

## Research Article

# Selection of Oviposition Sites by *Libelloides coccajus* (Denis & Schiffermüller, 1775) (Neuroptera: Ascalaphidae), North of the Alps: Implications for Nature Conservation

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(1) The survival of peripheral populations is often threatened, especially in a changing environment. Furthermore, such populations frequently show adaptations to local conditions which, in turn, may enhance the ability of a species to adapt to changing environmental conditions. In conservation biology, peripheral populations are therefore of particular interest. (2) In northern Switzerland and southern Germany, *Libelloides coccajus* is an example of such a peripheral species. (3) Assuming that suitable oviposition sites are crucial to its long-term survival, we compared oviposition sites and adjacent control plots with regard to structure and composition of the vegetation. (4) Vegetation structure at and around oviposition sites seems to follow fairly stringent rules leading to at least two benefits for the egg clutches: (i) reduced risk of contact with adjacent plants, avoiding delayed drying after rainfall or morning dew and (ii) reduced shading and therefore higher temperatures. (5) Furthermore, the study showed that it is possible to successfully create secondary habitats for *L. coccajus*, as shown by a road verge in one of our study areas. It is likely that other artificial habitats such as abandoned gravel pits and quarries may also provide suitable habitats.

## 1. Introduction

Peripheral populations are of particular interest in conservation biology. As species in peripheral populations tend to live under suboptimal conditions [1], these populations often show adaptations to local conditions and therefore can enhance the species' ability to adapt to a changing environment [2–4]. Guo et al. [5] also point out that monitoring marginal populations can improve the understanding of crucial site factors and, in consequence, enhance the chances of correctly predicting future developments. Accordingly, peripheral populations are of great significance for conservation biology [2, 6].

In northern Switzerland and southern Germany, the highly thermophilic *Libelloides coccajus* (Denis and Schiffermüller, 1775) (Neuroptera: Ascalaphidae) is an example of a peripheral species. *L. coccajus* has its core distribution around the Mediterranean coast, where this species can be

found in open forests, on rocky screes, and in meadows with quite dense vegetation that never becomes dry [7]. North of the Alps, the climate is substantially colder and in the summer months wetter than in the Mediterranean region, so that thermophilic species such as *L. coccajus* can survive only on exceptionally warm and dry sites which are mostly isolated [8, 9]. Such a shift in habitat preferences is widely known for several plant species (e.g., [10, 11]) as well as for various insect species [12–14]. It follows that global warming [15] might enhance habitat suitability for *L. coccajus* on sites with microclimatic conditions which up to now have been suboptimal, as has been shown for various species [16, 17]. On the other hand, any change in the size and/or number of such habitat islands, for example, due to changes in land use, may present a fatal threat and risk of local extinction. There is evidence that over the past 70 years *L. coccajus* has substantially declined north of the Alps [18–20], but no long-term monitoring of populations of *L. coccajus*, north of the

Alps, is currently available. On the Red List of endangered animals in Switzerland [21], *L. coccajus* is categorized as “endangered” in northern Switzerland as well as on the Red Lists for Bavaria and Baden-Württemberg, Germany [22, 23].

To date, knowledge of the autecology of *L. coccajus* is fragmentary [7, 8, 24]. Focusing on the habitat requirements of adult *L. coccajus*, north of the Alps, Gonthier [24] described the habitat of *L. coccajus* in the Canton of Neuchâtel as extensively used, south-facing grassy slopes at low altitudes (up to 1,200 m a.s.l.), often interspersed with rocks and shrubs, and adjacent to forests.

In Bavaria, several studies regarding the ecology of *L. coccajus* were carried out between 1995 and 2003 on five spatially very close and partially connected populations [9, 25–27]. Most of the habitats observed in Bavaria mainly correspond to the habitat description of Gonthier [24]. The authors’ results indicate that oviposition sites of *L. coccajus* are highly specific, and therefore small-scale habitat improvements may be a valuable conservation measure. Wolf [27] concluded that oviposition sites of *L. coccajus* are primarily characterized by (i) low vegetation cover and (ii) full exposure to the sun during the day. In addition, *L. coccajus* seems to prefer comparatively flat microsites on the upper part of a slope. The eggs are deposited exclusively on living or dead plant stems [27] between 10 and 30 cm above the soil surface [25].

Based on this rather limited knowledge, several questions about the autecology of *L. coccajus* arise. Wolf’s description of oviposition sites [27] as “patches of more or less open ground” suggests a considerable degree of variability. Several potentially important aspects in oviposition site selection remain unclear including (i) whether there is a maximum vegetation cover which should not be exceeded, (ii) if there are other relevant structural parameters, (iii) which dimension is most appropriate for the characterization of oviposition microhabitats, (iv) whether floristic composition is important, and (v) how an optimal oviposition substrate (plant stem) can be characterized. Regarding the behaviour of *L. coccajus*, it would be of great interest to know whether females search for oviposition sites using primarily visual, thermal, or other stimuli. There is also a need for further research on larval ecology (habitat, food sources, and development) and on population dynamics, especially as the dispersal potential of the imagines remains largely unknown.

As small-scale vegetation structure was found to be a crucial element of habitat quality for many insect species (e.g., [28–30]), we focused our study on the small-scale vegetation structure of oviposition sites. The general goal was to elucidate the sizes of the oviposition microhabitat and the related requirements of *L. coccajus* in northern Switzerland. In particular, we addressed the following questions.

- (I) Do small-scale vegetation cover and vegetation height vary significantly among circular areas of different radii around the oviposition sites of *L. coccajus*?
- (II) Based on the variation in small-scale vegetation structure around oviposition sites, which dimension is appropriate for characterizing the sites?
- (III) Can we characterize the oviposition site demands of *L. coccajus* in terms of vegetation-related parameters



FIGURE 1: Male owlfly resting in the vegetation (21.05.2010/SKK).

(vegetation height, vegetation cover, floristic composition, or indicator values) by comparison of known oviposition sites and adjacent control plots?


The knowledge acquired will hopefully lead to a deeper understanding of the oviposition site selection behaviour of *L. coccajus* and therefore help to improve conservation strategies. In particular, we are hoping to gain detailed information on how to create suitable oviposition sites without jeopardizing the floristic quality of the surrounding habitat, for example, by opening new gateways for invasive neophytes.

## 2. Material and Methods

**2.1. Study Area.** Fieldwork was conducted in 2010 on four different populations of *L. coccajus*, three in northern Switzerland and one just across the border in the southernmost part of Germany. The four study areas were located within 25 km of one another, and the two closest were separated by 12 km (center approx. 47.35°N, 8.37°W). They were situated between 360 and 620 m a.s.l., with a mean annual precipitation (1986–2010) of between 986 and 1,080 mm (data by MeteoSwiss, 2010). Based on the preliminary study carried out by Fischer [19], the main oviposition areas of the four populations were already fairly well known (Table 1).

**2.2. Study Species.** *Libelloides coccajus* is a medium-sized owlfly with a wingspan of 42–45 mm. On both forewings and hindwings, it has large yellow spots and black veins (Figure 1). It feeds on small flying insects [7]. North of the Alps, flying adults may be observed between May and the mid-June, with a tendency towards earlier activity in warmer years [9]. The maximum life span is approximately 50 days [9]. In northern Switzerland, *L. coccajus* occurs up to 1,200 m a.s.l. [24]. It undergoes a complete metamorphosis, but there is little data concerning its larval habitat and its presumably biennial larval development [7, 9, 18, 24, 25]. According to Tauber et al. [31], Ascalaphidae larvae live either epigeally or arboreally and develop over three larval stages. Even though several authors assume the larvae of *L. coccajus* to

TABLE 1: Description of the study areas.

Study area	Aspect	Size	Habitat <sup>1</sup>	Mean slope	Description	Sample photograph <sup>2</sup>
Hessenberg (HE)	S-SW	6,000 m <sup>2</sup>	<i>Molinio-Pinion</i>	15°	Open pine forest with broad clearings and heterogeneous vegetation, mown once a year but not before October 1	
Glattfelden (GL)	SE	6,000 m <sup>2</sup>	<i>Mesobromion</i>	30°	Steep roadside verge created in 1978 with homogenous vegetation, remaining uncut year-round but with selective mowing of areas with high coverage of <i>Erigeron annuus</i>	
Merishausen (ME)	S	6,000 m <sup>2</sup>	<i>Mesobromion</i> <sup>3</sup>	25°	Semidry grassland interspersed with shrubs and scarce vegetation at the upper edge due to more gravel soil. Every year one half of the area is mown, but not before August 1	
Rheinheim (RH)	SE	9,000 m <sup>2</sup>	<i>Mesobromion</i>	5°	Extensively used meadow, mown once a year but not before August 1	

<sup>1</sup>According to Delarze et al. [53]; <sup>2</sup>all photographs taken between May 1 and July 6, 2010, (M. Müller); <sup>3</sup>unusually high abundance of *Geranium sanguineum*.

be epigeal (e.g., [9, 24]), soil screenings performed by Wolf [9] in the surroundings of oviposition sites did not reveal any larvae.

**2.3. Field Work.** The four study areas were systematically searched from edge to edge for oviposition sites by slowly walking along approximately 4 m wide horizontal transects. Searching for oviposition sites (including marking the place with red wooden sticks) was performed between June 30 and July 8, 2010. Vegetation surveys were made between July 14 and August 27, 2010. An oviposition site was defined as a plant stem with at least one egg clutch of *L. coccajus* attached to it (Figure 2). Each stem was then taken as the centre of a set of three concentric circles with radii of 20, 40, and 60 cm, respectively. If two or more plant stems with egg clutches were found within a radius of 20 cm, this was considered as one oviposition site and the midpoint between these stems was used as the centre of the sampling circles. For every oviposition site, a control plot was established 10 m towards the centre of the study area, again consisting of three concentric circles with radii of 20, 40, and 60 cm, respectively.



FIGURE 2: Female owlfly during oviposition (5.6.2010/SKK).

For each sampling circle a vegetation relevé was made; that is, for each vascular plant species in the herb layer the cover was estimated using the extended scale of Braun-Blanquet according to Dierschke [32]. Vegetation height



TABLE 2: Description of the oviposition sites.

Study area	Number of oviposition sites	Total number of clutches	Mean number of clutches per oviposition site	Mean number of eggs per clutch $\pm$ SD <sup>1</sup>	Location above soil surface (cm) $\pm$ SD <sup>1</sup>
Hessenberg	4	4	1	33 $\pm$ 13 <sup>a</sup>	18.5 $\pm$ 3.1 <sup>c</sup>
Glattfelden	13	13	1	42 $\pm$ 9 <sup>a</sup>	18.8 $\pm$ 4.6 <sup>c</sup>
Merishausen	9	14	1.6	51 $\pm$ 8 <sup>b</sup>	24.1 $\pm$ 7.9 <sup>c</sup>
Rheinheim	10	16	1.6	50 $\pm$ 8 <sup>b</sup>	19.3 $\pm$ 6.1 <sup>c</sup>
Average	9	11.8	1.3 $\pm$ 0.3	46 $\pm$ 10	20 $\pm$ 6.4

<sup>1</sup>Values sharing the same letter are statistically not different for  $\alpha = 0.05$ .

was measured at the edge of each sampling circle at the southernmost, the westernmost, the northernmost, and the easternmost point, using a stick and a cardboard disk ( $r = 20$  cm, weight = 14.5 g) with a hole in the centre. Vegetation height was defined as the height where the disc stopped when dropped. In addition, for each egg clutch, the number of eggs and the height above the soil surface were recorded. If two clutches overlapped, which prevented the eggs from being counted accurately, the number of eggs was recorded as “uncountable” and excluded from any further analysis.

**2.4. Data Analysis.** VEGEDAZ software [33] was used to transform the ordinal vegetation cover values into percentage values (according to Dierschke [32]) and to calculate the weighted mean indicator values using Landolt’s indicator values [34] for each vegetation relevé. Statistical testing was performed using R-2.12.0 [35] and principal coordinate analysis (PCoA) was conducted with Canoco 4.55 [36].

Prior to analysis, each parameter was tested for normality of distribution and homogeneity of variances using the Shapiro-Wilk-test and the Bartlett-test, respectively. Where appropriate, a one-way ANOVA or a  $t$ -test for paired comparisons with correction for alpha-inflation [37] was applied. If normal distribution did not occur and could not be achieved by transformation, nonparametric tests were used, namely, the Friedman two-way ANOVA or the Wilcoxon signed-rank test. For subsequent pairwise testing based on the Friedman two-way ANOVA, the Wilcoxon signed-rank test with correction for alpha-inflation according to Holm [37] was applied. Floristic resemblance among the relevés was calculated using Bray-Curtis distance [38] and visualized with principal coordinate analysis (PCoA). Prior to analysis, cover percentages were subjected to square root transformation as suggested, for example, by Osborne [39] and Wildi [40].

### 3. Results

**3.1. Location and Characteristics of Egg Clutches.** On average, nine oviposition sites were found per study area (range 4–13; Table 2). The number of clutches per oviposition site ranged from 1 to 3 with an average of 1.3 clutches. On average, the clutches were located 20 cm above the soil surface (range 12–41 cm), with no significant differences among the study areas (ANOVA;  $P = 0.1$ ). The mean number of eggs per clutch, however, was significantly greater in Merishausen and

Rheinheim than in Glattfelden and Hessenberg (ANOVA;  $P < 0.01$ ), respectively.

**3.2. Small-Scale Vegetation Pattern.** Around oviposition sites, vegetation cover increased sharply from the 20 cm to the 40 cm radius and moderately from the 40 cm to 60 cm radius (Figure 3). Accordingly, significant differences between the three different-sized sampling circles were found for each study area separately (Friedman two-way ANOVA; HE:  $P = 0.018$ , GL:  $P = 0.0058$ , ME:  $P = 0.0043$ , RH:  $P = 0.0033$ ) as well as for all study areas combined (Friedman two-way ANOVA;  $P < 0.0001$ ). In contrast, no significant differences were found with regard to the mean height of the vegetation in the different-sized circles around the oviposition sites (Friedman two-way ANOVA,  $P = 0.23$ ).

For all study areas combined, differences in vegetation cover were statistically significant for all pairwise comparisons between the three different-sized sampling circles (Figure 3). Considering each study area separately, all three pairwise comparisons of the vegetation cover were significant only at Merishausen, whereas at Glattfelden and Rheinheim the difference between the areas with 40 cm and 60 cm radii was not significant (Figure 3).

On the sampling circles with a radius of 20 cm around the oviposition sites, vegetation cover varied substantially both among and within the study areas. At Hessenberg, for instance, vegetation cover ranged from 2.8% to 72.9%, while the mean cover on all four study areas ranged from 15% (Glattfelden) to 73.5% (Rheinheim) (Figure 3).

Since the differences in vegetation cover between oviposition sites and control plots were greatest on the smallest plots, we considered in the following analyses only data from 20 cm radius plots.

**3.3. Characterization of Oviposition Sites.** Considering the circular plots with a radius of 20 cm and the combined data of all four study areas, vegetation cover ( $P = 0.0007$ ), number of species ( $P = 0.0081$ ), and vegetation height at the different compass directions ( $P < 0.0001$ ) were significantly greater on the control plots than on the adjacent oviposition sites (Wilcoxon signed-rank test; Table 3). In contrast, no significant differences were found with regard to the mean indicator values (Table 3).

Performing the same analysis for each study area separately, only Merishausen revealed significant differences in vegetation cover (Wilcoxon signed-rank test;  $P = 0.012$ ) and

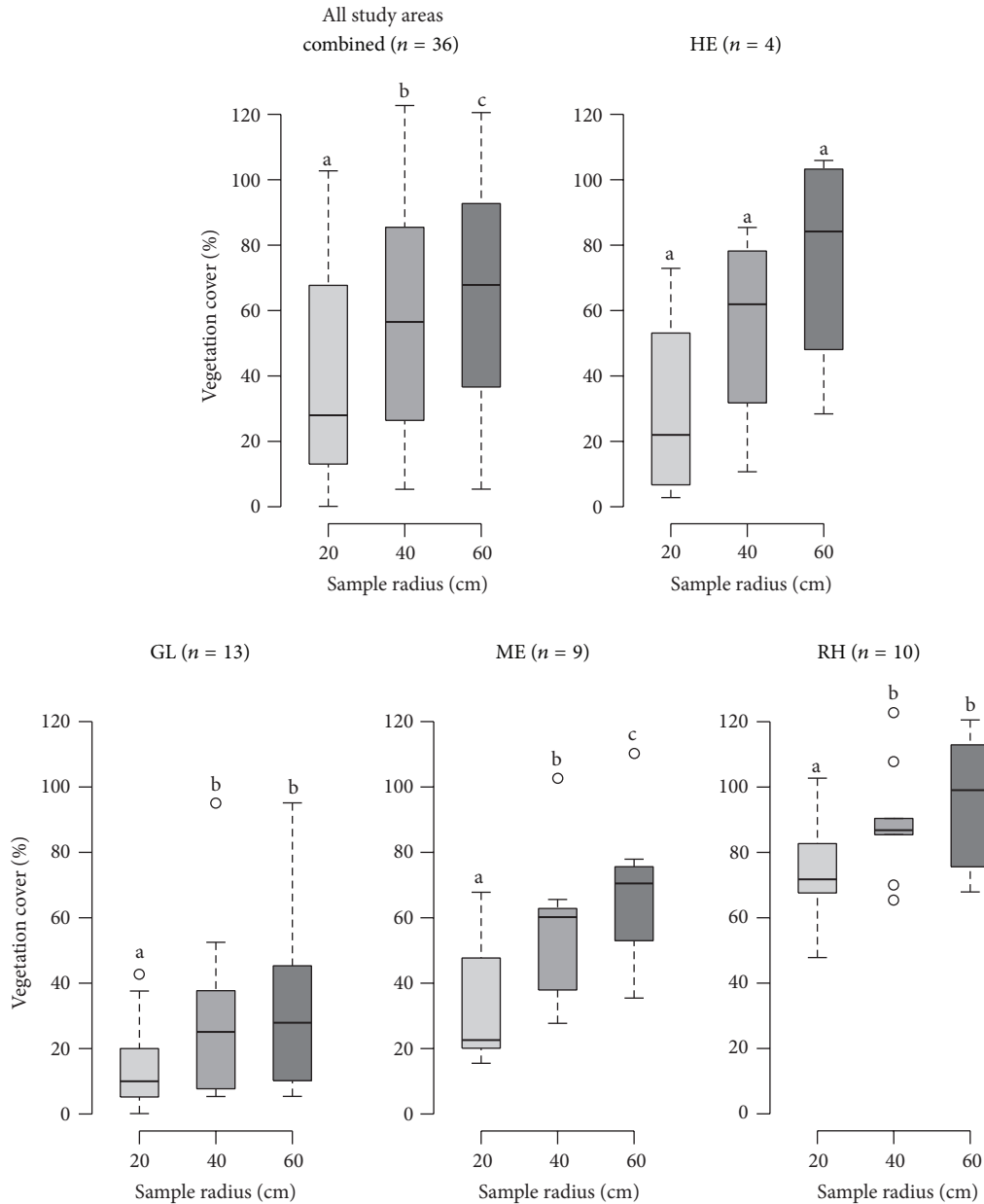


FIGURE 3: Vegetation cover on three different-sized concentric circles around the oviposition sites. (As plants may partly overlap, vegetation cover may be greater than 100%.) Boxes represent the interquartile range (IQR) including the median, whiskers being a maximum of 1.5 times the IQR. Values outside the whiskers' range are shown as circles. Within a study area, samples sharing the same letters were not significantly different according to a pairwise Wilcoxon signed-rank tests for  $\alpha = 0.05$ , corrected *sensu* Holm [37]. The acronyms of the study sites are explained in Table 1.

number of plant species ( $P = 0.029$ ) with greater values for both parameters on the control plots (Figure 4). For the other study areas, the differences were statistically not significant but showed the same tendencies (Figure 4).

At Glattfelden and Merishausen, the differences in vegetation height between oviposition sites and control plots were significant in all four compass directions (N, E, S, W). At Rheinheim, this was only true at the northern and the eastern edges, while at Hessenberg no significant differences were found (Figure 4).

**3.4. Floristic Resemblance.** Principal coordinate analysis (PCoA) of all 20 cm radius samples (oviposition sites and control plots) revealed three clusters corresponding to the study areas of GL, RH, and HE/ME (Figure 5). The first two axes of the PCoA explain 17.5% and 16.1% of the total variation, respectively. There was no obvious separation between oviposition sites and corresponding control plots (Figure 5). Samples from Rheinheim formed a clearly defined cluster with only one outlier. The RH cluster was characterized as extensively used meadow vegetation with high abundance of

TABLE 3: Results of a Wilcoxon signed-rank test comparing circular plots with a radius of 20 cm around oviposition sites and the corresponding control plots of all study areas combined. Differences represent the mean difference between each paired control plot and oviposition site, and SD is the respective standard deviation.  $V$  is the test statistic calculated by the Wilcoxon signed-rank test.

Parameter	Arithmetic mean			SD of difference	$V$	$P$
	Oviposition	Control	Difference			
Vegetation cover (%)	38.1	61	22.8	33.7	125	<b>0.0007</b>
Number of plant species	7.2	8.9	1.8	3.5	95	<b>0.0081</b> <sup>1,2</sup>
Vegetation height north (cm)	15.9	30.5	14.6	8.7	6	<b>&lt;0.0001</b> <sup>1</sup>
Vegetation height east (cm)	14.4	31.2	15.5	10.2	18.5	<b>&lt;0.0001</b> <sup>1,2</sup>
Vegetation height south (cm)	13.4	28.4	15.3	10.4	28.5	<b>&lt;0.0001</b> <sup>1</sup>
Vegetation height west (cm)	14.4	28.5	15	11	50	<b>&lt;0.0001</b> <sup>1</sup>
Mean indicator values according to Landolt [34]						
Moisture	1.9	1.9	0.03	0.3	281	0.4184 <sup>1</sup>
Light	3.6	3.6	0.04	0.2	267.5	0.3071 <sup>1</sup>
Temperature	3.5	3.6	0.02	0.3	302	0.6357
Soil reaction	3.4	3.4	0.07	0.3	293	0.5393
Soil nutrients	2.2	2.1	0.01	0.3	284	0.4507
Moisture variability	0.2	0.3	-0.03	0.2	289	0.4274 <sup>1,2</sup>

<sup>1</sup>Estimated  $P$  values due to the occurrence of ties; <sup>2</sup>estimated  $P$  values because of zeros.

grasses, mainly *Bromus erectus* (Poaceae), the GL cluster by a comparatively large abundance of herbs (e.g., *Origanum vulgare* (Lamiaceae), *Hieracium piloselloides* (Asteraceae)), and the joint HE and ME cluster by plant species related to open woodland and forest edge communities (such as *Geranium sanguineum* (Geraniaceae)).

## 4. Discussion

**4.1. Number of Clutches and Clutch Size.** In the four study areas, we found between 4 and 16 clutches per area with an average of 46 eggs per clutch. This is comparable to the figures reported by Wolf [9], who found averages of between 43.2 and 52.3 eggs per clutch. Wolf [9] hypothesized that the number of eggs per clutch depends primarily on the duration of the feeding period and on the availability of suitable food. These, in turn, depend on climatic conditions and other environmental stress factors, and it is well known that environmental stress can lead to a low maturation rate or even to oosorption (resorption of ripe or developing eggs). The correlation between food availability and the number of eggs deposited by females has also been described for other insect species, for example, for *Osmia pumila* (Megachilidae) [41] and for *Aphytis aonidiae* (Aphelinidae) [42]. In our study, the differences in the mean number of eggs per clutch found in the four study areas could therefore be due to differences in the amount of food available to the imagines or to differences in microclimatic conditions, which are crucial for successful foraging.

**4.2. Vegetation Pattern around Oviposition Sites.** Around the oviposition sites of *L. coccajus*, vegetation cover increased significantly with increasing distance, with an especially sharp increase after the first 20 cm. Our results are in accordance with the findings of Wolf [9], who reported low vegetation cover at and immediately around oviposition sites. Our study

showed that to ecologically characterize oviposition sites of *L. coccajus*, a plot with a radius of approximately 20 cm should be used. Other authors have used comparable plot sizes to investigate the microhabitat structure of oviposition sites of insect species. However, to the best of our knowledge, they selected the plot size subjectively and not based on any systematic approach. Beyer and Schultz [28], for instance, used plots of 0.1 m<sup>2</sup> to characterize the oviposition sites of the butterfly species *Polites mardon* (Hesperiidae). Randlkofer et al. [30] used plots with a radius of 10 cm to assess the vegetation structure around the oviposition sites of the leaf beetle *Galeruca tanacetii* (Chrysomelidae) and Gröning et al. [43] used a sample with a radius of 30 cm to study the microhabitat preferences of the grasshopper species *Tetrix ceperoi* (Tetrigidae).

**4.3. Differences between Oviposition Sites and Control Plots.** We found that oviposition microhabitats of *L. coccajus* can be characterized as small patches with comparatively (i) low vegetation cover and (ii) low vegetation height (at all four compass directions N, E, S, and W), which results in a somewhat warmer and drier microclimate than in its surroundings. The surprisingly high variance in mean vegetation cover among the oviposition sites examined at the four study areas (15%–75%) is in accordance with Wolf [9], who described oviposition sites as patches of “more or less open ground.” Oviposition sites are thus not completely restricted to open ground or very low vegetation cover. We hypothesize that (i) oviposition site selection is flexible, females choosing patches with the lowest vegetation cover within the meadow in question, or (ii) oviposition site selection is based on a combination of several factors and not exclusively on vegetation cover. Arguments supporting the first hypothesis are the general preference of *L. coccajus* for warm and dry microhabitats, which are generally found on patches with low vegetation cover. This seems to hold true for

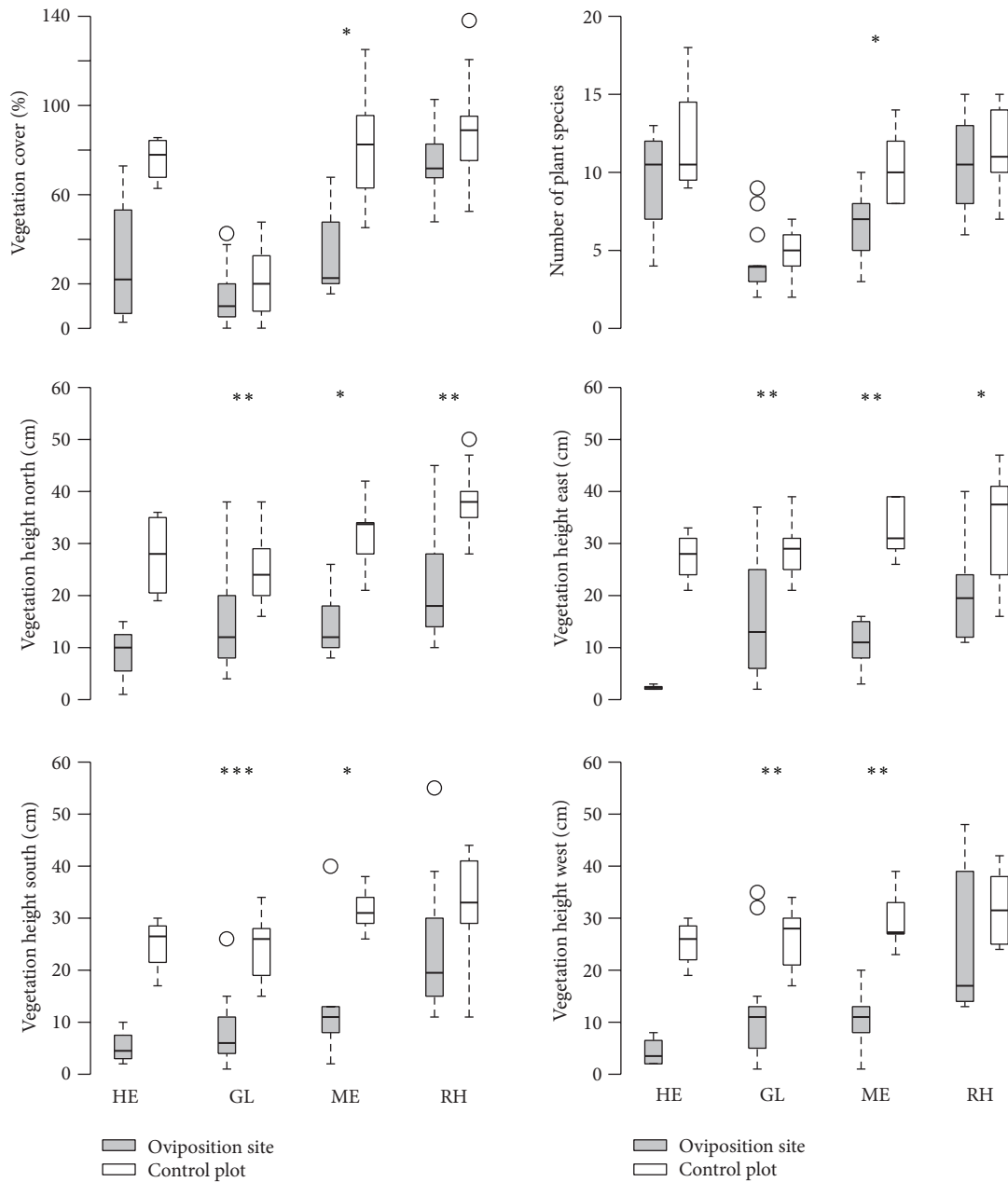


FIGURE 4: Differences between oviposition sites and control plots with a radius of 20 cm. Boxes represent the interquartile range (IQR) including the median, whiskers being a maximum of 1.5 times the IQR. Values outside the whiskers' range are shown as circles. (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , Wilcoxon signed-rank test). The acronyms of the study sites are explained in Table 1.

a variety of other thermophilic insect species, for instance, the grasshopper species *Chorthippus brunneus* (Acrididae) [44] and *Myrmeleotettix maculatus* (Acrididae) [45] as well as for several butterfly species, for example, *Hesperia comma* (Hesperiidae) [46]. The second hypothesis is supported by findings at one of our study areas (Rheinheim) where vegetation cover at oviposition sites attained up to 73%. This, however, was only the case when the height of the vegetation was very low due to the high abundance of low-growing plant species such as *Potentilla heptaphylla* (Rosaceae), *Sedum*

*acre* (Crassulaceae), and *Thymus pulegioides* (Lamiaceae). Consequently, for an attractive oviposition site, vegetation cover at the level of the egg clutch needs to be low, that is, approximately 20 cm above the soil surface.

We assume that the observed vegetation structure reduces the risk of direct contact between egg clutches and adjacent plants, particularly when they are wet, for example, following rainfall or because of morning dew. This view is supported by the findings of Wolf [27], who identified (i) delayed drying after rainfall as the main threat to the survival of egg clutches

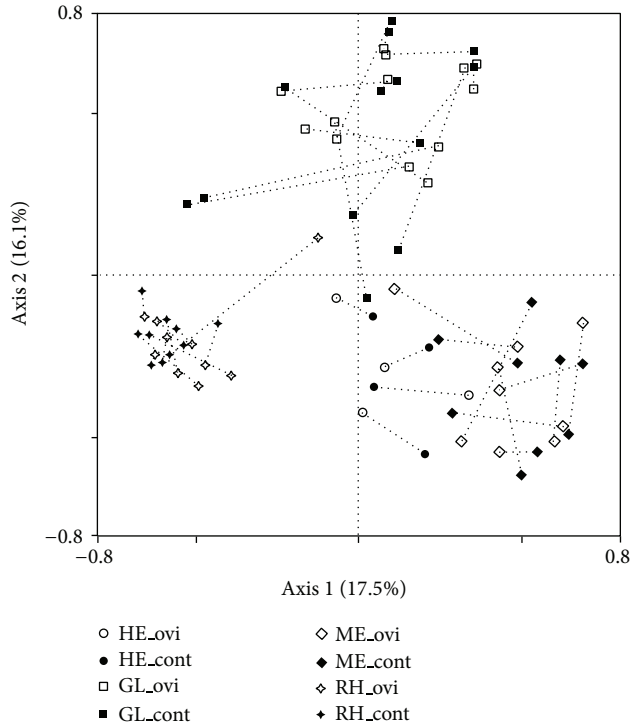


FIGURE 5: Ordination of vegetation on the oviposition sites and on the corresponding control plots with a radius of 20 cm. The first and second axes explain 17.5% and 16.1% of total variation, respectively. Oviposition site (ovi) and the corresponding control plot (cont) are connected by a dotted line (PCoA based on Bray-Curtis dissimilarities, with prior square root transformation of plant species cover). The acronyms of the study sites are explained in Table 1.

and (ii) direct contact with wet plant material as the main cause of delayed drying. Therefore, we conclude that tall-growing vegetation anywhere near an oviposition site might jeopardize egg survival and development. In addition, low-growing vegetation may reduce shading and, thus, lead to a warmer microclimate at the oviposition site which, in turn, will foster the development of the eggs.

To our knowledge, no data regarding the characterization of oviposition sites of *L. coccajus* in nonperipheral populations are available. It would be an interesting research topic to evaluate differences in oviposition site demands between peripheral and nonperipheral populations.

**4.4. Floristic Richness and Composition.** Even though fewer vascular plant species were detected on oviposition sites than on the adjacent control plots (an average of 7.2 versus 8.9 species per circular plot with a radius of 20 cm,  $P < 0.01$ , Wilcoxon signed-rank test), no clear differences in species composition were found. Moreover, none of the calculated indicator values was different between oviposition sites and control plots. However, based on the rather small size of the relevés, this result should not be overemphasized.

On the other hand, there were marked differences in floristic composition among the four study areas indicating

that different types of vegetation are used for oviposition. PCoA-ordination revealed three distinct clusters, a first cluster encompassing the vegetation relevés from the two study areas with trees and/or shrubs (Hessenberg, Merishausen), a second cluster corresponding to those from the completely open near-to-natural semidry grassland (Rheinheim), and a third cluster representing the relevés from the dry artificial roadside verge (Glattfelden). Inside the clusters, there was also no clear separation between oviposition sites and control plots. Consequently, we presume that floristic composition plays only a marginal role in the selection of oviposition sites. At a larger scale, however, floristic composition may be important since it has repeatedly been shown that floristic and invertebrate richness are closely related, for example, by Schaffers et al. [47] or Haddad et al. [48]. And for *L. coccajus* an ample supply of suitable prey is essential since both the larvae and the imagines are carnivorous.

**4.5. Practical Conservation Measures.** *L. coccajus* may be favoured by (i) improving and enlarging suitable existing habitats and (ii) by creating new habitats. Regarding habitat improvement, we may distinguish between large-scale and small-scale measures. The principal large-scale measure is to postpone mowing until after hatching, for example, in Northern Switzerland to the beginning of August [26, 49]. Among the small-scale measures, creation of suitable oviposition sites is suggested, for example, by removing the humus layer on patches with a diameter of about half a meter and/or by cutting selected shrubs or trees to reduce shading [14]. Another potentially suitable measure could be extensive grazing [50, 51].

As secondary habitats for *L. coccajus*, gravel pits or quarries seem to be promising since (i) they are not subjected to agricultural use, which often leads to clutch damage [26, 49], and since (ii) they provide the sparse vegetation highly suitable for oviposition. However, creation and active colonisation of new habitats should be performed only in the context of a broad species conservation program to assure connectivity among the newly established populations. In the Canton of Zurich (Switzerland), such a program has been started in 2010, and first (unpublished) results suggest that colonisation of abandoned gravel pits has been successful.

Since semidry grasslands are particularly species-rich and highly threatened throughout Switzerland [52], all the above-mentioned measures need to be carefully planned and properly monitored with regard to both *L. coccajus* and its habitat, namely, the vegetation. As shown by Wolf [9], *L. coccajus* shows highly fluctuating population sizes and long-term monitoring is a precondition to correctly evaluate and subsequently optimize the implemented conservation measures.

## 5. Conclusions

Firstly, the present study illustrated how demanding it is to identify the actual limiting site factor which, in turn, is the prerequisite for designing and implementing successful conservation measures. Obviously, both suitable general



microclimatic conditions and suitable oviposition sites are essential for the long-term survival of the highly thermophilic *L. coccajus*, north of the Alps. Regarding the oviposition sites themselves, however, not a dry and warm microclimate or a specific floristic composition of the vegetation seems to be crucial but rather minimal risk of contact between egg clutch and adjacent vegetation. The latter may be achieved by selecting for oviposition an isolated, 20 to 30 cm tall stem of a fairly sturdy plant growing either in a gap in the vegetation or on a patch of very low-growing vegetation. In both cases, contact with adjacent vegetation is largely excluded, mitigating substantially the risk of damage to the eggs resulting from delayed drying after rainfall or morning dew. Usually, such microhabitats tend to be particularly sunny and warm, which further promotes quick drying and egg development. At and around oviposition sites of *L. coccajus*, cover and composition of the vegetation may vary greatly, but its architecture or spatial structure needs to follow fairly stringent rules. About the larval habitat of *L. coccajus*, only little is known up to date [7, 9, 18, 24, 25].

Secondly, the present study indicates that it is possible to successfully create secondary habitats for *L. coccajus*, as shown by a road verge in one of our study areas where a habitat was artificially established approximately 30 years ago. Taking into account the above-mentioned characterization of oviposition sites, it is evident that other artificial habitats such as abandoned gravel pits and quarries may also provide suitable oviposition sites for *L. coccajus*.

## Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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