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Winter-green host-plants, litter quantity and vegetation structure are key determinants of habitat quality for *Coenonympha oedippus* in Europe

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Abstract

The knowledge on species' habitat preferences at local scales across its range is an essential condition for defining the most appropriate habitat management for the conservation of any species. In this study, we combined field observations from three European countries with breeding experiments under field conditions to identify oviposition and larval preferences of *Coenonympha oedippus* on micro-scale level across contrasting habitat types (wet vs. dry). Despite the wide geographical range and the different habitats we found some common features: (i) vegetation structure of the herb layer is an essential factor for oviposition site electivity and successful development of premature stages; (ii) high cover of litter and/or dwarf shrubs in the microhabitat (larval: 45–70% , oviposition: 40–50%) creates a herb layer rich in gaps; at their edges eggs are deposited and the caterpillars are adequately sun-exposed; (iii) egg-laying females are not selective regarding oviposition substratum; (iv) oviposition height is adjusted to positions with direct sunlight or warm substratum; (v) the host-plants coverage in oviposition sites was high: 45 and 50% (wet), 18% or 41% (including potential host-plants) (dry); (vi) the most important host-plant is *Carex panicea* (wet) and *Carex humilis* (dry), but *Molinia caerulea* (wet) and *Festuca rupicola* (dry) are also used regularly; (vii) the availability of winter-green host-plants in the vicinity of hibernated larvae plays a substantial role in their survival. As regular mowing or grazing would remove the litter and destroy the gaps, the management should be restricted to selective reed cutting or manual shrub removal. Only selective mowing during winter (December–February) can be recommended for keeping the habitat open where the reduction of bushes is not sufficient.

Key words: False Ringlet, microhabitat choice, oviposition preferences, larval ecology, successional habitats

Introduction

For the successful conservation of any species, knowledge of its habitat preferences at local scales across a species' range is required (e.g. Anthes et al. 2008), and an understanding of the perceptual world of the target organism and its interactions with the environment from the functional habitat point of view is a benefit (Dennis 2003; Dennis et al. 2006, Van Dyck 2012). The resource-based habitat concept based on species-specific resource distribution and individual movements considers all life stages of an organism and thus offers an advanced approach for successful conservation management of threatened butterfly species.

The False Ringlet, *Coenonympha oedippus* (Fabricius, 1787), is one out of twelve endangered European butterfly species (van Swaay et al. 2010), and listed on the Annexes II and IV of the Habitats Directive. Its distribution occupies only 3.92% of the area of Europe (Kudrna et al. 2011). The Climatic Risk Atlas of European Butterflies (Settele et al. 2008) placed the species in a category of "climate change risk (R)" due to more than 50% loss of its current grid cells under at least one of the three simulated scenarios. Previous studies represent the first important part of knowledge for better understanding the species' habitat use within the functional resource-based habitat approach including both, consumables and utilities. They aimed on habitat requirements (Bonelli et al. 2010, Bräu et al. 2010, Čelik & Verovnik 2010, Dušej et al. 2010, Örvössy et al. 2010, Sielezniew et al. 2010, Šašić 2010), adult movements and population ecology (Čelik 2003, 2004, Čelik et al. 2009a, Čelik & Verovnik 2010, Örvössy et al. 2010, 2013), together with some initial researches on ecology of early developmental stages (Bonelli et al. 2010, Bräu et al. 2010, Čelik 1997, 2003, Čelik & Verovnik 2010).

C. oedippus is a satyrine butterfly. Larvae of this subfamily feed on plants from the families Poaceae, Cyperaceae and Juncaceae (Munguira et al. 2009). Such grass-feeding species are generally thought to be less specific in their host-plant and oviposition-site choice (Wiklund 1984, Lindman et. 2013). Namely, the ability of larvae to utilize superabundant (i.e., graminoids) and multiple plant species as host-plants reduces limitations of females in oviposition-site selection (Gripenberg et al. 2010), but can also lead to a loss of benefits gained by female discrimination, as are favourable microhabitats for the premature stages (Zalucki et al. 2002, Eilers et al. 2013, Lawson et al. 2014), higher nutritional quality of hosts (Awmack et al. 2002), and reduced parasitism or predation or intra- and interspecific competition (Doak et al. 2006). Nevertheless, it has been discovered recently that grass-feeding species have specific requirements concerning the quality of host plants and microhabitat structures (e.g., Möllenbeck et al. 2009, Beyer & Schultz 2010, Weking et al. 2013) especially in terms of vegetation height and density, amounts of grass-litter and sun exposure.

Across its European range *C. oedippus* occurs in two contrasting habitat types regarding soil humidity: the majority of populations lives on semi-open wet grasslands (ordo Molinietalia, ordo Tofieldietalia) (Čelik 1997, 2003, 2004, Dierks 2006, Bonelli et al. 2010, Bräu et al. 2010, Čelik and Verovnik 2010, Dušej et al. 2010, Örvössy et al. 2010, Sielezniew et al. 2010, Šašić 2010), but at the southern range limit also on dry habitats (Ruehl 1895, Hafner 1910, Kolar 1919, 1929, Bischof 1968, Habeler 1972). However, populations occurring on dry abandoned grasslands (class Festuco-Brometea) are presently known only from Slovenia (Čelik 2003, Čelik and Verovnik 2010). Conservation of species using distinct habitat types most likely requires different management strategies (e.g. Kalarus et al. 2013). The habitats of the existent and last strong European populations of the False Ringlet are at least partially abandoned and if they are mown this happens only infrequently/extensively (Bonelli et al. 2010, Bräu et al. 2010, Čelik and Verovnik 2010, Örvössy et al. 2010), while regular mowing each summer within flight period leads to drastic declines and the extinction of populations (Čelik et al. 2009b, own obs.).

As already stressed by Thomas (1993), warm early successional habitats are often crucial for oviposition and larval development for Lepidoptera species that reach their northern limit in Central Europe. In contrast, *C. oedippus* inhabits late successional stages. The species seems to avoid large open ranges and prefers clearing-like habitats with interspersed bushes, enclosed by hedges (own obs., Örvössy et al. 2010). Such species of late successional habitats have been less studied compared to those of early successional stages, resulting in a higher demand of new information.

Previous studies on ecology of *C. oedippus* contributed to knowledge on habitat requirements and biology of early developmental stages within a single European country and habitat type. In this study, we used field observations and breeding experiments under field conditions to identify environmental parameters responsible for larval and oviposition microhabitat choice in three habitat types differing in soil humidity (wet vs. dry) and soil reaction (wet habitat: alkaline vs. acid). Then we compared three habitat types to determine common key features leading to the selection of larval and oviposition sites in *C. oedippus* across a large spatial scale.

Therefore, we hypothesized that (1) *C. oedippus*, as a grass-feeding species, is not very selective concerning oviposition substratum and host-plant species range within the contrasting habitat types; that (2) vegetation structure in larval/egg-laying microhabitats should be a more important factor in microhabitat selection than species composition of the vegetation; that (3) if differences in microhabitat structure between habitat types exist the required structure of larval/egg-laying microhabitat linking with microclimatic conditions most suitable for development of premature stages is achieved by adjusting micro-site selection across the macro-environmental gradient, meaning that larval/egg-laying habitat plasticity exists in the study species.

Based on the results from field observations and breeding experiments the implications for habitat management of the endangered *C. oedippus* are discussed.

Materials and methods

Study species

The False Ringlet is distributed from the Pyrenees in the west to Northeast-China, Korea and Japan in the east. At present, it is still very widespread and abundant in SE Transbaikalia and Altai (Gorbunov & Kosterin 2007). All populations east of the Ural Mountains are considered as different subspecies. In Europe, mostly isolated populations are still present in France, Germany, Liechtenstein, Austria, Italy, Slovenia, Croatia, Hungary, Poland, Belarus, Ukraine and Russia. Italy plays a central role in the conservation of *C. oedippus* in Europe as the species is still abundant in the north of the country, where over 100 populations are known and only 9 were documented to be extinct in recent times, mainly following habitat loss due to human activities (Balletto et al. 2007, 2014, Bonelli et al. 2010). In Slovenia, the species has a disjunct distribution, with two main centres: central (wet habitats) and south-western (dry habitats) part of the country. In central Slovenia only one metapopulation (ca. 2000 individuals) and 5 small neighbouring populations (each of them < 500 individuals) have been known within the last 15 years. During this period, three of the smaller populations have become extinct and total population size decreased by about 80%. Main reasons are regular mowing during or before flight season and destruction of the habitat by conversion into arable land. In south-western Slovenia, the species is more widespread but population densities are much lower than the density of the strongest wet subpopulation estimated 15 years ago (Čelik, own obs.). In Germany only few sites (wet habitats) are documented historically. They are all in the southern part of Bavaria mainly along the Isar river valley. At present, one of these sites still harbours *C. oedippus*, consisting of three habitat patches in close vicinity to each other. Before its rediscovery in 1996, the species was thought to be extinct in Germany (Bräu & Schwibinger 2013).

C. oedippus inhabits late successional habitats, which are not dominated by woody plants. According to Osthelder (cit. in Kolar 1929), *C. oedippus* may already have immigrated from its core territory in Asia to central and western Europe during the last interstadial (Allerød**)** of the Weichselian glaciation about 10.000 years ago.

Hence, primary habitats of the species may have been places where woodland could not completely close, but had larger open spaces because of very wet (e.g. in spring fens with continuously very wet soil or periodically flooded areas along rivers and brooks) or dry conditions, possibly combined with grazing of wild animals. This may be the reason why the species is also found, apart from wetlands, in dry abandoned grasslands of the karst regions of northern Italy (only old data exist which are not recently confirmed) and south-western Slovenia, and in folds of dry steppes on southern slopes with narrow strips of mesoxerophilous meadow vegetation and shrub-lands in southern Siberia (Gorbunov & Kosterin 2007). Specific ecological needs of *C. oedippus* together with a very low dispersal capacity (Čelik 2003, Örvössy et al. 2013) could explain the very scattered (presumably relict) distribution of the species in its western range. Many of the remaining habitats have changed due to human activities, such as lowering the water table for intensification of land use, peat ditching, and due to abandonment of extensive grazing.

Adults fly in one generation from June to July. Females lay single eggs on different substrata. Larvae are heliophilous and thermophilous: they are feeding during the day and basking in the sun in the warmest part of the day in late autumn and early spring (own obs.). Many food plants (grasses and sedges) have been published (e.g. Chretien 1886, Weidemann 1995, Lhonore 1996, Lhonore and Lagarde 1999, Lafranchis 2000, Tshikolovets 2003, Dierks 2006) but most of them refer to breeding experiments. Some of them are very likely to be used in the field as well (e.g. *Deschampsia caespitosa* (L.) P. Beauv.), while others were not confirmed in recent breeding experiments (e.g. *Schoenus nigricans* L., Dierks 2006, own obs.).

Study sites

Between 2008 and 2012, we studied larval and egg-laying habitats of *C. oedippus* in three countries (Germany – DE, Italy – IT, Slovenia – SLO) that represent the main three habitat types occupied by this species in Europe: wet grasslands on alkaline soil (DE), wet grasslands on acid soil (IT) and dry grasslands (SLO).

In DE, the only remaining population was studied, which inhabits a small and isolated area (ca. 1.1 ha, altitude 490 m) in open wetlands partially enclosed by hedges (Bräu & Schwibinger 2013). The wetter parts of the habitat patches can be classified as *Schoenetum ferruginei* Du Rietz 1925, with interspersed clusters of *Cladietum marisci* Allorge 1922. However, the *Schoenetum* is highly dominated by *Carex panicea* L. Outside depressions created by peat ditching in former times, vegetation is transient to *Allio suaveolentis-Molinietum caeruleae* Görs in Oberd. ex Oberd. 1983 merging with *Cirsio tuberosi-Molinietum arundinaceae* Oberd. et Philippi ex Görs 1974 in drier parts. The habitat patches have been abandoned for decades. While in some parts of the site bushes (mainly *Frangula alnus* Mill.) are highly abundant, they are rare in areas with high densities of *C. oedippus*.

In IT one site within the "Baraggia" Regional Oriented Reserve was studied (WGS 84: 45°31'39.6" N 8°09'17.4" E, altitude 300 m). The Reserve protects fragments of natural areas, surrounded by human-modified habitats, mainly rice fields. It is characterised by scattered woods (*Quercus robur* L., *Betula pendula* Roth, *Carpinus betulus* L.), interrupted by large clearings, which are dominated by *Calluna vulgaris* (L.) Hull and *Molinia caerulea* (L.) Moench. The study site is composed of three isolated (1600–5500 m apart) patches (1.0, 1.2, 1.7 ha). All are *Molinia caerulea* meadows, partially covered by *Calluna vulgaris* and with a shrubby perimeter (*Betula pendula*, *Populus tremula* L., *Frangula alnus*). One patch is regularly mown in its central part once per year; the second is extensively grazed; the third is unmanaged, but regularly used by tourists for recreational activities. All three patches are periodically used for military exercises.

In SLO one site on the Kras plateau (WGS 84: 45°52'12.17" N 13°36'27.32" E, altitude 260 m) was investigated. It consists of three adjoining (350–1000 m apart) patches (1.7, 1.5, 0.8 ha) characterised by abandoned, floristically poor, and overgrown submediterranean–illyrian dry grasslands (associations of *Danthonio–Scorzoneretum villosae* Ht. & Ht-ić in Ht-ić 1963 and *Carici humilis–Centaureetum rupestris* Ht. & Ht-ić 1934 on deeper soils). It is characteristic for these successional stages that sedges and grasses dominate the vegetation, while non-graminoid herbs are less abundant. Characteristic is also a high structural heterogeneity, which is composed of dense swards of *Sesleria autumnalis* (Scop.) F. W. Schultz scattered over a predominant cover of mainly lower and sparse herb layer consisting of other grasses and sedges. Individual islands of shrubs (*Cotinus coggygria* Scop., *Prunus mahaleb* L., *Ligustrum vulgare* L.) and young thermophylic low trees (*Fraxinus ornus* L., *Ailanthus altissima* (Mill.) Swingle, *Pinus nigra* Arnold) grow scattered over the entire abandoned grasslands and surround the study patches.

Larval microhabitat

To obtain data on host-plants and habitat preferences of larvae after hibernation, field surveys were carried out from April to May (DE: 2008, 2009; IT: 2009, SLO: 2010, 2011). For each detected larva we recorded the host-plant species (if feeding was observed) or plant species with feeding traces near the caterpillar, and the percent cover of main structural parameters within a radius of 50 cm around the larva: bare ground, rocks, mosses, litter, shrubs, herbs and known host-plants. Additional structural parameters were assessed for each country: percent cover of grass-like herbs (GLH, i.e. herbs with plant structure, that do not shade the lower parts of the herb layer;

e.g., *Allium* spp., *Anthericum ramosum* L., *Genista sylvestris* Scop.; DE, SLO), percent cover of plants from the families *Poaceace*, *Juncaceae*, *Cyperaceae* (PJC, i.e. plants with erectophile leaf orientation; DE, SLO), percent cover of *Calluna vulgaris* (IT), percent cover of each species from the group PJC (SLO), average vegetation height (i.e. prevailing height of herb layer in cm; SLO) and maximum vegetation height (SLO), the lattermost being the tallest plant in microhabitat. Those plants corresponded mainly to *Chrysopogon gryllus* (L.) Trin., *Bromopsis erecta* (Huds.) Fourr. s.str., *B. condensata* (Hack.) Holub, *B. transsilvanica* (Steud.) Holub and *Stipa* sp.; they deviated considerably from average vegetation height. In Germany and Italy, the percent cover of main and additional structural parameters were also recorded for random microlocations (May 2009) which were selected by a randomly thrown stick (Anthes et al. 2003), and represented the spectrum of available microlocations within the studied habitat type. In total, we recorded 49 random microhabitats (DE: 39, IT: 10) and 76 larval microhabitats (DE: 31, IT: 34, SLO: 11).

Oviposition microhabitat

We tracked egg-laying females on sunny days from June to July (DE: 2008, 2010 and some additional observations in 2011 and 2012; IT: 2009; SLO: 2010, 2011). Each female was chosen randomly and then followed for a maximum of 10 ovipositions. If no egg-laying occurred within 20 minutes, we selected another female. Females followed for multiple ovipositions clearly switched plant species during consecutive ovipositions, meaning that repeated sampling of the same female did not represent pseudo-replication and not bias the result on oviposition electivity. The same main and additional structural parameters were recorded for oviposition (DE: 76, IT: 101, SLO: 55) and random (DE: 35, IT: 150, SLO: 30) microlocations (DE, SLO: July 2010; IT: June 2009) as for the larval microhabitats (see above). Random microlocations again reflect the spectrum of available structures of the site. Additionally, we collected data on the oviposition substratum: plant species, plant part (leaf, steam, bud, other), support freshness (vital, dead), and oviposition height above ground.

Breeding experiments

Breeding of five generations of *C. oedippus* under field conditions (ex-situ) was performed in Germany from 2009 to 2014. Several vivaria of different size (minimum 20 x 30 x 30 cm) were planted with sods taken from the habitat, containing mainly *Molinia caerulea* and *Carex panicea*. The top of the vivaria was covered with gauze which was fixed with an elastic rubber band, allowing high air circulation. The vivaria were always kept outdoors, in the same region where the butterfly population lives. They received direct sunlight for several hours a day and were sheltered from rain and snow. Humidity was held at a high level by regular watering. Temperature and humidity were measured with a digital thermo-hygrometer over a long period under different weather conditions. Both were similar to the values occasionally measured at the species' habitat. For oviposition within the vivaria, some female butterflies were taken from the field (after observation of oviposition in the field, to ensure that they already started ovipositing) and some that emerged and mated in captivity could be used for maintaining the breeding stock as well. Depending on the year, between 26 and 92 pupae were achieved.

In Slovenia, only one young caterpillar was transferred from the field (i.e. study site) in October 2011 to a glass vivarium (50 x 50 x 50 cm) covered with gauze and planted with the sod taken from the location of the caterpillar. The vivarium was exposed to outdoor temperature and sunlight but sheltered from rain and snow. Its inside was humidified with water spraying through the mesh every time it rained or snowed out. The caterpillar was bred until the butterfly hatched (in June 2012).

In both experiments, the behaviour of caterpillars was observed and noted in short intervals.

Statistical analyses

Larval/oviposition microhabitat electivity within each habitat type was evaluated by comparison between larval/oviposition and random microlocations using multiple stepwise forward logistic regression. We fitted a presence-absence logistic model to our presence-only data (i.e., random microlocations represent pseudo-absences, cf. Ward et al. 2009) as we anticipate that the probability of selecting the random microhabitat with the presence of eggs/larvae must be very low given the high density of oviposition substrata (considering non-selectivity of egg-laying females) and host-plants (considering host-plants growth form and larval polyphagy) compared with the density of *C. oedippus* in each study site. Further, in the case that some of selected random microlocations contained the eggs/larvae, the difference between oviposition/larval and random microlocations were even underestimated (cf. Eilers et al. 2013), meaning that our estimations are conservative. Before regression analysis, all explanatory variables (i.e. structural parameters of microlocations) were tested for intercorrelations by calculating Spearman's Rho correlation coefficients. We defined two types of explanatory variables, i.e. “basic” and “derived” (see Table 2 and 4). Basic variables are main structural parameters of the microhabitat, while derived variables are structural parameters which represent only a part of the coverage of corresponding basic variable. Within both types, we distingushed between “composed” and “simple” variables. Composed variables can be substituted by more simple variables, e.g. Herbs can be substituted by HPs and

Herbs_without HPs, or PJC, GLH and NGLH. Simple variables can not be replaced by a set of other variables. In the case of strong correlation (Spearman Rho ≥ |0.9|) between two variables within pairs "basic vs. basic" or "basic vs. derived", the simple variable was maintained for entering in regression analysis. If two derived variables were strongly correlated, the one which correlated strongly with selected basic variables was excluded from further regression analysis. The last criterium was considered also in the case of strong correlation between two simple variables.

For identifying the differences between three habitat types for each structural parameter separately, the Kruskal-Wallis Chi test (KW) and Mann-Whitney U tests (MWU) were applied on all possible comparisons as post hoc procedures with Bonferroni correction.

To find out whether the difference in oviposition height between three habitat types depends on height of prevailing egg-laying support, the Jonckheere–Terpstra test was applied. Four categories of egg-laying supports were coded according to plant height (Lauber & Wagner 1996): 1 = *Carex humilis* (3–11 cm), 2 = *Calluna vulgaris* (10–50 cm), 3 = *Carex panicea* (20–40 cm), 4 = *Molinia caerulea* agg. (30–250 cm).

To detect the relationships between the type of oviposition support (dependent variable) and most abundant structural parameter (independent variable) in egg-laying microhabitats, Chi-Square tests using Likelihood ratio statistic were applied because of small sample sizes, which resulted in expected frequencies lower than 1 in some cases. For assessing the strength of association between both variables, Cramer's *V* was used. Standardized residuals were used to define the significant contributors to the overall chi-square value. For the purpose of Chi square testing, the egg-laying supports and most abundant structural parameters were arranged in the following categories: DE – *Molinia caerulea*, *Carex panicea*, other herbs, litter, shrub; IT – *M. caerulea*, *Carex* sp., *Calluna vulgaris*, other herbs; SLO – *Carex humilis*, *Poaceae*, other plants. As litter was the most abundant structural parameter in 76% of the Slovenian egg-laying microhabitats, the possible relationships between the type of oviposition support and the abundance of structural parameters was analyzed using the second most abundant structure parameter in the microhabitats.

All statistical analyses were performed using SPSS 13.0 (SPSS Inc. 1989–2004).

Results

Larval preferences

In our three habitat types, a total of 85 feeding observations were detected on 6 plant substrata: *Carex panicea*, *C. davalliana* Sm., *C. humilis, Carex* sp., *Molinia caerulea* and *Festuca rupicola* (Table 1). Sedges represented the majority of the larval diet after winter in all three habitat types (DE: 71%, IT: 94%, SLO: 77%), while observed alternative host-plants were *M. caerulea* in both wet grassland types and *F. rupicola* in dry habitat.

Larval microhabitats differed between three habitat types not only in the presence of main structural parameters (Table 2), but also in the coverage of those they had in common: litter (KW χ^2 = 22.67, df=2, p = 0.000), herbs (KW χ^2 = 11.94, df=2, p = 0.003) and shrubs (KW χ^2 = 60.34, df=2, p = 0.000) (Fig. 1a). Wet larval microhabitats were characterized by a higher coverage of litter and by lower abundances of herbs than dry microhabitats. Shrub cover was significantly higher in Italian microhabitats than in the other two countries. In Italy, the majority of shrub cover was formed by *Calluna vulgaris* (Table 2). If we presumed that this perennial dwarf shrub has a similar function as litter for overwintering larvae and add its coverage to litter, the larval microhabitats still significantly differed between Italy and Slovenia, but not between both wet habitat types (Fig. 1a). The cover of host-plants (Table 2) was significantly higher in German (median = 30%) than in Slovenian (median = 12%) larval microhabitats (DE vs. SLO, MWU Z = –4.23, p = 0.000; respective data not available for IT). If we assume that the other grass species present in dry habitats are also used as larval food-plants (PJC in Table 2), the host-plants abundances differ only slightly between both habitat types (MWU Z = –2.15, p = 0.032).

In Germany, occupied microhabitats had a significantly higher coverage of litter and of the preferred host-plant *C. panicea*, and lower abundances of shrubs, *M. caerulea* and non grassy-like herbs than available sites (Table 2). Due to lower coverage of *M. caerulea* and herbs with planophile leaf orientation, larval microhabitats were characterized by lower abundances of host-plants, graminoids (PJC), all herbs and herbs other than host-plants. Larval preferences for microlocations with high coverage of *C. panicea* revealed that this preferred host-plant has additional characteristics, which enable better survival of caterpillars after hibernation compared to the alternative host *M. caerulea* (see section *Ex-situ breeding observations*). In Italy, preferences of overwintering larvae showed a similar pattern as in Germany: they preferentially occurred on sites with higher coverage of litter or litter+*Calluna vulgaris* and lower abundance of herbs compared to the available microlocations (Table 2). Besides, larval microhabitats had lower coverage of bare ground. No information was available to assess the effect of host-plants on larval microhabitat selection in Italy. However, in both wet habitat types, the coverage of litter already explained most of the variation in microhabitat selection by overwintering larvae (Table 3). The likelihood of a microlocation being occupied by larvae after hibernation increased with litter coverage.

Preferences of egg-laying females

During this study we found out that females apply two oviposition modes in the pre-alighting phase of oviposition site selection, (i) “normal mode” – female lands on plants parts in the upper layer of the herb vegetation and remains there for post-alighting phase (egg-laying), and (ii) “dropdown behaviour” – female lands on plants parts in the upper layer of the herb vegetation, then crawls or drops down to the ground, and walks on the ground searching for suitable egg-laying support. The second mode is less frequently used and it was observed only in Germany.

The eggs were deposited on plants growing at the edge of gaps in the herb layer. In three habitat types, a total of 236 eggs were laid on 27 different egg-laying supports (Table 1), including herbs (71%), shrubs (19%), litter (2%) and undetermined plants (8%). All eggs were deposited singly on leaves (89%), stems (10%) or buds (1%). Three quarters (76%) of the eggs were attached on vital parts of plants, the remaining on dry parts or litter (20%) and undetermined substratum (4%).

The above described wide range indicates a rather unselective egg-laying behaviour. Nevertheless, some plant species dominate the plant spectrum used for ovipositon. The prevailing supports were *Molinia caerulea* (55%) and *Carex panicea* (28%) in Germany ($\chi^2 = 40.35$, d.f. = 1, $p < 0.001$), *Calluna vulgaris* (41%) and *M. caerulea* (34%) in Italy ($\chi^2 = 34.21$, d.f. = 1, $p < 0.001$), and *Carex humilis* (65%) in Slovenia ($\chi^2 = 5.27$, d.f. = 1, $p < 0.05$). The plant species used for oviposition and the most abundant structure parameter in the egg-laying microhabitat show a significant positive association (DE, LR = 40.90, df = 16, $p = 0.001$; Cramer's V = 0.560, $p = 0.000$; IT, LR = 43.47, df = 15, $p = 0.000$; Cramer's V = 0.406, $p = 0.000$; SLO, LR = 13.03, df = 4, $p = 0.020$; Cramer's V = 0.306, $p = 0.032$). Eggs are simply deposited on the most abundant plant species, which explains the regular use of the non-host *C. vulgaris* in Italy.

The vertical positions of eggs on substrata ranged from 0 to 44 cm and oviposition height increased with the height of prevailing egg-laying support (Jonckheere–Terpstra z = 5.12, No. of levels = 4, p=0.000). The eggs were deposited significantly higher in the most often applied (“normal”) oviposition mode (N = 67) than in dropdown mode (N = 9) (MWU $Z = –4.37$, p=0.000).

Oviposition sites differed between three habitat types not only in vegetation composition (due to different vegetation grassland communities) but also in microhabitat structure considering the presence and abundances of main structural parameters (Table 4). German and Slovenian microhabitats were denoted by a higher cover of litter and a lower cover of shrubs than Italian ones (KW, litter: $\chi^2 = 38.36$, df=2, $p = 0.000$; shrubs: $\chi^2 = 81.15$, df=2, *p* = 0.000; Fig. 1b). The coverage of herbs other than host-plants was significantly higher in dry than in wet microhabitats (KW χ^2 = 146.09, df=2, *p* = 0.000; Fig. 1b). Consequently, host-plants were more abundant in wet than in dry oviposition spots (KW χ^2 = 65.39, df=2, *p* = 0.000; Fig. 1b). But in dry habitats several further grass species occurred (PJC in Table 4); if they are taken into consideration as potential host-plants, the difference is equalled out (KW χ^2 = 5.91, df=2, *p* = 0.052). Litter is an important structure in oviposition microhabitats, because it creates a vegetation structure (herb layer) rich in gaps. Eggs are usually deposited at the edges of these gaps. As it was one of the most variable structural parameter in Italian oviposition microhabitats, and its median cover was much lower than in the other two countries (Fig. 1b), we presumed that other structures take over its role when its cover is very low, e.g. perennial *C. vulgaris* according to its significant negative correlation with litter cover (Spearman rho = –0.399, *p* = 0.000). Indeed, the sum of litter and *C. vulgaris* in Italian oviposition microhabitats was only slightly higher than litter cover in Germany and Slovenia (Fig. 1b).

In all three habitat types, the shrub cover was significantly lower in oviposition than in available sites (Table 4). In Germany, this was the only difference between both types of microlocations. Italian egg-laying microhabitats had significantly higher abundances of litter and *M. caerulea* than available sites. In Slovenia, oviposition microhabitats were characterized by a higher coverage of litter and maximum vegetation height than were in available microlocations, and also by lower abundances of all herbs and herbs other than observed host-plants. Thus, German oviposition microhabitats were the standard structure of the locality inhabited by *C. oedippus* as the difference in shrub cover between oviposition and available sites was not enough to improve a constant-only model. In both other countries, oviposition pattern/site selection was best explained by a combination of litter cover and abundances of shrubs and non-host plants. In Italy, the likelihood of a spot being accepted for oviposition increased with the litter coverage and decreased with the cover of shrubs other than *Calluna vulgaris* and herbs other than host-plants (Table 5). In Slovenia, the presence of high plant stems of *Chrysopogon gryllus*, *Bromopsis* sp., *Stipa* sp. which deviated from prevailing/average vegetation height positively influenced the selection of oviposition microhabitat, but high covers of shrubs and other herbs than host plants decreased the likelihood of a spot to be chosen by an egg-laying female (Table 5). Presence of high grass species indicates microlocations with higher coverage of *C. humilis* (Spearman rho, *C.h.* vs. *Bromopsis* sp. = 0.268, *p* = 0.014, *C.h.* vs. *C. gryllus* = 0.249, *p* = 0.022, *C.h.* vs. *Stipa* sp. = 0.269, *p* = 0.013) and litter (Spearman rho, *Bromopsis* sp. vs. litter = 0.233, *p* = 0.041), and lower abundance of *Sesleria autumnalis* (Spearman rho, *S. a.* vs. *C. humilis* = –0.363, *p* = 0.001; *S. a.* vs. *Bromopsis* sp. = –0.368, *p* = 0.001; *S. a.* vs. *C. gryllus* = –0.386, *p* = 0.000; *S. a.* vs. *Stipa* sp. = –0.282, *p* = 0.009) which creates a very homogeneous and dense sward. Furthermore, coverage of herbs with planophile leaf orientation was lower in occupied than in available microlocations although the difference was only close to significance (Table 4: Herbs without PJC).

Oviposition microhabitats were characterised by a clearly lower proportion of litter and a higher cover of herbs than larval spots (Table 2 and 4; MWU: litter, DE (40 vs. 70%): Z = –6.71, p = 0.000; IT (10 vs. 45%): Z = –5.01, p = 0.000; SLO (40 vs. 45%): Z = –2.70, p = 0.007; herbs, DE (60 vs. 30%): Z = –6.43, p = 0.000; IT (50 vs. 30%): Z = –2.70, p = 0.007; SLO (56 vs. 50%): Z = –0.98, p = 0.327), which is largely a seasonal effect.

Ex-situ breeding observations

Our observations from breeding under field conditions showed that caterpillars concentrate on the sun-facing side of tufts while feeding or resting, except during search for a place to pupate and during hibernation. From late October onwards, most caterpillars begin to retreat for hibernation: some overwinter at the base of sedges or grasses or even on upper parts of their food-plants hidden from the sun, presumably to avoid awakening too early on sunny winter days.

During breeding experiments we observed that caterpillars which hibernate in their third instar usually awake in spring when temperatures rise to about 20°C for several consecutive days. At that time not all host-plants are available. In Germany, the time lag between larval awakening and the start of *M. caerulea* growth varied from about 10 to 30 days (Table 6). In contrast, *C. panicea* which remains green during winter is always available for larvae as food resource. Hibernated caterpillars were observed feeding on it shortly after the start of activity. Moreover, caterpillars do not feed on *Molinia* leaves shorter than about 5 cm, thus even enlarging the time lag. In Slovenia, comparing awaking time with observations of host-plants growth status in the field and in ex-situ showed (Table 6) that besides known host-plants, *C. humilis* and *F. rupicola* which overwintered green, some other grass species, e.g. *Brachypodium rupestre, Sesleria autumnalis,* are also available.

Discussion

Habitat requirements of ovipositing females and larvae

Egg-laying females of *C. oedippus* are not selective regarding oviposition substratum, e.g. plant species or exact position on the plant. Eggs were mainly deposited on the most abundant structure parameter (plant/plant group) available in the microhabitat. This wide range is also reflected by previously known egg-laying plants from the species' European range (Table 7).

Such absence of electivity is in contrast to many butterfly species, who's females carefully choose the oviposition plant, e.g. *Phengaris* (*Maculinea*) butterflies (Dolek et al. 1998, Thomas & Elmes 2001, Kassai & Peregovits 2005), *Lycaena alciphron* (Dolek & Geyer 2001), *Boloria aquilonaris* (Turlure et al. 2013), *Euphydrays desfontainii* (Pennekamp et al. 2013), *E. maturna* (Dolek et al. 2013), *Colias myrmidone* (Dolek et al. 2005, Szentirmai et al. 2014). This contrast very likely relates to the wide host-plant range of *C. oedippus* larvae (i.e. different species from Poaceae and Cyperaceae), the growth form of host-plants (i.e. dense ground-covering plants growing mostly in tufts) and their relatively high stability in terms of growing period and abundance (e.g. due to possibility of vegetative reproduction).

Nevertheless, an important factor for suitable reproduction habitats is the availability of host-plants in close vicinity to the oviposition substratum, i.e within reach of young caterpillars. The host-plants coverage in oviposition sites was always high: between 45 and 50% in wet, and 18% (only observed host-plant species) or 41% (including potential host-plant species) in dry habitats. The finding that coverage of bare ground was highest in Italian microlocations, and only there larval microhabitats had significantly lower bare ground cover than random sites indicates that microlocations with higher amounts of bare ground are less suitable for overwintering larvae, possibly because bare ground can restrict larval movements and expose them to predation (e.g., Doak 2000). Alternatively, it could simply reduce the host-plants coverage and its connectivity around the caterpillar what could increase the time of larval searching for a new suitable host. We indentified six food-plant species in the field. Feeding on *M. caerulea* in the field was also observed in France (Dierks 2006) and Poland (Sielezniew et al. 2010). In former publications many additional grass and sedge species have been listed, but probably all of these refer to breeding experiments. Nevertheless, we are convinced that many more grass and sedge species are used, if they are present in the habitat.

Non-specificity for oviposition substratum, together with a high proportion of eggs (DE: 55%, IT: 34%) deposited on less frequently used host-plants (*M. caerulea*, DE: 27%, IT: 6%) or even on non-host plant material (Table 1) points out to other crucial factors observed by egg-laying females to maximize offspring performance (e.g., Mayhew 1997, Janz 2002). The models which best explain the oviposition and larval preferences of *C. oedippus* showed that vegetation structure of microlocation is an important parameter in oviposition site selection. High cover of litter and/or dwarf shrubs as *C. vulgaris* in selected microhabitats (median, larval: 45–70%, oviposition: 40–50%) creates a herb layer rich in gaps. Egg deposition mostly occurred at the edges of these gaps in order to allow helio- and thermophilous larvae to be adequately sun-exposed. Dry plant biomass provides warmer environments (WallisDeVries & van Swaay 2006) which is of special importance for overwintering larvae in early spring to enable them to reach optimal body temperature, and may also function as a microclimatic buffer (e.g., Turlure et al. 2010, Weking et al. 2013). In the field, most caterpillars could be found on sun exposed edges of tufts what is in harmony with the observations from ex-situ breeding. The lower abundances of shrubs in egg-laying microlocations than in random sites in all three habitat types also point to the importance of vegetation architecture with high solar insolation and low shading in oviposition/larval microhabitat selection.

Structure of host-plant/oviposition substratum and surrounding vegetation directly influences the microclimate, e.g. humidity, temperature and solar exposure (Beyer & Schultz 2010, O'Connor et al. 2014). Considering that there was a positive association between the type of oviposition support and the most abundant structural parameter in egg-laying microhabitat in all three habitat types, the height of prevailing egg-laying support could be used as an indicator for average vegetation height in egg-laying microhabitat. Thus, positive correlation between oviposition height and height of prevailing egg-laying support across three habitat types (from min to max height: *C. humilis* (SLO)–*C.vulgaris* (IT)–*C.panicea* (IT, DE)–*M.caerulea* (IT, DE)) suggests that female try to oviposit as high as possible on the selected substratum and within the vegetation (cf. Obermaier et al. 2006), meaning that eggs are deposited at positions that receive high solar radiation. The adjusting of oviposition height to the height of the local radiation surface to maximise heat absorption was also observed in two other satyrinae species which attach the eggs to a substratum (not simply drop them between the grasses), *Hipparchia fagi* (Möllenbeck et al. 2009) and *Coenonympha tullia* (Weking et al. 2013). However, in normal oviposition mode, females of *C. oedippus* laid eggs just below the top of the surrounding herb vegetation, but despite a limited number of field observations, it seems that dropdown mode occurs when air temperature unexpectedly decreases due to clouds temporarily covering the sun. In such cases, egg-laying females climbed down and deposited eggs on the surface of the litter cover, probably as dry plant biomass provides warmer environment than green plants (WallisDeVries & van Swaay 2006). Furthermore, the lower coverage of herbs with planophile leaf orientation in oviposition (SLO) and larval (DE) than in random sites indicates that shading of the lower herb layer is not favourable for the development of eggs and caterpillars. It seems that oviposition site selection in *C. oedippus* is influenced by the thermal requirements of eggs and larvae. This is additionally supported by the female's avoidance of dense tufts of *Sesleria autumnalis* in dry habitats, which do not offer adequate sun-exposition. These results are also in correspondence with a previous study on within-patch movements of *C.*

oedippus adults in Slovenian wet habitat (Čelik et al. 2009a) which showed that spatial and temporal patterns of female micro-distribution is affected by vegetation height, the homogeneity of host plant stands and the shading of the the lowest parts of the herb layer.

Preferences of overwintering larvae and egg-laying females for microlocations with high amounts of host-plants and litter and/or dwarf shrubs, and low amounts of bare ground, shrubs and herbs other than graminoids, together with adjusting the oviposition height as high as possible within the vegetation across all three habitat types revealed the high importance of vegetation structure in *C. oedippus* larval/oviposition microhabitat selection. At first sight, this is a relatively general pattern of habitat use across the macro-environmental gradient. The utilization of host-plants specific to the habitat type, and differences of preferred microlocations in presence and relative abundances of structural parameters between the habitat types showed that such patterns are a result of microhabitat selection conformed to local environmental conditions.

Winter green food-plants as key factor for larval survival

The butterfly host-plant synchronisation is a known phenomenon (e.g. review in Munguira et al. 2009), which directly influences larval growth and survival, and ultimately population fitness. A perfect synchronisation is of crucial importance for monophagous and oligophagous species overwintering as egg (e.g. de Vries et al. 2011) or as young caterpillar, as with *C. oedippus* (e.g. Gradl 1946). Based on breeding experiments Gradl (1946) already pointed out that a temporal mismatch exists between larval awakening and availability of the “prime” host-plant, *Molinia caerulea*. He reported that caterpillars awoke from hibernation very early due to enduring foehn weather in spring on March 20th, while their "normal" food resource *Molinia* was not yet available. Our breeding data and field observations after hibernation showed that caterpillars of *C. oedippus* awake from hibernation at a time period when only some host-plants are available (Table 6). At that time the larvae are still quite small (about 1.3 cm) and not able to move very far to search for food. Thus, they have to find host-plants in their immediate vicinity within a few days as their need for food and liquid is urgent after the long period of starvation during hibernation. Significant differences between larval and random spots in cover of the winter-green *C. panicea* support the assumption that the likelihood of larval survival is strongly influenced by the availability of this plant in German wetland habitats. *Molinia* starts to grow relatively late in spring, so in *Molinia*-dominated meadows *C. panicea* or other winter-green *Carex* species with soft leaves are needed as interim food. For *C. oedippus* habitats near Bordeaux, Dierks (2006) discussed the role of *Pseudoarrhenaterum longifolium* (Thore) Rouy which starts to grow earlier than *Molinia* and could serve as food for early awakening caterpillars. It seems that synchronisation between host-plants growing and larval diet requirements after hibernation is better harmonized in dry habitats of *C. oedippus* as the preferred food plant *C. humilis* overwinters green and sprouts already in early spring (March).

We hypothesize that winter-green host-plants play a substantial role also in the survival of overwintering caterpillars of several other butterfly species occurring in habitats with highly dominating non-winter green host-plants; a potential relationship that is so far not adequately taken into account. Namely, field observations on two satyrinae species, *Coenonympha hero* (Wagner 2010) and *Minois dryas* (Sachteleben & Winterholler 2013), living in *Molinia*-dominated habitats also showed that winter-green grasses (e.g. *Festuca* spp.) or sedges (*Carex* spp.) were used as interim food source immediately after larval awakening.

Late successional habitats

It is well known and demonstrated in detail for many butterfly species that their caterpillars need early successional stages, short turf, or otherwise hot and open habitats for their development (e.g. *Pyrgus malvae* Krämer et al. 2012; *Hesperia comma* Hermann & Steiner 1997; *Parnassius apollo* Geyer & Dolek 1995; *Lycaena alciphron* Dolek & Geyer 2001; *Scolitantides baton* Konvička et al. 2008; *Phengaris arion* Thomas 1980, Pauler et al. 1995, Fartmann 2005; *Polyommatus bellargus* Thomas 1983; *Chazara briseis* Königsdorfer 1997, Leopold 2001). The present study shows a contrasting habitat choice of *C. oedippus*, a species being restricted to largely unmanaged grassland with a dominating litter layer, but no substantial growth of woody plants. Our results on larval and oviposition preferences are in accordance with the findings from a population study of *C. oedippus* in Hungary (Örvössy et al. 2013) which reveals that large amounts of grass litter and structured vegetation with tussocks positively affect population size and density. Importance of late successional habitats, mainly characterised by pronounced litter layer, relatively nutrient-poor conditions, no considerable growth of shrubs and direct sun exposition, were also demonstrated for some other butterflies, e.g. *Coenonympha hero* (Steiner & Hermann 1999, Dolek 2011, Bräu & Dolek 2013), *Lopinga achine* (Geyer & Dolek 2013) and *Lycaena helle* (Nunner 1995).

Implications for conservation

The results of the present study showed that besides the availability of fresh-green host-plants in the vicinity of hibernated larvae, mainly the vegetation structure and microclimate of the herb layer are essential factors for oviposition site selection and successful development of premature stages of *C. oedippus*. The herb layer has to be rich in gaps (but not bare ground), usually created by large amount of litter or alternatively by dwarf shrubs. Such vegetation structure enables egg-laying females to adapt the oviposition height to local radiation surface with high heat absorption. In a gap–rich herb vegetation, the ectotherm and heliophilous caterpillar dependent on direct sunlight (i.e. when basking for elevation of body temperature) can select thermally favourable microclimates by behavioural thermoregulation (c.f. Stevenson 1985, Turlure et al. 2011), i.e. translocation of its position between the top of herbaceous plants, litter surface (warmer than upper green vegetation during colder/cloudy days) and the more balanced microclimate inside the litter in terms of temperature and humidity. A dense litter layer can also slow down the further secondary succession in the habitat as it prevents germination of groves (Ellenberg 2009, Ruprecht & Szabó 2012), and consequently affects the structure, diversity and dynamics of grassland plant communities (Ruprecth et al. 2010, Loydi et al. 2013). As litter in dry grasslands persists for longer periods than litter from wet areas due to higher lignin concentration (Fortunel et al. 2009), the site management in *C. oedippus* habitats must be diversified and adapted to meet the special needs of this highly endangered species across its range. Hence, in most of *C. oedippus* habitats some kind of management has become essential to avoid overgrowth with bushes and trees or, in wet habitats, with reed. Manual removal of groves should be preferred. Regular mowing or forms of grazing which create a uniform vegetation structure (i.e. close homogeneous sward) are thought to be detrimental. Furthermore, direct losses of larvae can be caused by cutting, as caterpillars partially feed on their food-plants until the onset of November and some keep sitting on upper parts of their food-plants even in winter (observations from breeding). In habitats where the reduction of bushes is not sufficient, only patchy mowing in winter period (December–February) can be recommended for keeping the habitat open without harming the population too much. Overgrowing with dense reed can be a problem in some wet habitats. Mowing experiments since 2009 (Bräu & Völkl unpubl.) have already shown promising results on reduction of reed if cutting is done during flight period with a cutter bar at a high level of about 30 cm above ground. However, this kind of mowing should be restricted just to parts of the habitat with dense reed to avoid emigration of butterflies and should mainly be used for habitat restoration.

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Table captions

Table 1 Substrata used by feeding larvae and egg-laying females of *C. oedippus* in Germany (DE), Italy (IT) and Slovenia (SLO). Given are the numbers of observations, in brackets percentage of all observations in the respective country

Table 2 Univariate comparison between larval microhabitats and available microlocations after winter (in May) of *C. oedippus* in Germany, Italy and Slovenia (note, that for Slovenia no information is disposable for available sites). Median (Min–Max) values of parameters and significance (*p*) of comparison using Mann-Whitney test are presented. B = basic variable, D = derived variable, C = composed variable, S = simple variable (see Material and methods for explanations)

Table 3 Analysis of preferences of overwintering larvae of *C. oedippus* based on occupied and available microlocations using binary stepwise-forward logistic regression

Table 4 Univariate comparison between oviposition microhabitats and available microlocations of *C. oedippus* in Germany, Italy and Slovenia. Median (Min–Max) values of parameters and significance (*p*) of comparison using Mann-Whitney test are presented. B = basic variable, D = derived variable, C = composed variable, S = simple variable (see Material and methods for explanations)

Table 5 Analysis of preferences of egg-laying females of *C. oedippus* based on occupied and available microlocations using binary stepwise-forward logistic regression

Table 6 Dates of *C. oedippus* larval awakening and of host-plants availability provided by field observations (on site) and by breeding under field conditions (ex-situ) in Germany (DE) and Slovenia (SLO)

Table 7 Egg-laying plants used by *C. oedippus* in Europe known before present study

Figure caption

Fig. 1 Coverage of main structural parameters in (a) larval and (b) oviposition microhabitats of *C. oedippus* in Germany (DE), Italy (IT) and Slovenia (SLO). Mann-Whitney tests: **(a)** *litter*, DE > IT: *p* = 0.000, DE > SLO: *p* = 0.000, IT ≈ SLO: *p* = 0.831; *herbs*, DE ≈ IT: *p* = 0.297, DE < SLO: *p* = 0.005, IT < SLO: *p* = 0.001; *shrubs*, DE < IT: *p* = 0.000, DE < SLO: *p* = 0.000, IT > SLO: *p* = 0.000; *litter+C. vulgaris*, DE ≈ IT: *p* = 0.724, IT > SLO: *p* = 0.001. **(b)** *litter*, DE ≈ SLO: *p* = 0.577, DE > IT: *p* = 0.000, SLO > IT: *p* = 0.000; *shrubs*, DE ≈ SLO: *p* = 0.545; DE < IT: *p* = 0.000, SLO < IT: *p* = 0.000; *Herbs without hostplants*, SLO > DE: *p* = 0.000; SLO > IT: *p* = 0.000; DE > IT: *p* = 0.000; *hostplants*, DE ≈ IT: *p* = 0.360; DE > SLO: *p* = 0.000; IT > SLO: *p* = 0.000; *litter+C. vulgaris*, DE ≈ IT: *p* = 0.053, IT > SLO: *p* = 0.021

Figure1a

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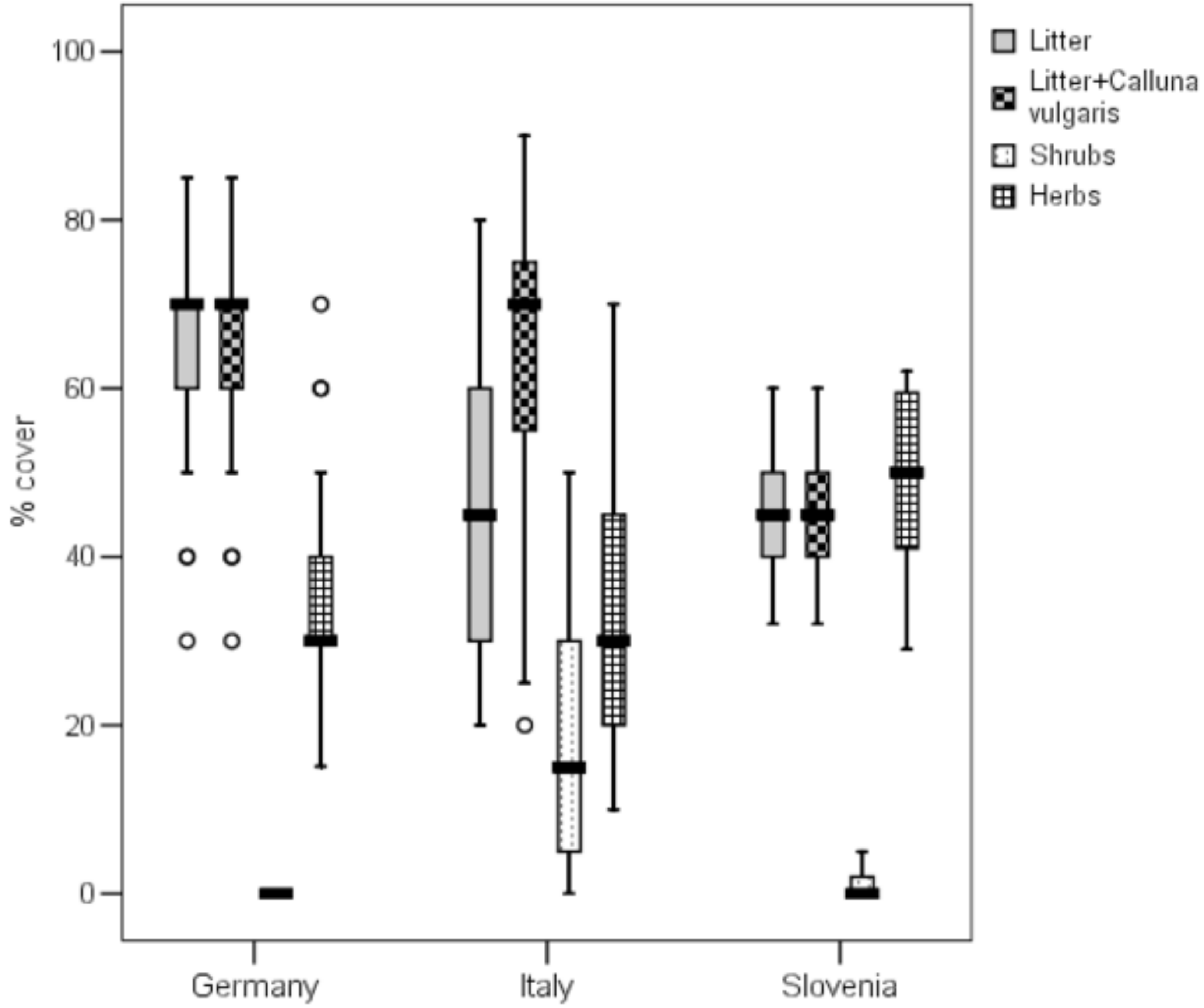

Figure1b

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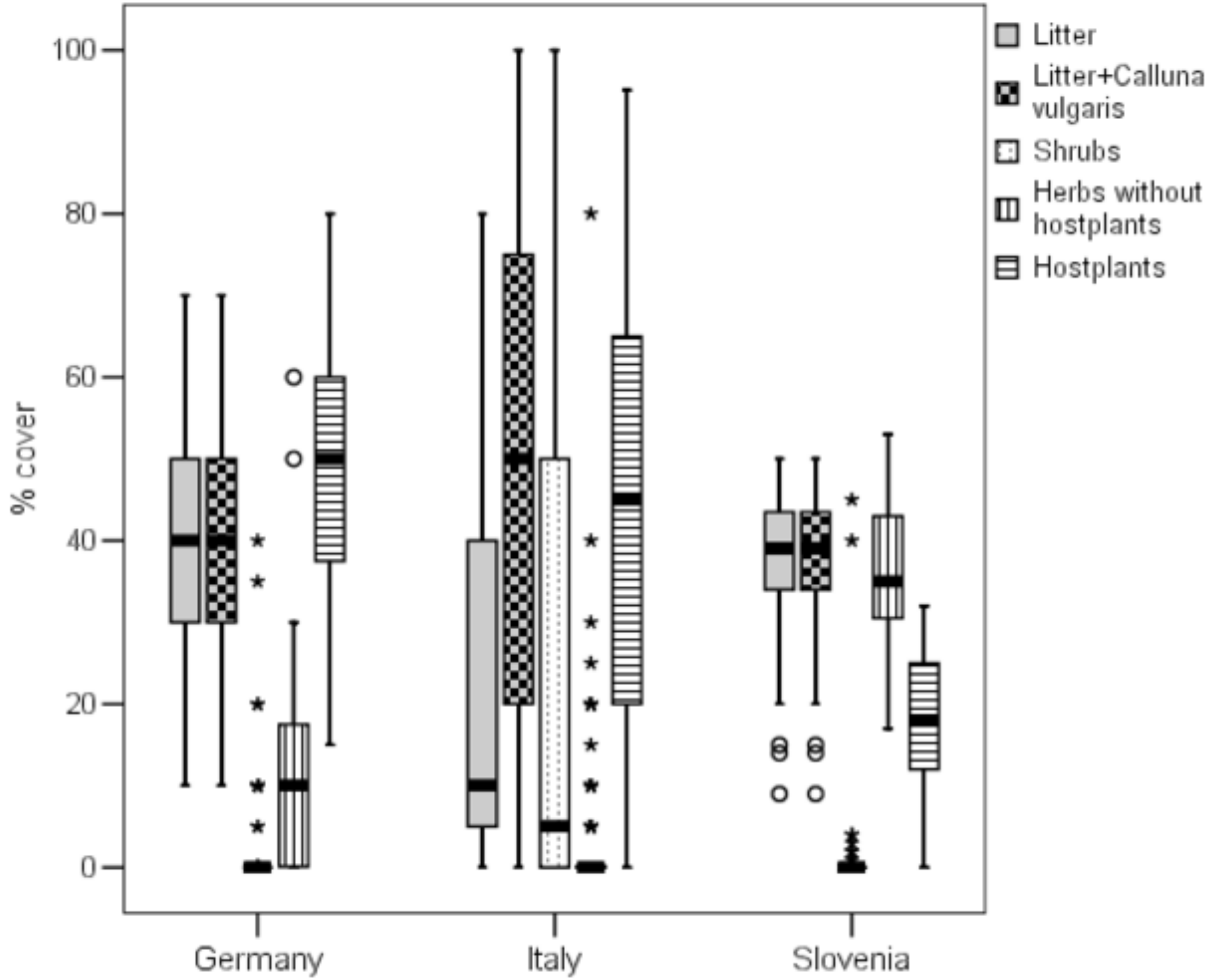

Table 1 Substrata used by feeding larvae and egg-laying females of *C. oedippus* in Germany (DE), Italy (IT) and Slovenia (SLO). Given are the numbers of observations, in brackets percentage of all observations in the respective country

Substrata		Larval host plants			Oviposition supports		
		DE	IT	SLO	DE	IT	SLO
		N = 38	N = 34	N =13	N = 79	N = 102	N = 55
Molinia caerulea	H	10 (26)	2 (6)	–	43 (54)	34 (33)	–
Deschampsia caespitosa	H	0	–	–	1 (1)	–	–
Festuca rupicola	H	–	–	3 (23)	–	–	3 (5)
Sesleria autumnalis	H	–	–	0	–	–	2 (4)
Bromopsis condensata	H	–	–	0	–	–	1 (2)
Bromopsis erecta	H	–	–	0	–	–	1 (2)
Stipa sp.	H	–	–	0	–	–	1 (2)
Chrysopogon gryllus	H	–	–	0	–	–	1 (2)
Melica ciliata	H	–	–	0	–	–	1 (2)
Anthoxanthum odoratum	H	0	0	0	1 (1)	0	0
Carex panicea	H	27 (71)	28 (82)	–	22 (28)	9 (9)	–
Carex davalliana	H	1 (3)	–	–	0	–	–
Carex humilis	H	–	–	10 (77)	–	–	36 (65)
other *Carex* species	H	0	4 (12)	0	0	0	0
Cladium mariscus	H	0	–	–	1 (1)	–	–
Eupatorium cannabinum	H	0	–	–	2 (3)	–	–
Valeriana dioica	H	0	0	–	1 (1)	0	–
Asperula cynachica	H	–	–	0	–	–	3 (5)
Anthericum ramosum	H	–	–	0	–	–	1 (2)
Galium purpureum	H	–	–	0	–	–	1 (2)
Genista sylvestris	H	–	–	0	–	–	1 (2)
Satureja montana	H	–	–	0	–	–	1 (2)
Calluna vulgaris	S	–	0	–	–	42 (41)	–
Rhamnus catharticus	S	0	–	0	1 (1)*	–	0
Frangula alnus	S	0	0	–	0	1(1)	–
Ligustrum vulgare	S	–	–	0	–	–	1 (2)
litter	L	0	0	0	3 (4)	0	1 (2)
NA		0	0	0	4 (5)	16 (16)	0

H = herb, S = shrub, L = litter
NA = undetermined substratum
0 = substratum present at the study site but not used
– = substratum not present at the study site

* This egg was erroneously given as laid on *Rhamnus frangula* (*Frangula alnus*) in Bräu et al. (2010)

Table 2 Univariate comparison between larval microhabitats and available microlocations after winter (in May) of *C. oedippus* in Germany, Italy and Slovenia (note, that for Slovenia no information is disposable for available sites). Median (Min–Max) values of parameters and significance (*p*) of comparison using Mann-Whitney test are presented. B = basic variable, D = derived variable, C = composed variable, S = simple variable (see Material and methods for explanations)

Parameter	Type of variable	Germany			Italy			Slovenia
		Larval (N = 31)	Available (N = 39)	*p*	Larval (N = 34)	Available (N = 10)	*p*	Larval (N = 11)
Bare ground (%)	B, S	0.00 (0–20)$	0.00 (0–10)$	0.854	0.00 (0–20)	10.00 (0–50)	0.001	0.00 (0–4)
Rocks (%)	B, S	[a]	[a]		[a]	[a]		0.00 (0–20)
Mosses (%)	B, S	[a]	[a]		0.00 (0–5.0)	0.00 (0–0)	0.689	0.00 (0–3)
Litter (%)	B, S	70.00 (30–85)	40.00 (20–70)	0.000	45.00 (20–80)	20.00 (10–30)	0.000	45.00 (32–60)
Shrubs (%)	B, C	0.00 (0–0)	0.00 (0–15)	0.001	15.00 (0–50)	10.00 (0–40)	0.591	0.00 (0–5)
Herbs (%)	B, C	30.00 (15–70)	55.10 (30–80)	0.000	30.00 (10–70)	47.50 (30–70)	0.005	50.00 (29–62)
HPs (%)	D, C	30.00 (15–65)	40.00 (20–70)	0.000	n.a.	n.a.		12.00 (8–20)
Herbs without HPs (%)	D, S	0.00 (0–20)	10.00 (0–40)	0.000	n.a.	n.a.		38.00 (12–51)
Herbs without PJC (%)	D, S	0.00 (0–10)	5.00 (1–30)	0.000	n.a.	n.a.		12.00 (3–24)
Calluna vulgaris (%)	D, S	[a]	[a]		12.50 (0–50)	10.00 (0–40)	0.572	[a]
Litter+*C. vulgaris* (%)	D, S	[a]	[a]		70.00 (20–90)	25.00 (15–70)	0.001	[a]
Shrubs without *C. vulgaris* (%)	D, S	[a]	[a]		0.00 (0–15)	0.00 (0–5)	0.923	[a]
Molinia caerulea (%)	D, S	15.00 (0–60)	30.00 (10–70)	0.000	n.a.	n.a.		[a]
Carex panicea (%)	D, S	10.00 (5–40)	5.00 (0–40)	0.022	n.a.	n.a.		[a]
Carex humilis (%)	D, S	[a]			[a]	[a]		10.00 (6–15)
Festuca rupicola (%)	D, S	[a]			[a]	[a]		2.00 (0–12)
PJC (%)	D, S	30.00 (15–67)	50.00 (30–70)	0.000	n.a.	n.a.		37.00 (24–54)
GLH (%)	D, S	0.00 (0–3)	0.00 (0–0.1)	0.604	n.a.	n.a.		2.00 (1–12)
NGLH (%)	D, S	0.00 (0–10)	5.00 (0–30)	0.000	n.a.	n.a.		8.00 (1–18)

HPs = Host plants (Germany: *M. caerulea* + *Carex panicea*; Slovenia: *Carex humilis* + *Festuca rupicola*)
PJC = Poaceace, Juncaceae, Cyperaceae (i.e. plants with erectophile leaf orientation)
GLH = Grass-like herbs (i.e. herbs with plant stature which does not shade the lower parts of herb layer; e.g., *Allium* spp., *Anthericum ramosum*, *Genista sylvestris*)
NGLH = Non grass-like herbs (i.e. herbs with plant stature which shades the lower parts of herb layer; plants with planophile leaf orientation) = cover of Herbs – cover of GLH
[a] Not existent in the microhabitat
n.a. = data not available
$ Bare ground was present only in one larval and one random microhabitat.

Table 3 Analysis of preferences of overwintering larvae of *C. oedippus* based on occupied and available microlocations using binary stepwise-forward logistic regression

Parameter	(B)	SE (B)	Wald	*P*	Exp (B)	95% CI for Exp (B)	
						Lower	Upper
(a) Germany[a]							
Litter	0.114	0.027	18.353	0.000	1.121	1.064	1.181
Const.	–6.560	1.544	18.047	0.000	0.001		
Model $\chi^2 = 31.186$, df = 1, $P < 0.0001$, Nagelkerke $R^2 = 0.481$, correctly classified 81.4% (larvae: 83.9%, available: 79.5%)							
(b) Italy[b]							
Litter	0.171	0.061	7.862	0.005	1.187	1.053	1.337
Const.	–3.814	1.606	5.642	0.018	0.022		
Model $\chi^2 = 21.011$, df = 1, $P < 0.0001$, Nagelkerke $R^2 = 0.577$, correctly classified 81.8% (larvae: 88.2%, available: 60.0%)							

(a) Larvae sites (N = 31), available sites (N = 39); *(b)* larvae sites (N = 34), available sites (N = 10)

[a] Variables entered into the regression analysis: coverage (%) of litter, bare ground, shrubs, HPs, herbs without HPs, *Carex panicea*, *Molinia caerulea*, GLH, NGLH; variables excluded from analysis because of multicollinearity: coverage (%) of herbs, PJC, herbs without PJC

[b] Variables entered into the regression analysis: coverage (%) of litter, bare ground, mosses, litter+*Calluna vulgaris*, *Calluna vulgaris*, shrubs without *C. vulgaris*; variables excluded from analysis because of multicollinearity: coverage (%) of shrubs, herbs

Table 4 Univariate comparison between oviposition microhabitats and available microlocations of *C. oedippus* in Germany, Italy and Slovenia. Median (Min–Max) values of parameters and significance (*p*) of comparison using Mann-Whitney test are presented. B = basic variable, D = derived variable, C = composed variable, S = simple variable (see Material and methods for explanations)

Parameter	Type of variable	Germany			Italy			Slovenia		
		Oviposition (N = 76)	Available (N = 35)	*p*	Oviposition (N = 101)	Available (N = 150)	*p*	Oviposition (N = 55)	Available (N = 30)	*p*
Bare ground (%)	B, S	0.00 (0–10)$	0.00 (0–0)		0.00 (0–75)	0.00 (0–50)	0.064	0.00 (0–5)	0.00 (0–3)	0.478
Rocks (%)	B, S	[a]	[a]		[a]	[a]		2.00 (0–55)	1.00 (0–15)	0.099
Mosses (%)	B, S	[a]	[a]		0.00 (0–0.1)	0.00 (0–70)	0.922	0.00 (0–3)	0.10 (0–5)	0.196
Litter (%)	B, S	40.00 (10–70)	40.00 (10–70)	0.823	10.00 (0–80)	5.00 (0–70)	0.000	39.00 (9–50)	33.00 (20–50)	0.010
Shrubs (%)	B, C	0.00 (0–40)$$	0.00 (0–40)$$	0.012	5.00 (0–100)	25.00 (0–100)	0.033	0.00 (0–45)	0.00 (0–55)	0.025
Herbs (%)	B, C	60.00 (30–90)	60.00 (30–80)	0.268	50.00 (0–95)	47.50 (0–100)	0.506	56.00 (25–75)	60.00 (20–70)	0.018
HPs	D, C	50.00 (15–80)	40 (20–70.0)	0.397	45 (0–95.1)	40.00 (0–100)	0.053	18 (0–32)	15 (0–42)	0.174
Herbs without HPs (%)	D, S	10.00 (0–60)	10.00 (0–50)	0.632	0.00 (0–80)	0.00 (0–95)	0.841	35.00 (17–53)	43.00 (14–67)	0.024
Herbs without PJC (%)	D, S	5.00 (0–30)	5.00 (0–30)	0.948	n.a.	n.a.		14.00 (6–33)	15.50 (3–35)	0.160
Calluna vulgaris (%)	D, S	[a]	[a]		5.00 (0–100)	20.00 (0–100)	0.327	[a]	[a]	
Litter+*C. vulgaris* (%)	D, S	[a]	[a]		50.00 (0–100)	40.00 (0–100)	0.307	[a]	[a]	
Shrubs without *C. vulgaris* (%)	D, S	[a]	[a]		0.00 (0–30)	0.00 (0–70)	0.000	[a]	[a]	
Molinia caerulea (%)	D, S	30.00 (0–70)	40.00 (0–70)	0.972	40.00 (0–95)	30.00 (0–100)	0.031	[a]	[a]	
Carex panicea (%)	D, S	10.00 (0–40)	10.00 (0–60)	0.277	0.00 (0–40)	0.00 (0–65)	0.087	[a]	[a]	
Carex humilis (%)	D, S	[a]	[a]		[a]	[a]		15.00 (2–30)	15.00 (0–40)	0.230
Festuca rupicola (%)	D, S	[a]	[a]		[a]	[a]		1.00 (0–13)	0.00 (0–15)	0.055
PJC (%)	D, S	50.00 (25–80)	40.00 (30–75)	0.223	n.a.	n.a.		41.00 (13–53)	41.50 (16–62)	0.596
GLH (%)	D, S	0.00 (0–0)	0.00 (0–0)	1.000	n.a.	n.a.		2.00 (0–8)	4.00 (0–15)	0.039
NGLH (%)	D, S	5.00 (0–30)	5.00 (0–30)	0.625	n.a.	n.a.		10.00 (3–30)	13.50 (2–30)	0.733
Average veget. height (cm)	S	n.a.	n.a.		n.a.	n.a.		20.00 (8–35)	20.00 (10–40)	0.205
Max. veget. height (cm)	S	n.a.	n.a.		n.a.	n.a.		45.00 (25–65)	40.00 (30–70)	0.027

HPs = Host plants (Germany, Italy: *M. caerulea* + *Carex panicea*; Slovenia: *Carex humilis* + *Festuca rupicola*)
PJC = Poaceace, Juncaceae, Cyperaceae (i.e. plants with erectophile leaf orientation)
GLH = Grass-like herbs (i.e. herbs with plant stature which does not shade the lower parts of herb layer; e.g., *Allium* spp., *Anthericum ramosum*, *Genista sylvestris*)
NGLH = Non Grass-like herbs (i.e. herbs with plant stature which shades the lower parts of herb layer; plants with planophile leaf orientation) = cover of Herbs – cover of GLH
[a] Not existent in the microhabitat
n.a. = data not available
$ Bare ground was present only in one oviposition microhabitat
$$ Mean±SD, oviposition: 2.44±7.14; available: 5.06±9.21

Table 5 Analysis of preferences of egg-laying females of *C. oedippus* based on occupied and available microlocations using binary stepwise-forward logistic regression

Parameter	(B)	SE (B)	Wald	*P*	Exp (B)	95% CI for Exp (B)	
						Lower	Upper
(a) Italy[a]							
Litter	0.024	0.007	10.750	0.001	1.024	1.010	1.039
Herbs without HPs	–0.020	0.010	3.923	0.048	0.980	0.961	1.000
Shrubs without *C. vulgaris*	–0.086	0.034	6.340	0.012	0.918	0.859	0.981
Const.	–0.524	0.200	6.868	0.009	0.592		
Model $\chi^2 = 35.868$, df = 3, P < 0.0001, Nagelkerke $R^2 = 0.180$, correctly classified 65.7% (eggs: 37.6%, available: 84.7%)							
(b) Slovenia[b]							
Shrubs	–0.119	0.034	12.117	0.000	0.888	0.830	0.949
Herbs without HPs	–0.146	0.038	14.686	0.000	0.864	0.802	0.931
GLH	–0.246	0.117	4.401	0.036	0.782	0.621	0.984
Max. vegetation height	0.114	0.039	8.641	0.003	1.121	1.039	1.210
Const.	2.759	1.787	2.383	0.123	15.784		
Model $\chi^2 = 33.948$, df = 4, P < 0.0001, Nagelkerke $R^2 = 0.456$, correctly classified 78.6% (eggs: 88.9%, available: 60.0%)							

(a) Oviposition sites (N = 101), available sites (N = 150); *(b)* oviposition sites (N = 54), available sites (N = 30)

[a] Variables entered into the regression analysis: coverage (%) of litter, bare ground, mosses, herbs, herbs without HPs, *Calluna vulgaris*, shrubs without *C. vulgaris*, *Carex panicea*, *Molinia caerulea*, litter+*Calluna vulgaris*; variables excluded from analysis because of multicollinearity: coverage (%) of shrubs, HPs

[b] Variables entered into the regression analysis: coverage (%) of litter, bare ground, mosses, rocks, shrubs, herbs, herbs without HPs, *Carex humilis*, *Festuca rupicola*, PJC, GLH, NGLH, average vegetation height, maximum vegetation height; variables excluded from analysis because of multicollinearity: coverage (%) of HPs (*C. humilis*, *F. rupicola*), herbs without PJC

Table 6 Dates of *C. oedippus* larval awakening and of host-plants availability provided by field observations (on site) and by breeding under field conditions (ex-situ) in Germany (DE) and Slovenia (SLO)

Year	Locality	Larval awakening	First observation of larval feeding on				Growing of *M. caerulea*
			C. panicea	*M. caerulea*	*C. humilis*	*F. rupicola*	
2008	on site (DE)	n.a.	n.a.	n.a.	[a]	[a]	27th April
2009	ex-situ (DE)	4th April	4th April	17th April	[a]	[a]	14th April
2009	on site (DE)	6th April	6th April	n.a.	[a]	[a]	n.a.
2010	ex-situ (DE)	23rd March	23rd March	3rd April	[a]	[a]	n.a.
2010	on site (DE)	n.a.	n.a.	n.a.	[a]	[a]	after 25th April
2011	ex-situ (DE)	6th February	20th March	n.a.	[a]	[a]	after 25th March
2011	on site (SLO)	2nd April	[a]	[a]	2nd April	2nd April	[a]
2012	ex-situ (DE)	16th March	18th March	21st April	[a]	[a]	n.a.
2012	ex-situ (SLO)	24th March	[a]	[a]	25th March	n.a.	[a]
2013	ex-situ (DE)	13th April	13th April	1st May	[a]	[a]	n.a.

n.a. = data not available

[a] Plant species not existent in the study site

Table 7 Egg-laying plants used by *C. oedippus* in Europe known before present study

Plant species	Country	Reference
Molinia caerulea	SLO, IT, DE, PL, CRO	Čelik 1997, Čelik et al. 2009a, Bonelli et al. 2010, Bräu et al. 2010, Sielezniew et al. 2010, Šašić 2010
Carex panicea	SLO, DE	Čelik 1997, Čelik et al. 2009a, Bräu et al. 2010
Carex davalliana	SLO, PL	Čelik et al. 2009a, Sielezniew et al. 2010
Carex hostiana	SLO	Čelik 1997, Čelik et al. 2009a
Carex gracilis	PL	Sielezniew et al. 2010
Carex tomentosa	CRO	Šašić 2010
Carex flacca	SLO	Rakar, Čelik, Vreš unpubl.
Gratiola officinalis	SLO	Čelik 1997, Čelik et al. 2009a
Angelica sylvestris	PL	Sielezniew et al. 2010
Inula hirta	SLO	Rakar, Čelik, Vreš unpubl.
Lotus corniculatus	SLO	Rakar, Čelik, Vreš unpubl.
Cirsium palustre	PL	Sielezniew et al. 2010
Calluna vulgaris	IT	Bonelli et al. 2010
*Rhamnus catharticus**	DE	Bräu et al. 2010
Cotinus coggygria	SLO	Rakar, Čelik, Vreš unpubl.

CRO = Croatia, DE = Germany, IT = Italy, PL = Poland, SLO = Slovenia
* This plant was erroneously given as *Rhamnus frangula* (*Frangula alnus*) in Bräu et al. (2010)