Department of Physics, Chemistry and Biology

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Habitat utilisation of burnet moths (*Zygaena* spp.) in southern Sweden: a multi-stage and multi-scale perspective

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Nyckelord
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Contents

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Keywords: Conservation, habitat cover, habitat requirements, life stages, occurrence probability, *Zygaena*

2 Introduction

Owing to their quick response to habitat fragmentation and deterioration, butterflies have commonly been considered as good indicators of general habitat health (e.g. Thomas, 1991; Erhardt & Thomas, 1991). Butterflies also fulfill several criteria for so-called "umbrella species" – species whose conservation is likely to improve the status of other organisms that require similar habitat conditions and are able to live in the same areas (New, 1997). However, like many other animal groups, butterflies have experienced long-term declines in both abundance and distribution throughout Europe, with about 12 % of the European butterfly species currently being threatened (van Swaay & Warren, 1999; Maes & van Dyck, 2001; Warren *et al.*, 2001; Douwes, 2004; Gärdenfors, 2005; van Swaay *et al.*, 2006; Wenzel *et al.*, 2006). The main reason for this decline is assumed to be the past and present loss of appropriate habitat types, e.g. semi-natural grassland (Ihse, 1995; Maes & van Dyck, 2001; Petit *et al.*, 2001; Gärdenfors, 2005; van Swaay *et al.*, 2006; Franzén & Johannesson, 2007). In Sweden, the area of semi-natural grassland decreased by 87-99 % between 1927 and the beginning of the 1990s (Ekstam & Forshed, 2000). The loss is mainly brought about by changed or intensified farming and by land abandonment, where the former leads to a reduced richness of flowering herbs or to overgrazing/-mowing and the latter results in overgrowth or afforestation of open areas. Both factors are likely to continue in the future, putting an even larger pressure on an already weakened group of species (Ihse, 1995; Petit *et al.*, 2001; Gärdenfors, 2005; Nilsson *et al.* 2008). In addition, fragmentation of the remaining semi-natural grasslands have resulted in decreased connectivity between the areas, and with that, reduced dispersal among populations (Ihse, 1995).

A species' presence is often limited by a variety of factors and can be seen as an interplay of biotic and abiotic elements. Traditional metapopulation studies have focused on the distribution of species in relation to size and isolation of habitat patches, stating that small and/or isolated patches are more likely to be unoccupied. Small patches often hold small local populations which are particularly prone to extinction, and isolated habitat patches are less likely to become colonised (e.g. Hill *et al.*, 1996; Thomas & Hanski, 1997; Hanski, 1999). On a more narrow scale, butterfly distribution is thought to be determined by the quality of individual habitats (e.g. Thomas, 1991; Bergman, 1999; Freese *et al.*, 2006; Albanese *et al.*, 2008). However, the relative importance of habitat area, isolation and quality remains under debate, and recent work is now emphasising the importance of including all factors in conservation strategies (Thomas *et al.*, 2001; Anthes *et al.*, 2003; Dennis *et al.*, 2003, 2006; Öckinger & Smith, 2006; Öckinger, 2008). Furthermore, in terms of habitat quality, the abundance and distribution of a species depend on the total availability of resources needed during separate life stages. The young stages of butterflies have been shown to require highly specific conditions, wherefore the distribution of adult individuals is restricted by the habitat requirements of eggs, larvae and pupae (Thomas, 1984; Thomas, 1991; Bourn, 1995; Bergman, 1999; Anthes *et al.*, 2003; Albanese *et al.*, 2008). On the other hand, factors affecting adult individuals, such as nectar resources, are also critical to maintaining butterfly populations, and the breeding grounds of butterflies are often the same as the areas inhabited by the imagines (Williams, 1988; Britten & Riley, 1994; Naumann *et al.*, 1999; Ellis, 2002 cited by Ellis, 2003; Dennis *et al.*, 2006).

As for most butterflies, the reduction of suitable habitat has also affected the burnet moths, Zygaenidae (Wenzel *et al.*, 2006; Naumann *et al.*, 1999), with six out of seven Swedish species currently being listed as VU (vulnerable) or NT (near threatened) on the Red list of Swedish species (Gärdenfors, 2005). Burnet moths have proved to be strongly correlated to the richness of butterflies and are predicted to act as good indicators of species-rich semi-natural grasslands (Franzén & Ranius, 2004; Franzén & Nilsson, 2008). Because they are readily recognised, sedentary, fearless and low-flying, they are also easy to survey (Naumann *et al.*, 1999). However, the exact ecology of this family of moths is still poorly known (Franzén & Ranius, 2004).

The aim of this study was to gain a better understanding of the total habitat requirements of three species of burnet moths: *Zygaena filipendulae*, *Zygaena lonicerae* and *Zygaena viciae*, in different life stages and on two spatial scales, assessing the importance of a multi-stage and multi-scale perspective. The results may bring about more effective conservation and management plans in order to protect and improve the status of burnet moths and other butterfly species.

3 Materials and methods

3.1 Study species

Burnet moths, within the family Zygaenidae, are diurnal lepidopterans easily recognised by their slow, buzzing flight and characteristic appearance. All life stages produce and release cyanide compounds as a defensive strategy, and their conspicuous features are considered to be aposematic (Naumann *et al.*, 1999).

Burnets usually prefer open and sunny biotopes; areas often being the direct or indirect results of human activities (meadows, woodland clearings and road verges), where their respective host plants and nectar sources are abundant (Naumann *et al.*, 1999; Gutiérrez *et al.*, 2001; Franzén & Ranius, 2004). Larvae of the subgenera *Zygaena* feed almost exclusively on plants of Fabaceae, and the imagines are attracted to red and violet Asteraceae flowers, but also to *Origanum vulgare*, *Valeriana officinalis* and *Inula salicina* (Hofmann, 1994; Naumann *et al.*, 1999; Söderström, 2006; Swedish Species Information Centre, 2007, 2008b, 2008c). Individuals are generally univoltine and larvae that hatch from eggs laid in the end of the flying season hibernate from late autumn to spring, when they resume feeding again. Pupation occurs in mid summer (Naumann *et al.*, 1999). In Sweden, *Z. filipendulae* and *Z. viciae* occur in south to mid Sweden whereas *Z. lonicerae* can be found sparsely up to more northern regions (Gärdenfors, 2005). Nomenclature for burnets follows Naumann *et al.* (1999), and for plants Tutin *et al.* (1964-1980), except for *Lathyrus linifolius* (Reichard) Bässler.

3.2 Study sites

Surveys of burnet moths were conducted on four sites on the Baltic island Öland, patches ranging from 0.14 to 1.3 hectares (Figure 1). The landscape is dominated by natural and semi-natural grassland and deciduous woodland, large areas being of high nature conservation values (Forslund, 2001). Sites were derived from the "Species Gateway" at the Swedish Species Information Centre (Swedish Species Information Centre, 2008a) and from local knowledge[1], and are henceforth referred to as A, B, C and D (Figure 1).

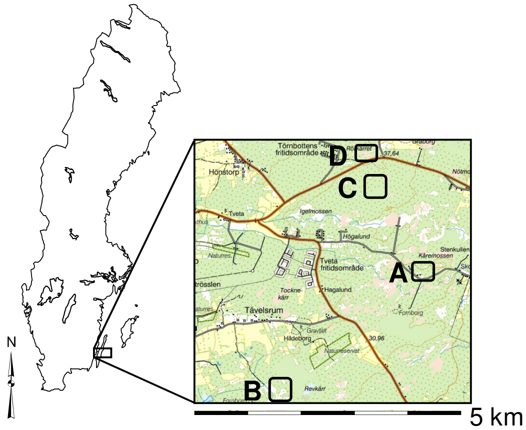

Figure 1. The four study sites on the Baltic island Öland.

3.3 Species surveys and habitat characteristics

Surveys of burnet moths took place between 3 June and 23 July 2008, covering mid to late larval instars, pupation and peak flight periods.

3.3.1 Larvae

From early June to early July, I systematically surveyed the four sites once, and actively searched for larvae on plants of Fabaceae, or on plants in the immediate vicinity of a Fabaceae plant. When an individual was observed, I recorded the plant species and the plant area (the total area of leaves, in cm^2). Moving larvae, or larvae found on plants not mentioned in previous literature, were not included in further statistical analyses of host plant choice. Within a circle of 1 m diameter centred on the larva, a set of habitat parameters was measured (Table 1). Due to identification difficulties, all *Vicia* species are henceforth referred to as *Vicia* spp, and the two *Trifolium* species *T. pratense* and *T. medium* are named *Trifolium medium/pratense*.

In a bigger circle of 5 m diameter centred on the larva, variables concerning nectar sources were measured (Table 1). Before surveying the 5 m circles, the ground within the circle was carefully examined so to not miss or harm larvae not yet found. Vegetation height was measured using the 'drop disc method': a 50 cm diameter disc made of hard material, weighing 430-440 g, is dropped down a vertically held ruler. The vegetation height where the disc comes to rest is recorded.

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[1] Bengt-Åke Bengtsson (Ph. D. h. c. at the University of Kalmar), Dave Karlsson (former part-time coordinator of The Swedish Malaise Trap Project) and Mats Lindeborg (biologist, the County Administrative Board of Kalmar).

3.3.2 Pupae

From late June to early July, pupae were surveyed by active search on larval host plants and on plants in the immediate vicinity of a larval host plant, all localities searched once. The cocoons of *Z. viciae* are often spun low down and hidden by vegetation, making them difficult to find, whereas the pupae of *Z. filipendulae* and *Z. lonicerae* are usually placed high up in the vegetation. Hence, I only searched for pupae of *Z. filipendulae* and *Z. lonicerae*. When a cocoon was located, the surrounding habitat was investigated similar to as described for larvae (Table 1). The height of individual pupae on their leaves of grass was also measured for further comparison with the vegetation height in their respective circles.

The cocoons of *Z. filipendulae* and *Z. lonicerae* are problematic to discriminate from one another and therefore, at site A where both species occurred together, cocoons that could not be distinguished were collected. When a burnet moth emerged from a collected cocoon, it was identified to species and brought back to the site. Of the ten pupae collected from site A, two proved to be parasitised by hymenopteran parasitoids (from the subfamilies *Cryptinae* and *Campopleginae*) and one remained unhatched. These pupae were not included in further anayses.

3.3.3 Imagines

Each site was visited twice during the peak flight period (2nd to 4th week of July). Burnets were surveyed along transects located 10 m apart, and all individuals observed within a semicircle 2.5 m ahead and 2.5 m to the sides of the observer were recorded and named to species. If a burnet individual could not be named to species immediately, photos were taken and sent to experts for later identification. Transects were oriented perpendicular to the short side of the site and were walked in a steady pace of about 50 m min^{-1} (following Wikström *et al.*, 2009). When spotting a resting, non-flying individual, the nectar source upon where it was found was recorded and its presence was marked on the ground with a coloured stick. After walking the transects, I revisited the marked positions where adults had been located and recorded a set of habitat variables within circles of 1 and 5 m diameter centred on the observation point, according to the procedure of larvae and pupae (Table 1). Possible nectar sources were selected according to main literature (Hofmann, 1994; Naumann *et al.*, 1999) and from field observations.

Table 1. Habitat variables measured around larvae, pupae or imagines.

Parameter	**Larva**	**Pupa**	**Imago**	**Definition, (diameter of circle)**
Area (cm^2) of chosen larval host plant	●	○	○	Total leaf area of the plant upon where a larva was observed.
Cover (%) of chosen larval host plant	●	○	○	Density of the plant species upon where a larva was observed, (1 m Ø).
Cover (%) of possible larval host plants	●	●	●	Density of possible larval host plants, (1 m Ø).
Chosen nectar source	○	○	●	Number of flowering flower heads of the plant species upon where an individual was observed, (5 m Ø).
Possible nectar sources	●	●	●	Number of flowering flower heads of possible nectar sources, (5 m Ø).
Sward height	●	●	●	Mean value of 5 measurements, (1 m Ø).
Cover (%) of bare ground	●	●	○	(1 m Ø).
Cover (%) of dry grass	●	●	○	(1 m Ø).
Sun exposure	●	●	●	The spot's estimated percentage daily exposure to light between 09:00 and 17:00 Swedish summer time, GMT+2.

● = Parameter studied
○ = Parameter not studied

3.4 Inventory criteria

Imago surveys were made according to Pollard and Yates (1993) and Wikström *et al.* (2009), i.e. during sunny conditions, temperatures above 17 ºC and wind speed below 8.0-10.7 $m\ s^{-1}$ (Beaufort scale force 5). As long as temperature was above 20 ºC, surveys were also made during partially cloudy conditions, since the importance of sunshine decreases rapidly above this level (Wikström *et al*., 2009). Larvae and pupae are less sensitive to weather conditions than imagines, and surveys of these earlier phases could be carried out during less favourable conditions than described above, although no surveys of larvae were made during rainy weather, as rain reduces their activity[2]. Inventories of adults took place between 12:00 and 16:00 (Swedish summer time, GMT+2), corresponding to the burnet moths' peak activity (Wikström *et al*., 2009).

3.5 Controls

Within each study site, plant and habitat characteristics around burnets were contrasted with that of 20 to 31 randomly selected control circles, scattered throughout the sites. Control circles were of the same size as the circles used during burnet surveys, i.e. 1 and 5 m diameter. In the 1 m control circles, the following variables were measured: percentage cover of possible larval host plants, percentage cover of bare ground, percentage cover of dry grass, sward height and sun exposure. Moreover, the area of any possible host plant being closest to the centre was measured. In the 5 m diameter circles, the number of flowering flower heads of possible nectar plants was counted. Positions of larval and pupal control circles were derived by random number generation of GPS coordinates. Control circles of imagines were placed at regular intervals along the imago survey transect, a total of 20 to 22 at each site. Data on habitat characteristics measured in control circles were compared between sites, and sites that did not differ significantly were treated together in further statistical analyses. (Table 2).

Table 2. Values of habitat variables in control circles, arranged site-wise (*mean* ± *SD*). *Period 1*, *2 and 3 refer to the time periods for larval*, *pupal and imaginal control surveys.*

Period	Site	Sward height (cm)		Cover of bare ground (%)		Cover of dry grass (%)		Sun exposure (% between 9:00-17:00)	
		Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
1	**A**	24.6	9.9	0.7	1.3	1.4	2.4	88.0	20.7
	B	21.9	6.1	0.3	0.9	1.4	2.0	98.2[b]	6.8
	C	10.8[c]	2.9	0.6	1.0	1.0	1.7	77.8	26.0
	D	20.5	10.8	9.7	21.4	10.6[d]	21.5	72.7	34.5
2	**A**	25.6	8.4	1.1	1.9	2.5	2.6	89.0[a]	15.6
	B	23.5	7.5	0.8	2.0	1.1	1.7	97.8[b]	5.1
	C	11.7[c]	2.7	0.5	0.7	2.6	6.2	68.1[c]	28.8
	D								
3	**A**	26.7	7.9					72.4	27.9
	B	25.7	9.5					92.9[b]	18.1
	C	9.8[c]	2.8					77.5	23.5
	D	23.3	9.7					70.3	34.3

[a] Site A differed significantly from remaining sites.
[b] Site B differed significantly from remaining sites.
[c] Site C differed significantly from remaining sites.
[d] Site D differed significantly from remaining sites.

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[2] pers. comm., Eric Öckinger, researcher at the Department of Ecology, Swedish University of Agricultural Sciences.

3.6 Large scale studies

To assess if there is a relationship between the amount of semi-natural grassland and the presence of burnet moths, and whether this possible relationship differs between species, I made map-based analyses using ARCVIEW GIS 9.0. Data on the distribution of meadows and pastures were downloaded from the Swedish Board of Agriculture (Swedish Board of Agriculture, 2005), based on a national inventory of valuable semi-natural meadows and pastures between 2002 and 2004 (Persson, 2005). Meadows and pastures no longer considered to be of interest (e.g. overgrown or planted areas according to Persson, 2005) were excluded. The total area of meadows and pastures was calculated within 10 x 10 km grid squares. A meadow or pasture that extended over two or more grid cells was not partitioned into the separate cells. Instead, each cell was given the entire areal value of the meadow or pasture, independently of the actual fraction of meadow or pasture being present. However, this overestimation of area did not cause any major areal change within each grid cell because most meadows and pastures were small in size. To minimise the impact of temperature on burnet presence or absence, semi-natural grassland and burnet observations north of a line corresponding to a mean annual temperature of 5 °C were excluded. Data on mean annual temperature between 1961 and 1991 were derived from the Swedish Meteorological and Hydrological Institute, SMHI.

Coordinates of burnet presence from 1990 onward were derived from the "Species Gateway" at the Swedish Species Information Centre (Swedish Species Information Centre, 2008a). *Zygaena viciae* is not present on the island of Gotland (Gärdenfors, 2005) and therefore, the island was omitted from analyses of this species.

3.7 Statistical analyses

Differences between controls, between life stages, and between each life stage and controls were evaluated using two sample t-test or, in the case of non-normally distributed data and/or heteroscedasticity, its nonparametric equivalent Mann-Whitney U test. For all tests, statistical significance was accepted as $P < 0.05$.

The effect of the total area of meadows and pastures on burnet presence was analysed with a Generalized Linear Model (GLZ): binomial distribution, logit link function, using STATISTICA 8.0. The presence (1) or absence (0) of burnet moths was used as dependent variable and the total area of meadows and pastures within 10 x 10 km grid cells was used as predictor variable. Data on the area of meadows and pastures were $\log_{10}$(area +1) transformed to reduce right skew prior to analyses. If area was significant, i.e. if it was shown to have some effect on burnet presence, the predicted probability values with 95 % confidence intervals were plotted and the areas required for 10, 30 and 50 % probability of burnet occurrence were calculated. All statistical analyses, except for GLZ, were performed by use of SPSS 15.0 for Windows.

4 Results

Each burnet species occurred at three of the four sites visited: *Z. filipendulae*: A, B and C; *Z. lonicerae*: A, C and D; *Z. viciae*: A, B and D. A total of 21-32 larvae and 28-32 imagines were observed, the number varying between species. Because the cocoons of *Z. viciae* are difficult to find, only pupae of *Z. filipendulae* and *Z. lonicerae* were searched for. However, the number of *Z. lonicerae* pupae found was too low (n = 3) to analyse statistically and therefore, concerning pupal evaluations, only the results of *Z. filipendulae* (n = 23) are presented hereafter. Results for host plants and nectar sources are henceforth reported for all sites together, whereas results regarding vegetation height, sun exposure, cover of bare ground and cover of dry grass are either reported for single sites or for combinations of sites, due to between-site dissimilarities (Table 2).

4.1 Larval host plants

For each burnet species, larval host plant choice was estimated as the proportion of times an individual larva was found on a particular plant. There was a clear difference in host plant choice between the three species. For *Z. filipendulae*, the dominating larval host plant was *Lotus corniculatus* (n = 18; 75 %), whereas *Z. lonicerae* chose *Trifolium medium/pratense* (n = 13; 93 %) and *Z. viciae* was mostly found on *Vicia* spp. (n = 18; 69 %). *Zygaena filipendulae* also used *Lathyrus pratensis* (n = 2; 8 %), *Z. lonicerae* was also found on *L. corniculatus* (n = 1; 7%) and *Z. viciae* was observed on *L. pratensis* (n = 5; 19 %), *L. corniculatus* (n = 1; 4 %) and *T. medium/pratense* (n = 2; 8 %) (Figure 1).

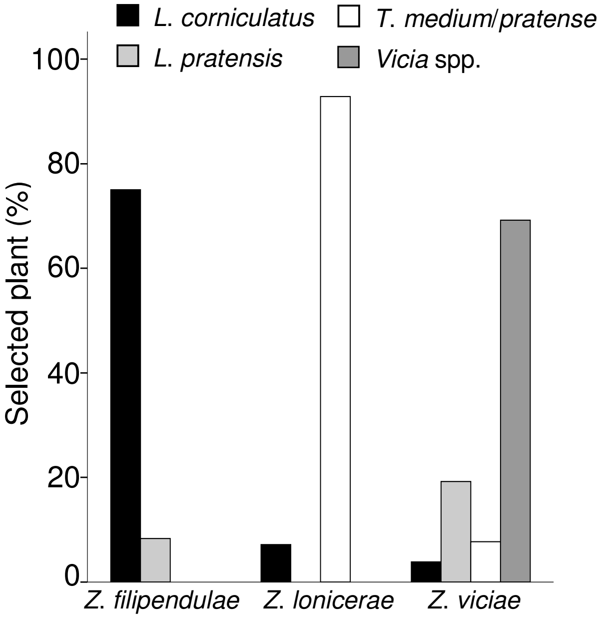


Figure 2. Frequency of larval observations on the most important host plants as compared to observations on other green plants, all sites in total.

4.2 Cover of larval host plant

4.2.1 Larva

The percentage cover of the most important host plant differed between larval and control circles (Figure 3a). For all three burnet species, the cover of their individual most important host plant was greater in larval circles as compared to control circles (*Z. filipendulae*, *L. corniculatus*: Mann-Whitney $U = 166.5$, $Z = -7.83$, $n_l = 32$, $n_c = 73$, $P < 0.01$; *Z. lonicerae*, *T. medium/pratense*: $U = 265.50$, $Z = -4.33$, $n_l = 21$, $n_c = 61$, $P < 0.01$ and *Z. viciae*, *Vicia* spp.: $U = 427$, $Z = -4.45$, $n_l = 27$, $n_c = 70$, $P < 0.01$).

4.2.2 Pupa

There was no difference in the cover of the most important larval host plant, *L. corniculatus*, between *Z. filipendulae* pupal and control circles (Mann-Whitney $U = 611$, $Z = -1.17$, $n_p = 23$, $n_c = 61$, $P = 0.240$).

4.2.3 Imago

In either species, no difference was observed between imagines and controls regarding the cover of the most important larval host plant (*Z. filipendulae*, *L. corniculatus*: $t_{(149)} = -0.55$, $P = 0.580$; *Z. lonicerae*, *T. medium/pratense*: $t_{(148)} = -1.02$, $P = 0.311$; *Z. viciae*, *Vicia* spp.: $t_{(173)} = 1.46$, $P = 0.146$).

4.2.4 Between stages

The cover of *L. corniculatus* was greater in *Z. filipendulae* larval circles as compared to the circles of pupae or imagines (larvae/pupae: Mann-Whitney $U = 59.5$, $Z = -5.427$, $n_l = 32$, $n_p = 23$, $P < 0.01$; larvae/imagines: Mann-Whitney $U = 110$, $Z = -5.45$, $n_l = 32$, $n_i = 31$, $P < 0.01$). Likewise, both *Z. lonicerae* and *Z. viciae* larvae were found on spots where the cover of their most important host plant, *T. medium/pratense* or *Vicia* spp., was higher than could be observed around imagines (*Z. lonicerae*: Mann-Whitney $U = 74.50$, $Z = -4.86$, $n_l = 21$, $n_i = 28$, $P < 0.01$ and *Z. viciae*: $U = 484.50$, $Z = -2.42$, $n_l = 27$, $n_i = 53$, $P < 0.05$). Pupae and imagines of *Z. filipendulae* did not differ regarding the cover of *L. corniculatus* ($t_{(52)} = -0.69$, $P = 0.492$) (Figure 4).

4.3 Larval host plant area

Except for one *L. corniculatus* plant, which was too reduced by the larva to be measured, the selected host plants were larger than randomly measured plants of the same species (the most important host plants considered: *Z. filipendulae*, *L. corniculatus*: Mann-Whitney $U = 38$, $Z = -2.08$, $n_l = 17$, $n_c = 9$, $P < 0.05$; *Z. lonicerae*, *T. medium/pratense*: Mann-Whitney $U = 34$, $Z = -3.33$, $n_l = 13$, $n_c = 18$, $P < 0.01$; *Z. viciae*, *Vicia* spp.: Mann-Whitney $U = 71.0$, $Z = -2.52$, $n_l = 18$, $n_c = 16$, $P < 0.05$) (Figure 3b).

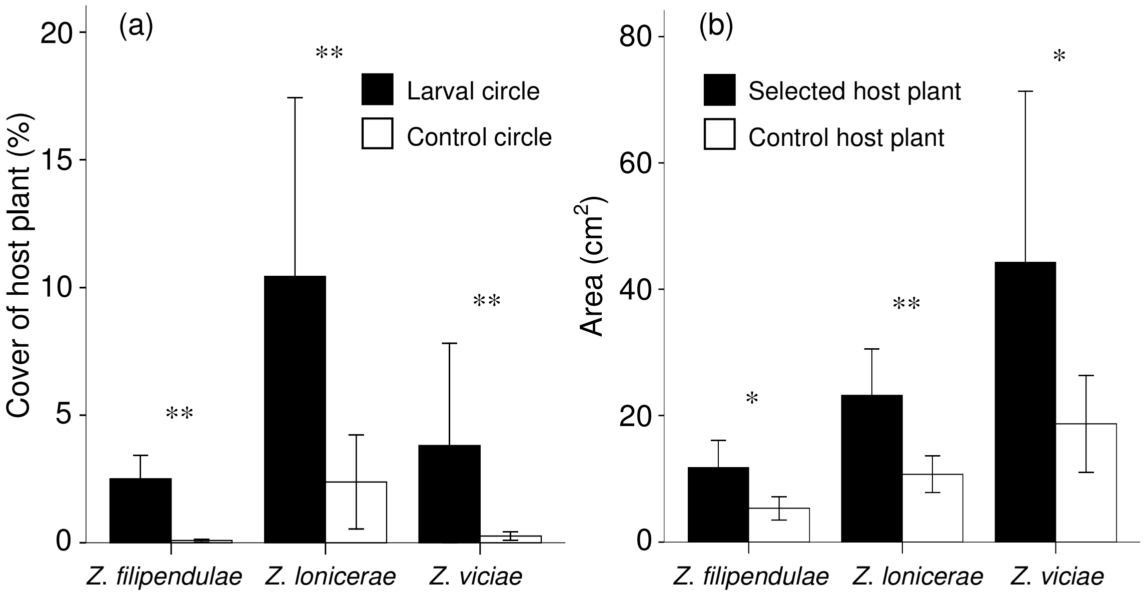


Figure 3. (*a*) *Mean percentage cover of host plants in larval and control circles, 1 m diameter, and* (*b*) *mean size of larval-selected and random host plants* (*the most important host plants considered*: L. corniculatus (Z. filipendulae), T. medium/pratense (Z. lonicerae) *and* Vicia *spp.* (Z. viciae)). *Level of significance is shown as* * $P < 0.05$, ** $P < 0.01$.

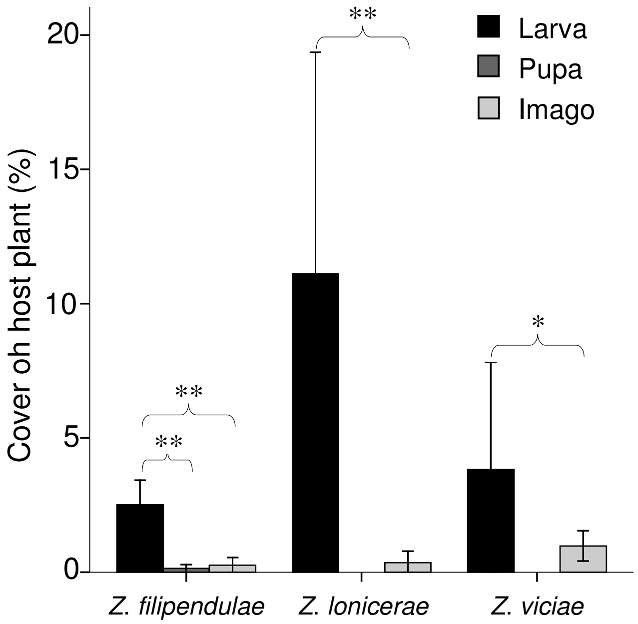


Figure 4. Mean percentage cover of the most important host plants: L. corniculatus (Z. filipendulae), T. medium/pratense (Z. lonicerae) *and* Vicia *spp.* (Z. viciae) *in circles of larvae, pupae and imagines, 1 m diameter. Only pupae of* Z. filipendulae *were analysed (see text for more information). Level of significance is shown as * $P < 0.05$, ** $P < 0.01$.*

4.4 Vegetation height

During the entire survey period, the overall vegetation height at site C was lower than at sites A, B and D (Table 2). Consequently, values for site A, B and D are henceforth reported in the combinations AB, AD and ABD, whereas site C is considered separately.

4.4.1 Larva

The *Z. filipendulae* larvae at site C were surrounded by a sward taller than average (Mann-Whitney U = 15, Z = -2.00, $n_l = 4$, $n_c = 21$, $P < 0.05$), whereas there was no significant difference between larval and control circles the AB site combination ($t_{(77)} = 0.57$, P = 0.568). For *Z. lonicerae*, there was no difference between larval and control circles, neither at site combination AD nor at site C ($t_{(47)} = -0.73$, P = 0.470 and $t_{(30)} = 0.78$, P = 0.443). For *Z. viciae*, all sites analysed together (ABD), larvae were found in vegetation higher than average ($t_{(96)} = 2.86$, $P < 0.01$) (Figure 5).

4.4.2 Pupa

There was a tendency towards a higher than average vegetation around *Z. filipendulae* pupae at the AB site combination, although not statistically significant ($t_{(60)} = 1.53$, P = 0.132). Only one pupa was found at site C, wherefore the individual was omitted from statistical analyses but is shown for comparison in Figure 5. Analyses of the height of individual pupae on their leaves of grass compared to the vegetation height within their respective circles revealed that pupae were placed significantly higher than the mean vegetation height within the circles ($t_{(23.871)} = 3.70$, $P < 0.01$).

4.4.3 Imago

The vegetation around imagines of *Z. filipendulae* at site C was significantly higher than the average sward (Mann-Whitney U = 31.50, Z = -2.48, $n_i = 5$, $n_c = 40$, $P < 0.05$). In contrast, an opposite trend was found at the AB site combination, although not statistically significant ($t_{(104)} = -1.76$, $P = 0.082$). The same pattern was observed for *Z. lonicerae*; the imagines preferring a sward taller than average at site C ($t_{(57)} = 3.57$, $P < 0.01$) but not different from controls at the AD site combination (Mann-Whitney U = 356, Z = -0.17, $n_i = 9$, $n_c = 82$, P = 0.863). For *Z. viciae*, all three sites pooled (ABD), the vegetation height around imagines was significantly higher than average ($t_{(173)} = 2.73$, $P < 0.01$) (Figure 5).

4.4.4 Between stages

At the AB site combination, pupae of *Z. filipendulae* were surrounded by higher vegetation than larvae and imagines. The difference was significant between pupae and imagines ($t_{(46)} = 2.37$, $P < 0.05$) and close to significant between pupae and larvae ($t_{(48)} = -1.99$, $P = 0.052$). Because there was only one pupa found at site C, this individual was omitted from analyses. Larvae and imagines did not differ, neither at the AB site combination ($t_{(52)} = 0.57$, $P = 0.568$) nor at site C (Mann-Whitney U = 7, Z = -0.74, $n_l = 4$, $n_i = 5$, P = 0.461). Likewise, neither *Z. lonicerae* nor *Z. viciae* displayed any difference regarding vegetation height between larvae and imagines, at any site or combination of sites (*Z. lonicerae*, sites AD: Mann-Whitney U = 31, Z = -1.14, $n_l = 10$, $n_i = 9$, P = 0.253, site C: Mann-Whitney U = 83.5, Z = -0.91, $n_l = 11$, $n_i = 19$, P = 0.365; *Z. viciae*, sites ABD: $t_{(78)} = -0.76$, $P = 0.450$) (Figure 5).

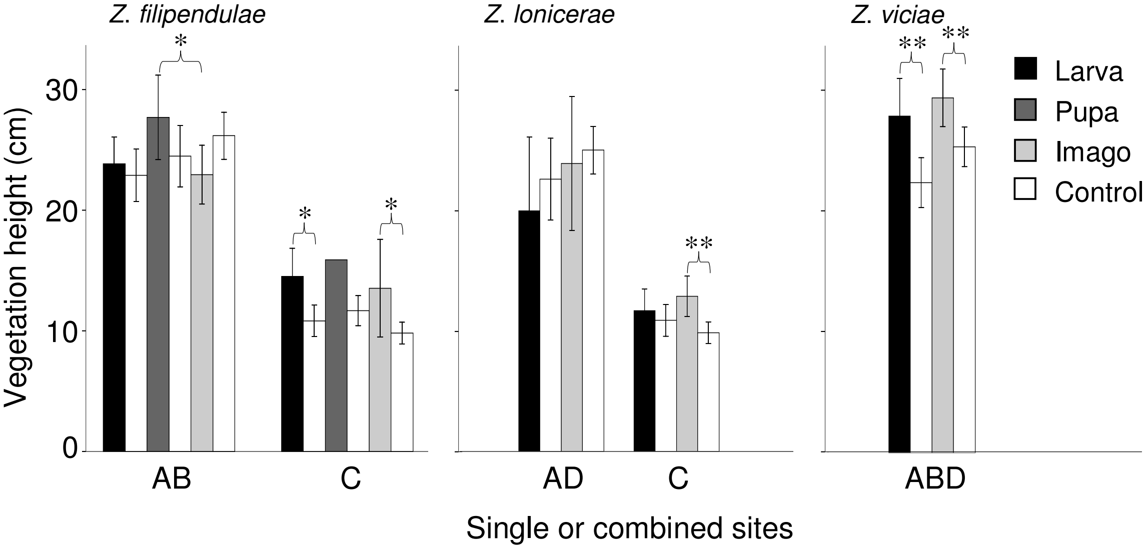


Figure 5. Mean vegetation height in circles centred on larvae, pupae or imagines and the corresponding vegetation height in control circles for each life stage, 1 m diameter. Only one pupae of Z. filipendulae *was found at site C, hence the absence of error bars. Level of significance is shown as * $P < 0.05$, ** $P < 0.01$.*

4.5 Cover of bare ground

During neither larval nor pupal surveys, the percentage cover of bare ground differed between sites (Table 2) and values are presented below in the site combinations ABC, ABD and ACD.

4.5.1 Larva

Zygaena filipendulae larvae were surrounded by less bare ground (i.e. more ground cover) than randomly selected spots (sites ABC: Mann-Whitney U = 923.5, Z = -2.28, $n_l = 32$, $n_c = 73$, $P < 0.05$), whereas no statistical difference was found between larvae and controls of *Z. lonicerae* and *Z. viciae* (*Z. lonicerae*, sites ACD: $t_{(80)} = -0.65$, $P = 0.515$; *Z. viciae*, sites ABD: $t_{(96)} = -1.10$, $P = 0.275$) (Figure 6).

4.5.2 Pupa

Pupae of *Z. filipendulae* were surrounded by less bare ground as compared to controls (sites ABC: Mann-Whitney U = 525, Z = -2.35, $n_p = 23$, $n_c = 62$, $P < 0.05$) (Figure 6).

4.5.3 Between stages

There was no difference between larvae and pupae of *Z. filipendulae* regarding the cover of bare ground (sites ABC: $t_{(53)} = -0.53$, P = 0.597) (Figure 6).

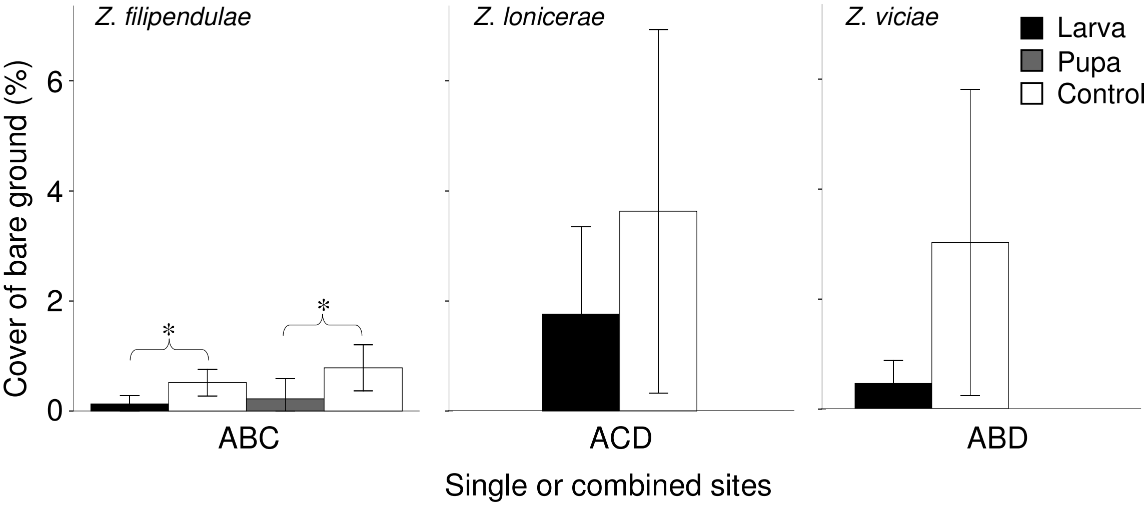


Figure 6. Mean cover of bare ground in circles centred on larvae or pupae and the corresponding cover of bare ground in control circles for each life stage, 1 m diameter. Pupae were only analysed for Z. filipendulae (*see text for more information*). *Level of significance is shown as * P < 0.05.*

4.6 Cover of dry grass

The cover of dry grass was significantly higher at site D during both larval and pupal surveys, than at the other three sites (Table 2). Hence, values for sites A, B and C are hereafter reported jointly in the combinations AB, AC and ABC, whereas values for site D are reported separately.

4.6.1 Larva

The cover of dry grass was significantly greater around *Z. filipendulae* larvae as compared to controls (sites ABC: Mann-Whitney U = 888.50, Z = -2.16, $n_l = 32$, $n_c = 73$, $P < 0.05$). For neither *Z. lonicerae* nor *Z. viciae*, the cover of dry grass around larvae differed from controls at any site or combination of sites (*Z. lonicerae*, sites AC: Mann-Whitney U = 262.5, Z = -0.97, $n_l = 13$, $n_c = 41$, P = 0.923, site D: Mann-Whitney U = 64, Z = -0.840, $n_l = 8$, $n_c = 20$, P = 0.401; *Z. viciae*, *s*ites AB: $t_{(71)} = 0.41$, P = 0.680, site D: Mann-Whitney U = 38.50, Z = -0.80, $n_l = 5$, $n_c = 20$, P = 0.422) (Figure 7).

4.6.2 Pupa

The cover of dry grass around *Z. filipendulae* pupae was lower than in control circles (sites ABC: Mann-Whitney U = 518.50, Z = -2.33, $n_p = 23$, $n_c = 62$, $P < 0.05$) (Figure 7).

4.6.3 Between stages

Larvae of *Z. filipendulae* were enclosed by more dry grass than pupae (sites ABC: Mann-Whitney U = 198, Z = -3.33, $n_l = 32$, $n_p = 23$, $P < 0.01$) (Figure 7).

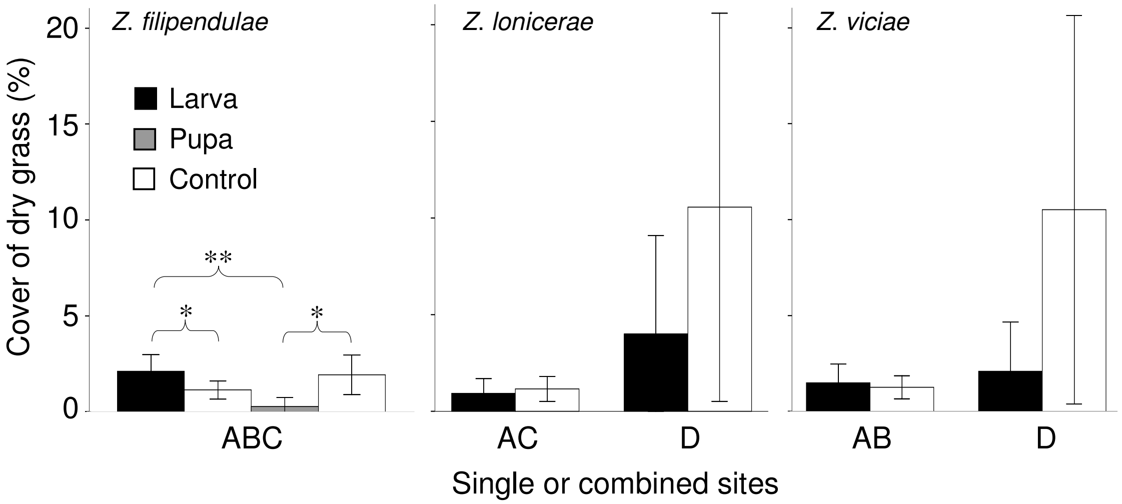


Figure 7. Mean cover of dry grass in circles centred on larvae or pupae and the corresponding cover of dry grass in control circles for each life stage, 1 m diameter. Pupae were only analysed for Z. filipendulae (*see text for more information*). *Level of significance is shown as * $P < 0.05$, ** $P < 0.01$.*

4.7 Sun exposure

During surveys of larvae and imagines, the overall sun exposure at site B was higher than at sites A, C and D (Table 2). During the pupal stage, all three sites of *Z. filipendulae* (A, B and C) differed, but because only one pupa was found at site C, both the individual and the site were omitted from analyses.

4.7.1 Larva

There was no significant difference in sun exposure between larvae of *Z. filipendulae* and controls (sites AC: Mann-Whitney U = 128.50, Z = -0.44, $n_l = 7$, $n_c = 41$, P = 0.659, site B: $t_{(55)} = 0.32$, P = 0.750). Neither *Z. viciae* larvae differed from controls (sites AD: Mann-Whitney U = 269.0, Z = -0.61, $n_l = 15$, $n_c = 40$, P = 0.545, site B: Mann-Whitney U = 174, Z = -1.09, $n_l = 12$, $n_c = 32$, P = 0.278), whereas the larvae of *Z. lonicerae* were observed in significantly more shady conditions than average (sites ACD: $t_{(80)} = -2.11$, $P < 0.05$) (Figure 8).

4.7.2 Pupa

Sun exposure did not differ between *Z. filipendulae* pupal spots and random control spots, neither at site A nor at site B (site A: Mann-Whitney U = 51.50, Z = -1.04, $n_p = 7$, $n_c = 20$, P = 0.296, site B: Mann-Whitney U = 133.0, Z = -1.08, $n_p = 15$, $n_c = 21$, P = 0.280) (Figure 8).

4.7.3 Imago

Imagines of all three species showed a tendency towards choosing sunnier conditions than average, although not always statistically significant (*Z. filipendulae*, sites AC: Mann-Whitney U = 276.50, Z = -2.76, $n_i = 13$, $n_c = 80$, $P < 0.01$, site B: Mann-Whitney U = 324, Z = -0.79, $n_i = 18$, $n_c = 40$, P = 0.432; *Z. lonicerae*, sites ACD: Mann-Whitney U = 1033.5, Z = -3.25, $n_i = 28$, $n_c = 120$, $P < 0.01$; *Z. viciae*, sites AD: Mann-Whitney U = 428.50, Z = -1.31, $n_i = 28$, $n_c = 80$, P = 0.191, site B: Mann-Whitney U = 925.50, Z = -1.39, $n_i = 25$, $n_c = 40$, P = 0.166) (Figure 8).

4.7.4 Between stages

Larvae, pupae and imagines of *Z. filipendulae* did not differ regarding sun exposure, at any site or combination of sites (sites AC, larvae/pupae: Mann-Whitney U = 23.50, Z = -0.13, n_l = 7, n_p = 7, P = 0.898; larvae/imagines: Mann-Whitney U = 25, Z = -1.71, n_l = 7, n_i = 13, P = 0.088; pupae/imagines: Mann-Whitney U = 23.50, Z = -1.83, n_p = 7, n_i = 13, P = 0.067, site B, larvae/pupae: Mann-Whitney U = 175.50, Z = -0.506, n_l = 25, n_p = 15, P = 0.613; larvae/imagines: $t_{(41)}$ = -0.57, P = 0.575; pupae/imagines: $t_{(31)}$ = -0.52, P = 0.607). Likewise, the larvae and imagines of *Z. viciae* choose spots with equal amounts of sun (sites AD: Mann-Whitney U = 204.50, Z = -0.14, n_l = 15, n_i = 28, P = 0.886, site B: Mann-Whitney U = 126, Z = -1.44, n_l = 12, n_i = 25, P = 0.149). Only the larvae of *Z. lonicerae* were encountered in significantly shadier conditions than imagines (sites ACD: $t_{(47)}$ = -3.84, P < 0.01) (Figure 8).

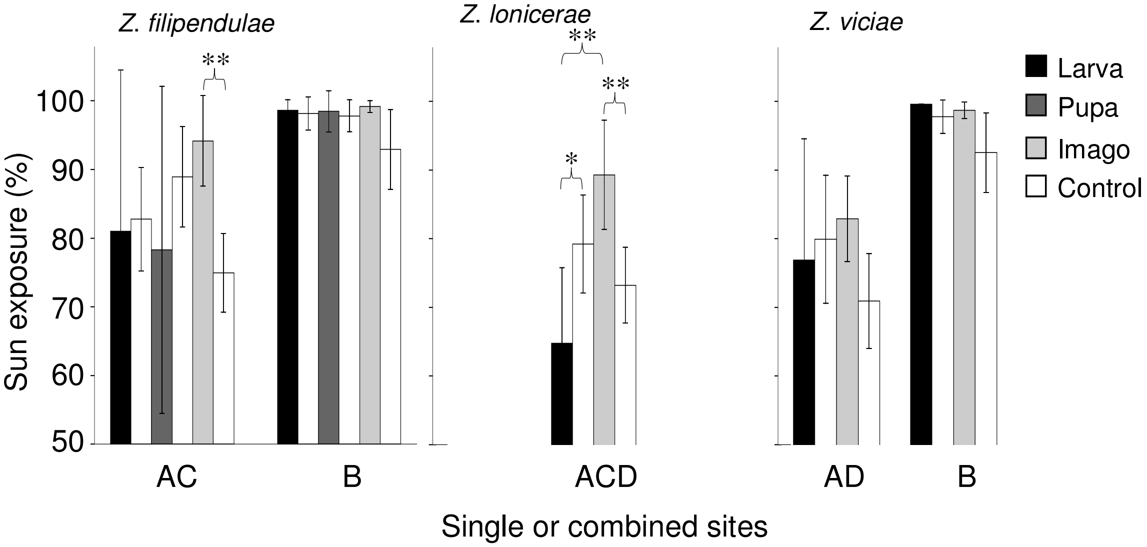
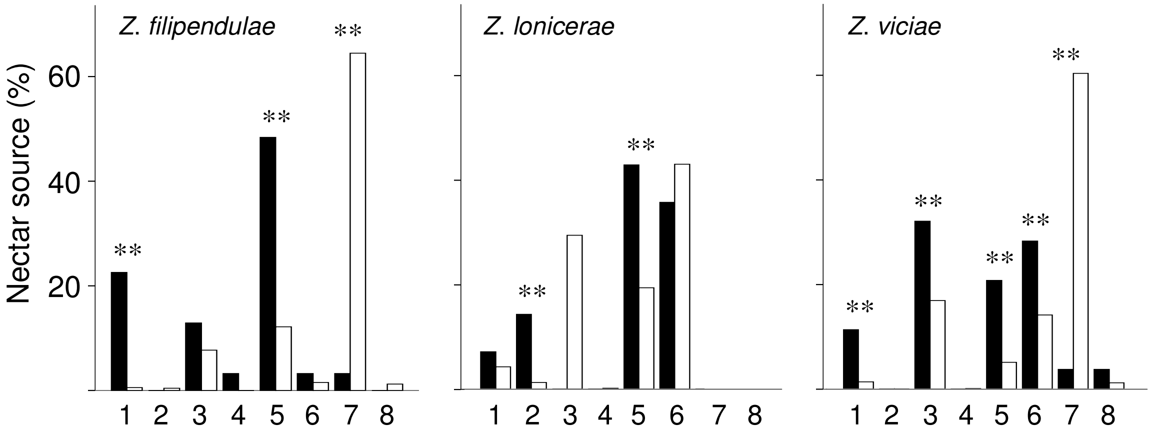


Figure 8. Mean light intensity (percentage sun exposure between 09:00 and 17:00 Swedish summer time, GMT+2) around larvae, pupae or imagines and the corresponding sun exposure in control circles for each life stage. Pupae were only analysed for Z. filipendulae *(see text for more information). Level of significance is shown as * P < 0.05, ** P < 0.01.*

4.8 Nectar plants

Centaurea jacea was the nectar plant most frequently visited by both *Z. filipendulae* (n = 15, 48 %) and *Z. lonicerae* (n = 12, 43 %), whereas *Z. viciae* used *Cirsium arvense* as main nectar source (n = 17, 32 %) (Figure 9). Binomial tests revealed that all three species of burnet moths were observed more frequently on their respective dominating nectar plant than would have been expected by chance alone, according to the overall proportion of *Centaurea jacea* or *Cirsium arvense* at the sites, P < 0.01 (Figure 9). *Zygaena filipendulae* also used *K. arvensis* as nectar source more often than would have been expected (P < 0.01), whereas *I. salicina* was visited less frequently (P < 0.01) (Figure 9). Likewise, the imagines of *Z. lonicerae* were foraging more frequently on *S. columbaria* (P < 0.01), and *Z. viciae* foraged more often on *K. arvensis*, *Centaurea jacea* and *Centaurea scabiosa* (P < 0.01), but was found less frequently on *I. salicina* (P < 0.01) (Figure 9). One flower head of *Valeriana officinalis* corresponded to 12 cm^2. No flowering nectar sources were found during larval and pupal surveys.



1) *Knautia arvensis*, 2) *Scabiosa columbaria*, 3) *Cirsium arvense*, 4) *Cirsium acaule*,
5) *Centaurea jacea*, 6) *Centaurea scabiosa*, 7) *Inula salicina*, 8) *Valeriana officinalis*

*Figure 9. Percentage frequency of imago observations on certain nectar plants (black bars) and the relative amount of each nectar plant in control circles of 5 m diameter (white bars). Level of significance is shown as ** P < 0.01.*

4.9 Large scale studies

For *Z. filipendulae* and *Z. lonicerae*, a total of 1580 grid cells were analysed, the burnets being present in 464 and 338 cells respectively. For *Z. viciae*, the island of Gotland was omitted from analyses, which resulted in 1526 grid cells being evaluated, the burnet being present in 354 of them. In a well-fitting GLZ model, the deviance divided by the degrees of freedom should be close to one. An alternative statistic to evaluate the goodness-of-fit is the ratio of Pearson χ^2 to the degrees of freedom, which should also be close to one. The overall fit of the three models revealed that they all conformed well to the data (*Z. filipendulae*: D/d.f. = 1.1, χ^2/d.f. = 1.0; *Z. lonicerae*: D/d.f. = 0.95, χ^2/d.f. = 0.98; *Z. viciae*: D/d.f. = 1.0, χ^2/d.f. = 0.99).

The total area of meadows and pastures within 10 x 10 km grid cells was shown to be a significant variable in each of the three burnet models ($P < 0.001$), and all three burnet species were positively correlated to it (Table 3, Figure 10). However, none of the species reached a presence probability of 100 % and hence, no upper limit of area could be discerned. Figure 11 shows the grid cells, south of the 5 °C limit, where the probability of finding burnets is 10, 30 or 50 %. The area required for a 50 % probability of burnet occurrence was 454 ha for *Z. filipendulae*, 925 ha for *Z. lonicerae* and 2055 ha for *Z. viciae*.

Table 3. Results of GLZ models analysing the effect of semi-natural grassland area within 10 x 10 km grid cells on burnet moth presence.

	Z. filipendulae	***Z. lonicerae***	***Z. viciae***
b1	-3.36559	-4.02002	-2.84336
SE1	0.23834	0.27770	0.23441
b2	1.26627	1.35514	0.85822
SE2	0.11243	0.12724	0.11286

Equation: $y = e^{(b1 + b2x)}/(1 + e^{(b1 + b2x)})$

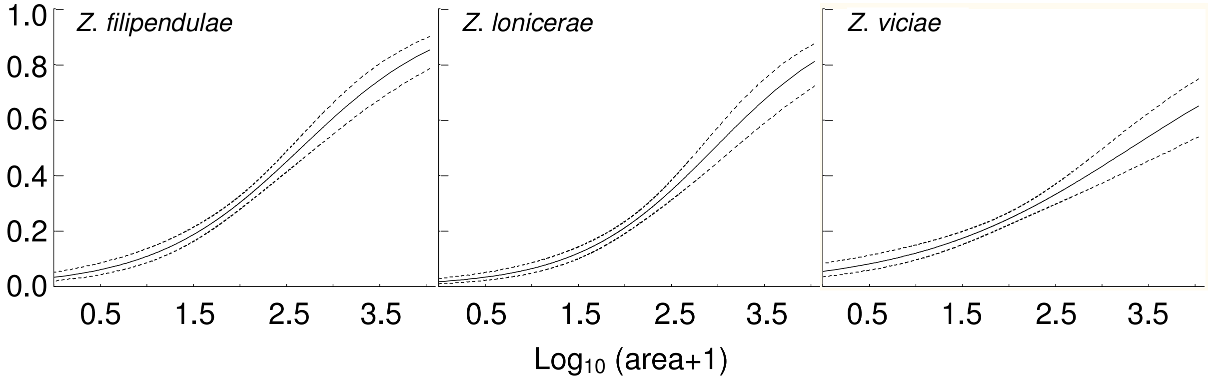


Figure 10. The probability of finding burnet moths (solid lines), with 95 % CI (dashed lines), depending on the area of meadows and pastures within 10 x 10 km grid cells (log_{10}(area+1)).

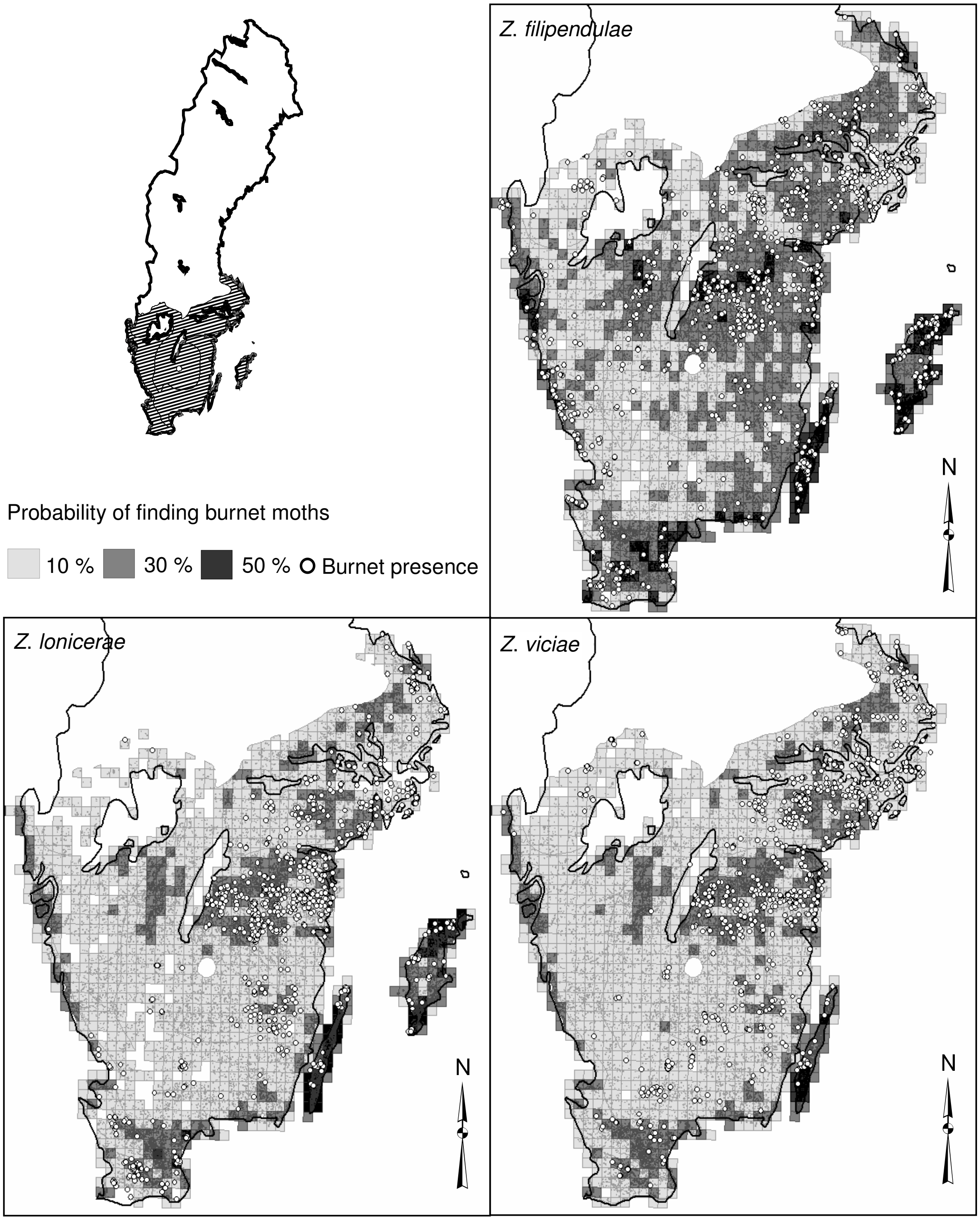


Figure 11. The area of investigation in southern Sweden (dashed lines) and the 10, 30 and 50 % probability of finding burnet moths based on the amount of meadows and pastures within 10 x *10 km grid cells.* Zygaena viciae *is not present on the island of Gotland, and the island was omitted from analyses and map of* Z. viciae.

5 Discussion

To halt and reverse the ongoing decline in butterfly and burnet moth species richness and abundance, there is an urgent need for quick and pointed actions. Identifying a species' habitat preferences and crucial resources makes it possible to construct effective conservation and management plans (Bergman, 1999; Anthes *et al.*, 2003; Ellis, 2003) and make estimations of habitat suitability among patches (Cowley *et al.*, 2000; Vanreusel *et al.*, 2007), or even to predict the occurrence of other species (Hein *et al.*, 2007). However, in order to be successful, conservational work must give attention to several parts of the lepidopteran life cycle, not solely focusing on only one life stage (Anthes *et al.*, 2003; Shreeve *et al.*, 2004; Öckinger, 2008). This study showed that within each burnet moth species (*Z. filipendulae*, *Z. lonicerae* and *Z. viciae*) the larvae, pupae and imagines differed with respect to their selection of microhabitat (Table 4 and 5). Between species, there was a difference in the preferred larval host plants and nectar sources. Moreover, the three species appeared to have various requirements at the landscape scale, concerning the amount of surrounding semi-natural grassland.

Table 4. Differences between larvae, pupae, imagines and controls regarding larval host plant characteristics and environmental parameters. Pupae were only analysed for Z. filipendulae (*see Results for more information*). *+ and – signs represent positive or negative differences.*

		Z. filipendulae			*Z. lonicerae*		*Z. viciae*	
Parameter	**Site(s)**	**L**	**P**	**I**	**L**	**I**	**L**	**I**
Host plant cover	ABCD	+	ns	ns	+	ns	+	ns
Host plant area	ABCD	+	x	x	+	x	+	x
Vegetation height	ABD	ns	+ [a]	ns	ns	ns	+	+
	C	+	na	+	ns	+	x	x
Sun exposure	ACD	ns	ns	+	–	+	ns	+ [c]
	B	ns	ns	+ [b]	x	x	ns	+ [d]
Bare ground	ABCD	–	–	x	ns	x	ns	x
Dry grass	ABC(D)	+	–	x	ns	x	ns	x

L = larvae, P = pupae, I = imagines, ns = not significant, x = parameter not studied or species absent, na = not analysed

[a] Trend, but not statistically significant.
[b] Trend, but not statistically significant.
[c] Trend, but not statistically significant.
[d] Trend, but not statistically significant.

Table 5. Differences between life stages regarding larval host plant characteristics and environmental parameters. Pupae were only analysed for Z. filipendulae (*see Results for more information*). *+ and – signs represent positive or negative differences between the first and second-mentioned stage.*

		Z. filipendulae			*Z. lonicerae*	*Z. viciae*
Parameter	**Sites**	**L/P**	**L/I**	**P/I**	**L/I**	**L/I**
Host plant cover	ABCD	+	+	ns	+	+
Vegetation height	ABD(C)	– [a]	ns	+	ns	ns
Sun exposure	ACD(B)	ns	ns	ns	–	ns
Bare ground	ABCD	ns				
Dry grass	ABC	+				

Abbreviations as in Table 4.
[a] Close to significant.

5.1 Host plants, nectar sources and sun exposure

In this study, the larvae of *Z. filipendulae*, *Z. lonicerae* and *Z. viciae* were found on host plants larger than randomly selected plants of the same species (*Z. filipendulae*: *L. corniculatus*; *Z. lonicerae*: *T. medium/pratense* and *Z. viciae*: *Vicia* spp.). Previous studies of butterfly species have shown both similar (Grundel *et al.*, 1998; Albanese *et al.*, 2008) and contrasting results (Ravenscroft and Young, 1996). However, Ravenscroft and Young (1996) denote plant size as the height of the plant while here, plant area was measured. Larvae often depend upon the amount of green mass provided, which is not necessarily correlated to the height of the plant but rather the total plant area. In this study, larvae of all three *Zygaena* species were found where the cover of host plants was greater as compared to controls. There is still to be investigated whether a high host plant cover is actively searched for by the larvae or if the larval position is a result of the female's ovipositing preferences (Gutiérrez *et al.*, 1999). The females of *Zygaena* species often place their eggs on plants other than the larval host plants (Bourn, 1995; Naumann *et al.* 1999; Gutiérrez *et al.*, 2001) and in order to provide enough nutrients for the larvae during the first critical larval instars, females may choose to place their eggs among, or in the vicinity of, closely grouped host plants (Porter, 1992). For species that deposit their eggs in clusters, like *Z. filipendulae*, *Z. lonicerae* and *Z. viciae*, a greater density of host plants within a short distance from the ovipositing site offers more food to a bigger group of larvae, and few larvae will have to move. The younger and smaller the larva, the less far it is able to move and the less likely it will find another host plant if host plants are not grouped closely together (Rausher, 1979). Furthermore, larvae of all three species were consistently found among a greater cover of their most important host plant as compared to later instars, indicating that the larvae move from their feeding areas before pupating. Other studies have shown that *Zygaena* larvae are able to move more than 5 meters, depending on the availability of host plants (Bourn, 1995).

Imagines preferred to rest and forage on plants of *Centaurea* or *Cirsium*, but other red and violet Asteraceae flowers were also favoured. Even larvae and pupae were often found in places surrounded by a high amount of nectar plants, although non-flowering. There is no obvious need for larvae and pupae to choose spots according to the quantity of flowering nectar sources, but the distribution of nectar flowers may influence the females during oviposition. Murphy *et al.* (1984) showed that the egg laying sites for the checkerspot butterfly *Euphydryas chalcedona* Doubleday and Hewitson were biased towards areas where nectar plants were abundant, implying the necessity for females to find easily accessible nutrients during oviposition. Similar results have been shown for the tiger swallowtail, *Papilio glaucus* L. (Grossmueller & Lederhouse, 1987).

Concerning sun exposure, the imagines of all three species preferred (or showed a tendency towards preferring) sunnier conditions than average. This finding is in concordance with previous studies showing that the burnet moths' peak activity occurs later in the day, i.e. during the lightest and warmest hours, as compared to many other butterfly species (Naumann *et al.*, 1999; Wikström *et al.*, 2009). The larvae of *Z. lonicerae* were found in more shady conditions than both controls and imagines, but whether this difference is due to the demands of the larvae themselves or to the conditions required by the food plants is still to be evaluated. The main host plant of *Z. lonicerae*, *T. medium/pratense*, was often found in the shadier parts of the sites such as at the edges of wood or close to trees and bushes, whereas nectar plants like *Centaurea jacea* and *C. scabiosa* grew in the more open central parts. These circumstances might explain the difference between *Z. lonicerae* larvae and imagines concerning sun exposure.

5.2 Surrounding vegetation

Pupae of *Z. filipendulae* were generally found in taller vegetation and surrounded by less dry grass than average, and also seemed to prefer a higher sward than larvae and imagines. The observed differences may be explained by the characteristic behaviour of *Z. filipendulae* larvae prior to pupation: cocoons are generally spun relatively high on stems of grasses and other plants, and the chance of finding such suitable elements rises with increasing vegetation height. The substrate also needs to be sufficiently firm to hold the pupae and not bend during bad weather conditions. Dry grass of soft texture is more prone to be knocked down by rain and strong winds and thus conceal a greater part of the ground. Consequently, within circles where the vegetation was weaker and more pliable, a higher percentage of ground was covered by dry grass as compared to circles with more robust grass. To some extent, this might explain why pupae were found on spots surrounded by a lower cover of dry grass, as compared to larvae and controls.

Comparisons between larvae and controls showed somewhat varied results. The sward height around *Z. lonicerae* and *Z. filipendulae* larvae did not seem to differ from controls, whereas larvae of *Z. viciae* preferred vegetation higher than average (even *Z. filipendulae* appeared in vegetation higher than average at site C, but these results require cautious interpretation as they are only based upon values for four larvae). These species-specific differences might be explained by the preferred host plants. Both *Z. filipendulae* and *Z. lonicerae* were mostly found on *L. corniculatus* and *T. medium/pratense*, plant species that seldom become particularly large in size and that primarily grow in lower vegetation, whereas the dominant food plant of *Z. viciae*, *V. cracca*, is generally larger and can manage to grow where the overall sward is higher. Even *L. pratensis*, the second most important host plant for *Z. viciae* (and the main larval host plant in Great Britain (Young & Barbour, 2004)), grow relatively large in size and can be expected to thrive in higher vegetation.

In terms of bare ground, only the larvae of one species, *Z. filipendulae*, differed from controls and were observed at spots with less bare soil than average. Studies on butterflies have shown that areas of bare ground and short vegetation are important for species living on the cool margin of their ranges, as more open conditions normally increase the temperature and improve the larval climate (Thomas, 1991; Ravenscroft & Young, 1996; Gutiérrez *et al.*, 2001; Bourn & Thomas, 2002). In contrast, other studies have shown that some butterfly larvae prefer host plants growing in tall vegetation (Bourn & Thomas, 2002). Such divergent results suggest that different species of butterflies require different types of grazing regimes, and that each species' preferences need to be investigated individually.

5.3 Large scale

While the specific habitat requirements of different life stages are important at the local scale, the surrounding landscape affects butterfly presence over time at larger spatial scales (Thomas *et al.*, 2001; Bergman *et al.*, 2004; Öckinger & Smith, 2006). In this study, I found that the three burnet species *Z. filipendulae*, *Z. lonicerae*, *Z. viciae* were all positively related to increasing proportion of semi-natural grassland in the landscape.

In studies of habitat cover and species occurrence, several authors report the existence of so called threshold points (Andrén, 1994; Bergman *et al.*, 2004; Betts *et al.*, 2007; Denoël & Ficetola, 2007; Rhodes *et al.* 2008). A threshold value is the critical amount of habitat cover below which a species declines rapidly in abundance. For *Z. filipendulae* and *Z. lonicerae*, a rapid decline in probability of occurrence could be distinguished around a 40-50 % probability, whereas the pattern is somewhat more obscure for *Z. viciae*. Bergman *et al.* (2004) studied the effect of habitat cover on butterflies and burnet moths. They concluded that for burnet moths (*Z. filipendulae*, *Z. lonicerae*, *Z. viciae* and *Z. osterodensis*) the proportion of deciduous forest/semi-natural grassland within a circle of 5 km radius must exceed 11.2 % for a 50 % probability of burnet occurrence. Within 10 x 10 km grid cells, 11.2 % would represent 1120 ha, a value that lies well within the range of the 450 ha to 2000 ha presented in my study. The amount of meadows and pastures within the grid cells can be considered a measure of both patch area and distance between patches, i.e. a large total area indicates either large patches and/or many patches within a relatively small distance. Both increasing patch area and decreasing distance between patches have been shown to favour the occurrence of butterflies (e.g. Thomas *et al.*, 1992; Bergman & Landin, 2001; Thomas & Hanski, 1997; Hanski, 1999). However, as can be seen in Figure 11, the presence of burnet moths does not always coincide with the areas rich in semi-natural grassland, and although promising, my results must be interpreted with some caution. The analyses of semi-natural grassland vs. burnet presence or absence are based on the total amount of meadows and pastures in southern Sweden. In reality, some of these areas are probably not fully suitable as burnet moth habitats, e.g. because of insufficient amounts of host plants or nectar sources, or intensive grazing – irrespective of their size. In other words, a large total area of meadows and pastures does not necessarily imply a large area of adequate habitat, but is still increasing the value of the predictor variable in statistical models. Furthermore, burnet moths are not exclusively found in semi-natural grasslands but also at fringes of wood and along roadsides. These latter land types were not included in this study, and the quantity of burnet moth habitats in the models may not be totally complete. Another potential source of variation in the models is the varying recording effort over the region. Data on burnet moth presence are based upon reports from private persons, suggesting that there are areas where burnet moths have not yet been surveyed, as well as areas where burnets have been observed but not reported.

There are no, or very few, findings of *Z. lonicerae* and *Z. viciae* in an area stretching diagonally from the lakes Vänern and Vättern and down along the west coast of Sweden (Figure 11). The area of semi-natural grassland within this area does not differ substantially from elsewhere in southern Sweden, and there are good reasons to believe that factors other than the amount of habitat affect burnet distribution in these regions. A similar eastward distribution shift has been shown for other groups of insects (Franc *et al.*, 2007), and might be due to a more favourable climate in eastern Sweden with less precipitation, more sunshine and higher temperatures; all important factors for warm-loving and sun-seeking species such as burnet moths.

5.4 Implications for conservation

This study shows that the habitat requirements of burnet moths differ between species and between life stages. To promote larvae, pupae and imagines of *Z. filipendulae*, *Z. lonicerae* and *Z. viciae*, successful management should aim at preserving sites with a high cover of their respective host plants (*L. corniculatus*, *T. medium/pratense* and *Vicia* spp) and important nectar sources such as *Centaurea*, *Cirsium* and other red and violet Asteraceae flowers. Some grazing or other types of management is recommended because no host plants or nectar sources are favoured by a complete lack of grazing, leading to grass domination (Young & Barbour, 2004). Management should also be carried out to keep the areas open and sunny. However, pupae of *Z. filipendulae* are often exposed on the stems of grasses and other plants, and require higher vegetation than other life stages. Management must therefore be executed with great care, or late in the season, to not harm unhatched pupae or reduce the amount of substrates suitable for cocoon attachment (*cf.* Dennis, 2005). Even the amount of important nectar sources might be negatively affected by too intensive management.

At the landscape scale, burnet moths are promoted by a high density of semi-natural grassland although other vegetation types, such as fringes of wood and road verges, are also important to manage and preserve. These results are in line with many other studies that demonstrate the general importance of semi-natural grasslands on butterfly occurrence (e.g.

Maes & van Dyck, 2001; Franzén & Ranius, 2004; Gärdenfors, 2005; Öckinger & Smith, 2006).

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