Final Thesis

Oviposition and habitat preferences of *Hamearis lucina* in the province of Östergötland, Sweden

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1. Abstract

Hamearis lucina is one of the threatened butterfly species that faces the risk of regional extinction in the near future due to changes in land use and habitat fragmentation. The aim of this study was to find out its oviposition and habitat preferences. About 2400 *Primula veris* were examined and a total of 145 eggs, larvae or feeding marks of *H. lucina* were found. The results showed that the species has specific host plant and habitat preferences. Females preferred to oviposit on flowering *P. veris* that were taller and had a higher number of leaves than average. This is probably because they were easier to find and gave a large amount of food for the larvae. Host plants with significantly higher nitrogen content were also preferred and these plants were shown to grow in a shadier environment. The preferred sward height for oviposition was 9-11 cm. When the sward exceeded 10 cm the females preferred a sward shorter than average, while they preferred a taller sward when the average was below 10 cm. Host plants situated closer together and in higher densities were significantly more often chosen for oviposition than other host plants. The females also preferred host plants growing closer to a forest edge or other shelter in the form of trees and bushes. The results give important management guidelines. Habitats suitable for *H. lucina* should be rich in bushes and woodland edges, lightly grazed and contain areas with high densities of *P. veris*.

Keywords: *Hamearis lucina, Primula veris*, oviposition, host plant preferences, host plant quality

2. Introduction

The increasingly intensive forestry and agriculture create a large threat to the European biodiversity (Kruys 1998). The main causes are habitat fragmentation and abandonment of semi natural grasslands, i.e. unfertilised pastures and meadows. These types of land are the habitats of many species, and therefore now in focus for conservation (Lindborg et al. 2005). Many species of butterflies are seriously affected, one of them being *Hamearis lucina* Linneaus 1758, which has become rare in most parts of northern Europe (Kruys 1998). About 40% of the previous British populations have disappeared (Bourn & Thomas 1993). In Sweden, the species has a very limited distribution and it has diminished steadily for many years (ArtDatabanken 2005). It is classified as vulnerable in the Swedish red list and since the beginning of the 21st century the species is almost completely dependent upon conservation measures (ArtDatabanken 2005).

Previous studies have concluded that to have a successful conservation of butterflies it is important to understand the precise habitat requirements at different stages of their lives (Bourn & Thomas 1993). It is therefore important to gather the necessary information as soon as possible to be able to save species at risk.

The oviposition preferences of *H. lucina* are complex and like many other butterflies they have very specific host plant preferences (Sparks et al. 1994). Most females lay their eggs exclusively on *Primula veris*, although in populations surviving in woodlands *Primula vulgaris* may be used (Emmet & Heath 1989). Studies in Sweden and Britain have shown that even though the larval host plant is present, it may not be sufficient for the survival of the species (Kruys 1998). Butterflies are often specialised to breed not only on one or a few plant species, but on plants growing in a precise situation (Warren & Key 1991). Factors that influence oviposition may be the apparency, which facilitates the localisation of the plant; the microclimate around it, which will affect larval survival; and sometimes also chemical and textural cues (Porter 1992). Early instar larvae have little choice what to eat and depend largely on the good judgement of the ovipositing female (Porter 1992). It may not always be possible for the female to find plants that correspond perfectly to the larval demands, but the closer the better (Porter 1992).

As mentioned above, the microclimate is among the factors influencing larval survival and oviposition preferences. Some sites can have a very different temperature and humidity than that of neighbouring sites, which is why the distribution of a specific microhabitat may have a strong influence on the distribution of a butterfly species, depending on its way of living (Shreeve 1992). *Hamearis lucina* often favours ride-intersections, sunken tracks or sheltered glades in scrub when choosing habitat (Emmet & Heath 1989), which may be due to their search for a certain microhabitat.

The nitrogen content in host plants is considered one of the most important factors deciding the performance in herbivorous insects (Fischer & Fiedler 2000). A study made by Bourn and Thomas (1993) showed that the *Aricia agestis* butterfly chose host plants with a higher concentration of nitrogen than that of randomly chosen plants.

The aim of my study was to find out what preferences *H. lucina* has on its habitat and oviposition sites. This includes factors as where *P. veris* grow and how various amounts of nitrogen in the individual host plant affect the choice of the butterfly. The influence of bush and tree structure was also examined. Different types of habitats were compared to try and see which were preferred by the butterflies and why.

3. Material and methods

3.1. Species description

Hamearis lucina is the only species in the genus, with remaining populations in most parts of Europe, even though it is declining severely in many places. In Sweden, it has a limited distribution in the southeastern parts, with the strongest populations found in the province Östergötland, southeastern Småland and on the island of Öland (ArtDatabanken 2005). Omberg has got one of the larger mainland populations in Sweden (Kruys 1998).

Hamearis lucina populations are found primarily in bushlands, e.g. former pastures or moderately grazed land where the host plant *Primula spp.* is present. The wings of the imago are dark brown with light yellowish brown and white spots and a wingspan of 25-29 mm (ArtDatabanken 2005).

The flight period is commonly from the beginning of June and a couple of weeks ahead, depending on the weather conditions. Males hatch first, choose a territory and defend it until they find a female to mate with (ArtDatabanken 2005). The females are somewhat nomadic and lay their eggs singly or in small batches of up to eight on the underside of the leaves (Emmet & Heath 1989). The eggs hatch after 10-20 days and the larvae emerge and start eating. After 4-6 weeks they pupate and overwinter in a dry, hidden site just above ground level in e.g. empty beechnut cases (ArtDatabanken 2005).

3.2. Site descriptions

All study sites were located at Omberg, in areas where previous observations had concluded the presence of *H. lucina* (e.g. Greiff Andersson 1998, Kruys 1998). Omberg is a ten-kilometre granite horst, situated on the eastern shore of Lake Vättern. It has a diverse and specialised flora and fauna, much due to the limestone-containing soil in the area (Ombergs Naturum 2005).

The following sites were included in the study: Bushy pasture 1, 2, 3 and 4, Plantation, Forest edge and Open pasture (Fig. 1, Table 1).

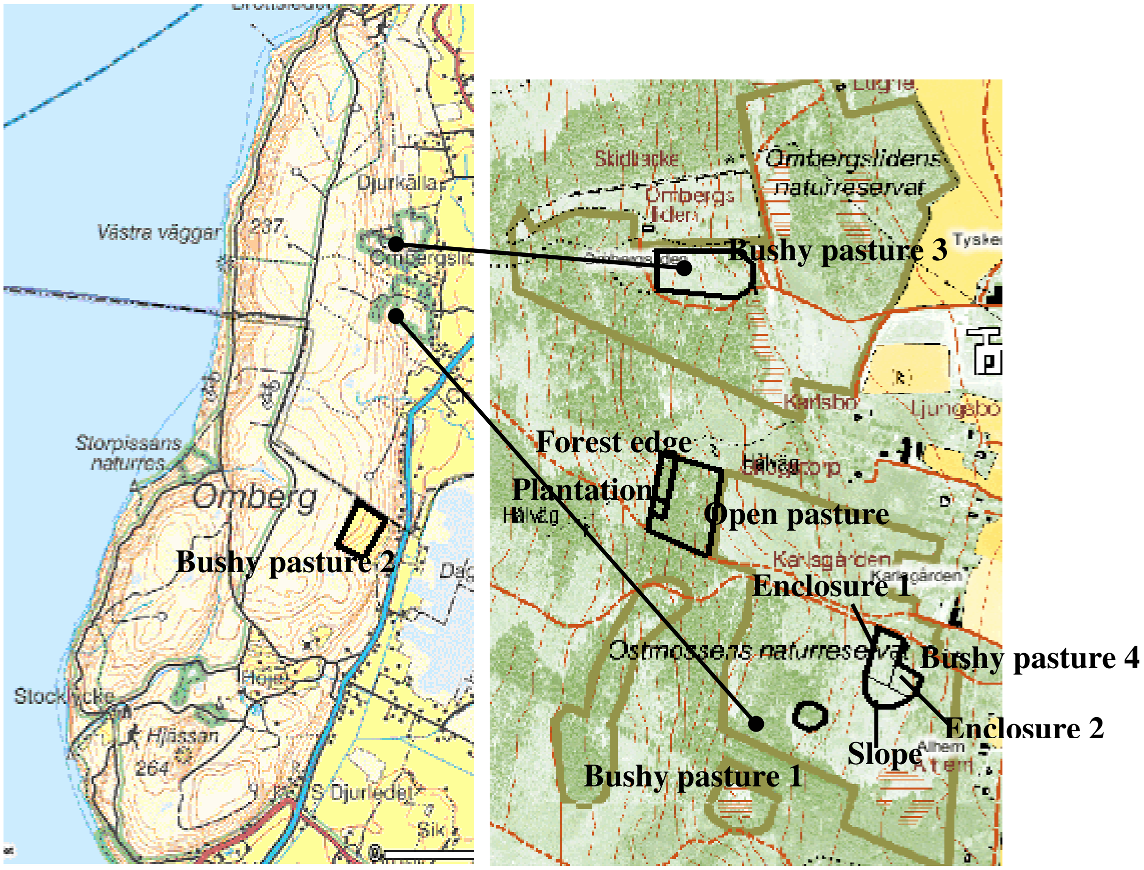

Figure 1*. Maps of Omberg and study sites marked with black colour. Enclosures 1 and 2 and the Slope were analysed together as "Bushy pasture 4".*

Table 1. *Site descriptions*

Study site	**Area (m^2)**	**Grazing**	**Occurence of bushes**	**Surroundings**
Bushy pasture 1 (Bp 1)	1 500	Cattle.	Bushes and trees creating glades and open sites.	Dense spruce forest on two sides and a few spruces and other trees on the other.
Bushy pasture 2 (Bp 2)	200 000	Horses.	Plenty of bushes and trees, creating glades and open sites.	Dense spruce forest.
Bushy pasture 3 (Bp 3)	1 800	Cattle, rotational grazing.	Juniper bushes and shrubs of varying sizes.	An open pasture where a forest recently was felled on one side, a ski slope and a forest on the other sides.
Bushy pasture 4 (Bp 4), comprising of: Enclosure 1, 2 and Slope	6 000	Cattle.	The two enclosures contained plenty of bushes and shrubs, but the Slope had only a few trees.	Dense spruce forest on one side and an open pasture on the other.

Open pasture	8000	Cattle, late summer.	Very few.	Forest edge on one side and another open pasture on the others.
Forest edge	810	No.	Bushes and shrubs of varying sizes.	Dense spruce forest on one side and the Open pasture on the other.
Plantation	250	No.	No.	Dense spruce forest on one side and the Open pasture on the other.

3.3. Measurements of *P. veris* and site characteristics

The 21st of June, as the flight activity had declined, the survey of *P. veris* and *H. lucina* eggs started. Every *P. veris* in 0.5 m wide randomly selected transects was searched for eggs or larvae. The total number of *P. veris* was counted and for each plant with eggs or larvae the following parameters were noted:

Plant characteristics and immediate surroundings
- If the plant was flowering
- Height of the plant, measured as the tallest leaf of the plant
- Number of leaves
- Nitrogen content
- Light intensity
- Sward height

Density of *P. veris*
- Distance to nearest *P. veris*
- Number of *P. veris* within one metre radius

Bush and tree structure
- Distance to the nearest tree or bush
- Distance to the nearest edge of forest

The plants collected for nitrogen analyses were examined at the lab with the Kjeldahl nitrogen method (Kjeltec 1987). A Kjeltec 1026 distilling unit was used together with a Technicon BD Heating Unit for the procedure. As oxidation and catalyst solution the following recipe was used for approximately one litre: 0.5 L of distilled water (H_2O) and 0.5 L of sulphuric acid (H_2SO_4) into which 2.5 g of copper sulphate ($CuSO_4$) and 7.5 g of potassium sulphate (K_2SO_4) were dissolved. For the receiver flasks used in the distilling procedure 0.1 M H_2SO_4 was used.

Light intensity was measured with a Hagner universal photometer type S2. The external cell of the instrument was put at the base of the plant, squatting at one arm's length. Every day a reference value was taken at the most open and sunny place in the sampling area. The values measured at the *P. veris* were then transformed into a percentage of the reference value of that day to eliminate the impact of the weather. Sunny days I was squatting so that the external cell was shaded by my head, because it was not possible to use it in direct sunshine.

The sward height was measured with a sward height ruler. It was a 17 cm wide and 100 cm tall graded ruler that was put down into the ground with a metal stick. At approximately 5 m distance it was read off while squatting, and where the sward height was perceived as covering 50 % of the ruler was noted as the height of the sward. All other measurements were done using a measuring tape.

After the investigation of several random transects at each area it was clear that the finds were very few. In addition, patches were chosen where all *P. veris* were searched. Within these patches it was emphasised that all plants were examined to avoid bias. In addition to searching for eggs or larvae, also feeding marks of the larvae were recorded as finds. Feeding marks are quite easily recognised, since the larvae eat small holes while leaving the vein structure of the leaves intact (Emmet & Heath 1989). Consequently they cannot be confused with the feeding marks of snails, which are much more indiscriminate, jagged and concentrated at the edges (Emmet & Heath 1989). According to Svensson (1993), there is no other butterfly species that eat the leaves of *P. veris* during this time of the year. Only clear cases were recorded as results.

Control *P. veris* were randomly selected in each sampling area and the same parameters were examined on them. The number of control plants was at Bushy pasture 1: 40; Forest edge: 30; Plantation: 31; Bushy pasture 2: 75; Bushy pasture 3: 30; Open pasture: 35 and at Bushy pasture 4: 95.

3.4. Seasonal host plant nitrogen content

Samples of *P. veris* were collected continuously to check for differences in nitrogen content over the summer. They were taken every second week and 80 plants were sampled each time. 20 plants were taken from a shady habitat, 30 from a bushy habitat and 30 from a sunny habitat. The samples were analysed in the lab with the Kjeldahl nitrogen method as mentioned above (Kjeltec 1987).

4. Results

About 2400 *Primula veris* were examined when transect search and the search of whole patches were put together. A total of 60 plants with eggs, 11 plants with larvae and 74 with feeding marks of the larvae were found, 145 altogether.

4.1. Plant characteristics and immediate surroundings

The females preferred flowering *P. veris* for oviposition. Out of the plants with eggs, larvae or feeding marks 59.3% (86/145) had flowers, while only 40.5% (135/333) of the control plants were flowering (χ^2=14.316, d.f.=1, p<0.001).

Primula veris used by *Hamearis lucina* females were both significantly taller and had a higher number of leaves than the control plants in three out of seven study areas (Fig. 2a, 2b). On an average the tallest plants were located at the Plantation, while the shortest were at the Bushy pasture 4.

For all areas pooled, the females preferred a significantly shadier environment than the average (Fig. 2c). However, at the two shadiest sites the plants used by the females were located in sunnier positions, although not statistically significant.

The females preferred to lay their eggs on *P. veris* growing in a significantly taller sward than the average (Fig. 2d). There were significant differences between used *P. veris* and control plants in five out of seven study areas. However, in the site with the tallest sward the used plants were located in shorter sward although not statistically significant.

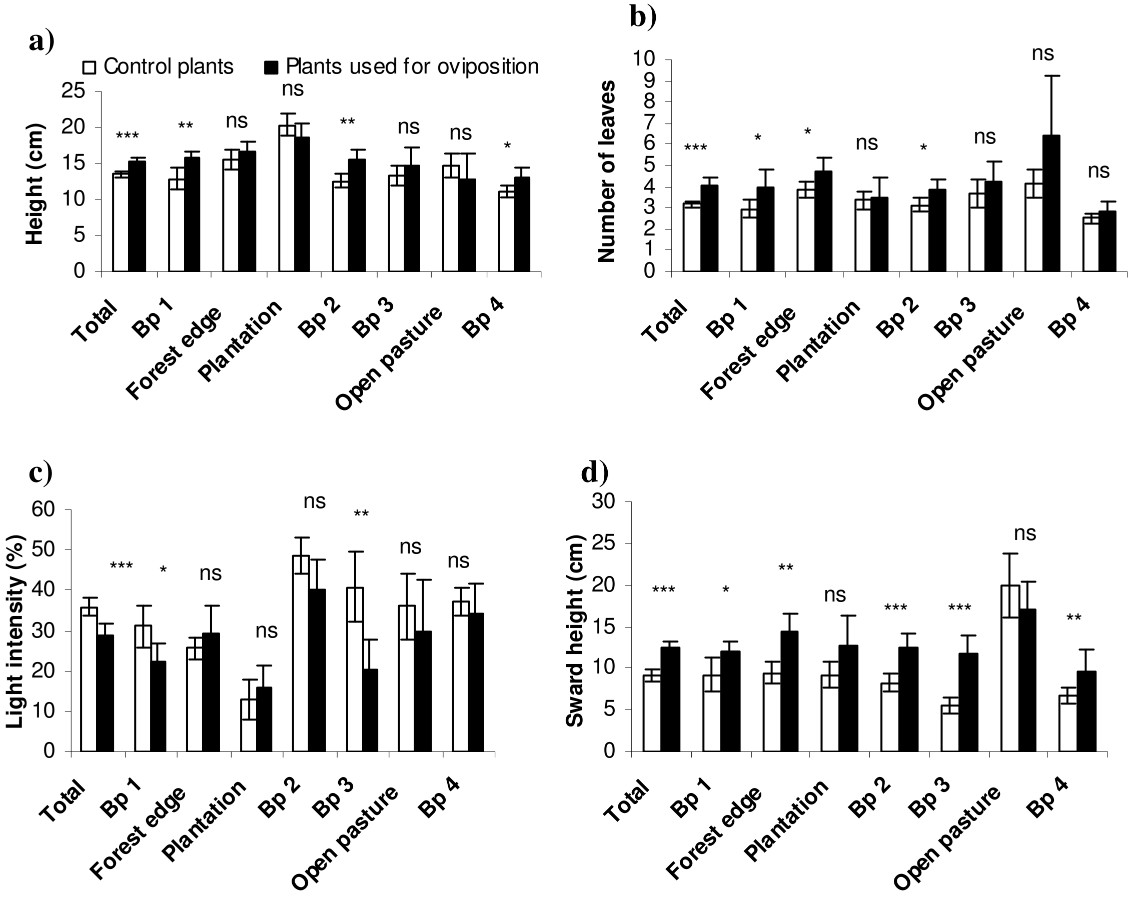

Figure 2a, b, c and d. *Height, number of leaves, light intensity and sward height of control plants and plants used by the butterfly for oviposition at the various study sites. The light intensity is shown in percent of the reference value of each day. The column denoted Total shows the average of all study sites. Error bars show 95% confidence interval for the mean. Level of significance (independent samples t-test) is shown for each study area as ns = not significant i.e. $p>0.05$, * = $0.05>p>0.01$, ** = $0.01>p>0.001$, *** = $p<0.001$. $N_{control}$, $N_{used\ for\ oviposition}$ for each study area: Total: 336,145; Bushy pasture 1: 40,35; Forest edge: 30,29; Plantation: 31,8; Bushy pasture 2: 75,26; Bushy pasture 3: 30,14; Open pasture: 35,9; Bushy pasture 4: 95,24.*

As light intensity increased, the height of *P. veris* decreased ($p<0.001$, $R^2=0.143$) (Fig. 3). At a light intensity of 10 %, the average height was about 16 cm, while at an intensity of 90 % the height was only 8 cm.

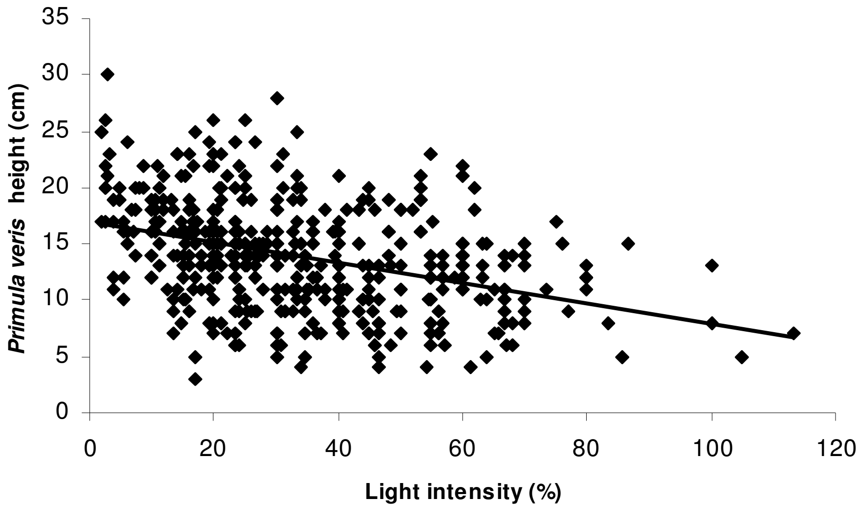

***Figure 3**. The relationship between* Primula veris *height and light intensity in percent of the reference value of each day. A linear regression gave $y = -0.0914x + 17.028$, $R^2 = 0.143$, $p<0.001$. All study sites were included. N = 426.*

The distribution of *P. veris* growing at various sward heights showed that the most preferred height for oviposition was 9-11 cm, while the peak for control plants was at 4-6 cm (Fig. 4). The preferred sward height surrounding *P. veris* used by the butterfly for oviposition showed a threshold at a height of 10 cm. In sward lower than 10 cm the females preferred *P. veris* growing in taller sward than control plants, while in sward taller than 10 cm they preferred plants in a lower sward.

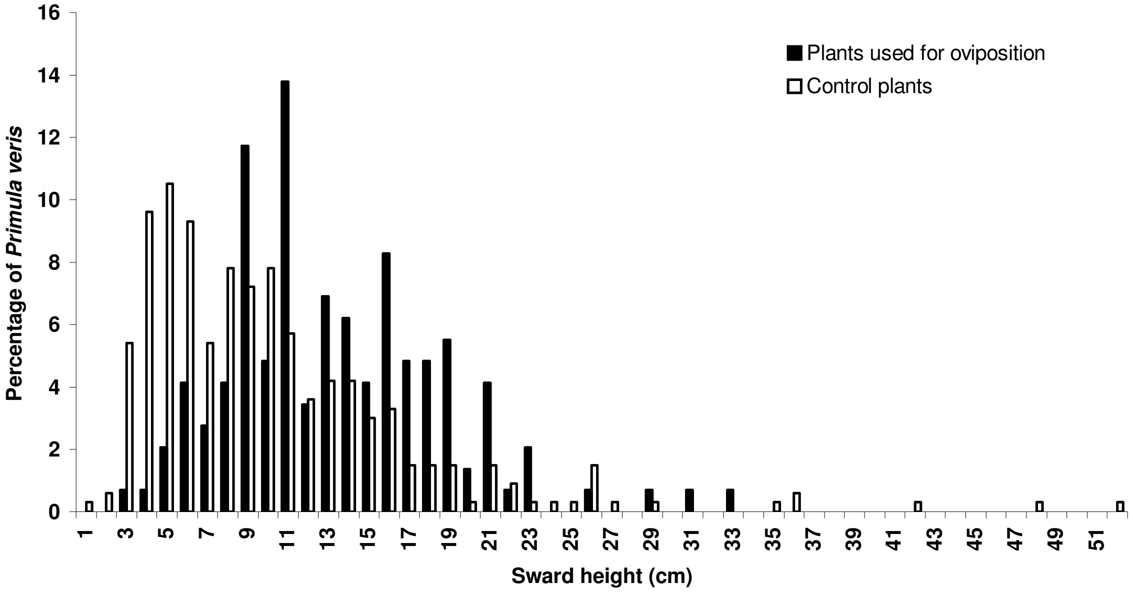

Figure 4. *Distribution of sward height at control plants and plants used by the butterfly for oviposition in all study areas.* $N_{used\ for\ oviposition}$ *= 145;* $N_{control}$ *= 333. The numbers are shown in percent of the total number of used and control plants respectively.*

Hamearis lucina females laid their eggs on *P. veris* with significantly higher nitrogen content than randomly selected plants (Fig. 5).

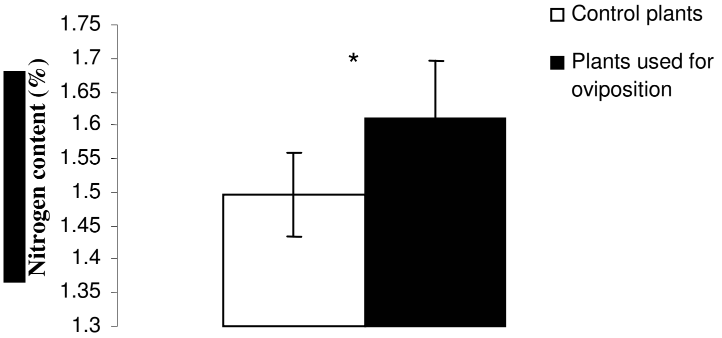

Figure 5. *Nitrogen content in percent of dry weight in control plants and plants used by the butterfly for oviposition. Error bars show 95% confidence interval for the mean. Independent samples t-test gave * = 0.05>p>0.01.* $N_{control}$ *= 61,* $N_{used\ for\ oviposition}$ *= 74.*

4.2. Density of *P. veris*

The *P. veris* density decreased during the summer in four study sites, although the density itself varied much between the different sites (Table 2). In Enclosure 2 at Bushy pasture 4 the density decreased more than four times and in Bushy pasture 1 it was halved from May to August.

Table 2. *Density of* Primula veris *in May and August at four different sites.*

	Enclosure 1 at Bushy pasture 4	**Enclosure 2 at Bushy pasture 4**	**Slope at Bushy pasture 4**	**Bushy pasture 1**
***P. veris*/m^2 in May**	0.306	1.701	0.532	1.043
***P. veris*/m^2 in August**	0.167	0.417	0.450	0.450

Primula veris showed a weak decreasing trend in density as the distance to the forest edge increased (Fig. 6). When the distance increased to more than 100 m from the forest edge the density was higher, however the number of studied plots was low and the variance high.

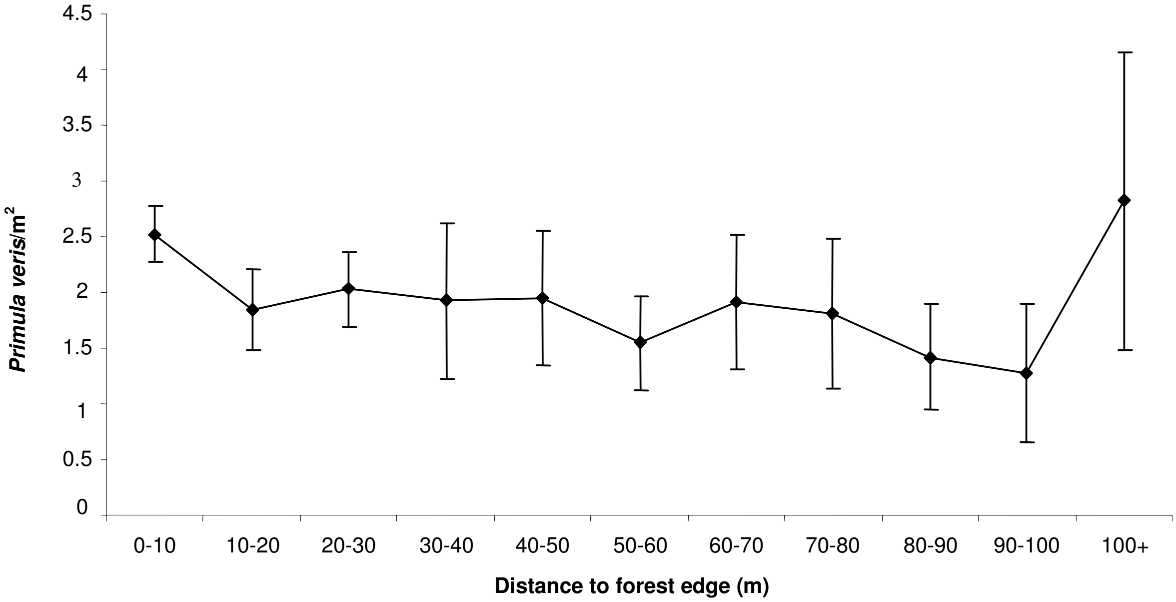

Figure 6*. Variation in density of* Primula veris *as the distance to the forest edge increased. All study sites were included. Error bars show 95% confidence interval for the mean.*

The females oviposited on plants with a high density of surrounding *P. veris* (Fig. 7a). The *P. veris* density was on average 91% higher around plants with eggs, larvae or feeding marks than around control plants. The females also chose plants that were situated significantly closer to other *P. veris* than to the control plants (Fig. 7b). Used plants were on average located 11 cm from the nearest plant, while the average distance of the control plants was 34 cm.

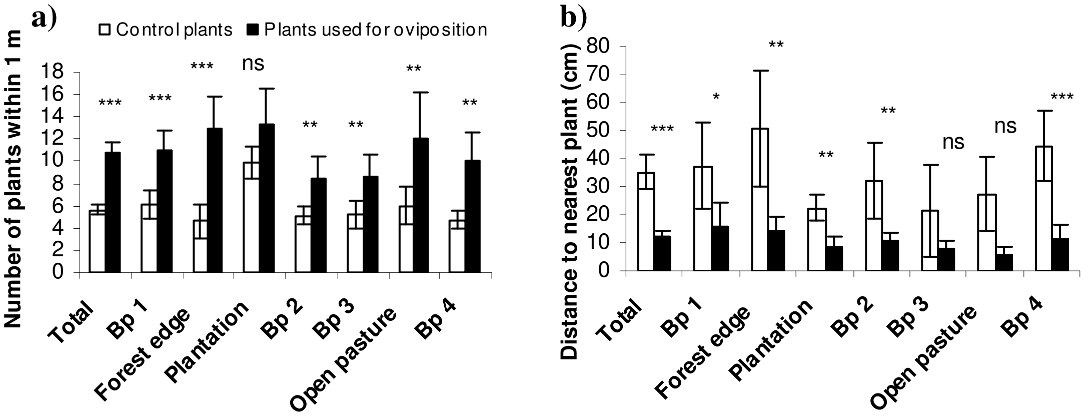

***Figure 7a and b**. Number of* Primula veris *within a radius of one metre (3.14 m^2) and the distance to the nearest plant of control plants and plants used by the butterfly for oviposition at the various study sites. The column denoted Total includes the average of all study sites. Error bars show 95% confidence interval for mean. For explanation of significance level (independent samples t-test) and N for each study site see Fig 2.*

When analysing *P. veris* density in a logistic regression the largest increase in probability of oviposition, with respect to density of *P. veris*, was found between approximately 3 to 5 plants/m^2 (Fig. 8). The equation used for the logistic regression model was p’ = -2.3 + 0.19**P. veris* density. The logistic equation calculated p’ and the probability of patch occurrence (p) was given by p’ = ln[p/(1-p)]. If the density of *P. veris* is raised from 3 to 5 per square metre the probability of oviposition is raised from 0.37 to 0.66. The average of *P. veris* density at all sites was 1.9 *P. veris*/m^2 for control plants and 3.5 *P. veris*/m^2 for egg-bearing plants.

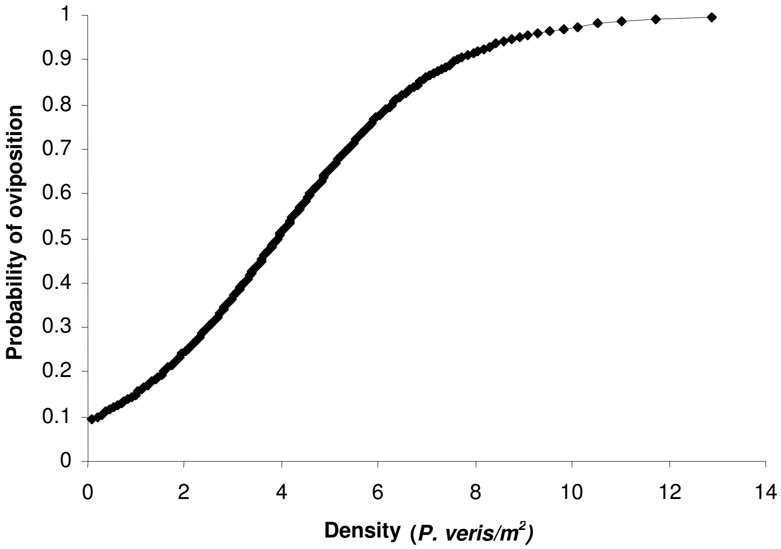

***Figure 8**. Probability of oviposition related to* Primula veris *density per square metre based on a logistic regression.*

4.3. Tree and bush structure

The females oviposited on *P. veris* situated significantly closer to a tree or a bush than randomly selected plants (Fig. 9a). The results were significant in three out of seven sites. The largest difference was at the site with the least amount of bushes and trees. At the densest site, plants with eggs, larvae or feeding marks were situated further away from trees and bushes than control plants, although it was not statistically significant.

Hamearis lucina females oviposited on plants located closer to the forest edge in two out of seven study sites (Fig. 9b). The Total column again showed highly significant differences. The large difference in average between the various areas was mostly due to differences in site structure. For example, at the Plantation and the Forest edge it is not possible to grow more than eight metres away from the forest, while at the Bushy pasture 2 the distance may be well over 70 metres.

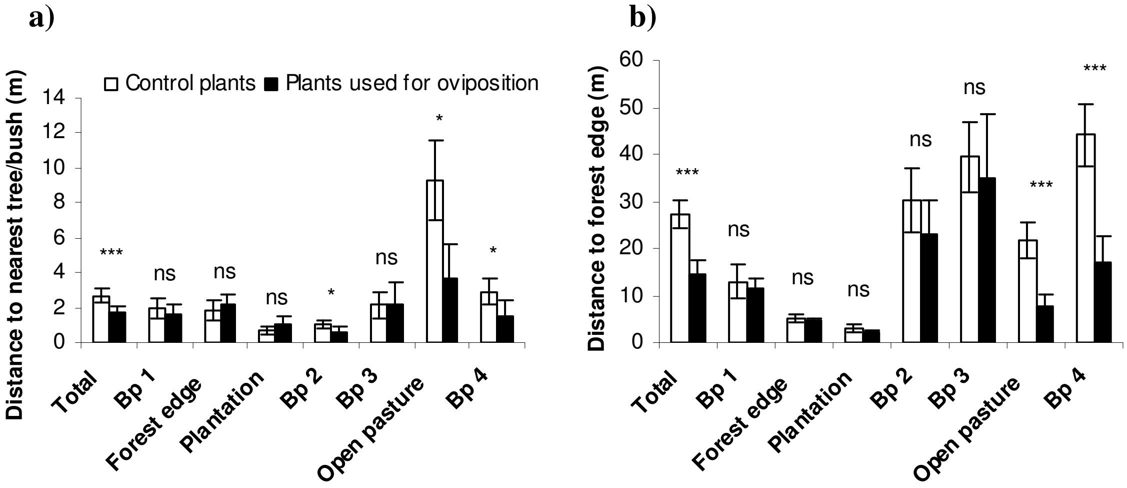

***Figure 9a and b**. Distance to nearest tree or bush and forest edge of control plants and plants used by the butterfly for oviposition at the various study sites. The column denoted Total includes the average of all study sites. Error bars show 95% confidence interval for mean. For explanation of significance level (independent samples t-test) and N for each study site see Fig 2.*

4.4. Seasonal host plant nitrogen content

Nitrogen content in *P. veris* generally decreased over the summer at all sites (Fig. 10). *Primula veris* at the shadiest site had the highest amount of nitrogen, while the bushy habitat had the least.

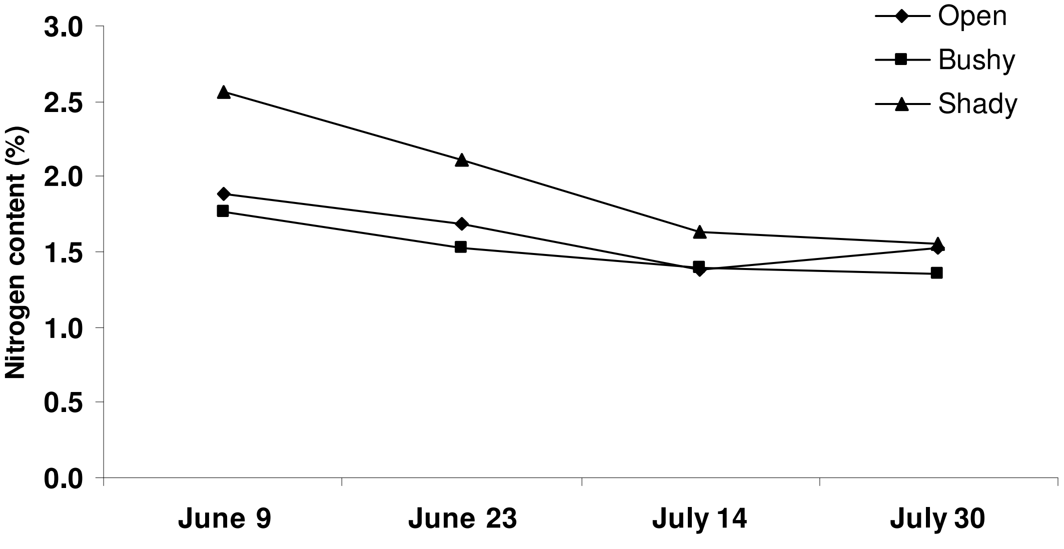

***Figure 10.** Seasonal variation in nitrogen content in percent of dry weight in* Primula veris *at three different types of habitat. Error bars show 95% confidence interval for mean.*

A significant negative correlation was found between light intensity and nitrogen content ($p<0.01$, $R^2 = 0.0643$) (Fig. 11). At a light intensity of 10% the nitrogen content was about 1.7% of the plants' dry weight, while it decreased to 1.3% at an intensity of 90%.

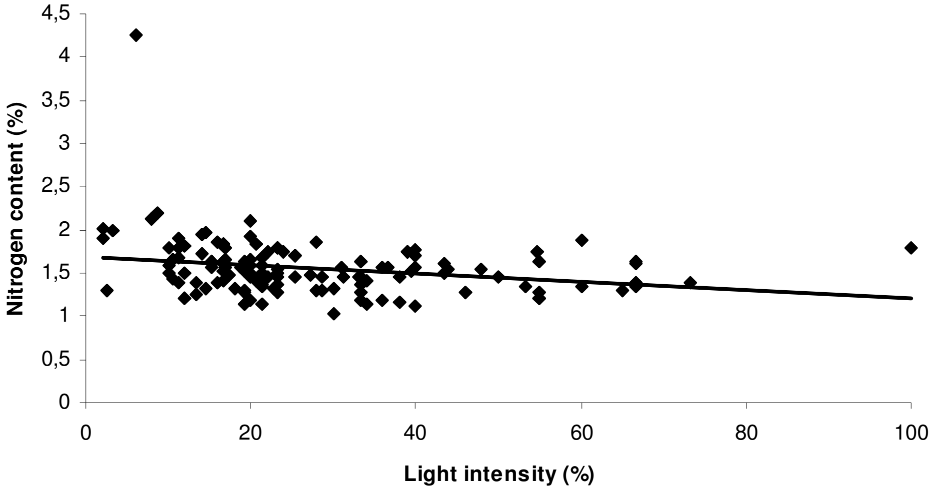

***Figure 11**. The relationship between nitrogen content in percent of dry weight in* Primula veris *and light intensity in percent of the reference value of each day. A linear regression gave $y = -0.4934x+1.6974$, $R^2 = 0.0643$, $p<0.01$. All study areas were included (N = 134).*

Nitrogen content showed no relationship with height in *P. veris* when tested in a linear regression ($p>0.05$), even though a weak trend pointed towards higher nitrogen content in taller *P. veris*. No significant relationship between the nitrogen content and the distance to the forest edge was found either ($p>0.05$). Again, there was only a weak pattern with more nitrogen in *P. veris* growing closer to the forest edge. A weak relation was found between the nitrogen content and the distance to nearest tree or bush, with higher nitrogen content closer to trees and bushes, but there was no statistical significance.

5. Discussion

The results of this study strongly suggest that *Primula veris* characteristics, plant density and the surrounding vegetation structure altogether influence the oviposition choice of *Hamearis lucina*. This is supported by several other studies on the same species (Sparks et al. 1994, Greiff Andersson 1998, Oates 2000, Kruys 2004).

Egg-laying females seem to prefer flowering plants that are taller than average. Similar results have been found both in England (Sparks et al. 1994, Oates 2000) and earlier at Omberg (Greiff Andersson 1998). The reason for choosing plants with these characteristics may be that they are easier to find since they are taller and have flowers on top guiding the way (Oates 2000). The results of a study made by Porter (1992) showed that the majority of the eggs were laid on the largest, most apparent plants. The exact cues used by *H. lucina* females to find good host plants are not clear, but visual searching is known to be important in many other butterfly species (Porter 1992). The females also preferred to oviposit on plants with a larger number of leaves than average. Larger plants with a higher number of leaves provide more food and shelter for the young larvae as they hatch. Food availability is important during the first larval instars, so that the larva is not forced to leave the plant when it is very small. Rausher (1979) concluded that small larvae leaving its host plant have a lower probability of finding another plant, and thereby a lower probability of surviving than larger larvae have.

Nitrogen content in host plants has in some studies been shown to limit phytophagous insect growth and development (Wheeler 2001). Increased larval performance would then be expected on high nutrient plants, which is one of the reasons that nitrogen content was measured in this study. If higher nitrogen content is beneficial to the larvae it is plausible to believe that the females prefer to oviposit on such plants. In a study conducted by Prudic et al. (2005) the results showed that female butterflies of the species *Junonia coenia* chose host plants with higher amounts of nitrogen. However, plants with higher amounts of nitrogen had a decreased chemical defense, which thus may have influenced the choice. Another study made by Fischer & Fiedler (2000) revealed that the butterfly species *Lycaena tityrus* was not able to discriminate between fertilised and unfertilised host plants. The results showed higher larval growth rates, higher pupal mortality and a reduction in adult size as the nitrogen content increased, i.e. not beneficial for the butterflies. These amounts of nitrogen were probably higher than those at my study sites, which are nutrient poor, and *P. veris* there are not likely to reach a harmful level of nitrogen. The results of my study showed that the females chose plants with a higher nitrogen content than average, but it is hard to say if it is because they grow where the light conditions are right, because the height is the preferred, because the distance to bushes or forest edge is the best or if it depends on the nitrogen content. All these factors are linked and probably some kind of balance is needed between them to make the habitat suitable.

Another factor that influences the probability for larvae to find another host plant is the density of *P. veris*. Many plants growing in the close proximity will of course increase the chances of finding a suitable food source. Also, if the female has laid a larger batch of eggs on a plant, it will not be sufficient for all the larvae until pupation, and some will have to move. The females in this study have been shown to follow that pattern by ovipositing on *P. veris* in clusters with a much higher density and also on specimens situated closer to another plant. When the probability of oviposition was plotted against *P. veris* density in a logistic regression the largest increase in probability was shown as the density rose from 2 to 5 plants per square metre. Within that range the probability was raised from 0.25 to 0.66. Of the control plants at all sites only the Plantation controls were within the high-density range (2-5 plants/m^2), though when looking at plants used by the butterfly for oviposition all sites were within the range. Consequently there are spots with a density high enough for oviposition at all study sites, even if the average site density often is much lower than that. However, further studies are needed to conclude if the area of high-density spots is large enough for long-term survival of *H. lucina*.

The seasonal decrease in *P. veris* density was examined at four different sites. In Enclosure 1 and 2, the number was more than halved during the summer. This is probably due to grazing and desiccation. The gates to the enclosures were supposed to remain closed until late summer in order not to disturb the larvae with grazing cattle. However, the gates were not closed at all this summer, a mistake that may have damaged parts of the *H. lucina* population, causing the area to be heavily grazed. The larvae need their host plant for food and shelter sometimes until the second week of August, when most of them have pupated (Emmet & Heath 1989). In other parts of the Bushy pasture 4 the *P. veris* density also decreased during the summer, which is not surprising, since the cattle graze the whole area and *P. veris* in open areas easily dried out. As *P. veris* density from the sampling in May was compared to the results of a study made in 1995 (Greiff Andersson 1998) it was apparent that it had decreased to a large extent at all sites. The largest decrease was found at the Open pasture with over four *P. veris* less per square metre than found in the earlier study. It may be possible that *P. veris* are outcompeted by the tall grasses growing in the pasture. This poses a management problem since the butterfly prefers an environment with taller grass and scrub, while the host plant needs heavier grazing in order to survive the competition from other plants and scrub (Oates 2000). At the Slope in Bushy pasture 4 the *P. veris* density was also much lower than in 1995. That part of the pasture was previously described as 'lush', while it today only contains a few trees. Probably the lack of bushes is the largest problem, causing the plants to be grazed, and to be situated in direct sunshine, which can cause the plants to dry out early in the season.

At the Plantation, the study in 1995 discovered a strong population of butterflies. The site consisted at the time of a plantation with small spruces (0.5-3 m tall). The spruces are now about 8 m tall and I found very few eggs, larvae or feeding marks there, all located at the edges of the plantation. Several butterfly species previously known to breed in woodland grassland, may temporarily find a habitat in young conifer plantations (Warren & Key 1991), *Hamearis lucina* being one of them (Warren 1992). Due to increasing shade as the trees grow these plantations are only suitable a few years, and are thereafter unsuitable for many years (60-80) until felling (Warren 1992). Many of the species in this habitat face the risk of local extinction as the plantations mature (Warren & Key 1991).

The preferred sward height for egg-laying was taller than the average of the randomly chosen *P. veris*. Warren (1992) has come to the same conclusion, but remarks that it is important to be careful not to allow the grass and scrub dominate too much, since *H. lucina* has died out on many sites for that reason. Sparks et al. (1994) has found that plants on bare ground, in very short sward or in rank vegetation are rarely selected as oviposition site. In a study made by Porter et al. (1992) it was found that the preferred sward height of *H. lucina* is 5-25 cm, which corresponds very well to the results of this study. The reasons for choosing taller sward for oviposition may be several: to hide from predators, the fact that host plants are less likely to dry out, or because of a more humid microclimate. One of the larger threats to butterfly eggs is desiccation, which is why females have to be careful to put their eggs in an environment humid enough (Porter 1992).

The distance to the nearest tree or bush from *P. veris* with eggs was significantly smaller than for randomly chosen plants. The same pattern was found with the distance to the nearest forest edge. In order to have a suitable structure of the landscape for the butterfly it is necessary to have a mixture of open and shaded sites. This is to make sure that the butterfly finds the important microhabitats for all stages of the life cycle. Porter et al. (1992) concluded that a suitable sward height is not sufficient, but that shrubs also are needed for breeding. This may be a problem for the population living at the Open pasture, where there are only a few bushes in the whole pasture. The proximity to bushes and forest edge may be important because of the shelter it gives both from predators of the butterfly and the host plant, when the area is grazed. Bushes and trees also provide shade during the hot parts of the summer to host plants. Senescent or yellow leaves are not accepted as food source by the larvae (Emmet & Heath 1989, Hellmann 2002), so if the host plant dies before the life cycle of the butterfly is completed, the larvae will have to switch to another plant, risking its life doing so (Rausher 1979).

Hamearis lucina females preferred *P. veris* in a somewhat darker environment than the randomly selected plants. This factor is connected to the sward height and the surrounding structure of bushes and trees. A higher sward and more bushes or trees give a darker habitat. The fact that the butterflies chose the darker patches supports the results of the preferred taller sward height and the preferred proximity to trees and bushes.

Nitrogen content in host plants was highest at the beginning of the summer when the leaves were fresh and the plants were flowering, and then decreased as time passed. The shade-grown *P. veris* had the highest amounts of nitrogen, when comparing different habitats. A study made by Grundel et al. (1998) on *Melissa samuelis* showed that larvae preferring shade-grown lupines over sun-grown ones had a significantly faster development, but not increased final size. This may be an advantage, because of less predation and parasitism. If shade-grown plants, which in my study were shown to contain more nitrogen, decrease development time, the females should search for host plants growing at shadier sites.

5.1. Conservation implications

This study has shown that *H. lucina* has specific host plant and habitat preferences, leading to important conservation implications. *Hamearis lucina* is sensitive both to heavy grazing as well as abandonment. The most preferred sward height was 9-11 cm and when the sward exceeded 10 cm the butterflies preferred a shorter sward than average. Conversely they preferred a taller sward in environments with a sward shorter than 10 cm. The dilemma is that in the absence of sufficient grazing, plants like *P. veris* gradually decline because of competition from other species (Oates 2000). If grazing of necessary intensity to keep the other species from invading is maintained, the habitat will not produce the preferred sward heights of the butterfly. *Primula veris* may well benefit from the increased grazing, but the butterfly will not find suitable oviposition sites until the grazing pressure is relaxed. Rotational grazing, when only a third or a quarter of the butterfly's habitat is grazed every year may be a good option if the scrub invasion is not too large (Bourn & Warren 1998).

Egg-laying *H. lucina* females also had specific preferences with regard to tree and bush structure. Forest edges or other shelter in the form of trees and bushes were important oviposition sites. During management some bushes and scrub must be left, even though it needs to be controlled and cleared locally to maintain glades in the landscape (Bourn & Warren 1998). This may sometimes be misinterpreted as a conflict with the conservation management of vascular plant communities. The conservation of a specialist butterfly as *H. lucina* clearly require good communication between vascular plant specialists and butterfly specialists. Bushes should be allowed to establish, especially in areas with high densities of *P. veris*, to create suitable oviposition sites for *H. lucina*. It is shown by Oates (2000) that larvae developing on *P. veris* clumps, whose leaves remained green, tended to be sedentary, which is a large advantage for vulnerable larvae of early instars. Also, taller plants with higher nitrogen content were located in shadier environments, which are both factors that were preferred by the females.

One of the larger problems with the conservation of *H. lucina* is that it prefers a middle successional stage, which is transient and requires quite a lot of management (Oates 2000). The combination of requirements as host plant density, bush and tree structure and sward height makes the conservation a challenge.

5.2. Practical site management guidelines

The results of the study allow specific site management guidelines for the long term survival of the *H. lucina* population at Omberg.

It is clear that the study site Plantation is in urgent need of management. Otherwise *H. lucina* will disappear completely from it within a few years time together with the *P. veris* population. At least two thirds of the spruces need to be thinned out to make the area more open, while letting a few smaller bushes grow up.

The late summer grazing at the Open pasture is good and should be continued. Maybe it could start at the end of July instead of August, to prevent the grasses from overshadowing *P. veris* completely. It would also be good if a few bushes could be planted or allowed to grow up in the parts of the pasture far away from the forest edge to create suitable egg-laying habitats for *H.*

lucina. The study site Forest edge seems to have a quite strong population of *H. lucina*, so if the bushes are kept down, the site needs no major changes. Since there is no grazing, the grass would preferably be cut at the same time as the grazing in the Open pasture starts.

Bushy pasture 3 seems to have lost parts of its *H. lucina* population since 1995. The grazing has increased since then and the forest just south of the study site has been felled, causing the woodland edge to disappear. The large open area that is left where the forest was must be managed to create an area rich in bushes, much in the same way as the study site. The study site should be left as it is, but there should only be allowed late summer grazing, since many *P. veris* were heavily grazed. The average sward height at Bushy pasture 3 has been halved among the control plants since 1995 (Greiff Andersson, 1998), which is a sign of too heavy grazing.

A comparison of *P. veris* density and number of egg-bearing plants at the study site Slope in the Bushy pasture 4 in 1995 and in this study gives important implications for management. In 1995, the area harboured one of the main populations of *H. lucina*. The area was then rich in bushes and trees and had a high density of *P. veris* and a high number of egg-bearing plants. Since then the site has been cleared, the *P. veris* density has decreased and very few egg-bearing plants were found in this study. In contrast to the Plantation, the area has become too open to be suitable to *H. lucina*. Some of the protective trees and bushes need to grow back in the Slope in order for the butterflies to inhabit that site again. Also, the gates to the two enclosures need to be closed at least until the start of August. For the rest of the Bushy pasture 4 to be suitable for the butterfly it may be needed to let more bushes grow up, creating glades in some places. Bushy pasture 1 should be left the way it is, because it seems to be working well with its mixture of open and shady spots. There was a light grazing that prevented the grasses and bushes from outcompete *P. veris*, and that should be continued.

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