditions, and allowed us to explore scenarios that would not have been feasible to observe in the field. We used our findings to provide information to managers to guide the design of a program to enhance *V. adunca* density.

Methods

Field observations of larval movement

To parameterize the larval movement model, we conducted larval foraging trials where we observed and quantified how hungry larvae of each instar moved through the environment at Cascade Head. We obtained diapausing first instar larvae from 11 half-sibships of *S. z. hippolyta* from the Oregon Zoo's captive rearing program and reared them in the laboratory, feeding them as needed on shade house-raised violets, regulating the temperature to keep their development rates synchronized with wild larvae. When larvae reached appropriate developmental stages for observations, we transported them to Cascade Head. We withheld food for at least 24 h before each trial, but kept larvae hydrated. To better observe the black larvae against the soil surface, we dusted them with pink fluorescent powder (T1-MG6618, Day-Glo Color, Cleveland, OH, USA). This dust has no effect on survival or development of larval Lepidoptera (Warner and Bierzychudek 2009), and no evident effects on their movement (unpublished observations).

For our observations at Cascade Head, we created eight observation arenas of ~1–2 m diameter. We used areas without host plants so our trials would not be cut short by larvae finding plants. We trimmed the vegetation (grasses and forbs) to a height of 7–10 cm and removed the clippings to facilitate seeing the larvae as they walked along the soil surface and over and under plant leaves. Because larvae spent virtually all of their time close to the ground surface, rarely moved vertically, and never reached the tips of the clipped vegetation, it is unlikely that shortening stems affected larval movement rates. Observations took place in mid-summer, between 1,000 and 1,700 h, when soil surface temperatures were between 14 and 37 °C. We shaded the arenas as needed to shield larvae from excessive sun that might have caused overheating; the shade thus created was similar to typical conditions in this foggy coastal grassland. Larvae within 24 h of molting were not used, as these individuals did not feed.

To quantify the movement of fifth and sixth instar larvae, we placed a larva in the center of an arena. When it began to move, we marked its location at 30-s intervals with plastic pins, taking care not to influence its behavior. We followed each larva for at least 30 timesteps (15 min). At the end of each trial, we photographed the pattern formed by the pins, including a ruler for scale and a compass bearing for reference. We performed 21 trials using 14 fifth instar larvae and 19 trials using 14 sixth instars.

Smaller larvae covered much less distance. To quantify their movements, we first photographed each arena from directly overhead and enlarged the photos. Each photo included a ruler and a compass bearing. On enlarged photos, we could recognize individual plants and other landmarks. For each trial, we placed a larva into the center of the arena and followed it as it searched, marking its location on the photo at regular intervals of either 30 s (for fourth instars) or 60 s (for second and third instars). Each trial lasted 30 timesteps or until a larva walked out of the photographed area. We performed 22 trials with 13 fourth instar larvae, 21 trials with 16 third instar larvae, and 19 trials with 14 s instar larvae.

Ants sometimes found larvae and bit them; we ended these trials to prevent further damage to this protected species. During a few trials, larvae were dragged underground by folding-door spiders (*Antrodiaetus* sp.). We recorded the frequency of all these attacks.

Data analysis

On the photographs, we connected the larval locations at successive timesteps with straight line segments, and decomposed these paths into their component move lengths (distance between successive positions) and turn angles (angle between the most recent move and the prior move) (Turchin et al. 1991; Turchin 1998). To avoid biasing the pool of observations with data from individual larvae that were observed for longer periods than others, we truncated the data sets for some trials so that each individual contributed the same number of observations (Wiens et al. 1993). After testing for autocorrelation (see "model validation"), we fit the move length observations for each instar to a lognormal distribution (which provided a better fit than other alternatives) and generated maximum likelihood estimates of μ and σ for each instar for use in the model. We assessed whether distributions of turn angles for each instar fit a von Mises distribution (also called the circular normal distribution) using Watson's goodness-of-fit test from the R package 'CircStats' (Lund and Agostinelli 2009). A von Mises distribution is characterized by a central tendency, μ (analogous to the mean of a normal distribution), and a measure of concentration, κ. We generated maximum likelihood estimates of these parameters for each instar.

We calculated the probability that a larva would experience predation by dividing the observed instances of attacks by ants or spiders ($n = 17$) by the number of observed moves ($n = 5{,}346$). We applied the same predation probability to all instars.

Model construction and parameterization

Our simulation of larval movement was based on the simple correlated random walk approach first applied to the movement of insects by Kareiva and Shigesada (1983) and subsequently elaborated by many others (e.g. Cain 1985; Crist et al. 1992; Turchin 1998; Goodwin and Fahrig 2002; Potting et al. 2005; Chapman et al. 2007; Heisswolf et al. 2007; Roslin et al. 2008). Modeling was simplified by the fact that the presence of food plants does not induce a bias in the movement of searching larvae (Bierzychudek et al. 2009). We constructed the model in MatLab [www.mathworks.com], using the statistics and image processing toolboxes. In the model, an individual larva was placed into a two-dimensional "patch" of individual host plants embedded in a matrix of non-host vegetation, and moved within this environment using rules described below. We recorded whether each larva (a) found enough hosts, soon enough, to develop to a pupa; (b) starved or was killed by a predator before pupating; or (c) wandered out of the host plant patch. In successive model runs we varied the density and spatial distribution of host plants. Details of model construction follow.

In the model, each pixel-sized cell represented a square of 4 cm diameter, the average size of a violet. The movement of model larvae was tracked to the nearest mm. Model larvae were allowed to move within a square habitat patch of 25 m diameter, the approximate size of suitable habitat patches at Cascade Head; this area contained cells representing violets as well as non-host cells. The patch was surrounded by a 10 m wide buffer without violets, and then by an absorbing edge. Cascade Head contains large expanses of habitat lacking violets.

Each model run began with a larva being placed on a violet (females typically lay their eggs near a violet) and consuming it. This violet was randomly chosen from those within 5 m of the patch's center. One violet plant typically provides enough biomass to support the development of a larva from hatching through its third instar (Bierzychudek,

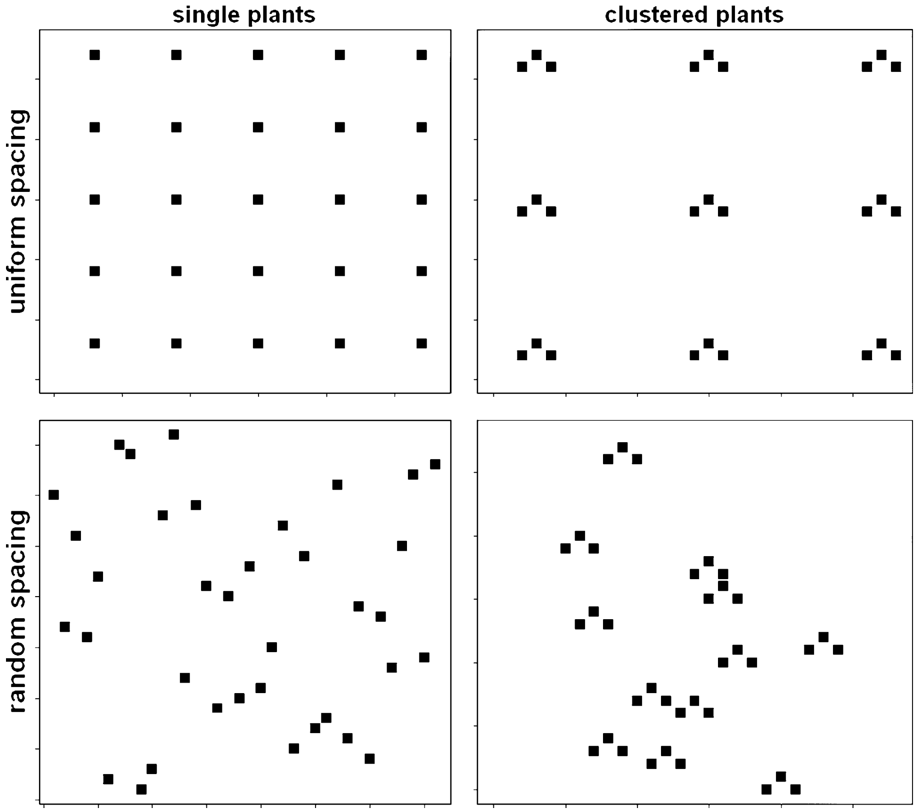

Fig. 1 The four spatial patterns of violets used in the simulation model. *Each black cell* represents a single host plant; white areas lack violets. Actual distances between *black cells* depended on the violet density used in a particular model run

unpublished results); field and greenhouse observations indicate that once larvae locate a violet, they typically shelter nearby until they have consumed it. We assumed that larvae were in the fourth instar when they began searching for additional plants.

Each timestep represented 30 s. For each successive timestep of a larval search, we applied a predation probability; predation ended the model run. If the larva survived, a move length and a turn angle were drawn from the instar-specific distributions of these parameters (see Data analysis). If the move brought a larva to a new violet, it consumed the violet; otherwise, it continued to search. Because larvae cannot detect the presence of a host from even a few cm away (Bierzychudek et al. 2009), the model required a larva to contact the pixel representing a violet before perceiving its presence.

In the model, we required a fourth instar larva to consume one violet in order to develop into a fifth instar, a fifth instar larva to consume two violets to become a sixth instar, and a sixth instar larva to consume eight violets to reach pupation. These values were based on the leaf numbers typically consumed by lab-reared larvae of these instars (for 5th instar larvae, $\bar{x}$ leaves = 12.3 ± 3.3, n = 18; for 6th instar larvae, $\bar{x}$ leaves = 82.7 ± 17.1, n = 19) and a mean violet size of 10 leaves plant^{-1} (P. Bierzychudek, unpublished data). The numbers of timesteps spent in each instar varied with food availability. As each violet was consumed, it was removed from the model environment.

We explored five different violet densities (1.1, 1.9, 4.5, 7.8, and 10 m^{-2}). The lower densities within this range represent the "best" habitat currently existing at Cascade Head, with the higher densities representing feasible enhancement targets. Within this range, we chose these particular densities because we could represent them using all four spatial patterns we wished to investigate (Fig. 1): single plants equidistantly spaced (uniform-single), single plants randomly spaced (random-single), plants in clusters equidistantly spaced (uniform-clustered), and randomly-spaced clusters (random-clustered). Clusters consisted of three violets located at the points of an equilateral triangle, with their centers separated from one another by 15 cm.

In the model, we set an upper limit on the time that a larva could actively search before starving. We based our upper limit on several factors. When reared in small jars, silverspot larvae can survive for well over 24 h without eating, but in these enclosed spaces they spend most of this time at rest. When Wint (1983) starved first-instar winter moth larvae at 20° C in small enclosures where their movement was limited, 60 % of them died within 1 day, and 100 % of them had died by the end of 3 days. Bauerfeind and Fischer (2009) found that 30 % of late-instar

Bicyclus anynana larvae housed in small containers died after 1 day of food deprivation. Since our model larvae were larger than first instars, but actively searching, we allowed them to search for food for up to 8 h, with an unlimited amount of time at rest.

We ran the model using three different estimates of predation probability. Our best estimate was the observed probability of predation, 0.0032 30-s move^{-1}. To determine how sensitive the model's results would be to alternative values, we also explored predation rates one-third as great (0.001 move^{-1}) and three times as great (0.01 move^{-1}).

A model run lasted until a larva pupated, starved, died of predation, or reached the absorbing edge (i.e. wandered out of the patch). Each new run began with a complete complement of violets; in nature, larvae are too rare to compete with one another for food. We observed 10,000 runs of each of the 60 combinations of five violet densities, four spatial patterns, and three predation levels. For each combination we calculated the proportion of runs ending in pupation, starvation, predation, and leaving the patch.

Model validation

We used three approaches to determine how faithfully the model represented the movement patterns of real larvae. First, to determine whether observed larval movements fit the assumptions of a correlated random walk, we tested for autocorrelation between successive move lengths and successive turn angles in observed paths. We used functions in the R package 'adehabitatLT' to calculate autocorrelation values, and tested observed paths for significant positive autocorrelation with a Wald-Wolfowitz test, using a Bonferroni correction (Calenge 2006; Dray et al. 2010). Second, we compared the fractal dimensions of observed and simulated paths for instars 4, 5, and 6 using Mandelbrot's basic divider method as implemented by Fractal 5.20 (Nams 1996), and compared the observed and simulated values for each instar with *t* tests. Because fractal dimension is scale-dependent, the simulated paths we analyzed were of the same number of steps as the observed paths. Finally, for each instar, we compared the net displacement of observed paths for each instar with that of 10,000 simulated paths of the same length.

Results

Field observations of larval movement

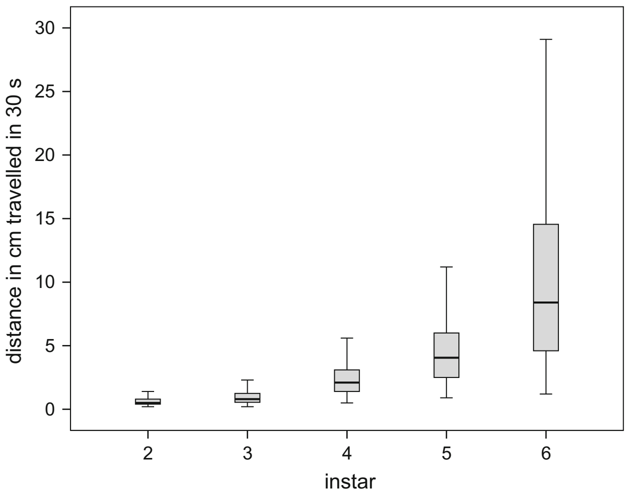

Fig. 2 *Box*-and-*whisker* plots of distances covered in one 30-s move by larvae of different instars. *Horizontal lines* represent medians, *boxes* and *whiskers* represent quartiles. Outliers are not shown. N = 409, 534, 440, 342, 351, respectively

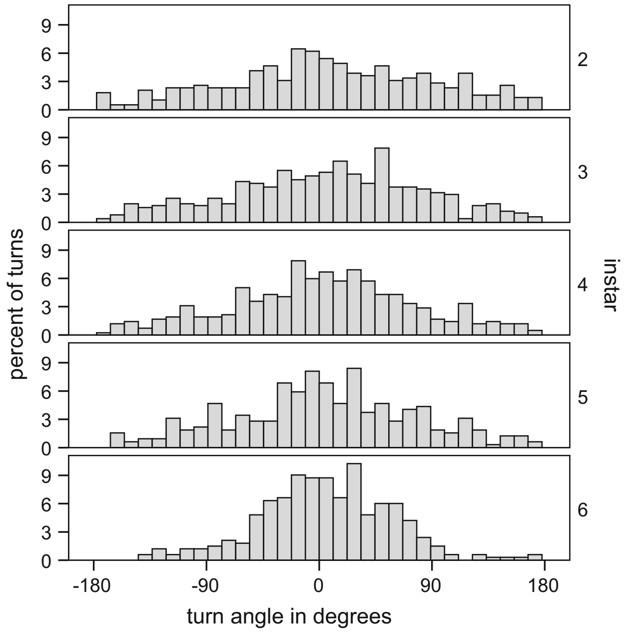

Fig. 3 Distributions of observed turn angles, in degrees, for larval instars 2 through 6. N = 387, 508, 419, 321, and 332, respectively

Larvae of different instars differed in their speed; smaller larvae covered much less distance in 30 s than did larger larvae (Fig. 2). They also differed in their turning behavior. The turn angles for third through sixth instar larvae fit the von Mises distribution (Fig. 3). However, early instar larval paths were strongly influenced by aspects of the vegetation's micro-structure. These larvae frequently followed horizontal grass blades to their tips, then doubled back, retracing their paths. Because of these reversals of direction (angles approaching 180), the turn angles of 2nd instar larvae did not fit the von Mises distribution (Fig. 3). Turn angles for all larval instars had a μ of 0 (Fig. 3). As larvae grew, their turn angles became increasingly concentrated about μ, with κ values of 0.776, 0.906, 1.012, and 1.710 for third through sixth instars, respectively. This increased concentration about 0 is particularly evident in sixth instars, for which most turn angles were less than 90°. Typical examples of observed movement patterns for fourth, fifth, and sixth instar larvae are shown in Fig. 4, along with examples of simulated movement paths for these instars. Larvae of all sizes spent a great deal of time circling the bases of *Hypochaeris radicata* rosettes, as if this plant held some particular attraction. *H. radicata*, a non-native species, is abundant at Cascade Head.

Model validation

Observed larval movements fit the assumptions of a correlated random walk model. In 92 % of 64 trials, successive move lengths (i.e. lag time = 1) were not autocorrelated ($P > .05$); for all 64 trials, successive turn angles were not autocorrelated ($P > .05$). Even fewer paths

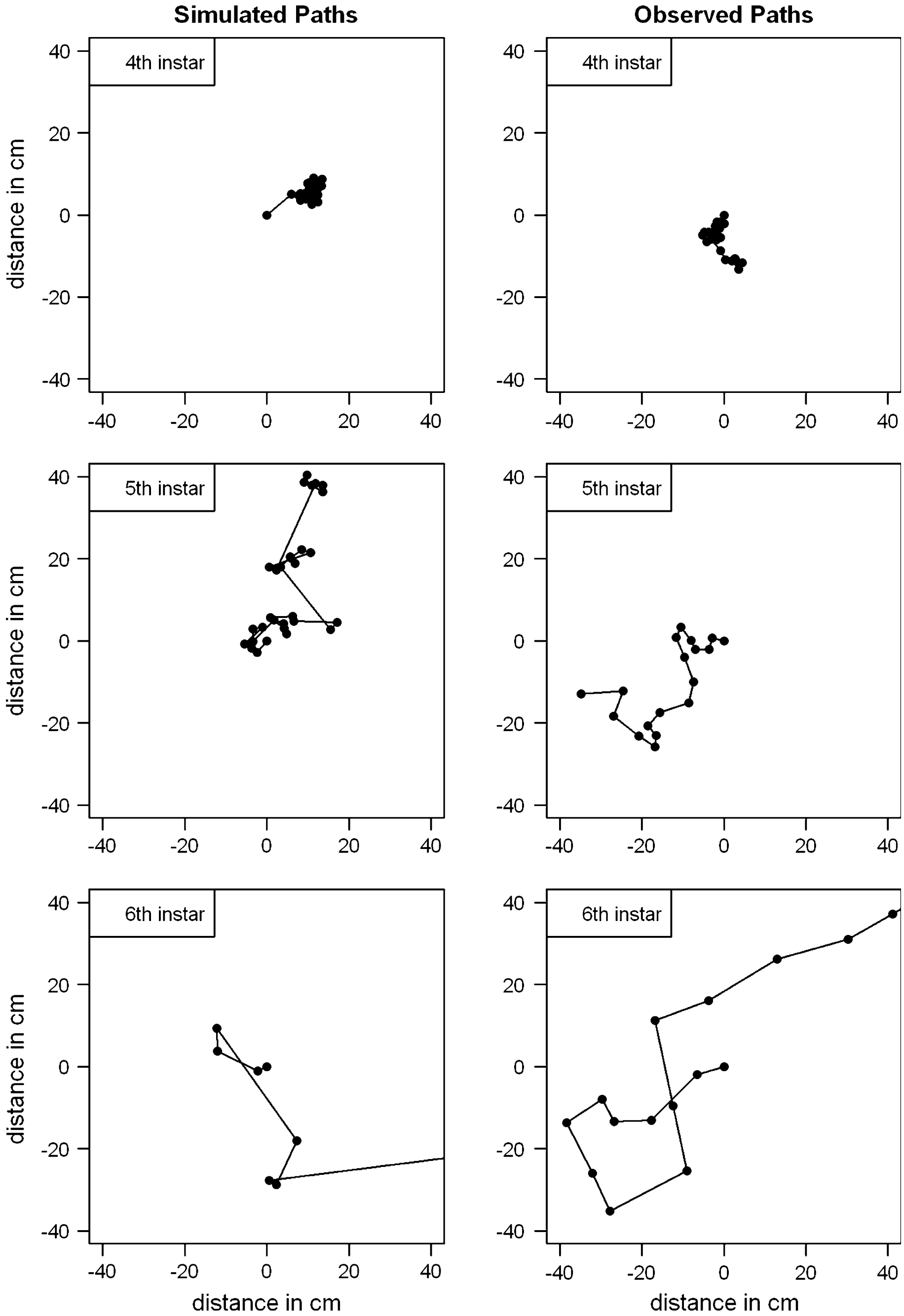

Fig. 4 Representative movement paths for 4th, 5th, and 6th instar larvae. *Circles* represent larval positions at successive 30-s time intervals. Larval starting position is at the center of each figure. (*right*) observed paths, (*left*) simulated paths

were significantly autocorrelated when larger time lags were examined.

Simulated paths were just as tortuous as observed paths. For 4th, 5th, and 6th instars, the mean fractalD of simulated versus observed trials was 1.25 versus 1.22 ($t = -.801$, $n = 22$, $P = .429$), 1.21 versus 1.22 ($t = .217$, $n = 21$, $P = .830$), and 1.15 versus 1.10 ($t = -1.787$, $n = 19$, $P = .082$), respectively.

Finally, the net displacements of 77, 92, and 89 % of the observed 4th, 5th, and 6th instar trials, respectively, fell within the 95 % confidence limits of 10,000 simulated trials for each instar.

Simulation model

Predicted pupation success increased dramatically and approximately linearly with host plant density (Fig. 5). Host plant spatial distribution also influenced the predicted probability of success, although less strongly than density did (Fig. 5). The different host plant spatial arrangements had consistent effects. Host-finding success was always highest when plants were clustered and when clusters were randomly distributed, and always lowest when individual plants were arranged in a uniform grid. At a violet density of 1.1 m^{-2}, fewer than 1 % of model larvae found enough host plants to permit successful pupation, regardless of the spatial arrangement of the plants. At the highest violet density, pupation success was as high as 29 % when plant clusters were randomly distributed (Fig. 5). The effect of changing predation rates affected the probability of successful pupation roughly proportionally to the magnitude of the change (Fig. 5).

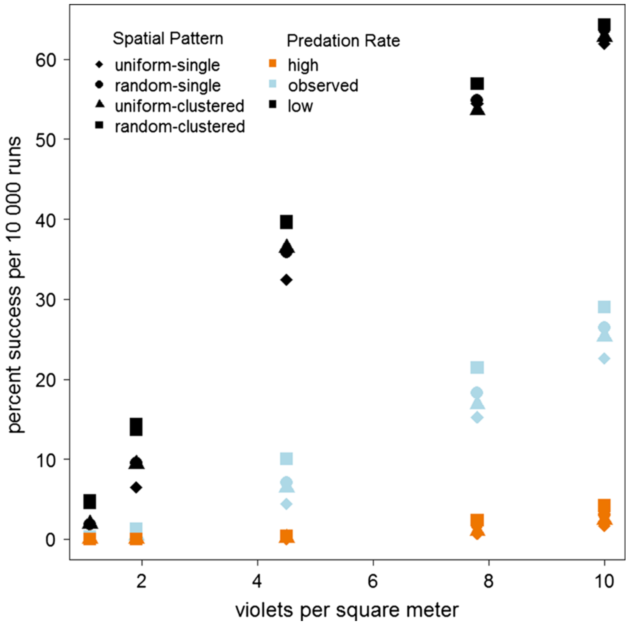

Fig. 5 Percent of model larvae reaching pupation as a function of violet density, violet spatial pattern, and predation rate (high = probability of 0.01 $move^{-1}$, observed = probability of 0.0032 $move^{-1}$; low = probability of 0.001 $move^{-1}$). Each *point* is the mean of 10,000 model runs

When model larvae failed to achieve pupation, predation was by far the most common reason. The frequency of other outcomes—starvation, leaving the patch—varied with violet density and predation probability. At observed predation levels (0.0032 probability of predation $move^{-1}$) and at a density of 1.1 violets m^{-2}, 3 % of model larvae starved before reaching pupation. This figure was much lower for higher violet densities. The percentage of model larvae that left the patch never exceeded 0.06 % for any violet density or predation rate, suggesting that the patch size used in the model did not affect the success of model larvae.

Discussion

Our approach demonstrates an effective strategy for acquiring information to establish management goals for a species of conservation concern. The clear formulation of such goals is an important determinant of a habitat restoration project's success (Miller and Hobbs 2007). We formulated our research question in close collaboration with land managers with local knowledge about the species and its requirements, as recommended by Thorpe and Stanley (2011). This collaboration revealed a knowledge gap about the foraging behavior of larvae of *S. z. hippolyta* in relation to their host plants. We filled this gap using a combination of field observations and simulations.

Our field observations of foraging larvae provided important insights into the process of searching for food. Differences in movement patterns between larvae of different instars show that larvae use different "movement rules" as they grow larger. The "back-tracking" behavior of early instar larvae, which keeps them near their original violet, was rarely exhibited by larger larvae, which were more likely to travel in nearly-straight lines, and thus to move into areas where resources are not yet depleted. The encounters we observed with ants and spiders illustrated the risks to which searching larvae are exposed, risks that increase with the amount of time spent looking for host plants. This information allowed us to model searching behavior more appropriately.

Our model predicted a strong and approximately linear relationship between violet density and pupation success of 4th instar larvae. When we initiated our study, most host plant patches at Cascade Head had densities less than one violet m^{-2} (Bierzychudek, unpublished data)—a level at which our model predicts a survival rate to pupation of less than 1 %. If adult butterflies oviposit where violet densities are insufficient, these areas could act as “sink” habitats. Our finding that current habitat conditions at Cascade Head are unlikely to sustain larval development is consistent with that population’s low numbers. Rebuilding declining Oregon silverspot populations is likely to require considerably higher larval survival rates. Our model indicated that at least four violets m^{-2} are required to achieve a probability of larval survival to pupation of approximately 10 %. If managers wish to achieve even higher survival rates, they can use the results of the model to decide how to distribute violet transplants within and among patches.

In addition to violet density, larval success in the model was also affected, though to a lesser extent, by the violet distribution pattern, with success highest when violets grew in clusters that were randomly distributed, and lowest when violets occurred singly and interplant distances were uniform. It is well-known that optimal search strategies depend on the spatial distribution of resources (e.g. Cain 1985; Zollner and Lima 1999; Nolet and Mooij 2002; Romero et al. 2009; Scharf et al. 2009). Unlike many vertebrates and even some invertebrates (e.g. McIntyre and Wiens 1999), *S. z. hippolyta* larvae appear to lack the flexibility to change search strategies when resource densities/distributions change, perhaps because they cannot perceive those changes (Bierzychudek et al. 2009). Random movement may be successful where host plants are dense and the habitat more open, but it is no longer a successful strategy in habitats, like Cascade Head, invaded with aggressive non-native pasture grasses. These findings are supported by Thomas et al.’s (2011) findings about the importance of larval habitat quality in determining habitat suitability for butterflies.

Models can serve many functions; we have used a model as a substitute for field experiments investigating the effect of host plant density/distribution that would have been impractical to perform. A similar approach has been employed by others interested in invertebrate behavior in relation to resources (e.g. Bukovinszky et al. 2005; Chapman et al. 2007; Roslin et al. 2008), but these studies were not attempting to set habitat improvement goals. Our approach has promise for evaluating habitat suitability and/or developing restoration goals for any insect species requiring multiple host individuals, as well as for larger, more vagile animal species that must move from one habitat patch to another (e.g. Lloyd and Marsden 2011).

While our model is based on field observations of larval behavior, it does not capture every detail. For example, because working with a threatened species meant that we could not cause the death of experimental animals, we had to make assumptions about how long larvae could forage before they starved. We also know rather little about rates of predation that larvae experience. Our presence may have protected larvae from attacks by birds, rodents, parasitic wasps, etc., leading us to underestimate true predation probability.

Our model results suggest that to achieve a pupation rate of approximately 10 %, enhancement efforts should aim to create numerous patches of at least four violets m^{-2}. Our findings indicate that higher densities would lead to even higher rates of larval survival, but the availability of violets for restoration is limited, creating a tradeoff between planting multiple areas and planting high densities. Secondly, while an evenly spaced planting arrangement is perhaps the easiest for a team of volunteers to understand and implement, the model results suggest that violets should be planted in randomly-distributed clusters. In addition, our observations of larvae “distracted” by *Hypochaeris radicata* (see Results—Field Observations) suggest that the management of this invasive species might be a useful strategy. Finally, given the strong effect of predation rate, additional information on predatory species, predation rates, and predator habitat preferences could be used to improve the model and management strategies in the future.

This work is part of a larger program of adaptive management for the Oregon silverspot; earlier stages involved assessing the effects of mowing and controlled burning on habitat quality and violet demography, and developing a captive rearing program to supplement butterfly numbers until habitat enhancement is achieved (Crone et al. 2007). Collaboration with conservation practitioners assured that our research was of maximum utility for guiding their activity. For example, most behavioral ecology studies of sensitive butterfly species have targeted adults (e.g. Schultz 1998; Sei 2009; and references in Dover and Settele 2009); the outcomes of previous management actions at Cascade Head prompted our focus on larval resource requirements. Our work has revealed how larvae of this sensitive species respond to important features of their habitat, and allowed us to set a goal to guide habitat enhancement activities at Cascade Head, at other population sites, and for areas where re-introduction is being considered. Our recommendations have been implemented by The Nature Conservancy and other partners at Cascade Head and elsewhere; population monitoring of the butterfly is assessing the success of these recommendations.

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