Caterpillars on the run – induced defences create spatial patterns in host plant damage

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Herbivores usually consume a mere fraction of available plant biomass. Spatial patterns in feeding damage may be attributable to induced defences by the host plant; a damaged plant reacts by lowering its nutritional value, thereby forcing herbivores to move on before food gets worse. In this study, we test this general hypothesis on a specific model system: caterpillars of the alpine butterfly *Parnassius smintheus* feeding on lance-leaved stonecrop *Sedum lanceolatum*. We first describe spatial patterns in host distribution and feeding damage within alpine meadows. We then use laboratory experiments to test a key assumption behind the proposed mechanisms: that the host plant exhibits an induced response with a negative impact on larval performance, and that this response is activated with a delay. Finally, we relate the patterns observed to the actual behaviour of *Parnassius* larvae.

Overall, we found the level of feeding damage to be low (on damaged plants, only 5% of all leaves were fed upon). Within meadows, both host plants and feeding damage were clumped at a small spatial scale. This pattern seemed directly explicable by the timing of the host's induced defence. Laboratory experiments revealed a delay of 1–2 d before the defence reached a level affecting larval performance, and wild larvae switch plants more quickly than this. A simulation model demonstrated that the spatial distribution of host plant damage can be generated by a simple random walk, based on the empirically observed step frequency, length and turning angles. Hence, as the most parsimonious explanation for the observed level and pattern of host plant damage, we offer a scenario where induced changes in host-plant quality limits the time spent per plant, but the herbivore moves throughout the landscape without any particular directionality.

Herbivores feeding on plants may have a strong impact on the local performance of their host (Louda and Rodman 1996, Crawley 1997, Maron and Gardner 2000, Maron and Crone 2006). Across a landscape, both the behaviour of individual insects (Singer and Wee 2005) and complex population dynamics (Roland 2005, Harrison et al. 2005) may contribute to dramatic variation in feeding damage. In studies of spatial patterns, host plant quality is often assumed to be equal, and the plants regarded as a passive template on which the herbivores then exhibit their dynamics (Gripenberg and Roslin 2007). Yet plants are not unresponsive fodder. They defend themselves against herbivores using thorns, trichomes, wax layers and other physical barriers, they may alert enemies of the herbivore to their own rescue (Turlings et al. 1995, De Moraes et al. 1998, Dicke 1999), and they produce noxious chemical substances which deter feeding, reduce the nutritional value of the food or are simply toxic to the herbivore (Schoonhoven et al. 2005).

Chemical defences may be grouped into two categories: constitutive and induced resistances (Schoonhoven et al. 2005). The latter type builds on compounds which are only produced after the plant is attacked (Green and Ryan 1972, Karban and Myers 1989, Karban and Baldwin 1997, Agrawal 1998, Agrawal et al. 1999, Dicke and Hilker 2003). Such mechanisms are taxonomically widespread, and have been reported from >100 plant species in 34 families (Karban and Baldwin 1997).

The speed with which induced responses arise once triggered varies substantially among herbivore-plant interactions. In some cases, like in the mountain birch, it may occur within minutes or hours (Haukioja et al. 1990, Neuvonen and Haukioja 1991). In other cases, full activation of the response may take over a week (Bashir Kahn and Harborne 1990). How quickly the relevant compounds can be produced will depend on the availability of precursors and their durability in the cell. Some delay will clearly occur in almost any biosynthetical process.

While induced responses have often been characterised from a chemical perspective, their impact on herbivore behaviour, and their implications for spatial interactions between hosts and herbivores, is still a topic of active research. In 1983, Edwards and Wratten (1983) suggested that damage-induced chemical changes would have a major

effect on patterns of insect feeding, causing insect herbivores to feed lightly on a large proportion of leaves rather than heavily on few leaves. In their seminal paper, these authors report tentative over-dispersion of herbivore damage in leaves from two out of five species of plants – an observation which has later received variable levels of support from other systems (Bergelson et al. 1986, Raupp and Sadof 1989, Mauricio and Bowers 1990, Edwards et al. 1991, Ravenscroft 1994, Kaitaniemi et al. 2004, Underwood et al. 2005).

In this study, we examine the potential impact of an induced response on patterns of feeding damage by the monophagous alpine butterfly *Parnassius smintheus* (Lepidoptera: Papilionidae) on its host, lance-leaved stonecrop *Sedum lanceolatum* (Crassulaceae). We first describe the spatial distribution of the host, and natural patterns of host plant damage. We then conduct a series of laboratory experiments to test the hypothesis that feeding by *Parnassius* induces a response by *Sedum*, and that there is a delay in this response allowing caterpillars to change host-plants within the time window of high host quality. Finally we examine *Parnassius* caterpillars in the wild, and relate their behaviour to the observed patterns of host damage by a simulation model. Through our multistep approach, we move from describing a fundamental pattern to resolving potential mechanisms behind it.

Material and methods

Study species and study site

At our study site in Alberta, Canada, larvae of the alpine butterfly *Parnassius smintheus* feed mainly on lance-leaved stonecrop *Sedum lanceolatum*. Infrequently, the species will also be found on ledge stonecrop *Rhodiola integrifolia*; see Results, and more commonly on other plant species in other parts of its range (Guppy and Shepard 2001). For the most part, the distribution of *P. smintheus* is limited to subalpine and alpine meadows where *Sedum* occurs (Sperling and Kondla 1991). Here, the adults fly from July to late August (Layberry et al. 1998) or sometimes into September (Bird et al. 1995). Female *Parnassius* do not lay their eggs directly on the larval host plant, but in the surrounding ground vegetation. Nevertheless, the presence of *Sedum* has been shown to elicit oviposition (Fownes and Roland 2002). The eggs then develop into pharate first-instar larvae which overwinter and emerge with the snow melt in the spring. The larval phase typically lasts until the end of June or early July.

The primary host plant *Sedum lanceolatum* is a perennial, overwintering as small rosettes. Flower stalks rapidly grow in late May or June. Since the species is long-lived, spatial patterns in host distribution will be fairly consistent among years. Within the study area, feeding damage on *Sedum* can be attributed pimarily to *P. smintheus*; while a few generalist Lepidoptera may occasionally feed on *Sedum*, quantitatively *P. smintheus* is its dominant herbivore (B. C. Schmidt pers. comm.).

In our study, we focused on *Parnassius* and *Sedum* in the foothills of the Canadian Rocky Mountains at both Jumpingpound Ridge and Powderface Ridge, Kananaskis

Country, Alberta (50°57′N, 114°55′W; for a map and meadow labels, see Roland et al. 2000). At these sites, subalpine meadows are separated from each other by intervening forests of lodgepole pine *Pinus contorta*, Engelmann spruce *Picea engelmannii* and subalpine fir *Abies lasiocarpa*. The vegetation of the meadows is dominated by white mountain avens *Dryas octopetala* ssp. *hookeriana*, grasses, sedges and other wildflowers interspersed with *Sedum*.

Spatial distribution of host plants and feeding damage

To describe patterns in the spatial distribution of the host, and in the damage inflicted by *Parnassius* caterpillars, we mapped *Sedum* within three alpine meadows in 2002. These meadows correspond to meadows F, g and M (border with L) in the maps of Roland et al. (2000). In each meadow, a 20 × 20 m plot was established and the location of every *Sedum* individual was mapped with an accuracy of 1 cm. For each plant, we scored whether there were any signs of feeding damage. On the succulent *Sedum,* past feeding is easy to detect in the form of whitish scars where leaves or parts of leaves have been consumed. In two of the meadows (g and F), plants were inspected in further detail. Here, every leaf was counted, as was the exact number of leaves damaged by *Parnassius* feeding.

While a 20 × 20 m plot may appear small, two observations reveal that the study was conducted at a relevant scale. First, aggregation of both host plants and feeding damage was found to occur at a small spatial scale (< 10 m and less than half a metre, respectively; cf. Results). Second, the size of the sampling plots was large compared to the scale of larval movement (cf. Results). Based on the observed rate of net displacement, it would take a larva more than three days to cross the diagonal of a 20 × 20 m plot – even without allowing for periods of inactivity during night or spells of bad weather.

Laboratory experiments

To examine the mechanisms behind patterns observed in nature, we conducted a series of experiments. Caterpillars (total n = 223) and host plants were collected in the field between 17 May and 5 June 2006, and brought to the Barrier Lake Field Station (51°02′N, 115°03′W, 1390 m a.s.l.). All plants brought from the field were selected to be of similar size, and completely undamaged. Plants were potted in soil from the alpine meadows. Outside of the experiments, larvae were kept in clear plastic boxes (25 × 25 × 15 cm; maximum 15 larvae per box) covered with polyester mesh, and fed with intact *Sedum* plants planted in a 2 cm layer of soil. To avoid any induced response in these stock cultures, host plants were renewed on a daily basis. All experiments were conducted under ambient conditions.

Growth experiment
To test whether and how quickly the plants react to damage, we examined the growth of *Parnassius* larvae on *Sedum* which had been exposed to damage at different time intervals before being fed to the caterpillars. Forty *Sedum*

plants were planted individually in 2 cm of meadow soil in plastic flower pots (diameter 8 cm, height 11 cm). Pots were numbered and then randomly assigned to one of four treatments: a undamaged control and *Sedum* individuals damaged one, two or five days before the start of the experiment. Damage was inflicted by removing three leaves from each plant with a pair of scissors. If the plant had more than one leaf rosette, damage was evenly distributed among the rosettes available. The damage level was selected to reflect natural conditions, since in 2002, average feeding damage on plants encountered by the larvae was 3.2 leaves (median 2 leaves, SD 3.0, range 1–26 leaves; for further details, see Results).

At the start of the experiment, a recently eclosed 5th instar larva was added to each pot. This larva was weighed before entering the experiment and reweighed at intervals of 24 h (24, 48 and 72 h after the start of the experiment). Weighing was done to a precision of 0.001 g using a laboratory balance (Mettler type PE 360, Houston, TX, USA). To keep experimental treatment levels at their nominal levels, every time a larva was weighed, it was also changed to a pot with a fresh plant damaged at the prescribed time before introduction. Larval growth was captured by two variables, of which relative growth refers to the change in weight between two weighing events divided by original weight, ([end weight (E) − start weight (S)]/S) and growth efficiency refers to change in weight relative to the amount of biomass (B) consumed, (E–S)/B.

To estimate biomass consumption from the individual *Sedum*, all leaves were counted at the start of the experiment and each leaf assigned to one of three size categories (large, medium, small). An extra set of plants was then used to determine the approximate biomass of leaves in each size category. For each category, 90 leaves were extracted from 5 plants (total n =450 leaves per size class, 1350 in total). To achieve separate estimates of biomass for leaves fully and partly consumed, we separately weighed 150 whole leaves, 150 half leaves and 150 leaf-tips. On experimental plants, we then calculated the number of large leaves completely consumed, half-eaten and chewed on at the tip, and the same for medium-sized and small leaves. By multiplying the matrix of size-specific weights with the matrix of size-specific consumption counts, we were hence able to estimate the total biomass ingested by a larva.

Choice experiments

To assess how host plant damage affected larval resource selection, we conducted two choice experiments. In the first one, each larva was offered an intact and a damaged *Sedum* individual. All plants had been collected two days earlier in the field and stored under similar conditions: damaged plants in plastic containers with larvae, undamaged plants in similar containers without larvae. The plants were then replanted in pairs at opposite ends of clear plastic containers (width 16 cm × height 8 cm × length 11 cm). Ten replicate containers were included. To each container, a 4th instar larva was added, and its resource selection monitored for three days. Every 24 h, we recorded which of the plants the larva was sitting on. If the larva was not on a plant, no choice was scored. At the end of the experiment, we also

recorded how much biomass the larva had consumed on each plant (cf. above).

To determine whether the timing of damage affected larval host plant selection, a separate set of larvae was offered a choice between two *Sedum* individuals damaged one and five days before the experiment, respectively. Ten replicates were run in the same 16 × 8 × 11 cm plastic containers as described above, and responses scored accordingly.

Behaviour of wild *Parnassius* larvae

Empirical data

To match spatial patterns in host plant damage to the actual behaviour of *Parnassius* larvae, we followed wild larvae in situ between 24 May and 23 June 2006. Each morning we located focal larvae in the field and monitored them for 1–6 h (depending on weather conditions). All aspects of behaviour were timed, and movement trajectories marked out with numbered flags and measured.

To examine whether the larvae modified their movements in response to host plant density, we assessed the number of host plants within 1 m² around the start of the movement trajectory (note that most larvae stayed within a short distance from the starting point; cf. Results). The distance moved by each larva was measured by two variables: total distance (the sum of all individual moves, i.e. the total length of the exact path followed by the larva) and net displacement (the Euclidean distance from the start to the end point of the movement path).

Simulation model

To model spatial patterns in host plant damage from first principles, we used empirical data on larval movement to simulate the expected pattern of feeding damage assuming that each larva performed a random walk solely defined by empirically observed step frequencies, lengths and turning angles. The rationale is simple: assuming that induced changes in plant quality limits the time spent per plant, but the herbivore otherwise moves through the landscape without any particular directionality, our simulation generated the "null pattern" to expect.

More specifically, the simulation model was constructed as follows: feeding damage within each of meadows F, g and M was modelled independently. For each meadow, we first created a buffer zone around the actual 20 × 20 m plot by mirroring the observed distribution of host plants in both the vertical and the horizontal plane, hence creating a simulation arena of 40 × 40 m. For computational convenience, we assumed periodic boundary conditions. We then simulated the lifetime movement trajectories of larvae by sampling individual move lengths and durations, turning angles between subsequent moves and stop-over durations from the observed distribution of these variables (n =350, 350 and 331, respectively). Since the distance and duration of an individual move are correlated, we sampled both characteristics from the same observed move. Moreover, since stop-over times spent off the plant, and stop-overs spent on the plant while feeding versus not feeding all differed in duration ($F_{2,328} = 16.1$, p < 0.0001), these values were sampled from different distributions.

Each larva was started from a random point within the 40×40 m arena and simulated for 28 d (with activity occurring for 12 h per day). If a larva came within 1.5 cm (our estimate for host plant radius) of the mid-point of a plant during a move, it stopped to feed with a probability of 0.9 (estimated from the empirical data, $n = 52$ observed caterpillar-plant encounters).

For the simulations, we recorded which exact plants were damaged (and thus the full spatial pattern). The meadow-specific density of larvae was fine-tuned by running 100 simulations for each meadow until the mean proportion of damage from the pilot simulations matched the actual proportion of damage observed in the meadow with an accuracy of two decimal places. For the final results, we ran 1000 simulations with the selected density.

To validate the simulation model, we first visually compared several simulated and empirically observed trajectories per meadow. We then mimicked the larval observation process in each meadow by sampling 1000 larvae and observing their movements for a randomly selected duration $< 25\,000$ s (the maximum time for which larvae were observed in the wild). For these larvae, we compared total distance moved and net displacement (cf. above) versus time observed to the patterns observed in real larvae (cf. Fig. 7, below). Finally, we visually compared spatial patterns in simulated and empirically observed feeding damage.

Statistical models

In order to describe the spatial arrangement of *Sedum* plants within alpine meadows, we conducted spatial point pattern analysis on the data collected in 2002 (Ripley 1976, Ovaskainen and Roslin 2007). To determine if the observed distribution of *Sedum* is more or less aggregated than a random pattern, we ask: for a randomly selected host plant, what is the density of other host plants at a distance d? For each focal plant, we calculated the observed number of neighbours within distance categories of 0.5 m. Whether the observed pattern was more extreme than expected by chance alone was then evaluated by comparing it to 95% confidence envelopes generated by 1000 simulations where the same number of plants was placed at random within the 20×20 m sampling area.

To examine spatial aggregation in feeding-damage among plants, we examined the frequency of feeding scars. For meadow M, where feeding damage had only been scored at the plant level (as "some damage" vs "no damage"), we asked: for a randomly selected host plant nibbled by a larva, what is the probability of another plant at distance d also being damaged? The observed pattern was compared to that generated by keeping each *Sedum* at its real location, but swapping damage status 1000 times randomly among plants.

For meadows g and F, where feeding damage had been scored at the leaf level, we asked: for a randomly selected leaf damaged by a larva, what is the probability that another leaf on another plant at distance d is also damaged? To resolve patterns among leaves within host individuals, we asked a nonspatial question: for a randomly selected leaf damaged by a larva, what is the probability that another leaf

inspected on the same plant is also damaged? Here, relevant confidence limits were obtained by keeping track of the damage status of each leaf in the data set, but randomizing leaves across plants. In other words, we held the underlying pattern of plants constant (i.e. the x, y coordinates of individual *Sedum*), but randomly shuffled plant-specific numbers of damaged and undamaged leaves among individuals.

To compare observed patterns to random patterns generated in simulations, distances d need to be "binned", i.e. discretized into distance classes. These bins need to be large enough to offer statistical resolution, but small enough to give spatial resolution. Since our material included pairwise distances between high numbers of points, we chose a relatively narrow bin size of 0.5 m. As an example, the minimum number of 174 plants mapped on meadow F offer $174 \times 173/2 = 15\,051$ pairwise distances (Fig. 1). We also chose to examine patterns of aggregation to a maximum of 14 m. This scale was dictated by the scale of the survey area: given that *Sedum* and feeding damage were mapped within areas of 20×20 m, any randomly chosen plant will have few neighbours at a distance of > 14 m. All calculations were implemented with pro-gramme Toast (Ovaskainen and Roslin 2007), and patterns within each meadow were analysed separately.

To analyse the movement trajectories of individual larvae in 2006, we first examined how the distance moved increased with time. Since we had several observations of each individual, we used a generalised linear repeated measures model to test the effect of time (as a fixed factor) on the total distance and net displacement of larvae as moved at time t (counting one observation per stop along the trajectory and including larval identity as a random effect). We next examined whether the movement trajectories of individual larvae differed in terms of characteristics unrelated to time. First, we used a one-way ANOVA to test whether the length of individual moves, and cosine-transformed turning angles between consecutive moves, differed among individual larvae. Second, we applied a repeated measures ANCOVA to test whether the density of host plants affected move length, i.e. whether larvae moved in longer bouts when faced with a sparse resource.

Observed movement trajectories were used to simulate expected damage patterns as described above (cf. Simulation model). To evaluate the consistency between simulated and observed patterns, we ran 1000 simulations of the feeding pattern in each meadow. For each replicate simulation, we then calculated exactly the same statistic as for the observed pattern – that is, the probability that for a randomly selected host plant damaged by a larva, another plant at distance d is also damaged. By repeating this for each of the 1000 simulations, we derived the mean and the 95% confidence envelope of the resulting distribution.

Data on larval growth were analysed by repeated measures ANOVA. The relative growth and growth efficiency of individual larvae was modelled as a function of fixed effects treatment, time (treated as a categorical variable) and their interaction. Since the same larva had been measured repeatedly, larval identity was included as a random effect. We did not detect any significant effect of treatment $\times$ time ($p > 0.3$), and hence this term was removed from the final models.
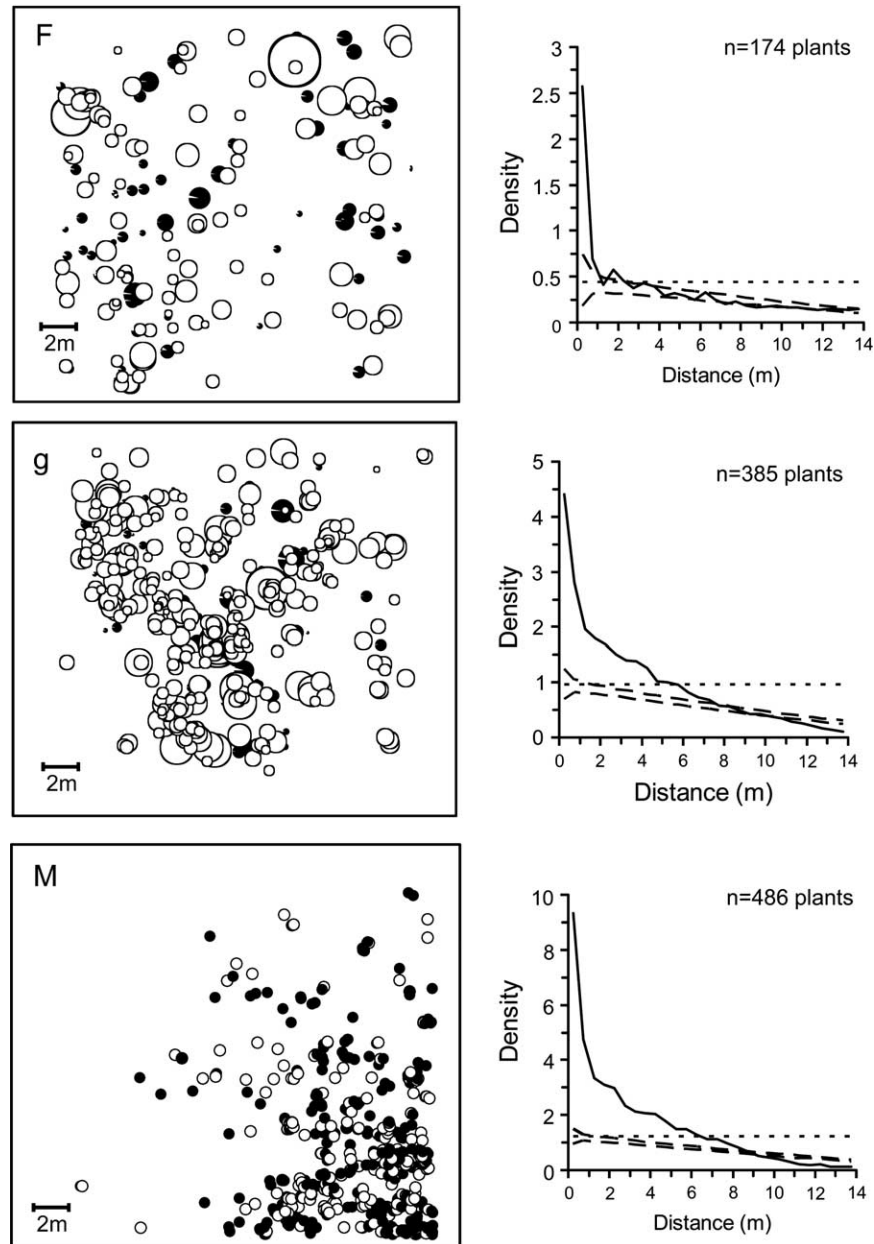
Fig. 1. Spatial distribution of *Sedum lanceolatum,* and of feeding damage among plant individuals, in three alpine meadows (F, g and M). Maps on the left-hand side show the exact location of each individual within 20×20 m sample plots. In all meadows, black circles indicate plants with some feeding damage, whereas white circles show plants left untouched by *P. smintheus*. Within meadows F and g, feeding damage was scored at the leaf level: here, the size of each map symbol shows the total number of leaves on respective plant, with the light grey fraction representing damaged leaves (note: small in all cases). Graphs on the right-hand side depict spatial aggregation in the density of *Sedum*. In each of the panels, the black line represents the observed spatial pattern, measured as the density of *Sedum* at distance d from a randomly chosen *Sedum*. The dotted line shows the average density in the whole meadow (*Sedum* m^{-2}). Dashed lines are 95% confidence limits based on redistributing *Sedum* randomly within the sampling plot. n indicates the number of plants within each plot.

All repeated measures models were fitted with procedure Mixed, SAS statistical package, ver. 8.01 (Littell et al. 2006) Since observations on the same subject are likely to be more similar the closer they were made in time, we assumed a first order autoregressive covariance structure.

Data from the choice experiments were analysed by Fisher's exact test as applied to 2×2 tables of the observed distribution of larvae as compared to an even distribution. In the first choice experiment, the 2×2 cell entries corresponded to the observed number of larvae sitting on the intact *Sedum* plant A and the damaged *Sedum* plant B (n_A versus n_B larvae) compared to an even distribution ($[n_A+n_B]/2$ versus $[n_A+n_B]/2$). In the second choice experiment, corresponding numbers were derived for larvae sitting on *Sedum* plant A damaged one day before the experiment and larvae sitting on *Sedum* plant B damaged five days previous. A separate test was applied to each (daily) scoring event. Total leaf consumption on the two plants (as

scored by the end of each experiment) was compared by a paired t-test. These analyses were conducted using Statistix 8.0 (Analytical software, Tallahassee, FL).

Results

Spatial distribution of hosts and feeding damage

In the *Parnassius-Sedum* system, the host plant is clumped at a relatively small spatial scale: in meadows g and M, clumping extends to <10 m, in meadow F to <1 m (Fig. 1; compare solid and dashed black lines). Among the clumped plants, feeding damage by *P. smintheus* is also aggregated in itself. While the level of feeding damage varied among individual meadows, its spatial distribution was nonetheless consistent among sites; in all but one case, significant aggregation occurred at a scale of less than half a metre (Fig. 2 and 3; solid versus dashed black lines). In meadow F, aggregation at the plant level did not differ significantly from random expectations (Fig. 2; solid versus dashed black lines). Within plants, the aggregation of feeding damage was particularly striking: a leaf on the same plant as a randomly chosen damaged leaf had a much higher probability of being damaged itself than a leaf picked at random from the total dataset (Fig. 3; compare open circle to confidence limits on black dot). In total, only 2% of all 18 490 leaves examined in meadows F and g had been affected by larval feeding (Fig. 1). On the plants that did exhibit feeding scars, an average of 5% of leaves per plant were affected (SD 4%; n =73 plants, 2644 leaves).

Delayed induced defence

In the laboratory experiments, we found no signs of any induced plant defence impairing survival: all larvae survived each experiment of 72 h. The effects on growth were more variable. In terms of relative growth, we found a significant effect of damage timing on the relative growth of the larvae (Fig. 4a). Here, the larvae grew significantly slower on plants damaged two (t = −2.89, DF =35, p =0.006) or five (t = −2.33, DF =35, p =0.03) days ago than on undamaged control plants (Fig. 4a). On plants damaged one day ago, growth was only marginally affected relative to controls (p =0.1; Fig. 4a). In terms of growth efficiency, larvae fed with control plants performed the best (Fig. 4b), but pairwise comparisons revealed significant differences only in the growth efficiency of larvae feeding on control plants compared to larvae feeding on plants damaged two days previous (t = −2.73, DF =35, p =0.01). Growth efficiency in other treatments did not differ significantly from the control (p >0.15).

Differences in larval growth were also reflected in larval resource selection. No selection was evident with respect to larval location; the distribution of larvae did not differ from an even distribution either among damaged vs undamaged plants (p ≥0.75), or between *Sedum* plants damaged one or five days before the experiment (p >0.75). Nevertheless, when offered a choice between a damaged and an undamaged plant, the larvae consumed more biomass on the originally undamaged than on the damaged plant (t_{19} = 3.20, p =0.005). The observed difference was relatively
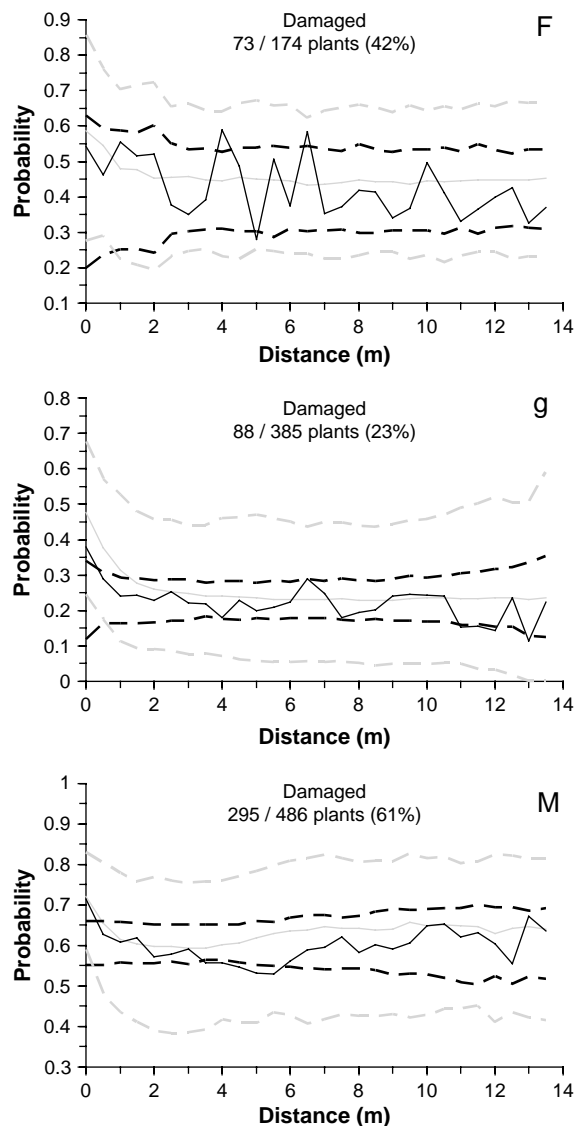

Fig. 2. Spatial aggregation of feeding damage at the level of individual plants within three alpine meadows (F, g and M). The solid black line shows the probability with which a plant at distance d from a randomly chosen damaged plant has been fed upon. The dashed black lines show the confidence envelope had the damage been distributed at random (i.e. 2.5 and 97.5% quantiles from 1000 randomisations where each *Sedum* was kept at its real location, but damage status swapped randomly among plants). These values are then compared to patterns generated by our simulation model (grey lines). Here, the solid grey line shows the average and the dashed grey lines show 2.5 and 97.5% quantiles from patterns generated by 1000 simulations of larvae performing a random walk.

large (mean pairwise difference 0.06 g, SE 0.02), since on average, the larvae had consumed only 0.01 g per plant. Surprisingly, the number of leaves fed upon differed in the opposite direction (average difference −4.9 leaves, SE 1.62, t_{19} =3.03, p =0.007). Hence, larvae "tasted" a higher number of leaves on the damaged plants, but ate larger pieces of the leaves of undamaged *Sedum*.

When offered a choice between a plant damaged one or five days before the experiment, there was a trend towards larvae consuming more biomass of the plants damaged
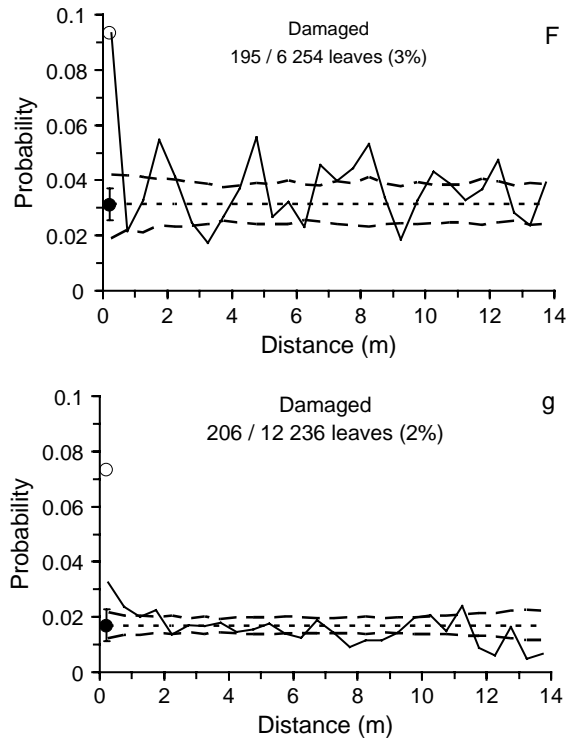
Fig. 3. Spatial aggregation of feeding damage at the level of individual leaves within two meadows (F and g). The solid line shows the probability with which a leaf at distance d from a randomly chosen damaged leaf has been fed upon. The dotted line shows the average proportion of damaged leaves on the meadow, and the dashed lines 95% confidence limits. Symbols at distance "0" show aggregation at the level of the plant individual. Here, we examine the probability that for a randomly chosen leaf, another random leaf within the same plant was also damaged. The filled black dot shows the average outcome of swapping the full pool of damaged and undamaged leaves 1000 times randomly among plants, with the error bars indicating 2.5% and 97.5% quantiles. The open circle shows the observed probability.
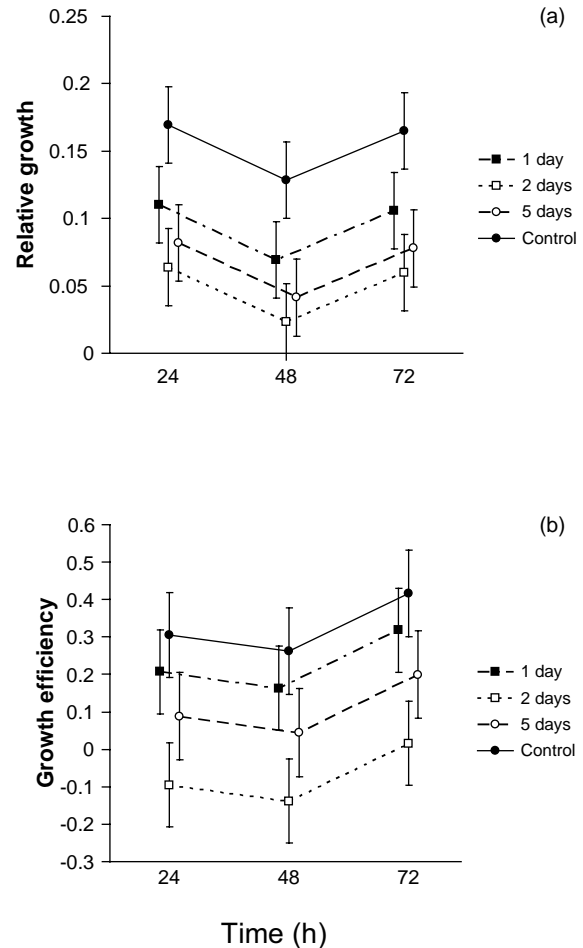

Fig. 4. Effects of host plant damage on: (a) relative growth; (b) growth efficiency. Since the same larvae were measured repeatedly, means and standard errors were estimated by a repeated measures model.

more recently (average pairwise difference 0.06 g, SE 0.03, $t_{19} = 1.98$, p = 0.06)

Behaviour of wild *Parnassius* larvae

In the field, *P. smintheus* larvae proved effectively monophagous on *Sedum lanceolatum*: out of 284 observations of larvae feeding on plants, only 5 (<2%) concerned feeding on ledge stonecrop *Rhodiola integrifolia,* and no other plant species were fed upon.

Larvae spent relatively little time on plants, and even less in actual feeding activities (Fig. 5). In total, we followed larvae for 74 h 8 min. Of this time, they spent about a third (23 h 9 min) on the host plant and two-thirds on the ground between host plants. In total, the larvae were observed to feed on 201 leaves, i.e. on average 2.7 leaves h^{-1}. Feeding was relatively quick: on average, a larva consumed a leaf in ca 3 min, the quickest time being 16 s and the longest time more than half an hour (range 16 s–37 min 47 s; mean 3 min 34 s, SD 4 min 5 s). From entering a plant to leaving it took an average of 16 min 57 s (median 10 min 51 s, SD 19 min 30 s, n = 82 plant

visits). Hence in nature, larvae will use much more time looking for food than actually eating it (Fig. 5)

Individual larvae were followed from one hour to nearly six hours, during which time they moved from less than half a metre to nearly 15 m. The length of invidual movement bouts (i.e. the length of "steps" in the trajectory) was comparable to the scale of aggregation in feeding damage estimated in 2003 (compare Fig. 2–3 vs 6); the vast majority of individual moves were <0.5 m (Fig. 6; mean 23 cm, median 14 cm, SD 26 cm, n = 365). One of the 28 larvae deviated from this pattern, making several consecutive movements of several metres. By the end of its path, this larva started to pupate, and the reason for its long moves might have been a need to find a pupation site rather than looking for suitable food. Therefore, this larva was removed from subsequent analyses.

Larvae moved forward at an average speed of ca 2.5 cm min^{-1} (Fig. 7a; generalised linear repeated measures model of total distance as a function of time: $F_{1,327} = 724.2$, p < 0.0001), and away from their point of origin at 0.6 cm min^{-1} (Fig. 7b, generalised linear repeated measures model of net displacement as a function of time: $F_{1,254} = 342.7$, p < 0.0001). Movement trajectories were not influenced by
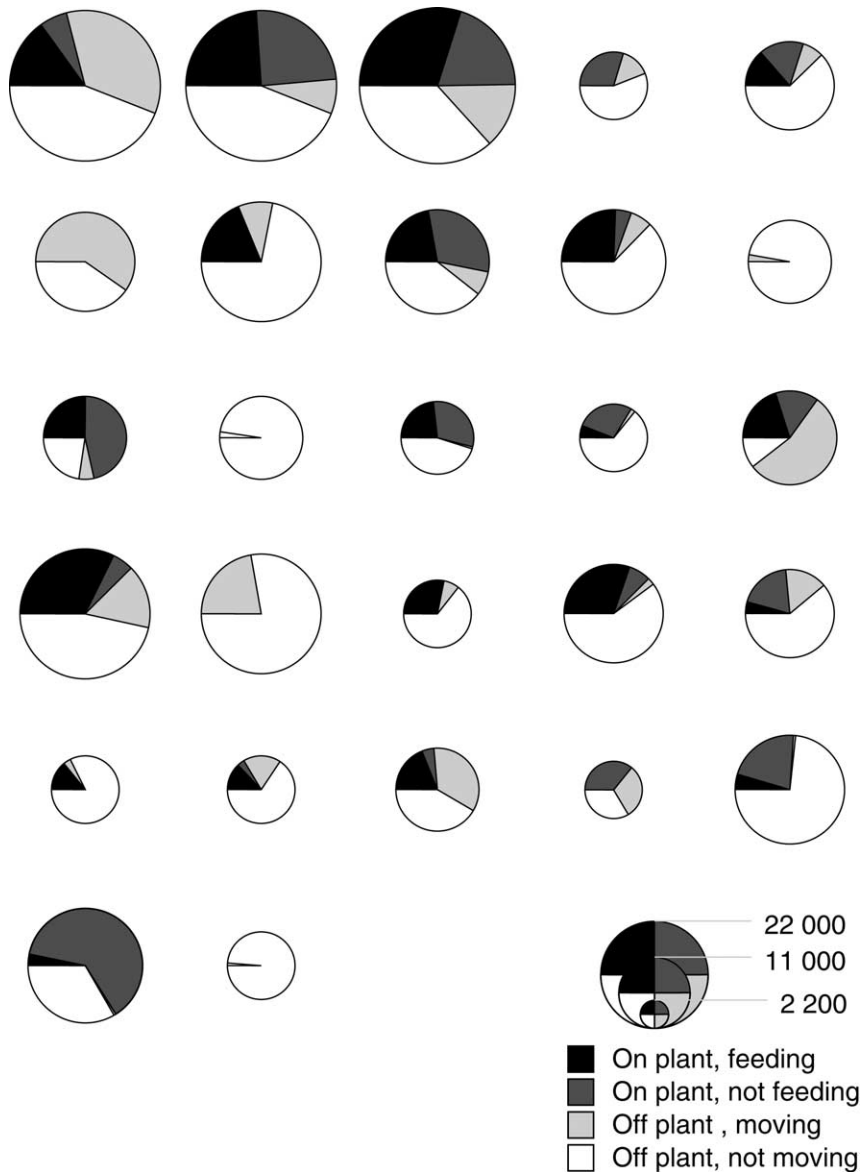
Fig. 5. Time budget for 27 individual *P. smintheus* larvae followed on alpine meadows. The total size of each pie chart is scaled to the total time each larva was observed for (in seconds), and within pies, different colours show the fraction of time spent on individual activities.

time alone, but they were also significantly different among individual larvae. The length of individual moves varied significantly among larvae (one-way ANOVA on ln-transformed distances, $F_{26,338} = 6.37$, $p < 0.0001$), and hence on average, some larvae moved longer distances than others – perhaps reflecting variation in short-term weather conditions. On the other hand, turning angles were not significantly different among individuals (one-way ANOVA of cosine-transformed angles, $F_{26,338} = 0.59$, $p = 0.92$). Therefore, we next analysed the relation between host plant density and movement length [the attribute that did vary among individuals]. Here, we detected no effect of host plant density on ln-transformed movement length (repeated measures ANCOVA; $F_{1,74.4} = 0.19$, $p = 0.67$). Hence, a larva walked no further per move even when host plants were sparse.

Simulations results

The density of larvae used in the simulation model per 20×20 m was 10.5 for meadow F, 5 for meadow g and 22 for meadow M. All our validations of the simulation model produced realistic results: simulated larvae moved forward (Fig. 7a) and away from their point of origin (Fig. 7b) at the same rate as real larvae. Simulated movement trajectories and spatial patterns of host plant damage were visually indistinguishable form observed patterns (data not shown). Most importantly, spatial aggregation in the simulated pattern of host plant damage quantitatively mimicked that of the observed pattern; within each meadow, the mean of the simulations closely tracked the observed curve (Fig. 2; compare solid black and grey lines), and all observed values fell well within the 95% confidence envelope generated by
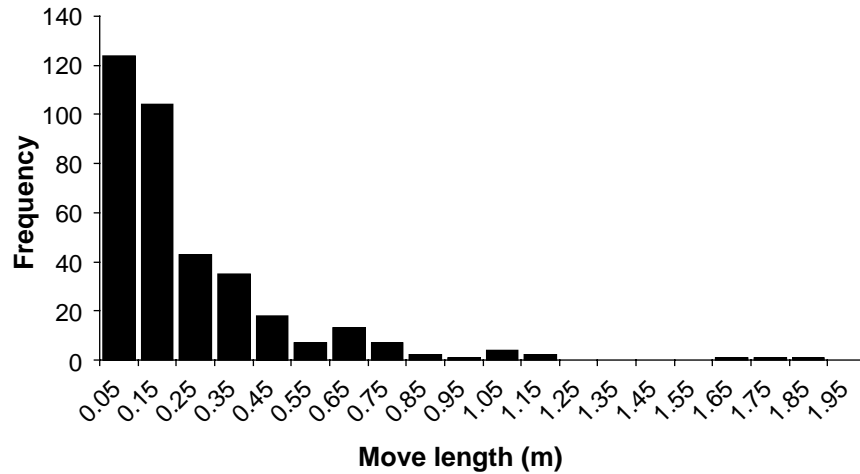
Fig. 6. Frequency histogram of the length of individual moves by *Parnassius* larvae.

the simulations (Fig. 2; solid black versus dashed grey line). Likewise, in two out of three meadows, the simulated pattern significantly deviated from that expected given no
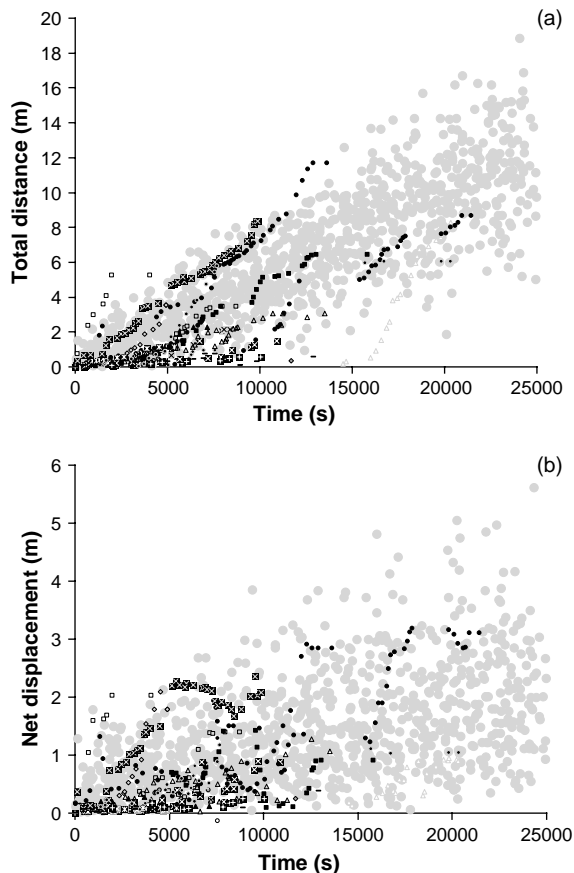

Fig. 7. Distance moved by *P. smintheus* larvae as a function of time: (a) total distance (i.e. the total length of the exact path followed by the larva) and (b) net displacement (the Euclidean distance between the start and end of the path). Empirically observed movement trajectories are shown by small black symbols (different symbol styles for different individuals), whereas larger grey dots show patterns observed in simulations for meadow M (results for other meadows quantitatively similar; not shown).

spatial aggregation (Fig. 2; solid grey line versus dashed black lines); exactly as did the observed pattern. In meadow F, neither the simulated nor the observed pattern showed any significant aggregation. Hence, not only did the simulation model accurately predicted aggregation where it occurred, but it also predicted the lack of it where it did not occur.

Discussion

This study shows that feeding damage on *Sedum lanceolatum* is spatially clumped at a scale of <0.5 m. Still, the level of damage is low: in 2002, only 5% of 2644 leaves on plants with any feeding damage had been chewed upon. Why would a 3 cm *Parnassius* larva eat so little, when moving to another plant will no doubt involve both risk and energy expenditure? Our results suggest that feeding damage induces a chemical response by the host plant, and that this response significantly affects larval performance at a time scale longer than that spent by wild larvae on individual plants. Hence, we suggest that apollo larvae hurry to switch host plant within the time window offering high nutritional quality. As shown by our simulation model, the spatial distribution of host plant damage can then be generated by caterpillars performing a simple random walk, based on the step frequency, length and turning angles observed in wild larvae. Hence, as the most parsimonious explanation for the observed level and pattern of host plant damage, we offer a scenario where induced changes in host-plant quality limits the time spent per plant, but the herbivore moves throught the landscape without any particular directionality. Such random movement has been suggested by work on *Pieris* larvae (Chew 1974), and proposed as the fundamental null model to be used in studies of animal movement (Turchin 1998).

In the basic scenario that we propose, the rate of caterpillar movement will be largely determined by the rate of plant response. Here, the rate of response observed in *Sedum lanceolatum* (1–2 d) is comparable to that observed in the birch *Betula pendula*, where a local increase in phenolic levels can be observed within 24 h from

pin-pricking (Bergelson et al. 1986). This response is first observed only in the immediate vicinity of the damage, but then spreads within the leaf so that between 24 h and 8 d the phenolic contents of the full leaf will differ from that of control leaves. The time frame of the response is also comparable to that observed in *Senecio jacobae* and *Cynoglossum officinale,* where alkaloid levels changed within 6–12 h and 24 h from damage, respectively (van Dam et al. 1993), and in tomato, where a response is observed within one day of feeding damage (Edwards et al. 1991, Stout and Duffey 1996, Kant et al. 2004). It seems somewhat quicker than in *Atropa acuminata,* where mechanical damage resulted in maximal induction of alkaloids after eight days (Bashir Kahn and Harborne 1990). We also note that the time scale is consistent with the observed level of aggregation in damaged *Sedum* leaves. Larvae feed quickly on leaves and will typically leave a plant in less than half an hour, well before the defence would be activated.

Once activated, we have no further information on the temporal persistence of an induced defence in *Sedum lanceolatum.* While our experiments reveal a delay of about one day in its induction, it is unclear whether it then extends for a week or for several years (cf. Haukioja and Neuvonen 1985a, Haukioja et al. 1990, Neuvonen and Haukioja 1991, Kaitaniemi et al. 1998, Nykänen and Koricheva 2004). It seems to persist for at least five days following induction, given that larvae grew significantly worse on plants damaged five days previous than on undamaged control plants. In the choice experiments, larvae also preferred leaves on plants damaged one day before to leaves on plants damaged five days before, suggesting a persisting response. The temporal dynamics of the defence offer an interesting topic for future research.

One potential mechanism behind the observed induced defense is the activation of the jasmonate pathway. In a seminal study, Rodriguez-Saona and Thaler (2005) showed that while larvae of the moth species *Spodoptera exigua* grew best on tomato plants deficient in producing jasmonate-related defensive proteins, damaged wild-type plants had more than twice as many leaves and leaflets damaged, and twice as many feeding holes eaten by *S. exigua* larvae compared to jasmonate-deficient plants. These findings suggest that induction of the jasmonate pathway plays a key role in determining the amount and distribution of feeding damage on tomato plants. Since jasmonate can trigger induced plant defenses in a wide range of plants (Baldwin 1996), and interact with other defense pathways (Thaler et al. 2002), the results may well extend to other taxa – but whether this is really the case can only be resolved by further studies.

In our experiments, the results from different data sets largely support each other. Nevertheless, the results from the choice experiments may first seem confusing. Here, the larvae distributed themselves evenly among plants of different types. This observation contrasts with clear-cut differences in the amount of biomass consumed on plants damaged at different times or to a different extent. Nevertheless, the even distribution of larvae per se likely reflects how small a proportion of their total time they actually spend feeding (cf. Fig. 5). In fact, larvae seem to spend most of their time moving between host plants, touching and tasting them – and are thereby as likely to be observed on either plant in the choice experiment, although they will then, in fact, feed mostly on one of them. This interpretation is also supported by our observations from the experiment where larvae were given a choice between damaged and undamaged plants; although larvae consumed more biomass on undamaged *Sedum* plants, they actually tasted a higher number of leaves on damaged plants.

Our observations from the *Parnassius-Sedum* system have clearcut implications for both the host plant and for the larvae. Most importantly, the realised spatial distribution of host plant damage may create spatial variation in both plant and insect fitness – the basic currency of both population dynamics and evolutionary response. From the perspective of the host plant, large variation in feeding damage among individual meadows correspond to large variation in the per capita risk of a plant being damaged (ranging from 23% in meadow g to 61% in meadow M; Fig. 2). Since feeding damage may drain vital resources, and since feeding larvae will often destroy the flowers of *Sedum,* this will likely result in meadow-to-meadow variation in plant fitness. Within meadows, the scale of aggregation in feeding damage is proportional to the length of larval movements. Since damage is clumped at a small scale, it may be detrimental to a host plant to have neighbours closer than 40 cm. Nevertheless, Singer and Wee (2005) have suggested that it may be more beneficial for a plant to grow in a group than to be more isolated, because growing in a group serves to spread the risk in the event of herbivore attack. Their reasoning does not hold in the current system, however, because when damage does occur, it is higher on a per-leaf (and per-plant) basis than it would be had the leaves (and plants) been distributed randomly (Fig. 2 and 3). Regardless of the exact shape of the relation between plant location and feeding risk, the mere existence of such a relationship may affect the spatial distribution of the host. In *Sedum,* there are no signs of overdispersion, but rather of clumping (Fig. 1; cf. Fownes and Roland 2002). So far, we have not conducted any specific experiments to reveal the effect of host plant distribution on biological fitness, but experimental transplantation of host individuals would be easy, thus opening avenues for future research.

From the perspective of *Parnassius* larvae, the spatial distribution of the host plant may affect larval survival. Although female *Parnassius* do not lay eggs directly on the larval host plant, *Sedum* presence does elicit oviposition (Fownes and Roland 2002). Because females oviposit off the host plant, hatching first-instar larvae must locate and move to a *Sedum* plant. Successful orientation and establishment of *Parnassius* on a host plant should therefore result from a combination of both *Sedum* availability and its spatial pattern. For example, a randomly searching *Parnassius* larva will have less chance of encountering a host plant in a meadow with small clumps of host plant. Our current observations suggest that the larvae do search at random, and do not modify their movements in reponse to the density of host plants. Preliminary observations from European *Parnassius apollo* suggest the same; here, the larvae seem not to detect the host pant *Sedum telephium* from any distance, nor do ovipositing females react to the fine-scale distribution of *Sedum* (M. Fred pers. comm.).

Nevertheless, the issue is further complicated by the fact that adult movements are influenced both by the distribution of habitat with *Sedum* and by nectar resources (Brommer and Fred 1999), a pattern also observed in *P. smintheus* (Matter and Roland 2002).

Most importantly, the induced response observed in *Sedum* will affect the growth rate of *Parnassius* larvae. In general, the growth rate of insects will have important fitness consequences (although the exact relationship may be complex; Gotthard et al. 1994, Gotthard 2000), and so will their eventual size; larger females are more fecund in a wide range of taxa (Haukioja and Neuvonen 1985b, Roff 1992, Tammaru et al. 1996, Nylin and Gotthard 1998), including *P. smintheus* (Reed and Matter unpubl.). Therefore, the induced response of *S. lanceolatum* may have important effects on the performance of *P. smintheus*, and result in behavioural choices largely determining the spatial pattern of host plant damage. Since the larvae do not modify their movement trajectories in reponse to the local density of the host plant, both local damage levels and the local performance of *P. smintheus* should vary significantly in space. Spatial variation in damage levels is well evident in Fig. 1–3, but so far we have no data on spatial variation in larval performance. The pattern observed at the plant level does suggest that plant-herbivore interactions may add to the list of factors affecting local and regional buttefly population dynamics (Matter et al. 2003, Roland and Matter 2007). This interesting predicition – and its implications for population dynamics – will be tested in forthcoming work.

In conclusion, this study adds a spatial perspective to the interaction between *Parnassius smintheus* and its host plant *Sedum lanceolatum*. While several factors may favour host-switching (Mody et al. 2007), we offer induced reponses as a key factor behind observed low levels of herbivore damage in the *Sedum-Parnassius* system. We end by identifying an interesting corollary: while we show that some compounds produced by *Sedum lanceolatum* are obviously harmful to larval growth in *P. smintheus*, the larvae may also use noxious chemicals produced by the host plant for their own defence. The larvae of *P. smintheus* are aposematic and have been shown to sequester a bitter-tasting compound from at least one *Sedum* species, the wormleaf stonecrop *Sedum stenopetalum*; Nishida and Rotschild (1995). The sequestered compound has been identified as the cyanoglucoside sarmentosin (also known from *Sedum lanceolatum*; Garrigan 2002), but whether it is part of the host's constitutive or induced defence is not known. At least it is present in relatively high amounts in undamaged plants. What specific compounds are involved in the induced response revealed by our study we do not know (for general discussions of allelochemicals in *Sedum* and other Crassulaceae, see Stevens et al. 1995, Kim et al. 1996, Korul'kin 2001). That its net effect is harmful is shown by decreased growth and active avoidance by the larvae. It would be interesting to learn whether they are involved in larval defence, too, in which case larvae will be caught between a rock and a hard place; increasing chemical protection will be associated with reduced growth. Identifying the compounds involved will then be a key priority for future work.

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