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Titel der Diplomarbeit

**Habitat and host plant use of the Large Copper Butterfly *Lycaena dispar rutilus* (Lepidoptera: Lycaenidae) in Vienna (Austria)**

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## Habitat and host plant use of the Large Copper Butterfly *Lycaena dispar rutilus* (Lepidoptera: Lycaenidae) in Vienna (Austria)

**Key words:** *Lycaena dispar rutilus*, immature stages, spatial distribution, Vienna, habitat utilization, host plant species, plant characteristics.

**Abstract.** This study was designed to investigate egg placement patterns at three different spatial scales for the Large Copper butterfly (*Lycaena dispar*), a species of considerable conservation interest. In Austria the subspecies *L. d. rutilus* is bivoltine, with the first generation occurring from the end of May to mid June and the second in August. Females deposit their white eggs onto the leaf surface where they are visually easy to detect. Earlier studies have demonstrated that searching for pre-imaginal stages in *Lycaena dispar* is a far better way to prove the incidence of this species at particular locations than the observation of adults. Accordingly, this study was based on searching for eggs on appropriate food plants in Vienna. In order to assess the importance of characteristics that influence host plant selection and habitat choice by egg laying females at the site, plant, and leaf scale, different biotic and non-biotic factors were measured.

23 study sites with potential food plants were investigated at the end of the flight period of the two generations of *Lycaena dispar rutilus* in the year 2008. A total of 2457 eggs and 271 larvae were counted. Most eggs and larvae were encountered at dry fallows and urban waste land. Statistical analyses revealed that on site scale only the landscape zones according to the classification of the Vienna municipality had a significant effect on egg densities. The sparsely or densely built up urban zones harboured nearly half of the whole egg records. Six different *Rumex* species were confirmed as host plants for *Lycaena dispar rutilus* in Vienna, two of which had not been mentioned as food plants for this species in the literature. *Rumex crispus* was found to be the most abundant and most important host plant for egg-laying females of both generations harbouring 87.55% of the total number of egg counts. *Rumex crispus* (4.4 eggs/plant) was preferred over *Rumex obtusifolius* for oviposition (1.1 eggs/plant). At the plant scale more eggs were found on higher plants and on plants with a higher potential daily sunshine duration. Mowing had a significantly negative effect on egg densities at plant level. At the leaf scale tall leaves were preferred by egg laying females. The degree of infection through a phytopathogenic fungus (*Uromyces rumicis*) did not affect oviposition preference. For the future persistence of the Large Copper Butterfly in Vienna conservation strategies should focus on the maintenance of appropriate habitat patches, i.e. so called “wasteland” like e.g. fallows. Natural succession of such areas should be prevented by extensive management, e.g. by mowing parts of the habitat every 2-3 years. This will not only support the Large Copper but also many other threatened insects.

## Habitat- und Wirtspflanzennutzung durch den Großen Feuerfalter (*Lycaena dispar rutilus*) in Wien

**Zusammenfassung.** Diese Studie wurde entworfen, um das Eiablageverhalten des Großen Feuerfalters (*Lycaena dispar*), einer naturschutzfachlich bedeutenden Tagfalterart, auf verschiedenen räumlichen Skalenebenen zu untersuchen. Die Unterart *Lycaena dispar rutilus* bildet zwei Generationen aus, wobei sich die Flugzeit der ersten Generation von Ende Mai bis Mitte Juni erstreckt. Die zweite Generation hat ihre Hauptflugzeit im August. Die weißen Eier, mit ihrer charakteristischen Oberflächenstruktur, werden von den Weibchen auf den Blättern der Ampferpflanzen abgelegt und sind hier leicht zu entdecken, wobei selbst geschlüpfte Eier noch gut zu erkennen sind und deshalb auch mit aufgenommen werden können. Frühere Studien haben gezeigt, dass sich Präimaginalstadien besser zum Nachweis dieser Art eignen als das Falterstadium, weshalb in dieser Studie in erster Linie die Suche nach Eiern von *Lycaena dispar* zum Einsatz kam. Um mögliche Präferenzen der Weibchen bei der Eiablage zu erfassen, wurden verschiedene biotische und abiotische Parameter auf Flächen-, Pflanzen-, und Blattebene erhoben. Insgesamt wurden 23 potentiell geeignete Flächen in fünf verschiedenen Kulturlandschaftszonen innerhalb Wiens auf die Präsenz von Eiern im Jahr 2008 untersucht. Es konnten während der Studie insgesamt 2457 Eier und 271 Raupen erfasst werden. Als günstige Reproduktionshabitate erwiesen sich vor allem trockene Brachen und diverse Ödflächen. Auf der Ebene der Fläche erwies sich der Faktor Kulturlandschaftszone als statistisch signifikanter Einfluss auf die Eidichten. Flächen, die der dicht- bzw. dünn bebauten Kulturlandschaft zuzuordnen waren, enthielten fast die Hälfte der gesamten nachgewiesenen Eier. Als Eiablagepflanzen konnten sechs verschiedene Ampferarten nachgewiesen werden. Neben den in der Literatur schon erwähnten Futterpflanzen (*R. crispus*, *R. obtusifolius*, *R. sanguineus*, *R. hydrolapathum*) konnten für Wien zwei weitere Ampferarten (*R. stenophyllus*, *R. patientia*) als Futterpflanzen bestätigt werden. Als die häufigste und damit auch die wichtigste Futterpflanze für den Großen Feuerfalter in Wien erwies sich der Krause Ampfer (*R. crispus*), der gegenüber *Rumex obtusifolius* deutlich bevorzugt wurde. Während an *R. crispus* durchschnittlich 4,4 Eier/Pflanze gefunden wurden, waren es an *R. obtusifolius* nur 1.1 Eier/Pflanze. Auf der Ebene der Pflanze wurden hohe Ampferpflanzen sowie Futterpflanzen, die eine längere Besonnungsdauer aufwiesen von Weibchen des Großen Feuerfalters bevorzugt zur Eiablage genutzt. Der Faktor Mahd hatte auf Ebene der Pflanze einen signifikant negativen Einfluss auf die Zahl der abgelegten Eier. Auf der kleinsten räumlichen Ebene, der Blattebene, konnte eine Präferenz der Weibchen für längere Blätter aufgezeigt werden. Die Zahl der Eier wurde auf der Ebene des Blattes nicht vom Befallsgrad durch einen Rostpilz (*Uromyces rumicis*) beeinträchtigt. Damit Vorkommen des Großen Feuerfalters in Wien auch in Zukunft gesichert sind, sollten getätigte Schutzmaßnahmen vor allem die Erhaltung von geeigneten Lebensräumen, wie etwa Ödflächen und Brachen, zum Ziel haben. Die natürliche Sukzession solcher Flächen sollte durch extensives Management verhindert werden, z.B. durch partielle Mahd alle 2-3 Jahre. Dadurch werden neben dem Großen Feuerfalter auch viele andere gefährdete Insekten gefördert.

## I. Introduction

One key factor in the ecology of phytophagous insects is the interaction with their natural host plants, thus maternal host choice is a particularly important step in the life-cycle of all herbivorous insect species (Rabasa et al., 2005; Janz et al., 2005; Batáry et al., 2008). Recognition and selection of the best quality foods available by ovipositing females is crucial for optimal and successful larval performance (Hódar et al., 2002; Liu et al., 2006; Ngu et al., 2008; Talsma et al., 2008). Due to the low dispersal ability of the juvenile stages compared to adults; especially during the young instars; the selection of optimal quality host plants and suitable habitats is a critical step in the life-cycle of all Lepidoptera (Fartmann & Timmermann, 2006; Eichel & Fartmann, 2008). Oviposition patterns are a result of female choosiness at different spatial scales, i.e. the host plant scale and the site scale (Anthes et al., 2003; Wiklund & Fridberg, 2008). Therefore several studies have focused on the selectivity of egg depositing female butterflies at different spatial scales (e.g. Rabasa et al., 2005; Fartmann, 2006; Loritz & Settele, 2006; Batáry et al., 2008; Eichel & Fartmann, 2008).

Generally host plant choice has been shaped by selection to maximize fitness, i.e. the opportunities of survival and growth of a female's offspring. Egg laying strategies vary strongly across butterflies: some species lay their eggs as singletons, while others lay numerous eggs in clusters at the same place. Egg laying behaviour is rarely indiscriminate but very often specific. Mostly eggs are laid on particular plant species or plant parts at climatically favourable spots. Visual and chemical stimuli that are used during host plant selection include plant height, the size of the leaves, and the phenological or nutritional status of the plant (Thompson & Pellmayr, 1991; see also references in Fartmann & Hermann, 2006). Eichel & Fartmann (2008) analysed ovipositional choice of *Melitaea aurelia* and reported that females preferred to oviposit on tall plants. This is consistent with the findings of several other authors exploring egg-laying behaviour of butterflies (Anthes et al., 2003; Árnayas et al., 2006; Liu et al., 2006; Talsma et al., 2008b). Stefanescu et al. (2006) revealed that *Euphydryas aurinia* selected the greenest leaves of their host plant for egg placement. Janz et al. (2005) found that at the plant scale females of *Polyommatus icarus* exhibited a significant preference for flowering plants when ovipositing (Janz et al., 2005).

At the larger spatial scale, i.e. the site scale, female imagines are intended to be able to discriminate between local characteristics, e.g. local microclimate, vegetation structure and food quality (Anthes et al., 2003; Rabasa et al., 2005; Batáry et al., 2008). In the case of the Duke of Burgundy Fritillary Fartmann (2006) found that a higher number of eggs were deposited at sites which had more than 60% herb cover and a high potential duration of insolation was also favoured when searching for suitable sites for oviposition. An increase in the potential duration of sunshine was also positively affecting egg densities in other butterfly species (e.g. Eichel & Fartmann, 2008). Some butterfly species were shown to preferentially occupy breeding sites if a high number of larval host plant individuals were present (Anthes et al., 2003; Krauss et al., 2004; Krauss et al., 2005).

Appropriate egg laying sites and thus larval habitats are of imminent importance for the persistence of butterfly populations. Successful management strategies should aim at improving the availability or quality of these resources (Hermann & Fartmann, 2006). Therefore, during the last decade much research in butterfly conservation biology has focused on this life-cycle aspect (e.g. Bergman, 2000; Anthes et al., 2003; Krauss et al., 2004; Bergström, 2005; Krauss et al., 2005; Küer & Fartmann, 2005; Rabasa et al., 2005; Árnayas et al., 2006; Liu et al., 2006; Batáry et al., 2008; Eichel & Fartmann, 2008; Talsma et al., 2008a+b). Here I use surveys of eggs and larvae of one focal species of conservation relevance, viz. the Large Copper Butterfly (*Lycaena dispar*), to gain insight into habitat use and host plant preferences in the city of Vienna (Austria). Although the species is known to be

widespread in Vienna (Höttinger et al., 2006) most records are based on single observations of adult individuals and not much is known about its breeding habitats. The species is regarded as a low density species and imagines show high dispersal ability with a medium migration distance of 5 km (Settele et al., 2000). In comparison, the largest distance covered by the related butterfly *Lycaena hippothoe* during a mark-release-recapture study performed in western Germany was 325 metres, showing its sedentary nature (Fischer, 1998). A successful survey method for species occurring in low densities is the search for pre-adult stages and for approximately one quarter of the Central European butterfly species this method is relevant (Fartmann & Hermann, 2006; Fartmann & Timmermann, 2006).

Ecological studies on *L. dispar* have so far mainly focused on the ssp. *batavus* (including the reintroduced populations in Britain) (Duffey, 1968; Webb & Pullin, 1996; Pullin, 1997; Nicholls & Pullin, 2000; Webb & Pullin, 2000; Nicholls & Pullin, 2003; Martin & Pullin, 2004 a; Martin & Pullin, 2004 b). Only one study on egg placement patterns for the bivoltine Central European populations of *Lycaena dispar rutilus* was performed until now (Loritz & Settele, 2006). This study mainly focused on egg deposition decisions at two spatial scales; i.e. the plant scale and the leaf scale. In the present study I used biotic and abiotic factors at three different spatial scales to model which of them affects oviposition selectivity of females of *L. dispar rutilus*.

Even though *L. d. rutilus* is still extant throughout much of mainland Europe, regional declines of this species in previous decades have lead to it being listed in several regional Red Lists, e.g. in Austria (Huemer et al. 1998) and Germany (Pretscher et al., 1998) but also on the European scale (Van Swaay & Warren, 1999). According to recent analyses, however, most populations appear to be stable or even expanding and hence the species was delisted, e.g. in Austria (Höttinger & Pennerstorfer, 2005) and Europe (van Swaay et al., 2010). In the most recent Red Lists of the Butterflies of Vienna and Lower Austria it is still listed as vulnerable ("gefährdet"; Höttinger, 1998; Höttinger & Pennerstorfer, 1999). *Lycaena dispar* is also listed under the 1979 Convention on the Conservation of European Wildlife and Natural Habitats and it is included in Annexes II and IV of the European Community Habitats Directive requiring strict protection in its own right and designation of Special Areas of Conservation. Therefore the intention of this work is to contribute to the knowledge about the species' ecology in eastern Austria as a sound scientific basis for future conservation and management strategies. The main objectives of the study were as follows: 1. to assess the differential importance of habitats (site scale) situated in the five landscape zones of Vienna for the reproduction of the Large Copper by searching for pre-imaginal stages; 2. to record which *Rumex* species are used for oviposition and to investigate the influence of host plant characters at different scales (plant and leaf scale) on oviposition preferences; 3. to assess the factors which are important for egg laying females on site, plant, and leaf scale.

Accordingly, the following specific working hypotheses were formulated:

- Prominent, vigorous *Rumex* plants protruding above surrounding vegetation and growing in a sunny position are preferred by egg-laying females
- Females exhibit a preference for one particular *Rumex* species
- Host plants suffering from massive leaf damage caused by herbivorous competitors and/or being heavily infested by fungi are less attractive for oviposition
- Large leaves higher above the ground are preferred by egg laying females
- In both broods maternal host and habitat choice is consistent
- Both generations of *rutilus* use the same habitats for their reproduction
- Uncultivated places (agricultural fallows or urban waste lands) are favoured by *L. d. rutilus* for oviposition
- Egg density is balanced across landscape types.

## II. Material & methods

### II.1. Study species

The trans-palaeartic distribution of *Lycaena dispar* reaches from Western Europe across temperate Asia to the Amur region and Korea (Ebert, 1993; Nicholls & Pullin, 1999; Kühne et al., 2001). Across Europe *L. d. rutilus* has a large but disjunct distribution, occurring throughout much of mainland Europe southwards of 60° latitude (Väisänen et al., 1983; Pullin et al. 1998; Lai & Pullin 2004). Its vertical range is restricted to the plains and foothill zone approximately up to 400 m (Ebert, 1993). In Austria its distribution is limited to the eastern lowland areas occurring in Lower Austria, Burgenland, Vienna, and southern Styria (Reichl, 1992; Slamka, 2004; Stettmer et al., 2007). *Lycaena dispar* is mostly considered as a hygrophilous butterfly species which becomes ever more bound to wetland habitats towards the northern margin of its range (Pullin et al., 1998). In the Netherlands, Poland, Finland and northern Germany the species is restricted to fenland habitats. In central and southeastern Europe, however, the habitat requirements are different and less specific since a wider range of habitats is occupied by the Large Copper. *Lycaena dispar rutilus* is an oligophagous species consuming *Rumex* species that contain little or no accumulations of oxalic acid ('docks') while 'sorrels' are avoided. The actual *Rumex* species used vary across the butterfly's range. *L. d. rutilus* is known to utilize the following food plants throughout its distribution: *Rumex hydrolapathum* HUDS., *R. crispus* L., *R. obtusifolius* L., *R. conglomeratus* Murray, *R. sanguineus* L., *R. aquaticus* L., and rarely *R. acetosa* L. (SBN, 1987; Pullin et al. 1998; Kühne et al., 2001; Werner & Möller, 2003; Loritz & Settele, 2006). The caterpillars of *Lycaena dispar*, like those of many other butterfly species, are foliophagous which means that they only consume plant leaves. *L. d. rutilus* has a bivoltine life cycle in most localities and even a third generation is possible in more southerly locations in favourable years (Pullin et al., 1998; Lai & Pullin, 2004). The first generation of *rutilus* is on the wing from May to June, the flight period for the second generation is from August to early September. Adults are very active fliers with a high dispersal capacity and can be found at places far away from their native habitats. The abundance during the second generation tends to be noticeably higher than in the first (Kühne et al., 2001; Loritz & Settele, 2006). Females of *Lycaena dispar* lay their eggs singly or in small groups on the leaves of their host plants. Eggs are laid on the upper leaf surface of the larval food plant hatching ca.10 days post oviposition. Data about the number of eggs produced per female vary greatly and reach from a mean of 50 eggs (Pullin, 1997), 60.8 eggs (Duffey, 1968); 300 (Pullin, 1997) and 400 in captivity (SBN, 1987). Even up to 750 may be produced under good conditions (Bink, 1986). In contrast to the majority of Lycaenid species larvae of *L. dispar* are only sporadically visited by ants (Fiedler, 1991, 2006). Ant-associations have been observed with two ant species (*Myrmica rubra* L., *Lasius niger* L.: Kühne et al. 2001; see also Appendix Fig. A6). First the larvae feed on the underside of the leaves, creating characteristic windows since the upper epidermis is avoided (Pullin, 1995). As a result of this behaviour first instar larvae can be detected easily by an experienced observer. Later, as the larvae increase in size they eat through the leaf making irregular holes. As a consequence of the shortening photoperiods in early September diapause is induced. Diapause is characterized by cessation of feeding, followed by migration to the base of the host plant. Depending on climatic conditions resumption of feeding occurs between the latter half of March and the beginning of May. The life span of *Lycaena dispar* imagines varies from about 20 to 36 days (Bink, 1986; Duffey 1968).

## II.2. Study sites

Potential study sites were located using infrared aerial photographs of Vienna. Vegetation structure can be identified on the shots which enables the location of sites suitable for investigation. Primarily open places were searched on the available shots since the occurrence of *Rumex* plants on such open places is more likely than on sites completely overgrown by trees or other kind of brushwood. Areas considered for further investigation were all potential sites detected, without regard to their size or other characteristics but they had to be of the following type: fallows, meadows, open river banks, various waste areas, green stripes and waysides. On the basis of the available photographs these kinds of habitat types were easy to detect (Fig. 1).

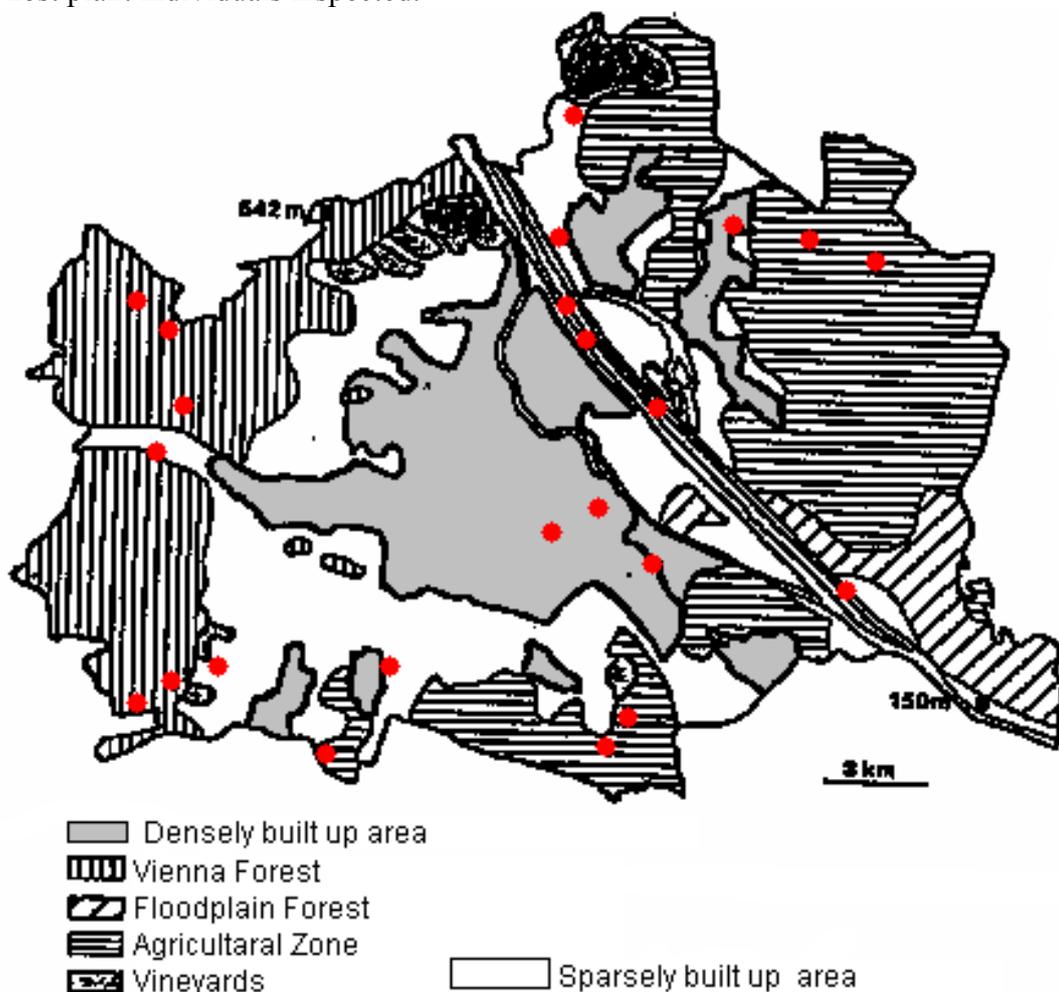


**Fig. 1** Example of an infrared aerial photograph showing a large area with fallow land marked in green. Photograph courtesy Municipality of Vienna (MA 22).

Every pre-selected site, which according to the aerial photographs appeared to provide potential habitat for *Lycaena dispar*, was then examined on the ground for the occurrence of *Rumex* plants. Sites which had no or less than 10 potential *Rumex* host individuals were excluded from further research, as well as those areas where trespassing was forbidden. The objective was to search at least 10 plant individuals per study site in order to make examination and subsequent statistical analyses meaningful.

Vienna was divided up into six landscape zones (after Zahner, 1994) in order to assess whether the frequency of *Lycaena dispar* differs among habitats in these zones. The zones are zone 1: densely built-up urban area; zone 2: sparsely built-up urban area; zone 3: Danube river bank and Danube island; zone 4: region dominated by agricultural land excluding

vineyards; zone 5: Vienna Forest; zone 6: area with vineyards (Fig. 2). The intention was to locate five study sites within each zone. The final study sites within each zone were randomly chosen to avoid bias in sampling. Unfortunately I had to exclude zone 6 from my investigations since sites with host plants present were too scarce there. Finally I arrived at 23 study sites in five zones (Fig. 2). Each site was then characterized by its (1) size (calculated with ArcGIS 9.2 software (by ESRI 2006) on aerial photographs; the habitat boundary was defined either if a marked change to another vegetation structure occurred or if the area was surrounded by anthropogenic structures (i.e. roads, buildings, fences, rails); (2) type of habitat it represents (see above II. 2.); (3) kind of management of vegetation (mowing, grazing, no management); (4) the abundance of flowering plants as an indicator for nectar availability on a rank scale from 0 (=no flowering plants present) up to 4 (=very rich in nectar plants ) for the day of survey; (5) distance to the next body of water (in m) as a proxy to the importance of wetland habitats for this species in the Viennese region (calculated as straight line to the next body of water with ArcGIS 9.2 software on aerial photographs); (6) the total number of *Rumex* host plant individuals inspected.



**Fig. 2** Map of Vienna with the location of the study sites within 5 (out of 6) landscape zones. For the geographical coordinates of each site see appendix.

### II.3. Host plants

Each of the 23 study sites was monitored twice at the end of the flight season of both generations of the Large Copper. In the first generation field work was carried out from 17<sup>th</sup> June 2008 to 3<sup>rd</sup> July 2008 and in the second generation observations were made from 16<sup>th</sup> to 28<sup>th</sup> of August 2008. The intention was to examine 20 *Rumex spp.* on each study site but at least 10 plants had to be present. The following plant features were recorded for each plant individual during field work: (1) plant species (after Fischer et al. 2005); (2) plant height (this was recorded by measuring the highest plant part, which was either the flowering stem for plants with inflorescences, or the leaf protruding highest above ground in non-flowering plants); (3) the mean height of the surrounding vegetation directly adjacent to the *Rumex* plant (mean calculated from measures of vegetation height at four points within a radius of 10 cm around each *Rumex* plant); (4) number of stems and leaves per plant (in flowering plants leaves on the stem were counted and, if present, also basal leaves; in non-flowering plants the total number of leaves was recorded); (5) leaf damage caused by herbivores scored on a rank scale from 0 (= no damage at all) up to 4 (= highly damaged); (6) externally visible fungal infections on leaves, again scored on a rank scale from 0 (= not infected) to 4 (=highly infected); (7) average potential duration of daily sunshine in hours for each plant (measured at medium height on both flowering and non-flowering plants with a horizontoscope after Tonne (1954) (Institute of daylight engineering in Stuttgart, Germany) for June in the first observation period and August in the second). The reason for taking this latter measurement was to find out whether plants potentially exposed longer to sunshine are preferred for egg deposition. On the leaf scale (1) the length (cm) of each leaf carrying eggs was measured as well as (2) its height above ground.

### II.4. Immature stages

Targeted search for pre-imaginal stages is considered an essential method for the identification of habitats for butterfly reproduction (Hermann & Fartmann, 2006). Since nowadays many butterfly populations are severely fragmented and their densities reduced in man-made landscapes, some butterfly species have become scarce to the extent that their occurrence has become difficult to prove. An important complementary method for monitoring certain species is the search for eggs and larvae on their food plants. By targeted search in the right season at suitable sites immature stages of these species can be found with little effort on their specific food plants. Hence this method enables the detection of reproductive habitats of certain species much more easily than the search for adult butterflies, especially when adult densities are low and/or if adults frequently disperse away from their reproduction habitats.

*Lycaena dispar* eggs are highly characteristic in shape, size and colour (Figs. A3, A4) and can unequivocally be identified even when hatched. Females usually deposit their eggs, either as singletons or in pairs, onto the upper side of leaves of their host plants, but some eggs are also laid on the underside (Kühne et al. 2001). Larger egg clusters indicate that oviposition involved more than one female (Kühne et al. 2001) or that a single female repeatedly visited the same plant. After hatching the empty eggshells remain on the host leaves for several days or even for a few weeks, since they are not eaten by the hatching larvae.

At the end of the flight period of each generation all study sites were monitored once and potential host plants were systematically checked for the existence of immature stages. First, all eggs were counted on each host plant and the following data were recorded: (1) number of

eggs per leaf (hatched and non-hatched eggs on both upper- and underside of the leaves were recorded); (2) number of eggs per plant; (3) height above ground and length of leaves carrying eggs (on plants with stems leaf height was measured from the ground; on non-flowering plants the height of the deposited eggs on a leaf was measured; leaves without eggs were not measured).

## II.5. Statistical analyses

Data were compiled in spreadsheets and were transformed if necessary in order to achieve an approximately normal distribution. Data with a skewed distribution were square-root or log-transformed, proportions were arc sin-square-root transformed, and environmental variables (e.g. the abundance of flowering plants) were standardized to a mean of zero and a standard deviation of one. For further statistical procedures I used the program STATISTICA 7.1 (StatSoft 2005). To test whether certain biotic and non-biotic parameters have a significant influence on the egg numbers on study site, plant and leaf level, I constructed General Linear Models (GLM). GLMs allow for a simultaneous analysis of the effect of different parameters on egg densities. The dependent variables (eggs/study site; eggs/plant; eggs/leaf) were tested with continuous (e.g. plant height, sunshine duration) and categorical predictor variables (e.g. mowing: yes or no) in the GLM. Prior to statistical analysis continuous predictor variables were checked for multicollinearity. When a high ( $r > 0.5$ ) and significant ( $p < 0.05$ ) correlation was found (e.g. between dock height and the height of its surrounding vegetation) then one of these variables was not considered in the statistical model. If more than one leaf on the same plant was found to carry eggs, these leaves were modelled as being nested within the respective plant individual. Additionally to the full model a simplified GLM was calculated. Not significant parameters gained from the full model were excluded from analysis in the simplified model.

## III. Results

### III.1. Egg numbers at site scale

Egg records proved that all 23 sites distributed over five landscape zones of Vienna were used as reproduction habitats by *L. dispar*. The number of sites with egg records at the end of the flight period of the first and second generation was 22 and 19, respectively. One site was not used for egg deposition by Large Copper adults in the spring generation, but the same site actually served as reproduction habitat for the summer generation (Tab. 1). In the summer brood four sites had no egg records, three of which were located within the Vienna forest landscape zone.

In total 750 *Rumex* plants were inspected on which 2457 eggs (or egg shells) and 271 larvae were observed. In the first generation I detected 698 eggs on 386 host plants, and in the second generation 1759 eggs on 364 host plants. This contrasts to the low number of adult sightings (2 males in the first, 3 males and 3 females in the second generation) during approximately 190 hours of field work. The exact numbers of egg records for each landscape zone and site separated for each brood are summarized in Table 1. The majority of study sites showed a higher egg number in the second brood but a few exceptions existed where the situation was reversed (Tab. 1). With a total of only 74 eggs, the sites situated in the Vienna forest zone had the lowest number of egg records. On the other hand the densely built-up urban areas harboured most eggs (761 eggs), followed by the sparsely built-up urban areas (701 eggs).

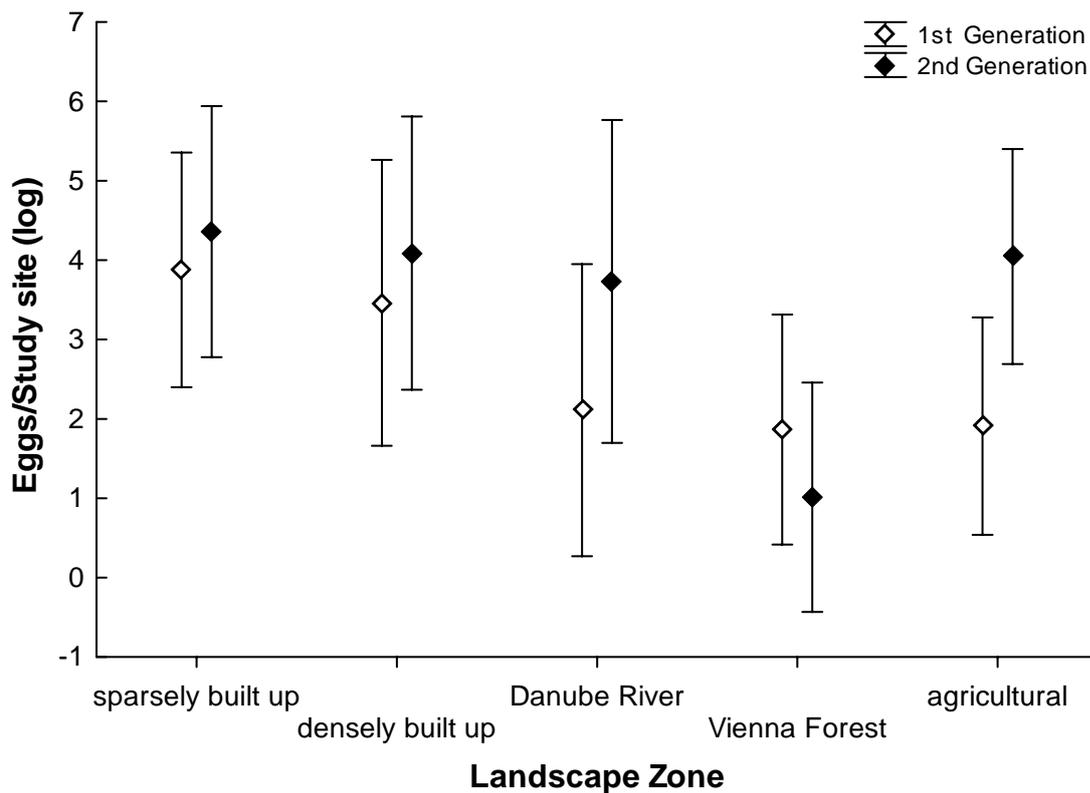
Table 1. Egg numbers at each study site in each landscape zone for the two generations. Plants – number of *Rumex* plants scored for the presence of eggs. A dash (--) indicates that no appropriate fifth replicate site was available in the respective zone.

Landscape zone	Generation	Plants	Replicate 1	Replicate 2	Replicate 3	Replicate 4	Replicate 5	Sum
sparsely built up	spring	86	48	21	156	67	5	297
	summer	94	76	173	34	104	17	404
densely built up	spring	71	52	8	52	63	--	175
	summer	65	0	161	199	226	--	586
Danube river	spring	53	2	4	32	10	--	48
	summer	47	59	168	22	4	--	253
Vienna forest	spring	98	23	5	27	4	5	64
	summer	85	0	3	0	7	0	10
agricultural zone	spring	78	57	0	17	35	5	114
	summer	73	10	39	49	338	70	506

Egg numbers per site mainly differed between the landscape zones (Tab. 2). The highest egg numbers were found at sites located in the sparsely and densely built-up landscape zone (Fig. 3). The Danube River zone and the zone dominated by agricultural land had only slightly lower egg numbers, while distinctly fewer eggs were recorded at sites in the Vienna Forest zone (Fig. 3). This low relevance of sites in the Vienna Forest zone as breeding habitat of *L. dispar* was more pronounced in the second than in the first generation. None of the other variables tested had a significant effect on egg numbers per study site. Neither the number of *Rumex* plants investigated on a site, nor the area size, the availability of nectar sources nor the distance to the next body of water were significantly associated with egg numbers. Mowing had a slightly negative effect ( $\beta = -0.294$ ) on egg numbers although it narrowly failed to be significant. Fewer eggs were found in the first as compared to the second generation ( $\beta = -0.250$ ), but this was again only marginally significant (Tab. 2 and Fig. 3). In a simplified GLM only those factors that had attained a *p*-value below 0.10 in the full model were considered. Results of the simplified model revealed a significant influence of mowing on egg densities at the site scale (Tab. 2).

Table 2. Results of GLM analysis of egg numbers on the site level. Significant effect ( $p < 0.05$ ) printed in bold. Overall model fit ( $N=46$ ), full model:  $R^2=0.541$ ;  $F(14)=2.614$ ;  $p=0.013$ ; simplified model:  $R^2=0.512$ ;  $F(10)=3.677$ ;  $p=0.002$ .

Effect	<i>full model</i>			<i>simplified model</i>		
	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
Number of plants investigated per site (square root)	1	0.655	0.424			
Distance to the next water body (standardized)	1	0.909	0.347			
Mown fraction of site (arc sin square root)	1	3.572	0.068	<b>1</b>	<b>5.046</b>	<b>0.031</b>
Area of study site (standardized)	1	0.083	0.774			
Number of flowers (standardized)	1	0.118	0.734			
Generation(Landscape zone)	5	2.202	0.079	5	2.317	0.064
<b>Landscape zone</b>	<b>4</b>	<b>3.093</b>	<b>0.029</b>	<b>4</b>	<b>3.234</b>	<b>0.023</b>
Error	31			35		



**Fig. 3** Mean number of eggs per study site ( $\pm 95\%$  confidence intervals), adjusted at the means of covariates from the full GLM (see Table 2), segregated for the two generations and the five landscape zones in Vienna. See Table 2 for details of statistical model.

### III.2. Egg numbers in relation to host plant species

Six different *Rumex* species were confirmed to serve as food plants of *L. dispar* in Vienna during this study: *Rumex crispus*, *R. obtusifolius*, *R. hydrolapathum*, *R. patientia*, *R. stenophyllus*, and *R. sanguineus*. The total number of eggs per plant species as well as the average egg load per plant individual and per leaf for the whole observation period is listed in Table 3. The portion of surveyed plants which had no eggs, aggregated over all six *Rumex* species, was 59.7% (see Fig. 4). The number of hosts with low egg numbers (1-5 eggs) was dominating and only a few food plant individuals received massive egg loads. In the first brood the share of plants without eggs was 64.5% (386 plants investigated), and in the second brood it was 54.7% (out of 364 plants). Hence, the fraction of *Rumex* plants carrying *L. dispar* eggs was significantly higher in the second brood ( $\chi^2_1=7.54$ ,  $p=0.006$ ).

*R. stenophyllus* and *R. patientia* are two new hosts being added to the list of food plants for the Large Copper. They were not common at the study sites, but both attained rather high egg loads per leaf if available. *R. crispus* was the overall most abundant host plant of *L. dispar* in Vienna, contributing 87.5% of all egg records. On average 4.4 eggs per plant occurred on this host. *R. crispus* also had the largest egg number per plant (78 eggs counted in the second brood), and the highest egg number per leaf (31 eggs recorded on one leaf in the first brood; Tab. 4). One *R. hydrolapathum* plant received 31 eggs which was the second largest egg number observed, followed by one *R. obtusifolius* plant which harboured a total of 23 eggs.

*R. obtusifolius* was the second most abundant food plant species assessed in this study, but egg numbers per plant were low (Tab. 3). Even though two host species (*Rumex hydrolapathum*, *R. stenophyllus*) were extremely rare they often received relatively high egg

numbers. *R. hydrolapathum* had the highest average egg density with 8.5 eggs per plant. This species is scored as a highly endangered in Vienna (Adler & Mrkvicka, 2003) as a result of river regulation. *R. stenophyllus*, another rare and endangered *Rumex* species occurring in Vienna (Adler & Mrkvicka, 2003; Fischer et al., 2005), also had high egg numbers per plant. *R. patientia* was originally cultivated as vegetable (“English spinach”), but is now quite abundant as neophyte in Vienna. Females of *L. dispar* used this plant as host as well. The lowest egg number was observed on *R. sanguineus*.

Table 3. Overview of egg distribution across six *Rumex* species used as host plants by *L. dispar* in the Vienna area. n: number of plants investigated.

	<b>Total egg number</b>	<b>Share (in % of total)</b>	<b>Eggs/Plant</b>	<b>±SE</b>	<b>Eggs/Leaf</b>	<b>±SE</b>
<i>R. hydrolapathum</i> (n= 4)	34	1.38	8.5	7.5	0.53	0.25
<i>R. stenophyllus</i> (n= 2)	7	0.28	3.5	3.5	0.19	0.12
<i>R. obtusifolius</i> (n= 195)	209	8.51	1.1	0.2	0.05	0.01
<i>R. sanguineus</i> (n= 36)	4	0.16	0.1	0.1	0.01	0.01
<i>R. patientia</i> (n= 21)	52	2.12	2.5	1.0	0.24	0.91
<i>R. crispus</i> (n= 492)	2151	87.55	4.4	0.5	0.40	0.03
<b>n=750</b>	<b>2457</b>	<b>100</b>	<b>3.3</b>	<b>0.3</b>	<b>0.24</b>	<b>0.01</b>

SE= standard error of the mean

Egg numbers per plant, segregated for the two generations and the six host plant species, are given in Tab. 4. In *R. hydrolapathum* the average egg number/plant was ten times higher in the second brood (15.5 eggs/plant) compared to the first (1.5 eggs/plant), and in *R. crispus* it was almost three times higher in the second generation. Accordingly, in *R. crispus* the amount of plants deposited with eggs was significantly higher in the second brood ( $\chi^2_1=15.15$ ,  $p=0.001$ ). In *Rumex patientia* and *R. obtusifolius* egg densities per plant were almost equal between the two generations. Hence, there were no significant differences in egg densities between the generations in *Rumex obtusifolius* and *R. patientia* ( $\chi^2_1=2.31$ ,  $p=0.129$  and  $\chi^2_1=0.17$ ,  $p=0.677$ , respectively). *Rumex stenophyllus* received an average of 3.5 eggs per plant in the first generation but no data for the second generation are available since plants had been covered by a rosebush. On *Rumex sanguineus* plants egg numbers were the lowest of all host plant species.

Table 4. Use of six *Rumex* host plants by *L. dispar* in the Vienna area segregated for the two broods.

Species	Generation	mean eggs/plant	±SE	max. eggs/plant	max. eggs/leaf
<i>R. hydrolapathum</i>	spring	1.5	1.5	3	1
	summer	15.5	15.5	31	10
<i>R. stenophyllus</i>	spring	3.5	3.5	7	3
	summer	0	0	0	0
<i>R. obtusifolius</i>	spring	1.2	0.3	23	10
	summer	1.0	0.2	10	5
<i>R. sanguineus</i>	spring	0.05	0.05	1	1
	summer	0.2	0.2	3	3
<i>R. patientia</i>	spring	2.4	1.2	19	6
	summer	2.7	1.7	10	5
<i>R. crispus</i>	spring	2.2	0.4	64	31
	summer	6.3	0.8	78	30

SE= standard error of the mean

*R. obtusifolius* plants predominantly received few eggs. About 75% of the plants examined for the first butterfly generation, and 82% for the second generation, harboured only 1-4 eggs. More than 10 eggs per plant were rarely encountered for both the first and second generation in this *Rumex* species (10% and 5%, respectively). In contrast, the proportion of plants with more than 10 eggs was substantial in *Rumex crispus* (first generation: 15.1%, second generation: 36%). Nevertheless low egg loads on *R. crispus* (1-4 eggs per plant) were prevailing in the first generation (63%) and less so in the second brood (40.7%). For *R. patientia* the situation was very similar (incidence of high egg densities (10+), first generation: 11.1%, second generation: 33%). However, low egg loads were most common (first generation: 77%). In the other three *Rumex* species either plant or egg numbers were too low for a meaningful consideration in this context.

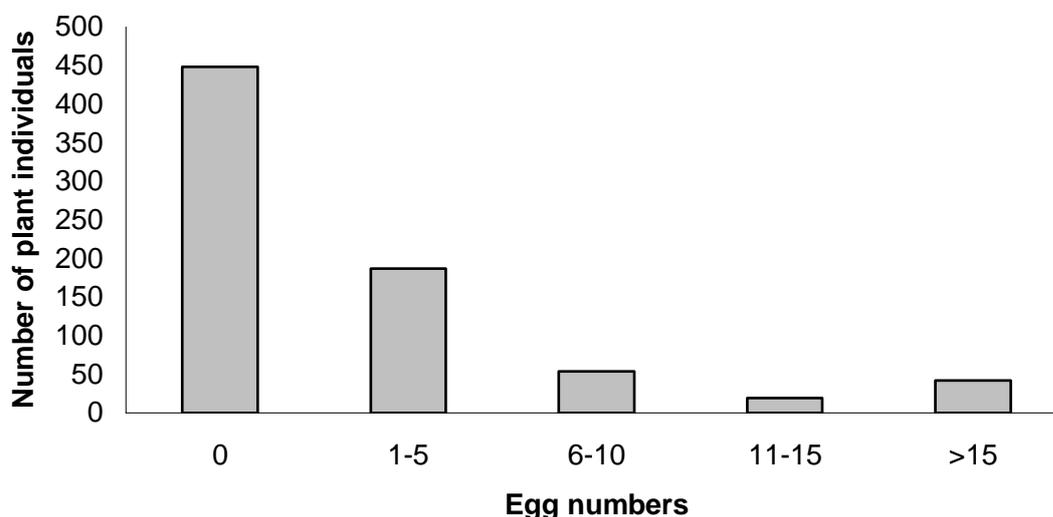


Fig. 4 The absolute number of eggs/plant scored in five categories.

To test which host plant species was favoured by *Lycaena dispar* females when egg-laying the four most abundant *Rumex* species were compared in a GLM while simultaneously accounting for some other variables that usually are relevant for host plant choice in

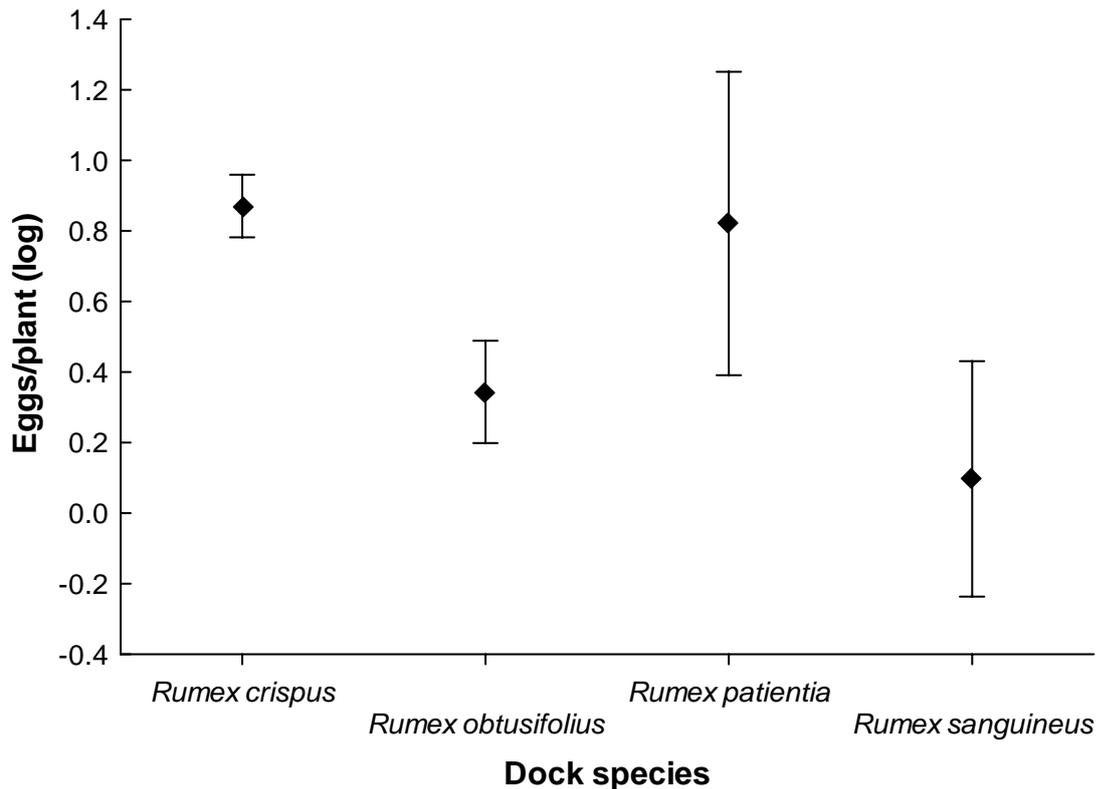
herbivorous insects (Tables 5 and 6). *Rumex hydrolapathum* and *R. stenophyllus* had to be excluded from analysis due to their rarity. This analysis revealed a strong relationship between egg densities and dock species ( $p < 0.001$ ; Tab. 5 & Fig. 5). Most eggs per plant were laid on *R. crispus*, and *R. patientia* plants had nearly identical egg densities (Tab. 6). In contrast, *R. obtusifolius* plants carried significantly fewer eggs, and *R. sanguineus* plants harboured the lowest egg number. The potential insolation of host plants did not influence egg densities (see below for an analysis lumping all *Rumex* species). Interestingly plant height and egg densities were negatively related ( $\beta = -0.111$ ;  $p = 0.012$ ), whereas there was a positive association between egg number and leaf number ( $\beta = 0.086$ ;  $p = 0.035$ ). No significant effect on egg densities on plant level was found for the intensity of herbivore leaf damage and of fungal infections.

Table 5. Results of a GLM for *L. dispar* egg numbers per *Rumex* plant, modelling the four most common dock species as categorical predictor. Significant effects are given in bold. Overall model fit (N=744 plants), full model:  $R^2 = 0.072$ ;  $F(8) = 7.077$ ;  $p < 0.001$ ; simplified model:  $R^2 = 0.061$ ;  $F(5) = 10.174$ ;  $p < 0.001$ .

Effect	Full model			Simplified model		
	df	F	p	df	F	p
<b>Plant height (sqrt)</b>	<b>1</b>	<b>6.268</b>	<b>0.012</b>	<b>1</b>	<b>3.928</b>	<b>0.048</b>
Duration of sunshine (sqrt)	1	0.838	0.360			
Fungal infection	1	0.722	0.395			
Herbivore damage	1	1.810	0.178			
<b>Leaves per plant (sqrt)</b>	<b>1</b>	<b>4.417</b>	<b>0.035</b>	<b>1</b>	<b>5.621</b>	<b>0.018</b>
<b>Dock species</b>	<b>3</b>	<b>16.118</b>	<b>&lt;0.001</b>	<b>3</b>	<b>16.780</b>	<b>&lt;0.001</b>
Error	735			738		

Table 6. Effects of continuous variables tested in a GLM on *L. dispar* egg densities across the four most common *Rumex* species at plant level (see Table 5 for further details). Given are standardized regression coefficients  $\beta$  plus their statistical evaluation.

	$\beta$	t	p
<b>Plant height</b>	<b>-0.111</b>	<b>-2.503</b>	<b>0.012</b>
Duration of sunshine	0.034	0.915	0.360
Fungal infection	0.034	0.849	0.395
Herbivore damage	0.051	1.345	0.178
<b>Leaves per plant</b>	<b>0.086</b>	<b>2.101</b>	<b>0.035</b>



**Fig. 5** Mean number of eggs per plant ( $\pm 95\%$  confidence intervals), adjusted at the means of covariates from the full GLM (see Table 7), for the four most abundant *Rumex* species. See Tables 7 & 8 for details of statistical model.

### III.3. Egg numbers on the host plant individual scale

In the subsequent analysis I addressed which factors are related to egg densities, if all *Rumex* individuals are treated equally, irrespective of their species affiliation. High and significant positive correlations were found between plant height and the number of inflorescence stems per plant ( $r=0.615$ ;  $p<0.01$ ), and between plant height and the height of the vegetation surrounding the *Rumex* plants ( $r=0.634$ ;  $p<0.01$ ). Therefore these two predictors were not considered in the GLM. Statistical evaluation (Tabs. 7 and 8) revealed a highly significant positive association between egg densities and plant height ( $\beta=0.399$ ;  $p<0.001$ ). Plants with longer exposure to sunshine were significantly ( $\beta=0.148$ ;  $p<0.001$ ) preferred by egg laying females, as were plants with larger number of leaves ( $\beta=0.109$ ;  $p=0.003$ ). Contrary to expectation, the intensity of herbivore leaf damage and of fungal infections had no significant effect on egg densities.

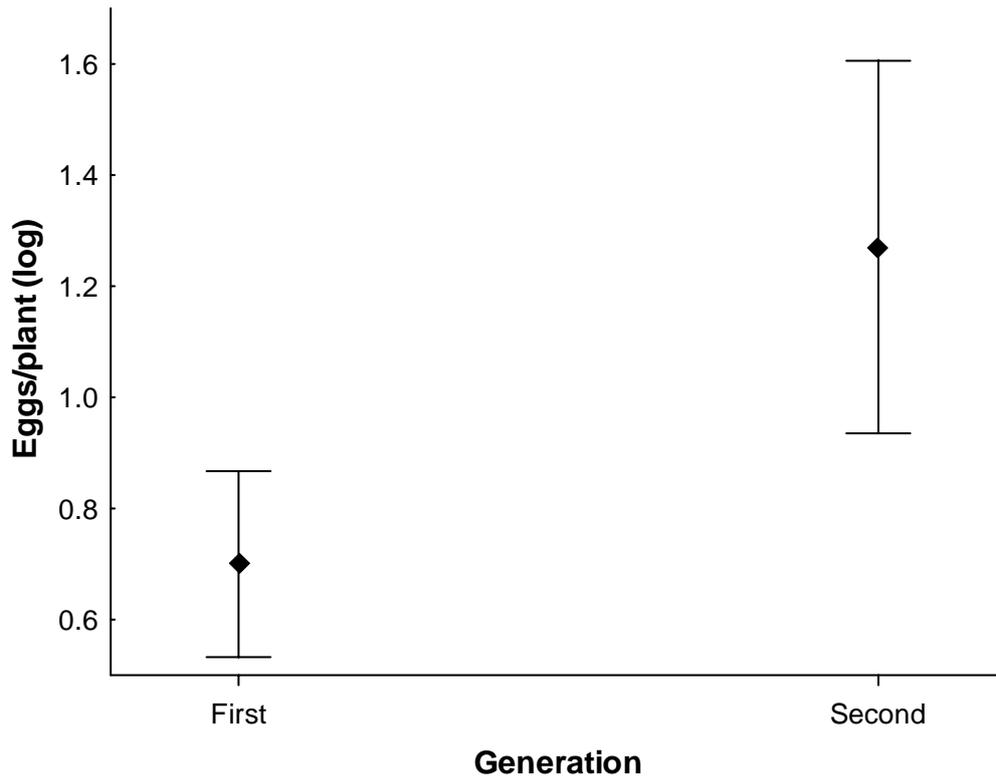
Table 7. Results of GLM for *L. dispar* egg numbers per *Rumex* plant. Significant effects are given in bold. Stems (y/n) denote whether the plant had inflorescence stalks at the time of surveying. Overall model fit (N=750 plants), full model:  $R^2=0.228$ ;  $F(12)=18.110$ ;  $p<0.001$ ; simplified model:  $R^2=0.156$ ;  $F(6)=22.750$ ;  $p<0.001$ .

Effect	Full model			Simplified model		
	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
<b>Plant height</b>	<b>1</b>	<b>32.926</b>	<b>&lt;0.001</b>	<b>1</b>	<b>25.884</b>	<b>&lt;0.001</b>
<b>Duration of sunshine</b>	<b>1</b>	<b>18.316</b>	<b>&lt;0.001</b>	<b>1</b>	<b>16.645</b>	<b>&lt;0.001</b>
Fungal infection	1	0.054	0.816			
Herbivore damage	1	0.354	0.551			
<b>Leaves per plant</b>	<b>1</b>	<b>8.447</b>	<b>0.003</b>	<b>1</b>	<b>8.403</b>	<b>0.003</b>
<b>Generation</b>	<b>1</b>	<b>8.770</b>	<b>0.003</b>	<b>1</b>	<b>24.877</b>	<b>&lt;0.001</b>
<b>Stems (yes/no)</b>	<b>1</b>	<b>13.336</b>	<b>&lt;0.001</b>	<b>1</b>	<b>29.740</b>	<b>&lt;0.001</b>
<b>Mowing</b>	<b>1</b>	<b>24.257</b>	<b>&lt;0.001</b>	<b>1</b>	<b>36.914</b>	<b>&lt;0.001</b>
<b>Generation × Stems</b>	<b>1</b>	<b>6.453</b>	<b>0.011</b>			
Generation × Mowing	1	0.282	0.595			
<b>Stems × Mowing</b>	<b>1</b>	<b>4.585</b>	<b>0.032</b>			
Error	737			737		

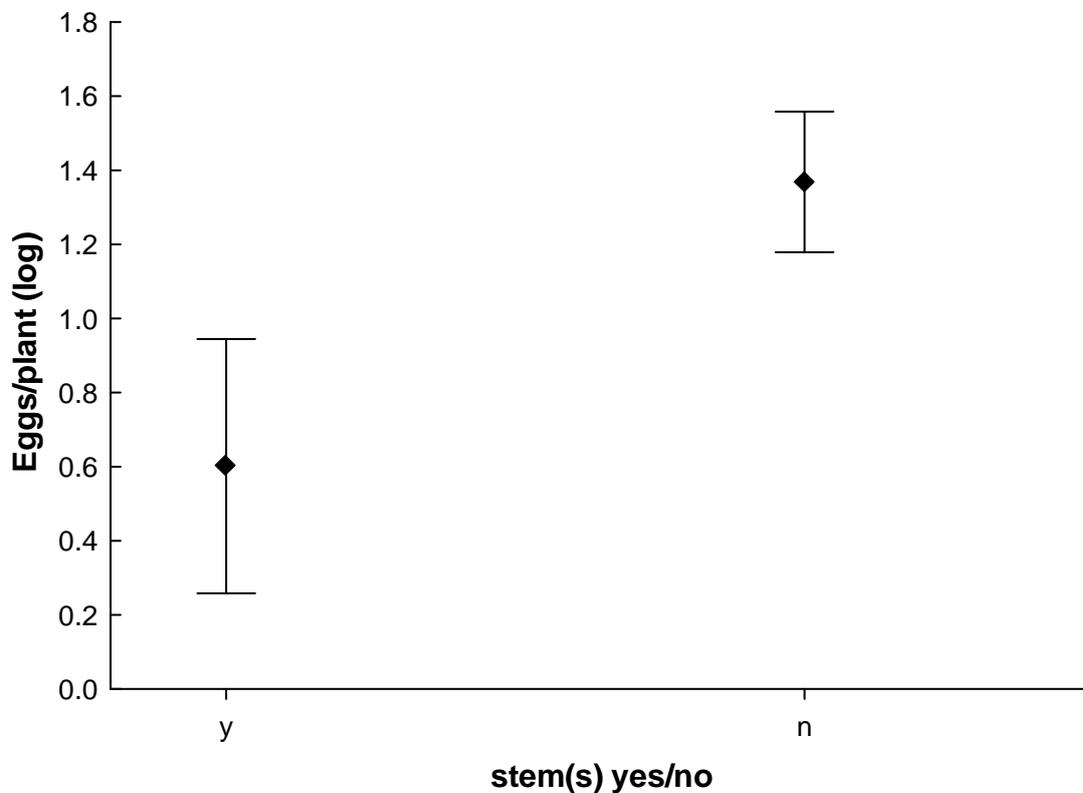
Table 8. Effects of continuous variables tested in a GLM on *L. dispar* egg densities at plant level (see Table 7 for further details). Given are standardized regression coefficients  $\beta$  plus their statistical evaluation.

Effect	$\beta$	<i>t</i>	<i>p</i>
<b>Plant height</b>	<b>0.399</b>	<b>5.738</b>	<b>&lt;0.001</b>
<b>Duration of sunshine</b>	<b>0.148</b>	<b>4.279</b>	<b>&lt;0.001</b>
Fungal infection	0.008	0.232	0.816
Herbivore damage	0.020	0.595	0.551
<b>Leaves per plant</b>	<b>0.109</b>	<b>2.906</b>	<b>0.003</b>

Egg densities on plant level differed significantly between the generations: in the first generation plants received significantly fewer eggs than plants in the second generation (Tab. 7 and Fig. 6). Egg densities also varied depending on whether or not a dock plant had developed an inflorescence shoot (Fig. 7). Plants without flowering or fruiting stems received far more eggs.

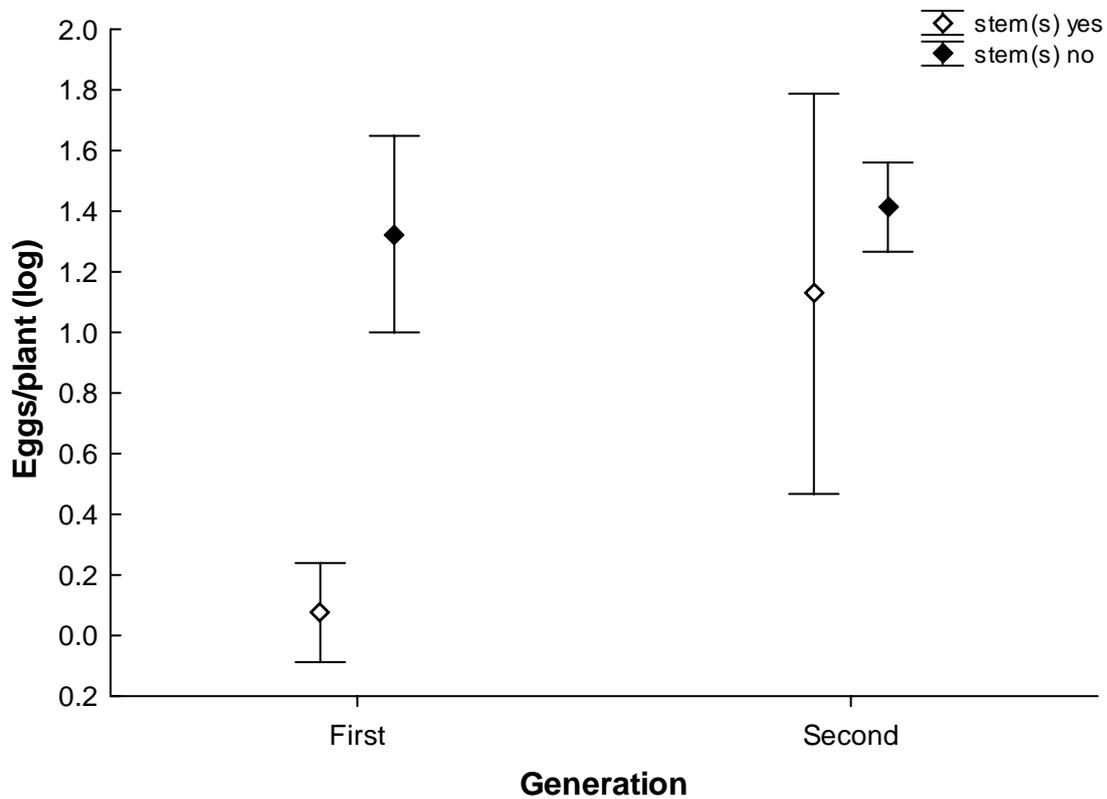


**Fig. 6** Mean number of eggs per plant ( $\pm 95\%$  confidence intervals), adjusted at the means of covariates from the full GLM (see Table 9), for the two generations.



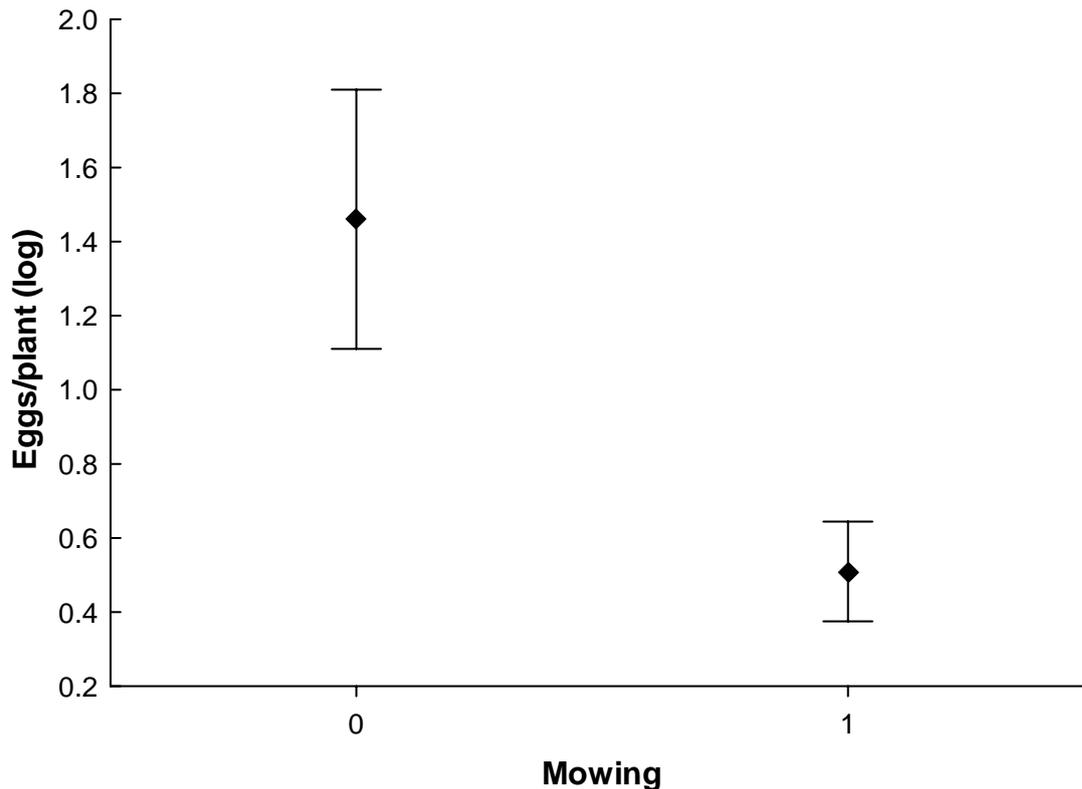
**Fig. 7** Mean egg densities on plant level ( $\pm 95\%$  confidence intervals), adjusted at the means of covariates from the full GLM (see Table 9), in relation to the existence of inflorescence stems.

There was also a significant interaction between generations and the existence of flower stalks with regard to egg densities (Fig. 8). In the first generation plants with stems received significantly fewer eggs than plants with stems, whereas in the second generation there was no such difference.



**Fig. 8** Mean egg densities on plant level ( $\pm 95\%$  confidence intervals), adjusted at the means of covariates from the full GLM (see Table 9), separated for the generations and for plants with and without stems.

Egg densities of *L. dispar* were significantly higher on plants which were not cut (Fig. 9). This effect was equally strong in both generations, as evidenced by the lack of a significant interaction term Generation  $\times$  Mowing (Tab. 7).



**Fig. 9** Mean egg numbers per plant ( $\pm 95\%$  confidence intervals), adjusted at the means of covariates from the full GLM (see Table 7), in relation to mowing regime. Plants which were cut (1) show significantly lower egg numbers

#### III.4. Host plant use at the leaf scale

Finally I constructed a GLM to assess the relevance of various parameters for the numbers of eggs laid per *Rumex* leaf. Since several leaves on the same plant cannot be viewed as independent units, I modeled leaves nested in the respective plant individual. The two most relevant predictors for egg density at the leaf scale were the number of leaves per plant and mowing (Tabs. 9 and 10). The more leaves a *Rumex* plant had, the less clumped the eggs appeared on the leaves. Fewer eggs were found per leaf when the sites were mown, and in the first generation. In addition, egg-laying females exhibited a significant preference for longer leaves, whereas leaf height above ground did not significantly affect egg densities. Fungal infections were also not relevant, whereas there was a very weak, but just significant positive association between egg densities per leaf and leaf damage by herbivores.

Table 9. Results of GLM for *L. dispar* egg numbers per *Rumex* leaf. Significant effects are given in bold. Overall model fit (N=650), full model:  $R^2=0.339$ ;  $F(125)=2.151$ ;  $p<0.001$ ; simplified model:  $R^2=0.337$ ;  $F(123)=2.172$ ;  $p<0.001$ .

Full model				Simplified model		
	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
<b>Leaf length</b>	<b>1</b>	<b>4.802</b>	<b>0.029</b>	<b>1</b>	<b>4.715</b>	<b>0.030</b>
Leaf height	1	0.058	0.809			
Fungal infection	1	1.831	0.176			
<b>Herbivore damage</b>	<b>1</b>	<b>4.053</b>	<b>0.044</b>	<b>1</b>	<b>4.053</b>	<b>0.044</b>
<b>Leaves per plant</b>	<b>1</b>	<b>37.906</b>	<b>&lt;0.001</b>	<b>1</b>	<b>40.582</b>	<b>&lt;0.001</b>
<b>Generation</b>	<b>1</b>	<b>8.915</b>	<b>0.002</b>	<b>1</b>	<b>13.222</b>	<b>&lt;0.001</b>
<b>Mowing</b>	<b>1</b>	<b>11.672</b>	<b>&lt;0.001</b>	<b>1</b>	<b>11.772</b>	<b>&lt;0.001</b>
Leaf(Plant)	118	1.139	0.171	118	1.140	0.170
Error	524			526		

Table 10. Effects of continuous variables tested in a GLM on *L. dispar* egg densities at leaf scale (see Table 9. for further details). Given are standardized regression coefficients  $\beta$  plus their statistical evaluation.

	$\beta$	<i>t</i>	<i>p</i>
<b>Leaf length</b>	<b>0.089</b>	<b>2.191</b>	<b>0.028</b>
Leaf height	0.012	0.241	0.809
Fungal infection	-0.056	-1.353	0.176
<b>Herbivore damage</b>	<b>0.082</b>	<b>2.013</b>	<b>0.044</b>
<b>Leaves per plant</b>	<b>-0.284</b>	<b>-6.156</b>	<b>&lt;0.001</b>

## IV. Discussion

### IV.1. Use of urban habitats as reproduction sites

All of the 23 study sites checked were confirmed as breeding habitats of the Large Copper. Significantly fewer eggs occurred on sites in the zone adjacent to the Vienna Forest. This might be due to the fact that, firstly, at these sites repeated and intensive mowing at unfavourable times occurred and secondly as a result of the colder microclimate. The annual mean temperature of the western outskirts of Vienna is about 1.5°C lower compared to the densely built up city centre (Auer et al., 1989). Between 1951 and 1980 the recorded annual mean temperature of the densely built up urban areas was 10-11°C, whereas in the Vienna Forest it was only 8-9.5°C. Lower annual mean temperatures in the Vienna Forest zone result in shorter vegetation period of about 10 days. The egg numbers found for each of the other four remaining landscape zones were almost identical suggesting that their suitability for egg deposition is well balanced. One reason for this could be that these sites were mostly waste areas without much anthropogenic intervention.

Statistical testing on study site scale revealed no significant relationship between egg density and the majority of the variables tested. No influence on egg numbers were found for the number of plants investigated per study site, the distance to the next water body, the size of the study site, the number of flowers available, the generations and the mown portion of the study site (see Tab. 2). It is therefore considered that females of the Large Copper do not select their reproduction habitats in relation to the number of potential food plants available.

Consistent findings were made for brimstone butterflies as the abundance of larval food plants were reported to be an inadequate measure of the suitability of a habitat for oviposition (McKay, 1991). In the case of *Euphydryas aurinia* larval food plant quantity had no significant influence on egg deposition decisions (Anthes et al., 2003). For sedentary butterfly species like *Cupido minimus* and *Lycaena helle* larval food plant abundance was found to significantly affect patch occupancy (Krauss et al. 2004; Bauernfeind et al.; 2009). So it can be predicted that species with moderate dispersal ability preferentially colonize habitats with a large amount of food plants present and that highly mobile species with a high dispersal capacity do not depend on large food plant populations at one particular location. A good disperser like *Lycaena dispar* has the ability to search for appropriate patches with larval food plant individuals whilst the sedentary species rely on a high portion of larval resources in the habitat.

Expectations that the density of flowers as a factor of nectar availability on research sites would have had an influence on egg densities were not confirmed, although nectar is suggested to be essential for egg production (Bink, 1986; Kühne et al., 2001). Additionally, Fischer & Fiedler (2001) revealed that in the sedentary butterfly *Lycaena hippothoe* females laid significantly more eggs when fed with highly concentrated sucrose solution compared to females fed only with water. Thus the fecundity of sedentary species seems to rely more on nectar in close spatial vicinity than of highly mobile species. For instance, the sedentary species *Lycaena hippothoe* preferred to occupy habitats with flowering plants (Fischer, 1998). In the case of *L. dispar rutilus* in Vienna the importance of nectaring plants in breeding habitats is suggested to play a minor role as imagines show a high dispersal ability indicating they are able to meet their demand on nectar elsewhere. Hence it can be stated that the choice of larval breeding habitats by *Lycaena dispar rutilus* is not correlated with adult nectar resource availability. Concordantly, Werner and Möller (2003) state that nectar availability at reproduction habitats of the large Copper is only of secondary importance. Likewise, females of *Leptidea sinapis* were found to search for nectar and host plants in different habitats (see references in Thompson & Pellmyr, 1991). On the other hand for *Lycaena alciphron* nectar sources in close spatial vicinity to the breeding sites seem to be important since no eggs were found on patches far away from flowery meadows although host plants were present (Hermann & Steiner, 1998). Nectar availability was also found to be relevant for other butterfly species (Janz et al., 2005; Freese et al., 2006).

Furthermore, a larger habitat size does not seem to increase the probability of occupancy by ovipositing females. Even small stripes, e.g. along roads, and small patches with docks present were used as breeding habitats. Similarly, patch size did not increase the likelihood of high egg numbers in other studies of butterfly oviposition (Rabasa et al., 2005; Batáry et al., 2008). Contradictory results were found for some butterflies species preferring large habitat patches for egg deposition (Anthes et al., 2003; Krauss et al., 2004; Eichel & Fartmann, 2007; Bauernfeind et al., 2009). Unfortunately, no comparable data concerning demand on breeding site size of *L. dispar rutilus* are available from the literature.

Distance to the next water body showed no significant effect on egg density thus leading to the conclusion that the Large Copper in Vienna does not chose its breeding site in relation to the degree of its dampness. This is in agreement with the statement of Pullin et al. (1998) that habitats used by *L. dispar* in central Europe also include drier areas. They state this primarily for the second generation but in Vienna the first and second generation appear to behave similarly. I conclude that both generations populate the same kind of habitat types and that the absence at sites is due to the fact that they were cut recently after oviposition happened. Pullin et al. also mention that in Belgium breeding areas have been recorded in fallow land for both generations which is in agreement with my findings. Likewise, the butterfly is not restricted to damp habitats in SW-Germany (Loritz & Settele, 2006). This suggests that a strong linkage to

damp habitats seems to be exhibited mainly in the northern regions but further south this tendency seems to be much less pronounced and dry places become more important habitats for this species. *Maculinea arion* and *Lycaena alciphron* e.g. also have been reported to show variability in their demand on breeding habitats along different climatic gradients (see references in Fartmann & Hermann, 2006; Fartmann & Timmermann, 2006).

The habitat fraction subject to mowing has been shown to negatively affect egg densities although slightly not attaining significance in the full model. However, in the simplified model it gained significance thus it can be stated that the higher the portion of mowing on a site, the more detrimental its impact for eggs densities. Statistical analysis on plant and leaf scale supported the negative influence of mowing. Johst et al. (2006) found the same negative impact of mowing for two endangered butterfly species.

Only one site in the first generation was not populated with eggs of the Large Copper and in the second generation no eggs were found at four sites.

Egg densities between the generations slightly missed to be significant with fewer eggs in the first generation. However, the trend for higher egg numbers in the second generation is well supported by the results of statistical calculations in the host plant and leaf model.

## IV.2. Differential use of host plant species

Comparison of the different *Rumex* species used by *Lycaena dispar rutilus* showed that *Rumex crispus* plants contained 87.6% of all eggs recorded during this survey. The strong preference for *Rumex crispus* is in agreement with the findings of Loritz & Settele (2006) who investigated the host plant choice of *Lycaena dispar rutilus* in Southwest Germany and found 68.4% of the eggs on *Rumex crispus*. In their survey the mean egg numbers for *crispus* were approximately 2 eggs/plant. With 4.4 eggs/plant the average number of eggs/plant for *R. crispus* in Vienna was more than twice as high. For France, Lafranchis et al. (2001) report 4.3 eggs/plant on *R. crispus* which is nearly identical with the value for Vienna. Additionally, data for egg records on *R. conglomeratus* are given with 5.5 eggs/plant for France. During their research Kühne et al. (2001) found more than 90% of the larvae on *R. hydrolapathum* and only one caterpillar was found on *R. crispus* indicating that in the North-German lowlands *R. hydrolapathum* is the main food plant of the Large Copper. *R. hydrolapathum* was also assessed as the most important food plant in the Upper Rhine valley (Ebert, 1993) and in Brandenburg (Werner & Möller, 2003). On the four *R. hydrolapathum* individuals observed in Vienna an average of 8.5 eggs per plant was found. This was the highest average egg number compared to the other dock species. This leads to the assumption that *R. hydrolapathum* might be the most suitable host plant species also in Vienna if it would be more abundant. So the host shifts within *L. d. rutilus* across its range is considered to be a result of the absence of its more preferred host. Where *R. hydrolapathum* is abundantly present it is preferentially used for oviposition (see above) but in drier areas other *Rumex* hosts are more widespread and *L. d. rutilus* is able to shift on other hosts. Such host shifts throughout different latitudes are also documented for other oligophagous and polyphagous butterfly species (see references in Fartmann & Hermann, 2006). Statistical analysis showed that there was a significant positive correlation between the dock species *Rumex crispus* and egg density so that it is assumed not only as the most abundant dock species in Vienna but also one of the most favoured hosts by *Lycaena dispar*. *Rumex patientia* was also shown to be highly preferred for egg deposition although being markedly less abundant. On the other hand *Rumex obtusifolius* harboured only 8.51% of the whole egg proofs although abundantly present in Vienna. In comparison to that Loritz & Settele (2006) found 23.8% of their egg records on *R. obtusifolius* which suggests that in Southwest Germany *R. obtusifolius* is a more

important food plant for *Lycaena dispar rutilus* than it is in Vienna. The reason for this preference for *Rumex crispus* could be explained differently. First of all *R. crispus* tends to grow in open places and in sunny position and is more tolerant of drier condition whereas *obtusifolius* tends to grow in shady habitats with less warmer microclimate, i.e. in the Vienna Forest Zone. So the preference for *R. crispus* over *R. obtusifolius* probably is not related to the plant species per se but to its preferred habitat with more suitable microclimatic conditions for optimal larval performance. The highest egg numbers per leaf (31 eggs per leaf) were recorded for *Rumex crispus*. In comparison *Rumex obtusifolius* and *R. hydrolapathum* had a maximum of 10 eggs per leaf. The maximum egg numbers per leaf for the other three *Rumex* hosts (*R. patientia*, *R. sanguineus*, and *R. stenophyllus*) were even lower. The average number of eggs per leaf for *R. crispus* was 0.40 (see results Tab. 3) which is in agreement with the findings of Loritz & Settele (2006) who reported the same number of eggs per leaf for *R. crispus*. Marked differences in the number of eggs per leaf were found for *Rumex obtusifolius* bearing only 0.05 eggs in Vienna compared to 0.30 eggs in Southwest Germany (Loritz & Settele, 2006)

The potential duration of insolation was significantly influencing egg numbers in a positive way, so the preference for *crispus* is probably a consequence of the fact that females prefer plants in sunny position and may have nothing to do with the dock species itself. Kühne et al. (2001) also recorded high egg densities on plants in sunny position, whereas eggs were rarely deposited on shaded plants. This is in agreement with Webb & Pullin (2000) as they never found eggs on totally shaded plants (Hermann & Steiner, 1998). In Baden-Württemberg *Lycaena alciphron* was shown to prefer *Rumex acetosella* over *Rumex acetosa*. The authors suggested that this might have been a result of the fact that the former occurred predominantly at warmer and drier sites as the latter and *alciphron* seems to prefer these warmer microclimates for oviposition. The preference for host individuals well exposed to direct insolation was also reported for other butterfly species (Anthes et al, 2003; Fartmann, 2006; Eichel & Fartmann, 2008). In contrast to that host plant exposure to sunshine seems to have little influence on egg deposition decision in the butterfly *Zerynthia cretica* (Dennis, 1996) and in *Euphydryas aurinia* increasing duration of sunshine was even detrimental for larval survival (Freese et al., 2006).

Plants in sunny position may allow larvae of the Large Copper to grow faster and finish development within a shorter period as a result of higher temperatures (e.g. Anthes et al., 2003). Since the larvae are ectothermal they may have a longer time of activity on plants with more hours of sunshine and therefore need less time to achieve maturity. Temperature is considered to have a major influence on developmental time with lower temperatures causing lower growth rates and longer development times (Fischer & Fiedler, 2002). For instance, developmental time of *Lycaena hippothoe* markedly increased with lower temperatures, ranging from 16 days to 66 days at temperatures of 30°C and 15°C, respectively (Fischer & Fiedler, 2002). Concordantly, larval development rate of *Pararge aegeria* and *Papilio machaon* was shown to be dependent upon temperature (Shreeve, 1986; Wiklund & Fridberg, 2008). Also the pupal stage is strongly temperature dependent and may be finished after 10 days under favourable conditions but may last up to 14 days under unfavourable conditions (Kühne et al., 2001). Hence local microhabitat conditions are considered to be one important factor for females searching for suitable hosts to oviposit on. Searching for hosts in open and sunny habitats appears to be advantageous for females allowing them maximum flight time and the opportunity for basking between egg-laying (McKay, 1991). As a consequence host plants growing in unfavourable light conditions might be avoided by ovipositing *L. d. rutilus* females.

Martin & Pullin (2004) showed in feeding experiments that larvae of *L. dispar batavus* on *Rumex obtusifolius* and *Rumex crispus* had a lower intake of food than on *Rumex*

*hydrolapathum* which suggests a higher efficiency of utilization. Additionally they found that larvae on *R. crispus* consumed significantly less food than either larvae on *R. obtusifolius* or *R. hydrolapathum* suggesting that the conversion of digested food to body mass is more efficient with *R. crispus*. Hence, the preference for *crispus* in Vienna is possibly an interaction between its nutritional value and the warmer microclimate where it grows. Besides *R. crispus* and *R. obtusifolius*, *Rumex patientia* was found to be the third most important food plant for egg-laying, containing 2.12% of the whole egg records. The other three dock species (*R. hydrolapathum*, *R. stenophyllus* and *R. sanguineus*) do not represent important food plants in Vienna as they are too rare but the fact that these were used for egg deposition shows that *rutilus* is able to use a wide range of different dock species in the wild. On the contrary *batavus* was found to utilize only *hydrolapathum* as food plant in the wild despite others being available (Martin & Pullin, 2004). *R. sanguineus* is a dock species which occurs more often at shaded places and additionally it is a visually inconspicuous small species with small leaves (see also Ebert, 1993).

### IV.3. Factors affecting egg densities at the plant scale

Most of the 750 plant individuals checked for egg presence were not used as oviposition substrates (see Fig. 4) predicting a very specific selection of hosts by ovipositing females in my study.

The maximum number of eggs in Vienna counted on a single *R. crispus* plant was 78, and 23 on *R. obtusifolius*. Loritz & Settele found a maximum egg number of 14 for *crispus* and 11 for *obtusifolius*. Pullin (1997) recorded a maximum of 42 eggs for *batavus* on one large *R. hydrolapathum* plant and Webb & Pullin (2000) found 73 eggs of *batavus* on one *R. hydrolapathum* plant. Plants with such high egg densities must have been selected repeatedly by one or several ovipositing females (Webb & Pullin, 2000) since single oviposition events mostly result in small egg clusters (SBN, 1987; Webb & Pullin, 2000; Kühne et al., 2001; Loritz & Settele, 2006). The reasons for disproportionately high number of eggs per plant are not clear and it is impossible that one plant individual provides enough foliar biomass to support all the 78 larvae to maturity. Such excessive egg loading could result in complete defoliation of the food plant thus forcing larvae to disperse and seek for new hosts and thus leading to an increased mortality (Dennis, 1996). Additionally, high concentrations of eggs on one plant may enhance host location by parasitoids or predators. Therefore it is expected that a plant which already bears many eggs is avoided as egg-laying substrate in order to minimize direct intraspecific competition. Intraspecific competition between larvae on hosts which received high egg numbers increased offspring failure (see references in Fartmann & Hermann, 2006). For instance, *Euchloe ausonia* avoid potential oviposition sites occupied by conspecific eggs and therefore display egg avoidance behaviour (Dennis, 1995). This is also the case for the butterfly *Mechanitis lysimnia* as females recognize conspecific eggs and tend to select egg free hosts (Vasconcellos-Neto & Ferreira Monteiro, 1993). Conversely, oviposition on plants may be facilitated by the tendency of females to add to egg batches laid by other females (Dennis, 1996). Excessive egg densities might be a result of the so called edge effect, thus a plant being isolated and easily accessible receiving more eggs than a plant located in a group of suitable host individuals (see references in Fartmann & Hermann, 2006). Egg densities of *Hamearis lucina* e.g. were the highest on isolated plants compared to clumped host groups (Fartmann, 2006). However, massive egg loads are the exception and the majority of the host plants harboured low (1-5) egg numbers (see Fig. 4). Likewise, over occupation of hosts were scarce in a study on *Maculinea alcon* in Northern Germany (Kür & Fartmann, 2005).

Furthermore, egg densities on host plant scale were shown to be dependent on plant height in this study. This is in contrast to Webb & Pullin (2000) who found no significant relationship between the egg numbers present on a plant and any of the plant attributes measured. Since visual recognition of host plants may be crucial for locating potential hosts for egg laying females it is quite obvious that plants which are tall and prominent will be visually detected first. In Southwest Germany Loritz & Settele (2006) found that docks harbouring eggs were taller than their average surrounding vegetation. This is in coincidence with other surveys on butterfly egg placement patterns, where females have been reported to be attracted to larger plants (e.g. Dennis, 1995; Anthes et al., 2003; Küer & Fartmann, 2005; Rabasa et al., 2005; Árnayas et al., 2006; Eichel & Fartmann, 2008; Talsma et al., 2008). Another possible explanation for higher egg numbers on taller plants, besides the fact of visual appearance, could be a smaller probability of a female leaving a plant occupying a large fraction of space (Rabasa et al., 2005).

Statistical analysis revealed that an increase in leaf number on a host plant led to more eggs. The leaf number of a host plant is a good indicator for the phytomass available for the larvae (Duffey, 1968) and ovipositing females may favourably choose such vigorous plants in order to secure enough resources for their offspring. For instance, more *Zerynthia polyxena* eggs were found on plants with increasing leaf number in Hungary (Batáry et al., 2008). In contrast to that no significant relationship was found between egg density and number of leaves for *Lycaena dispar batavus* in the Netherlands (Webb & Pullin, 2000). However, statistical analysis showed that although higher egg numbers were found on taller plants, those plants which had already developed flowering/fruitlets stems were less attractive for egg placement. Females preferred to oviposit on host plants without stems which might be an indicator for non flowering/fruitlets plants to be a better quality host to support the larvae. I hypothesize that flowering/fruitlets may be an indicator of lower food plant quality for females since such plants have already invested a lot of their nutrients into stem developing and may therefore not contain much nitrogen in the leaves. Nitrogen is an important component for larval development and larvae on non flowering/fruitlets plants may grow faster with less food intake and hence being less exposed to different mortality factors such as predation and parasitoids. Bink (1986) found that pupae of *L. dispar* reared on docks with high nitrogen content had the highest weights. Two studies on *Lycaena dispar batavus* showed no significant relationship between egg densities on flowering versus non-flowering *R. hydrolapathum* plants (Nicholls, 2000; Webb & Pullin, 2000). The preference of females for plants without stems for oviposition was strong in the first generation and also present in the second generation. Generally, it can be assumed that females prefer *Rumex* hosts without stems in both generations, but in the second generation plants with stems increase in number as a consequence of their phenology and females are forced to select plants with stems for egg placement more frequently. Fartmann & Timmermann (2006) suggest that young shoots could invest all their energy into leaf growth and therefore are preferred for egg placement by *Thecla betulae* compared to older flowering plants.

In the first generation the number of eggs per plant was significantly lower than egg densities in the second generation. Due to the high larval mortality during winter diapause (mean winter survival for *batavus*: 18.3%; Webb and Pullin, 1996) in the first generation there are fewer imagines who reproduce leading to lower egg numbers. In the second brood the population density of *Lycaena dispar* must have been higher since firstly, more imagines were sighted and secondly, the egg numbers were more than two times higher. Accordingly it is suggested that the population density of imagines was at least two times higher in the second generation. This is in agreement with the statement of Ebert (1993) that the second generation normally has a much higher population density. A higher population density in the second brood should be advantageous to compensate for losses during hibernation. On the other hand

this would also lead to the assumption that in the second generation competition between larvae for resources must be stronger.

Another interesting result is that neither fungal infections nor leaf damage by other herbivores had a significant influence on egg densities on plant level although a negative influence was expected. Competition is a strong selective pressure influencing the evolution of strategies that optimize resource utilization (Vasconcellos-Neto & Ferreira Monteiro, 1993). For instance, brimstone butterflies appear to avoid host plants damaged by other herbivores (McKay, 1991) and Ngu et al. (2008) found that volatiles of herbivore injured plants deter ovipositing females of *Pieris rapae*. Larvae of the herbivore beetle *Gastrophysa viridula* were often found on *Rumex* plants, especially on *R. obtusifolius*, where they caused considerable leaf damage. However, *G. viridula* was rarely encountered on *R. crispus*; nevertheless high leaf damage caused by slugs, snails, herbivorous insects and by larvae of the Large Copper was frequently observed. Although direct competition could be minimized by females searching for plants without much leaf damage this does not seem to be the case for *L. dispar*. In the case of my study in Vienna it was illustrated that the presence of competitors is not a key factor for ovipositional choice. Anecdotal field observations also suggest this for *L. dispar batavus* (Martin & Pullin 2004).

Additionally, the portion of foliage affected by fungal infections did not significantly influence the egg numbers negatively (nor positively) indicating that females laid their eggs irrespective of fungi infection. Likewise females of *Maculinea alcon* oviposited irrespective of the presence of fungal infestation on its larval host plant (Árnyas et al., 2009). It could be assumed that fungal infection may have rendered food plant quality unsuitable for egg laying females since e.g. females of the beetle *Cassida rubiginosa* preferred to oviposit on healthy thistles and avoided infected ones (Kruess, 2002). The author also found that larval development time and pupal mortality was higher when feeding on infected leaves. Consumption of host plants attacked by phytopathogenic fungi e.g. prolonged larval development of two species of alpine leaf beetle (Röder et al., 2007), and that of the butterfly *Melitaea cinxia* (Laine, 2004). Pathogen infection may alter host plant nutritional quality; i.e. changes in carbohydrate, nitrogen and water content (Kruess, 2002; Martinková & Honěk, 2004); appearance and defence chemistry (see also references in Biere et al., 2002). As a consequence preimaginal performance might be negatively affected. Feeding on fungal-infected plant tissues with reduced nutritional quality was also shown to decrease survival of diapausing larvae (Laine, 2004). Accordingly, over-wintering larvae of the Large Copper consuming fungally infected plant tissues may have a higher mortality rate. Laboratory feeding experiments are required to investigate if rust has detrimental effects on *L. dispar* larval performance.

Comparing all significant variables affecting egg densities on plant scale illustrates that, according to the F-values, some factors had a stronger effect on egg densities than others. Based on the statistical evaluation egg placement patterns in the plant scale model were best explained by plant height, mowing, potential duration of sunshine, generation and stem presence. The number of leaves only had a minor modulating role in this survey, whereas fungal infection and herbivore damage had no significant effect.

#### **IV.4. Factors affecting egg load at leaf scale**

Eggs were found to be preferentially laid on the uppersides of the docks' leaves by females of the Large Copper though some eggs were also found on the undersides of leaves in both generations. Concordantly, the majority of *Lycaena dispar* eggs were found to be predominantly deposited on the adaxial surfaces of leaves by other authors (SBN, 1987; Ebert, 1993; Webb & Pullin, 2000; Kühne et al., 2001). The preference for the uppersides of

leaves concerning oviposition may be due to the shorter time of development of such eggs receiving more sunshine than eggs on the abaxial surfaces of leaves. Actually the hardly mobile first instar larvae always feed on the underside of the leaves hence laying eggs on the underside would be expected in order to enable immediate feeding commence. Eggs on the leaf uppersides might be detected by parasitoids more easily and are more exposed to adverse weather conditions, such as e.g. hail or desiccation. Egg placement on a leaf's underside is mentioned to be one strategy to escape desiccation (see references in Fartmann & Hermann, 2006). For instance, in Crete the endemic butterfly *Zerynthia cretica* lays the vast majority of its eggs on the underside of its host's leaves (Dennis, 1996). Females of the thermophilous *Lycaena alciphron* were found to oviposit preferentially on the upper leaf surface of their hosts (*Rumex acetosa*, *R. acetosella*), at least in Germany which is near its northern range limit (Hermann & Steiner, 1998). In the case of *Lycaena dispar* the stems of docks were not used for egg deposition by females, only a single egg was found on a stem. This is in agreement with Hermann & Steiner (1998) who noted that the related *Lycaena alciphron* also avoids ovipositing on host stems. The number of leaves per plant was found to have a significant negative influence on egg densities per leaf. The same effect was already shown by Loritz & Settele (2006). A higher number of leaves results in more possibilities of selection for the females and as a result the average egg numbers per leaf decrease. A high number of leaves are an indicator of high phytomass amount, thus supporting more larvae to maturity. This reduces intraspecific competition since eggs are more evenly spread over the leaves avoiding one leaf to receive excessive egg numbers.

Larger leaves received significantly more eggs than shorter ones. This leads to the conclusion that large leaves are preferred for oviposition probably as a result of the higher amount of food resources they provide or the easier visual localisation. Similarly, egg clusters of *Mechanitis lysimnia* were larger on very large leaves than clusters on small leaves (Vasconcellos-Neto & Ferreira Monteiro, 1993). In *Melitaea cinxia* females most often oviposited on leaves with intermediate length (Talsma et al., 2008). It is therefore assumed that ovipositing females may be able to discriminate between leaf sizes. Apparently *L. dispar* females do not prefer juvenile leaves for oviposition since that would have resulted in a higher egg density on shorter leaves. E.g. *Thecla betulae* females showed a strong preference for young plants suggesting that they represent a better quality foodplant for the offspring (Fartmann & Timmermann, 2006). Young and soft leaves are reported to be favourably consumed by larvae of other butterflies (Jordano & Gomartz, 1994; Haddad & Hicks, 2000).

In contrast, leaf height did not have a significant effect on egg deposition selectivity. Leaf height does not seem to play a decisive role in the female's choice. It is hypothesized that the size of the leaf is a more important cue for the females than the leaf's position. In agreement with the findings on plant level fungi infection was not shown to significantly influence egg densities. At the leaf scale frass was found to have a slightly significant positive effect on egg density but no significant effect was seen on the plant scale. Therefore deterring effects of volatiles on ovipositional choice do not seem to exist. Higher egg numbers per leaf in the second generation are mainly a result of higher overall egg numbers. Leaves on uncut plants contained a significantly higher number of eggs showing the negative impact of mowing from the biggest spatial scale to the smallest scale. Characteristics explaining egg numbers on leaf scale were mainly the number of leaves per plant, mowing and generation (see Tab. 10).

#### **IV.5. Management and conservation aspects**

For the location of habitats of the Large Copper the search for immature stages is an important method and is much more effective than the search for adults. An essential part of conservation strategy should consider the management of suitable reproduction habitats.

Management of breeding habitats of the Large Copper in Vienna should concentrate on preserving open patches with appropriate *Rumex* plants in sunny position as larval hosts. It is emphasized that it is not the size of a patch that is decisive for the colonization by the Large Copper and therefore small sites should also be considered in management. Dry fallows and dry waste areas even with a small number of appropriate food plants can be important breeding sites for the species and should be maintained. Apparently habitats preferentially chosen for oviposition have a warm microclimate for optimal larval development. The high dispersal ability of the Large Copper allows colonization of even isolated patches in the densely built up urban area. Supporting small abandoned patches with a suitable vegetation structure and appropriate host plants in Vienna would ensure the persistence of *Lycaena dispar* in Vienna in the future. Patches with heterogeneous vegetation are also essential for the survival of other arthropods in the city. Hence one important aspect of nature conservation in cities is to provide space for spontaneous vegetation on so-called "wastelands". Vienna currently still has some larger areas of fallow land, e.g. on abandoned former train stations, but most of these habitats are due to be destroyed for building developments within the next decade. Therefore it is recommended to allow natural succession in other unsealed places, e.g. in dedicated areas of recreational parks. These habitats only need a low level of management (e.g. by extensive mowing, see below) to avoid succession to woodland.

Mowing had a strong negative impact on egg densities at the plant and leaf scale, and a negative tendency was also found at the site scale. This is in agreement with Nicholls & Pullin (2000) who found that larval survival on host plants from cut areas was significantly lower than on food plants amongst unmown vegetation. Ebert (1993) considered repeated intensive mowing as a main threat to immature stages of the Large Copper. Plants which are mown after egg-laying will cause disastrous losses since the majority of the eggs will be destroyed and newly hatched larvae will mostly die of starvation (Loritz & Settele, 2006). Larvae who have already reached higher instars may be able to drop to the ground and may wait a few days without food intake till the docks sprout again (Loritz & Settele, 2006). Hence, time of mowing should not be chosen arbitrarily, especially not at important reproductive habitats for the Large Copper. Implementation of mowing should, if possible, not take place every year but e.g. every second year or every third year and only a portion of habitats should be mown each year to enable recolonization from other unmown sites. Probably mowing after the onset of caterpillar hibernation in late autumn would be an alternative to mowing during butterfly activity. For instance, mowing in autumn after pupation is recommended in the case of the hygrophilous butterfly *Lycaena helle* (Bauernfeind et al., 2009). Another important aspect is that if mowing is done in late autumn it should be taken into consideration that plants must not be cut directly above the ground since hibernating larvae prefer to rest at the base of the host plants. However, extensive mowing is important since otherwise sites will become overgrown by shrubs and trees which will lead to the disappearance of *Rumex* hosts and as a consequence to the demise of populations of *Lycaena dispar* (Kühne et al., 2001).

In this study *Lycaena dispar* eggs were recorded on every site checked for its presence, which demonstrates that the species is more widespread in Vienna than previously thought and able to colonize habitats, even in the densely built up area. The search for juvenile stages has proven a successful strategy to prove the incidence of this low density species and is recommended for further surveys.

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## Appendix

Table A1. Geographical coordinates of the study sites (centres).

Site	District	Landscape Zone	x-coordinate	y-coordinate	Altitude m a.s.l.	Habitat size (m <sup>2</sup> )
1	14.	Sparsely built up	48.205	16.223	227	10616
2	23.	Sparsely built up	48.139	16.315	203	2270
3	23.	Sparsely built up	48.140	16.258	246	3100
4	21.	Sparsely built up	48.274	16.386	160	15100
5	21.	Sparsely built up	48.300	16.393	162	1120
6	3.	Densely built up	48.191	16.406	167	2760
7	3.	Densely built up	48.191	16.396	179	5640
8	11.	Densely built up	48.179	16.426	155	5470
9	21.	Densely built up	48.270	16.456	158	2680
10	22.	Danube River	48.178	16.494	154	1880
11	22.	Danube River	48.222	16.425	156	1225
12	21.	Danube River	48.259	16.381	157	1950
13	22.	Danube River	48.242	16.396	154	4620
14	14.	Vienna Forest	48.219	16.231	265	15120
15	14.	Vienna Forest	48.241	16.237	365	3180
16	23.	Vienna Forest	48.137	16.225	264	1220
17	23.	Vienna Forest	48.141	16.241	265	1910
18	14.	Vienna Forest	48.245	16.227	466	12800
19	23.	Agricultural zone	48.125	16.303	215	610
20	10.	Agricultural zone	48.132	16.410	180	720
21	11.	Agricultural zone	48.134	16.417	172	3930
22	22.	Agricultural zone	48.257	16.505	156	680
23	22.	Agricultural zone	48.274	16.480	156	9500

**Color Plates**



Fig. A1: *Lycaena dispar rutilus* male basking



Fig. A2: *Lycaena dispar rutilus* female nectaring



Fig. A3: Eggs of *L. d. rutilus* on a dock's leaf



Fig. A4: Hatched and unhatched eggs of the Large Copper



Fig. A5: Caterpillar of the Large Copper.



Fig. A6: Caterpillar-ant interaction with *Lasius niger* (only observed once on 16<sup>th</sup> April 2008).



Fig. A7: Example of a leaf infested by fungi.

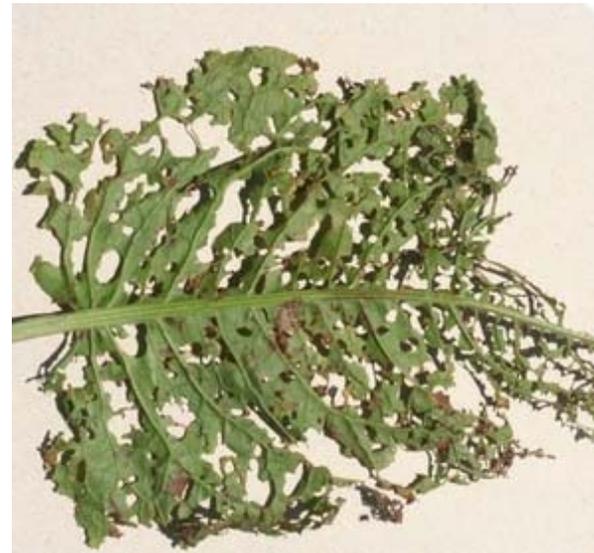


Fig. A8: Leaf damage caused by larvae of *Gastrophysa viridula*.

## Curriculum Vitae



Name: Martin Strausz  
Date of birth: 09<sup>th</sup> February 1982  
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### Education

1988 – 1992 Primary school in Vienna  
1992 – 2001 Secondary school in Vienna  
since 2001 Study of Biology with major in Zoology at the University of Vienna – with special focus on Lepidoptera

### Employment

2007 & 2008 Participation in a research project of the University of Vienna (BINATS) by monitoring butterflies in agricultural landscape in Austria  
2010 Monitoring butterflies in the Örség National Park in Hungary for two years on behalf of the National Park.