Influence of spreading woody plants and surface cover on the distribution of *Calliptamus italicus* and *Oedipoda caerulescens* (Saltatoria, Caelifera) in a steppe habitat

ABSTRACT

The Rottensand is a nature reserve located alongside a braided alpine river in Valais (CH). Due to the prevention of flooding by dams, pine forest is spreading and fragmenting the xeric steppes. We investigated the influence of surface cover and the shading by trees on egg-laying sites and on the distribution of larvae and adults of *Calliptamus italicus* and *Oedipoda caerulescens*. The abundance of *C. italicus* was more than two times higher than that of *O. caerulescens*. Both species preferably laid their oothecae in places with little shadow and medium to low vegetation cover. Both species always avoided shrubs and trees. In both species areas with low grass coverage were more preferred by early instars than by late instars and adults. *O. caerulescens* needs much bare soil (75-100% of the surface) whereas *C. italicus* prefers areas with a mosaic of bare soil and moderate to high grass coverage (50-75% of the surface). By capture-recapture method we showed low dispersal in both species and that larvae have lower dispersals than the adults. In conclusion, at the study site both species are threatened by the spreading pine forest and *O. caerulescens* additionally by a receding percentage of bare soil.

TABLE OF CONTENTS

1. INTRODUCTION

The nature reserve Pfynwald (Central Valais, CH) is located in an inner alpine valley, therefore it is one of the warmest and driest regions in Switzerland. The reserve offers several habitats with different microclimata (BILLE & WERNER 1986), such as the largest pine forest (*Ononido-Pinion*) in Central Europe (WERNER 1985) and unique xeric steppes (*Stipo-Poion*). Therefore it features an exceptional biological diversity.

The Rottensand, a part of the Pfynwald, borders on one of the last remaining braided sections of an alpine river (Rhône) in Switzerland. After a severe flood in 1860 the construction of dams along the river began (BILLE & WERNER 1986). In the 1960's the last dams were finished and the former floodplain Rottensand was completely separated from the riverbed. As a result the once dominating steppe areas decreased while pine (*Pinus sylvestris*) forests increased (WERNER 1985).

The spreading pine forest fragments the steppes. Habitat fragmentation impedes gene flow or even prevents it (WITH et al. 1999). RÖSER (1990) showed that the invasion of wood into a xeric steppe renders this habitat unattractive for Caelifera species (less bare soil, shading). According to SÄNGER (1977) the spatial structure is a crucial factor for the preference of habitats in Saltatoria. Due to the absence of flooding the steppes must be kept open by a controlled management. It is the long-term aim to bring back the alluvial dynamic while not endangering the steppe areas (pers. comm. ZETTEL).

For a successful habitat management an exact knowledge of the demands of the concerned species is needed. The research group of J. Zettel has done several investigations with the aim to provide a basis for management plans for the Rottensand. So far these investigations covered ants (GROSSRIEDER & ZETTEL 1999, KELLER & ZETTEL 2002), digger wasps (ZEHNDER & ZETTEL 1999), wild bees (LOEFFEL et al. 1999), grasshoppers (MÜLLER & ZETTEL 1999, HOLDEREGGER 1999, WUNDER 2001, MÜHLHEIM 2002) and true bugs (WITSCHI & ZETTEL 2002).

The Rottensand hosts a number of stenotopic and xerothermophilic grasshopper species (MÜLLER & ZETTEL 1999) being mentioned in the Red List by NADIG & THORENS (1994). Therefore the Rottensand is an important habitat for endangered grasshoppers in Switzerland. Grasshoppers show conspicuous bonds to certain habitats, thus being good indicators for their condition (BROCKSPIEPER 1978).

As the demands may change during development, investigations on egg-laying sites and on every developmental stage are necessary. Furthermore larvae mostly show more definite habitat preferences being more suitable therefore for determination of a species' preferences than the more vagile adults (DETZEL 1998). According to SÄNGER (1977) a lot of grasshopper species' larvae were bond to different habitats than the adults.

According to WUNDER (2001), who covered the same site in her investigations, adult *C. italicus* avoided woody plants and dense grass vegetation. In Rottensand the temperature on the surface dropped by 30 °C within ca. one hour after becoming shaded by a nearby tree (MÜHLHEIM 2002). Furthermore *C. italicus* showed significantly lower frequencies in the strongly fragmented steppe area in the eastern part of the Rottensand than in the more open steppes (MÜLLER 1999).

The present study is a continuation of the investigation of WUNDER (2001), who studied the distribution of adults of several grasshopper species on the same study site. We investigated the influence of the shading by trees and the surface cover on the distribution of the oviposition sites, the larvae and the adults of the Caelifera species *Calliptamus italicus* and *Oedipoda caerulescens*. These two species are typical for the xeric steppes of Rottensand (MÜLLER & ZETTEL 1999, HOLDEREGGER 1999, WUNDER 2001).

In summer the females of these two species lay their eggs into the soil. The eggs hibernate and undergo a compulsory diapause (UVAROV 1966, INGRISCH & KÖHLER 1998). Most of the adults, however, die during the first frosts. After winter the development of the embryos proceeds and the larvae hatch from end of April onwards (DETZEL 1998).

We examined the following hypotheses:
- *C. italicus* and *O. caerulescens* show a clumpy distribution on the study site.
- Both species avoid dense grass vegetation and long shaded areas.
- *C. italicus* and *O. caerulescens* have different habitat preferences.
- The larvae have the same habitat preferences as the adults.
- Adults are more mobile than larvae.

2. MATERIAL AND METHODS

2.1. Study area

The nature reserve Pfynwald is located 560 m a.s.l. in Central Valais (CH), between Susten and Sierre. The climate is dry and hot in summer and cold in winter. ZEHNDER & ZETTEL (1999) give a detailed description of the area.

The study area was situated in a xeric steppe (*Stipo-Poion*, DELARZE et al. 1999) and measured 2450 m^2 comprising a mosaic of diverse surface covers and being surrounded by forest. Moreover, it hosts a large population of *Calliptamus italicus* and *Oedipoda caerulescens* (WUNDER 2001).

We laid a 5x5 m grid over this steppe. The study area covered 98 squares (Fig. 1) providing plots with different surface covers and different times and durations of shading. Squares completely covered with woody plants were excluded because no grasshoppers were expected. To delimit the plots we marked the corners with tent pegs before the hatching of the first larvae, i.e. between mid and end of April (MÜHLHEIM 2002). The plots were numbered as follows: first number = row, second number = column (e.g. • 4 in Fig. 1 is located in square 8.10.).

The following parameters were investigated:
- Distribution of oothecae, larvae and adults
- Shadow and its influence on the temperature
- Surface cover
- Dispersal of larvae and adults

2.2. Shadow and its influence on soil and surface temperature

On a cloudless day, we monthly (30.4., 30.5. & 4.7.02) drew the shadow margins at 7:30 h and 17:45 h on a map.

We chose four spots for temperature measurements, which differed in the daily shading periods (Tab. 1); their localisation is shown in Fig. 1.

Tab. 1: Occurrence of shadow (yes or no) on the four measurement spots 1-4 (Fig. 1) at 7:30 and 17:45.

	spots			
time	1 M_{me}	2 M_m	3 M_e	4 M_0
7:30	yes	yes	no	no
17:45	yes	no	yes	no

Two thermologgers Grant-Squirrel SQ-1000 (each with four probes) were used for the temperature measurements at 5 min intervals. At each measurement spot we dug a hole of 10 cm in diameter and 8 cm in depth being refilled with the same kind of sand providing an equal soil quality. One probe was installed in 5 cm depth and one on the surface. The measurements started on July 1st 2002 and for analysis we considered data until the end of October 2002.

We calculated the duration of insolation and the average time above the temperature threshold for oviposition (being 23.5 °C, SAMIETZ & KÖHLER 1998).

2.3. Surface cover

Every plot was mapped individually before the hatching of the first larvae. We estimated the %-cover of the habitat variables moss, woody plants, grass (height <10 cm and >10 cm), herbs (height <10 cm and >10 cm), sand, humus, stones and dead wood in five categories: 0-5 %, 5-25 %, 25-50 %, 50-75 % and 75-100 %.

Data analysis was carried out only with three variables: grass, moss/bare soil and woody plants. The other parameters recorded showed a coverage too low to have an influence on grasshopper distribution. Because sand, humus and stones were represented in negligible quantities, they were pooled together with moss to the category bare soil, which could also be termed as "surface free of grass and herb vegetation. Grass with a height <10 cm was very rare, therefore we equated grass > 10 cm as grass.
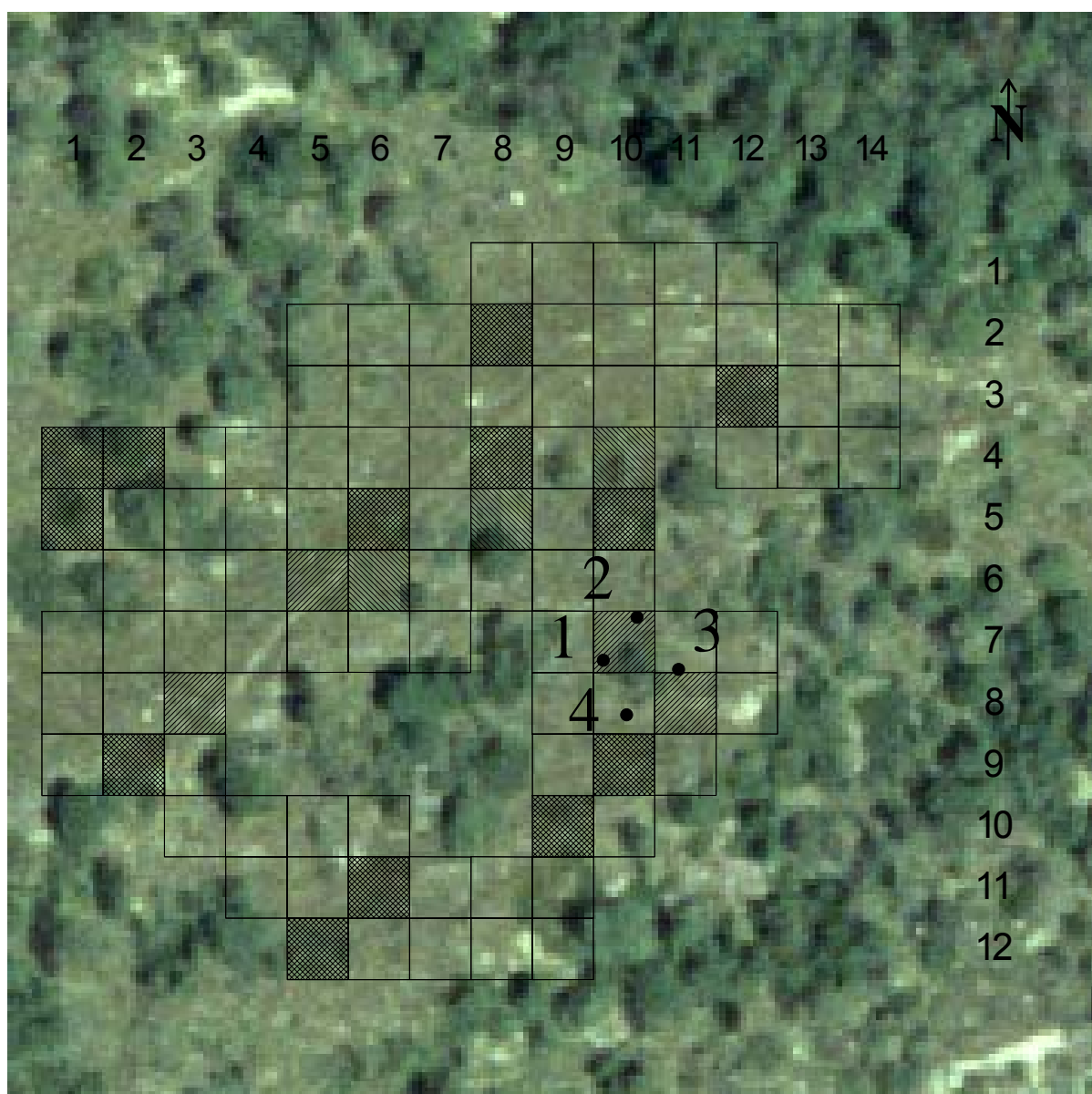
Fig. 1: Study site with 98 5x5 m plots. Vertical numbers: row numbering, horizontal numbers: column numbering. ●: Position of four thermologger-probes. Plots of marking of each species:

C. italicus   *O. caerulescens*   *C. italicus & O. caerulescens*

2.4. The distribution of oothecae, larvae and adults

Due to the reduced mobility of the first instar larvae, their distribution matches more or less that of the oothecae (DETZEL 1998).

We scanned a plot while walking slowly five loops covering the whole surface. We startled the animals by moving the foot slowly from one side to the other and caught them with a dip net; specimens of the two studied species were put individually in perspex tubes, other species were released immediately. The tubes were stored in a cold box to protect the animals from heat. For sex determination as well as for measuring the hind femur and the pronotum the animals were transferred into a spipot (ROBERTS 1995). The examination was carried out with a magnifying glass (8x) containing a scale in tenth of millimetres. The **determination of the instars** was made after CARRON (1994), THORENS (1991) and PICHLER (1956). The last two instars could definitely be separated according to the wing pads' length after their reversal. Finally, all larvae were released in the middle of the scanned plot. The sampling was carried out five times between mid May and end of July 2002 (Tab. 2). The sampling always started at plot 1.8 (Fig. 1) and went on in loops through the rows (1.8-1.12 then 2.14-2.5 etc.). We tried to sample the squares at regular intervals; this was not possible, however, due to varying weather conditions and varying time needed for measurements and marking (Tab. 2). Because we never caught an adult *Oedipoda germanica* (whose larvae cannot be distinguished from those of *O. caerulescens*), we assumed that all larvae caught belonged to *O. caerulescens*.

The **data analysis** was carried out separately for each developmental stage. We tested the distribution with the Variance-Mean Ratio Test for Clumped Distribution (KREBS 1989).

For a visual illustration of the distributions, we categorised the frequencies per plot as follows: 0 catches, 1-3 catches, 4-8 catches, 8-12 catches and >12 catches. These categories were plotted (with GIS-program Idrisi 32.1) on a map of the study area.

Tab. 2: The time periods of the 5 samplings

sampling	1	2	3	4	5
time period	14.05. - 22.05.02	27.05. - 12.06.02	17.06. - 05.07.02	08.07. - 22.07.02	22.07. - 25.07.02

2.5. Shadow and its influence on the distribution

In order to investigate the influence of shading on the occurrence of each developmental stage of the studied species, we superimposed the distribution maps with these shadow maps drawn during the occurrence of the studied group. We visually correlated the distribution with absence/occurrence of shadow. As the precise localisation of individuals within a plot was not recorded a statistical analysis was not reasonable.

2.6. Surface cover preferences

We tested our null hypothesis - the use of each habitat variable in proportion to its availability - using the χ^2-goodness of fit (NEU et al. 1974, BODURTHA et al. 1989). Each developmental stage of both species was tested separately. If the null hypothesis had to be rejected for a particular category, we checked selection for that category by using a modification (MESING & WICKER 1986, TODD & RABENI 1989) of STRAUSS' (1979) linear index of food selection:

$$L = r_i - p_i$$

L being the habitat selection value, r_i the percentage use of category i (i.e. number of catches within category i divided by the total number of catches of this larval instar or adults), and p_i representing the percent availability of category i (i.e. number of plots with category i divided by the total number of plots (98)). Values of habitat selection (L) range from +1 to -1; positive values indicate habitat selection, negative values indicate habitat avoidance and values of zero indicate random use of that variable within the study site.

2.7. The dispersal of larvae and adults

The procedures were the same as described in chapter 2.4., but the animals were marked before being released. The larvae were marked with one or two triangle shaped cuts at the hind edge of the pronotum (Fig. 2). Such a marking endures several ecdyses (GANGWERE et al. 1964). Only the last two to three instars could be marked because the risk of a severe injury within the first instars was too high. The adults were marked on the pronotum with dots of acrylic colour (Humbrol). Individuals cut-marked as larvae were not marked again.

All animals caught on one marking plot got the same tag, which allowed us to assign a recapture to its plot of marking. Due to the limited pattern possibilities for the cut marking, we marked animals only on 14 (*C. italicus*) and 15 (*O. caerulescens*) plots (Fig. 1). Choice criteria for these plots were sufficient number of individuals and different surface cover. Because the animals could not be marked individually, the time between capture and recapture was unknown.

For the recaptured individuals, we calculated the average distance between the recapture plot and the origin plot (= distance between the two plot centres) being categorized as: 0 m, 5 m, 6-10 m, 11-15 m, 16-20 m and >20 m. The frequency of each category was counted per species and marking-group (colour-marked adults, adults being cut-marked as larvae and cut-marked larvae). The differences between the three groups within one species were tested against each other by comparing them pairwise for independence with contingency tables (PÉLADEAU 1996).

Fig. 2: *O. caerulescens*, L5 ♀, freshly marked with two cuts on the left side of the pronotum.

3. RESULTS

3.1. Shadow and its influence on soil and surface temperature

a) 23.07.2002
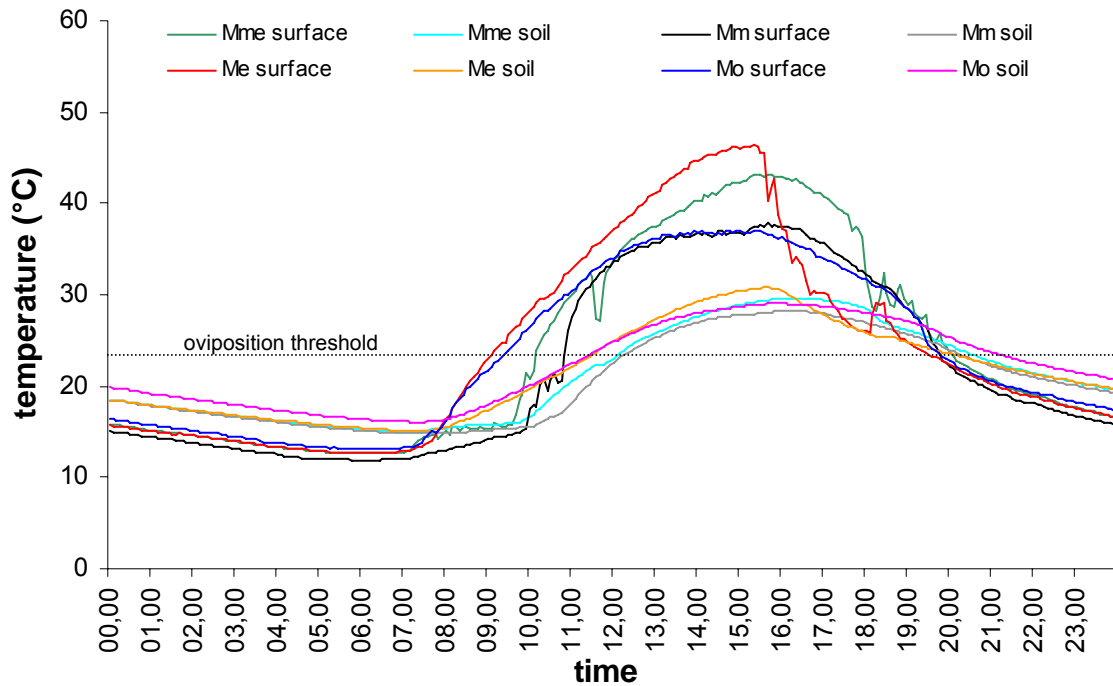
b) 17.08.2002
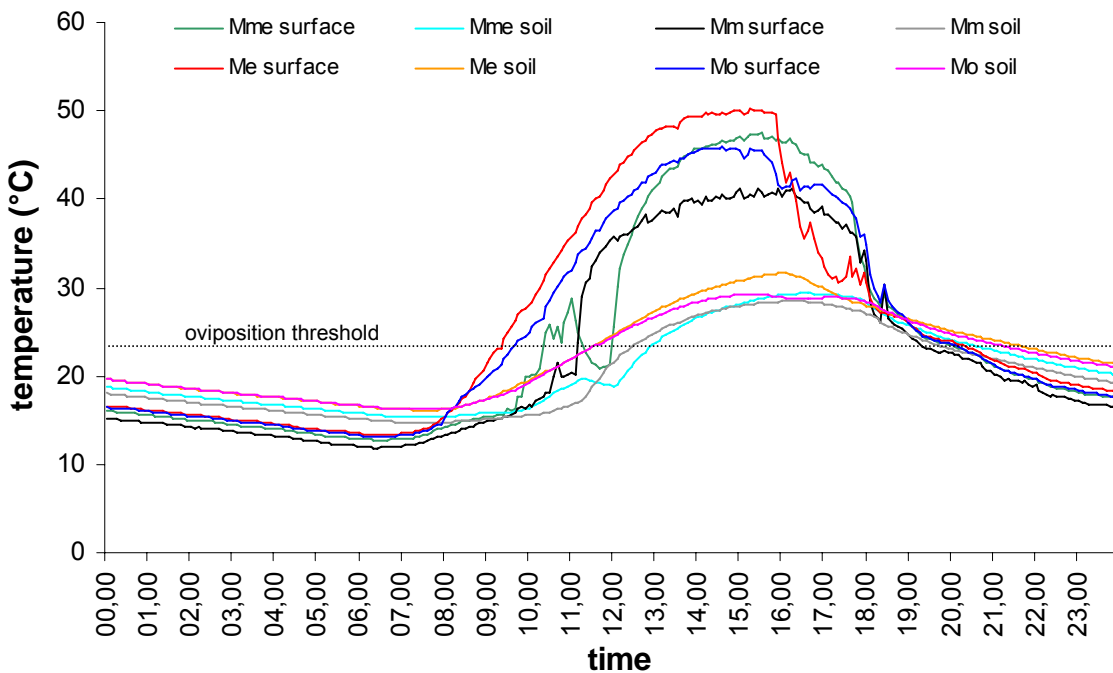
Fig. 3 a-d: The temperature pattern at four measurement spots on the surface and in the soil (5 cm) on one bright day in July (a), August (b), September (c) and October (d). M_{me}: morning and evening shadow, M_m: morning shadow, M_e: evening shadow, M_0: no shadow (Localisation see Fig. 1). Oviposition threshold = 23.5 °C (SAMIETZ & KÖHLER 1998). Continued next page.

c) 18.09.2002
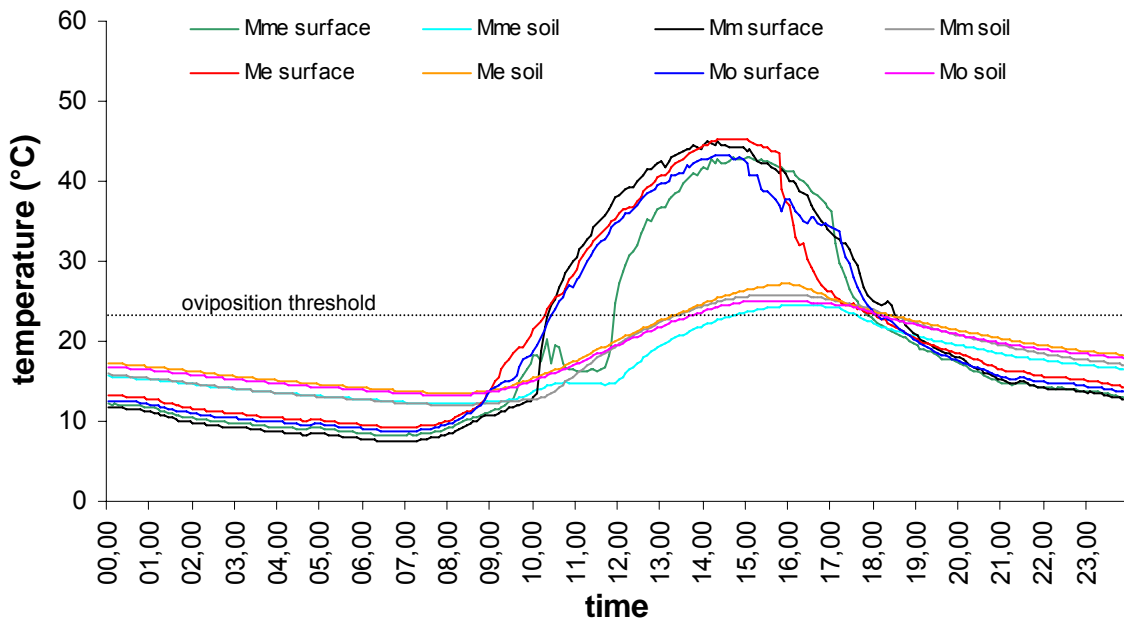
d) 13.10.2002
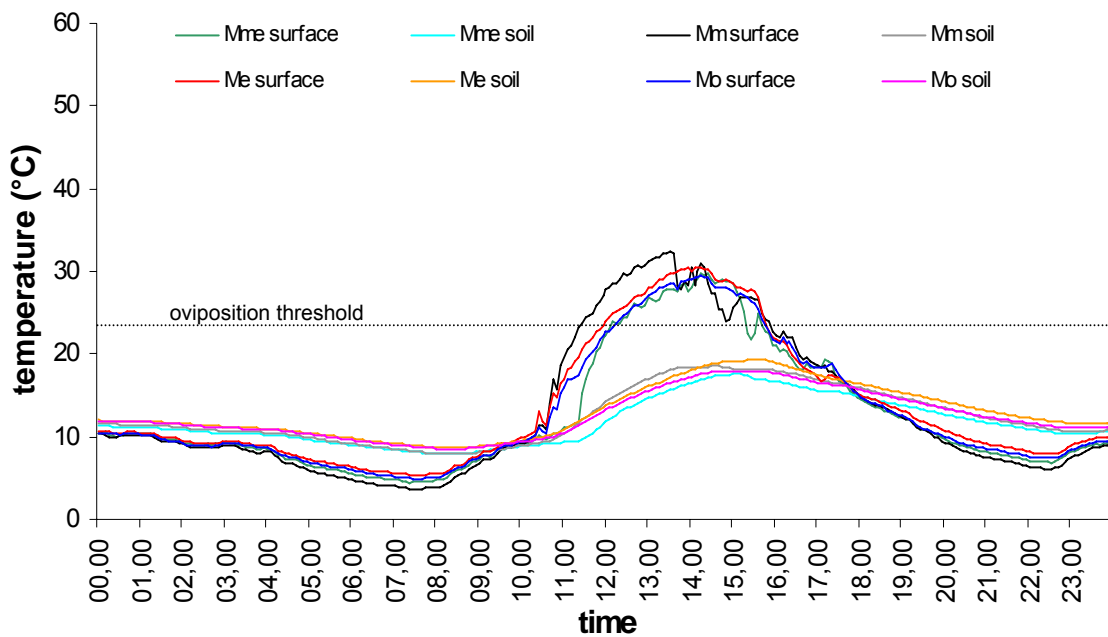
Fig. 3 a-d: (continued). The temperature pattern at four measurement spots on the surface and in the soil (5 cm) on one bright day in July (a), August (b), September (c) and October (d). M_{me}: morning and evening shadow, M_m: morning shadow, M_e: evening shadow, M_0: no shadow (Localisation see Fig. 1). Oviposition threshold = 23.5 °C (SAMIETZ & KÖHLER 1998).

The temperature course differed between the measurement spots as well as over time. The daily temperature pattern in the soil was more constant than on the surface (Fig. 3 a-d). Due to different shadow periods, the temperature rise in M_{me} and M_m was delayed in comparison to M_e and M_0; for the same reason M_e had an earlier temperature decline than the other three spots in the evening.

The maximal soil temperature in M_{me} seldom reached the values of the other three spots. The soil temperatures at the four spots differed 5 °C at most in July and became more and more equal until October. The highest surface temperatures were measured in M_m (62.7°C) and M_e (62.4°C), followed by M_0 (59.35°C) and M_{me} (59°C).

Tab.3: The insolation time per day and the average number of hours (h) per day, during which the temperature on the surface was above the oviposition threshold (23.5 °C, SAMIETZ & KÖHLER 1998), for the four measurement spots and two time periods. M_{me}: morning and evening shadow, M_m: morning shadow, M_e: evening shadow, M_0: no shadow.

measuring spot	M_{me}	M_m	M_e	M_0
insolation time (h)				
July - August	7.5-8.5	9-10	8.5-10	11-12
September - October	5.5-7.5	7-8.5	4.5-7.5	6-8
average time per day above oviposition threshold (h)				
July - August	7.67	7.54	8.32	8.68
September - October	2.72	3.21	2.98	2.89

From July to October the photoperiod became shorter (Tab.3), resulting in lower temperatures (Fig. 3 a-d). The insolation times as well as the times with temperatures suitable for oviposition were influenced by the duration of shading (Tab.3). In the first period (July-Aug.) M_0 had on average 4.5 hours more sunshine than M_{me} and two hours more than M_m and M_e. From September to October, in contrast, the duration of exposition to the sun was more or less equal at all four spots, due to the lower elevation of the sun causing more shadow from the surrounding forest.

In the early egg-laying period (July-Aug.) the temperature stayed more than twice as long above the threshold for oviposition than in the following time period (Sept.-Oct.). In July and August 50 to 70 minutes more time was available for oviposition (T ≥ 23.5 °C) on M_e and M_0 compared to M_{me} and M_m, in September and October the difference was reduced to less than 30 minutes.

In the morning (7:30) between 25 % (July) and 40 % (October) of the study site were shaded, while only between 10 % (July) and 15 % (October) in the evening (17:45) (Appendix 1-3). Ca. 5 % of the study site were shaded at both times. One contiguous area was shaded neither in the morning nor in the evening.

3.2. Surface cover

More than half of the plots had a **moss** cover between 25 and 50 % and none were dominated by moss (Tab. 4, Appendix 4).

The dominating **grass** species was the tall *Stipa pennata*. Most of the plots had a grass cover between 5 and 75 % (Tab. 4, Appendix 4) particularly long shaded plots had a grass cover of more than 50 %.

Half of the plots were not or only little covered with **woody plants** (Tab. 4). We considered only the woody plants within the plot, but not those at the periphery. Shrubs were mainly young *Pinus sylvestris*, *Berberis vulgaris* and *Hippophaë rhamnoides* and trees were mostly *Pinus sylvestris*.

Herbs were evenly distributed covering between 0 and 25 % of the surface; no species was dominating.

Tab. 4: The relative abundance for each category of the three surface cover variables: grass, moss/bare soil and woody plants (bold = most frequent categories of one variable, n = 98 plots).

	0-5 %	5-25 %	25-50 %	50-75 %	75-100 %
grass	0.12	**0.28**	**0.35**	0.20	0.05
moss / bare soil	0.03	0.27	**0.57**	0.13	0.00
woody plants	**0.51**	0.21	0.14	0.09	0.03

3.3. Larval instars and phenology

In *C. italicus* the females ran through six and the males through five instars, whereas in *O. caerulescens* both sexes ran through five instars (Fig. 4 a-d). First instar larvae of both species were observed from the beginning of the investigation (01.05.02). The first adults were caught from 26.06.02 onwards.

a) *C. italicus* ♀♀   b) *C. italicus* ♂♂

c) *O. caerulescens* ♀♀   d) *O. caerulescens* ♂♂

post femur length (mm)
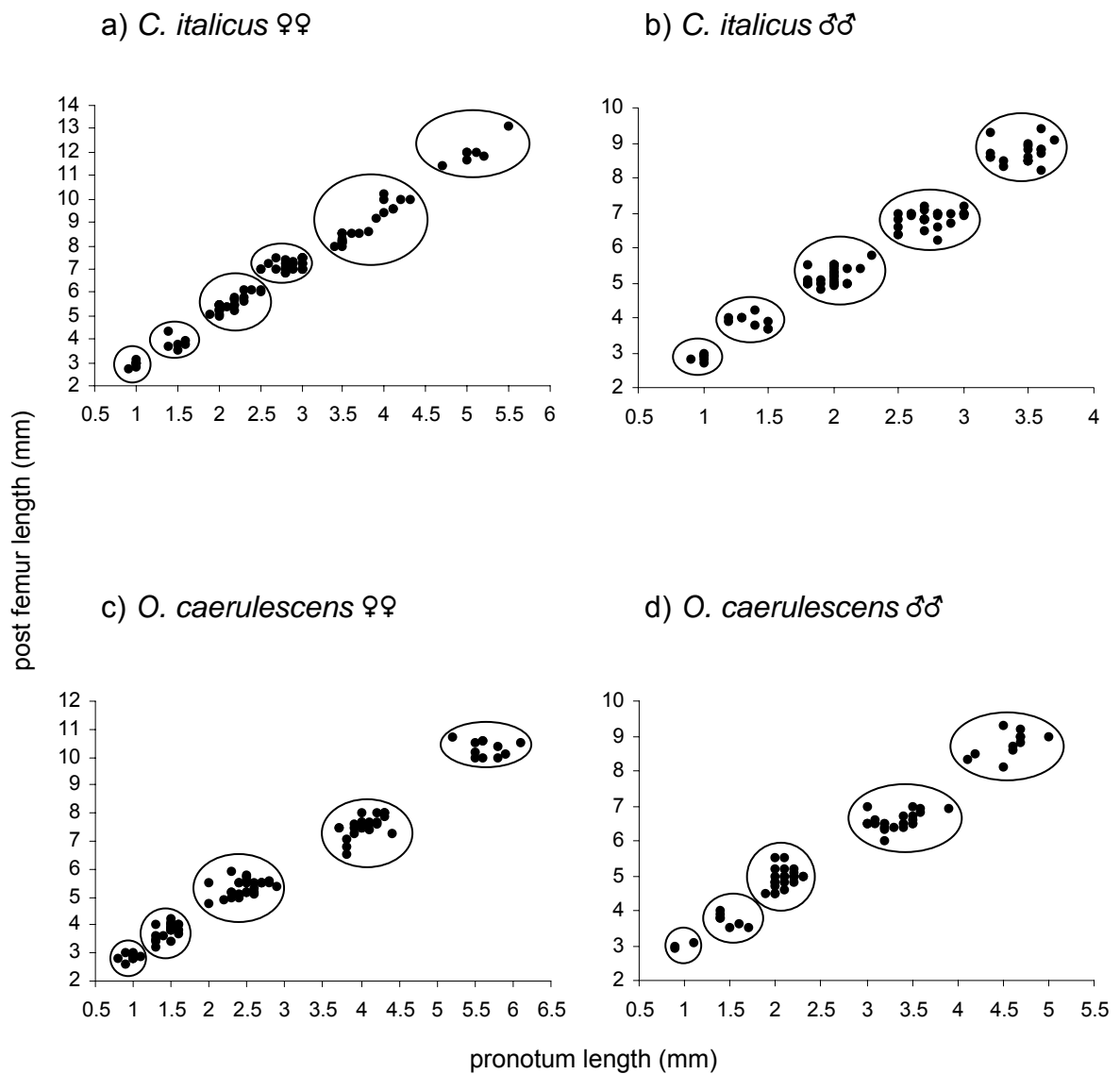
pronotum length (mm)

Fig. 4 a-d: Correlation between the lengths of the pronotum and of the femur. The black ellipses represent the different larval instars in both sexes.

The number of caught L1 of both species was quite similar (Tab. 5), but in total we caught twice as much *C. italicu*s than *O. caerulescens*, which indicates that the former species was more frequent on the study area. The number of catches per instar decreased from L1 to L3/L4 in both species, but then increased again.

Both species showed a hatching asynchrony within oothecae, as described by INGRISCH & KÖHLER (1998).

Tab. 5: Number of catches per instar and species.

	L1	L2	L3	L4	L5	L6	Adult	Total
C. italicus	291	178	147	167	474	268	645	2170
O. caerulescens	261	121	105	96	203	---	143	929

3.4. The distribution of oothecae, larvae and adults

Larvae and adults of both species were distributed clumpy on the study site (p < 0.001 for all developmental stages of both species). The distribution of oothecae can be considered to be the same as that of the L1. Both species showed high hatching rates on plot 10.9. (Fig. 5a & 6a).

In both species the distribution changed from instar to instar and more plots became colonised with growing age (Fig. 5 & 6). Larvae and adults of *C. italicus* colonised far more plots than those of *O. caerulescens*. Both species avoided plots bordering on wood in the east or west and preferred plots in the open steppe.

C. italicus

First instar larvae were most abundant on the plots 1.8., 3.7., 7.1. and 10.9. (Fig. 5 a). Most of the early instars could be found on plots that were in the open steppe (e.g. 4.6., 4.7., 5.6. or 6.5.) and the abundance of L1 near wood (especially such bordering the plot in the west or east) was very low or zero (Fig. 5 a-d). L5, L6 and adults stayed also near wood and in places with dead wood (6.10., 11.6., Fig. 5 e-g). The instars L2 - L4 were distributed more evenly than older ones, but this might be due to the low number of catches.

O. caerulescens

First instar larvae were most abundant on the plots 3.8., 3.9., 3.12., 3.13., 8.9. and 10.9. (Fig. 6 a). The older instars were found on fewer plots with total catches rarely exceeding eight individuals (Fig. 6 b-f). The adults were distributed more evenly than the larvae, the catch-frequencies per plot of all instars exceeded eight catches only on 10.9. (Fig. 6 f). All developmental stages avoided plots bordering on wood in the east or west.

18

a) L1
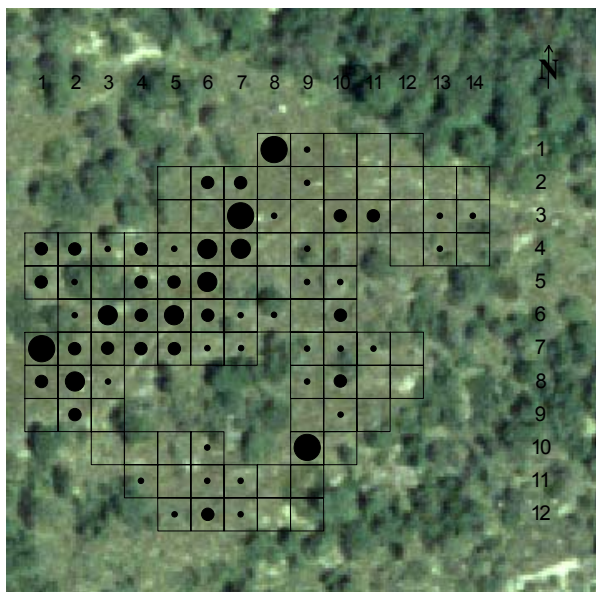
b) L2
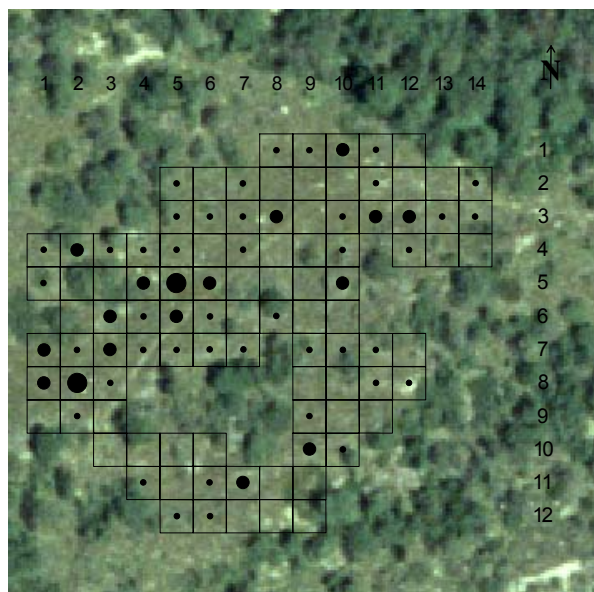
c) L3
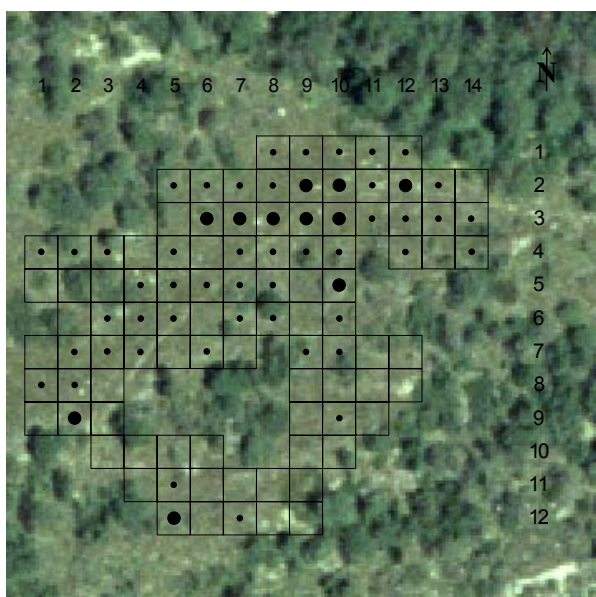
d) L4

Fig. 5 a-g: Distribution of each developmental stage of *C. italicus* on the study site.

Continued on next page.

Number of catches: ☐ 0   ⊡ 1-3   ● 4-8   ● 9-12   ● >12

e) L5

f) L6
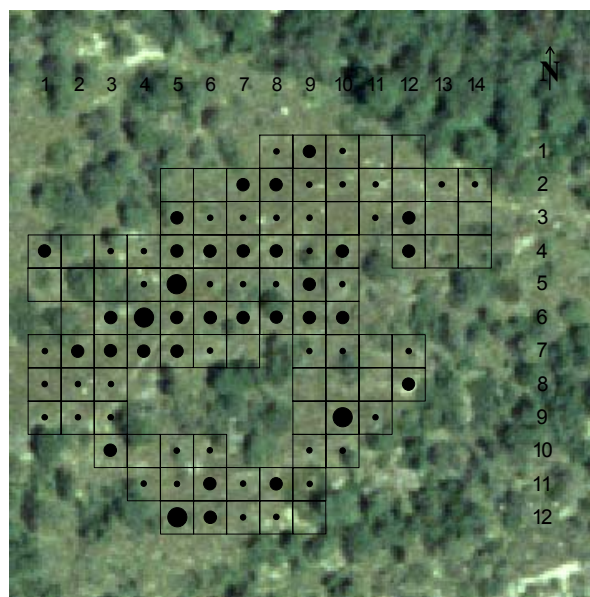
g) adult
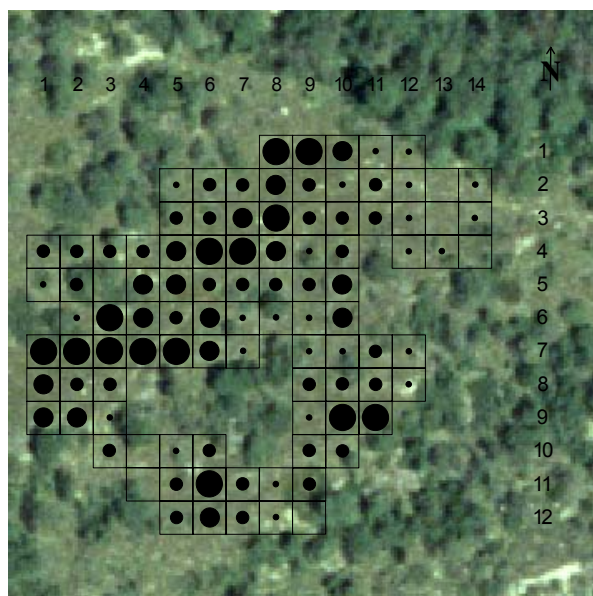
Fig. 5 a-g: Distribution of every developmental stage of **_C. italicus_** on the study site (continued).
Number of catches: ☐ 0   ⊡ 1-3   ⬤ 4-8   ⬤ 9-12   ⬤ >12

a) L1
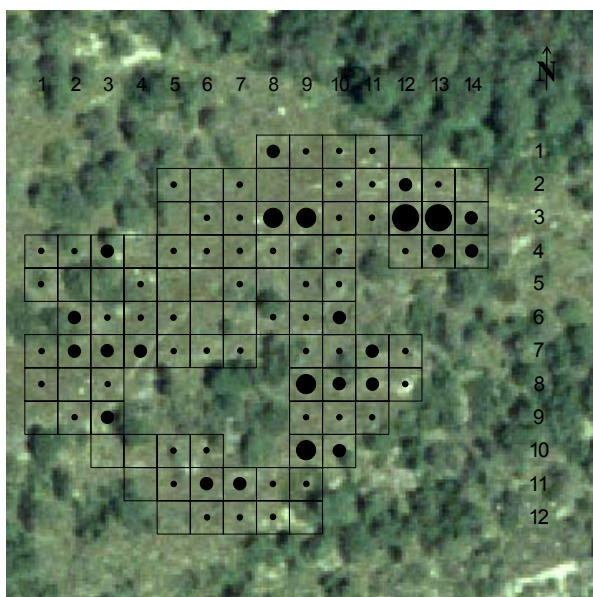
b) L2
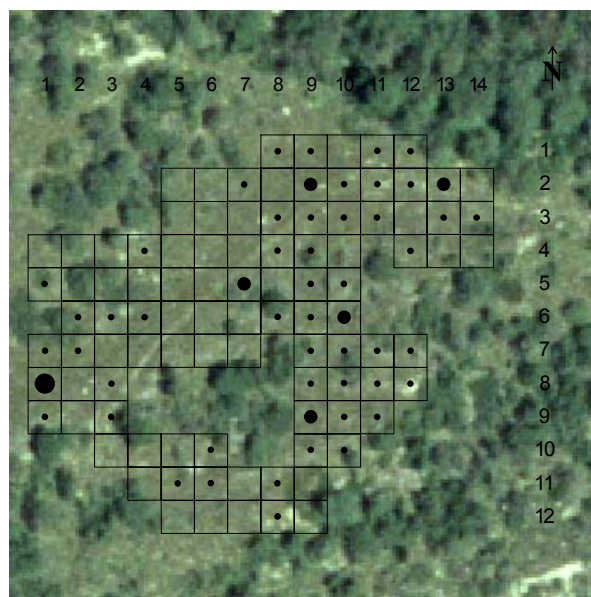
c) L3
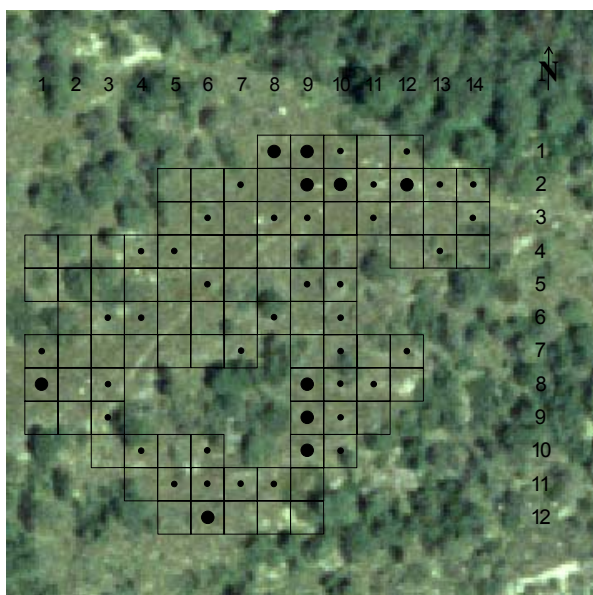
d) L4

Fig. 6 a-f: Distribution of each developmental stage of **O. caerulescens** on the study site.

Continued on next page.

Number of catches: ☐ 0   ▪ 1-3   ● 4-8   ⬤ 9-12   ⬤ >12

e) L5
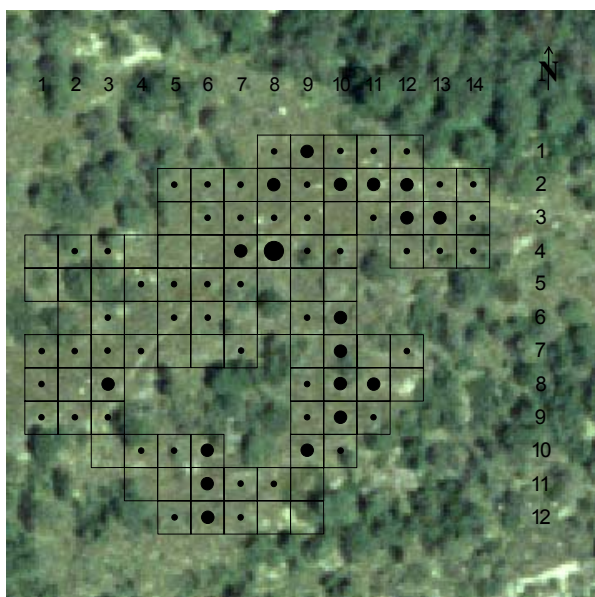
f) adult
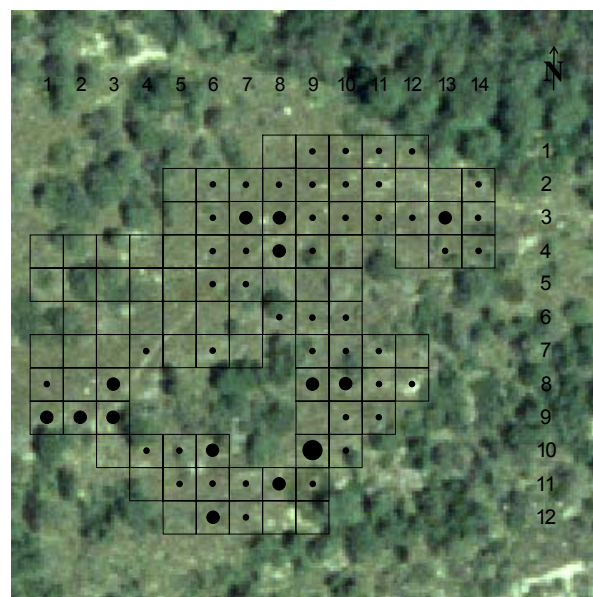
Fig. 6 a-f: Distribution of every developmental stage of *O. caerulescens* on the study site (continued).

Number of catches: ☐ 0 ▪ 1-3 ⚫ 4-8 ⬤ 9-12 ⬤ >12

3.5. Shadow and its influence on the distribution

The plots with several L1-catches of one or both species (>8 catches, e.g. *C.italicus*: 3.7., 4.7., 7.1.) had little shading, while plots with longer shading times had only few individuals (≤ 3, e.g. *C.italicus*: 1.11., 2.5., 10.4.)(Figs. 5 & 6, Appendix 1-3). However, there were plots with short shading periods and only few catches. The results were the same for the subsequent developmental stages in both species.

We rarely caught adults or late larval instars of both species directly in the shadow; nevertheless we found them on some plots becoming shaded in the morning and/or in the evening.
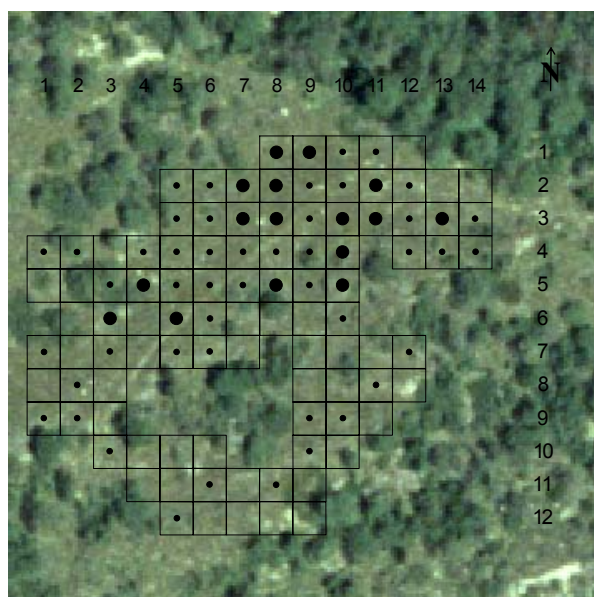
Plot 10.9 provided lots of catches of both species and had long shading periods (Figs. 5 & 6, Appendix 1-3); but besides the shadow the surface cover was another important criteria (Chapter 3.6.).

3.6. Surface cover preferences

C. italicus

The preferred habitat type on the study site consisted of a moderate grass cover and no woody plants; moss/bare soil had no direct influence. However, *C. italicus* was also found in areas covered with a carpet of *Arctostaphylus uva-ursi* as well as in bushy herbs.

The larvae show selectivity respectively avoidance for two habitat variables (grass, woody plants) while using moss/bare soil randomly, the adults showed selectivity for all variables (Tab. 6). E.g. a third of all plots had a grass cover between 25 and 50 % (Tab. 4), yet between 40 and 50 % of the early instar larvae were restricted to these plots. Although plots with 75-100 % cover of woody plants comprised 3 % (Tab. 4), we obtained less than 0.6 % of all catches on these plots. We found at least 70 % of all L1 and L2 on plots with a cover of 0-5 % woody plants, which represented half of the plots (Tab. 4).

Tab. 6: Significance of the χ^2-goodness for selectivity of habitat variables (positive or negative) by *C. italicus* on 98 plots.

	L1	L2	L3	L4	L5	L6	adult
grass	***	*	***	***	***	***	***
moss/bare soil	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	*
woody plants	***	***	***	**	***	***	***

Plots with low grass cover (0-25 %) were avoided (L ≤ -0.0339, Tab. 7) by each developmental stage. But they preferred plots with 25-75 % (L ≥ 0.0519) grass cover and selected plots with 75 to 100 % randomly (0.0291 ≥ L ≤ -0.0061). A grass cover of 25-50 % was selected by the first four instars (L ≥ 0.0519), while L5 and L6 preferred plots with 50-75 % grass cover (L ≥ 0.0871). Adults were found almost exclusively on plots with grass cover between 25 and 75 % (L = 0.0438, 0.0796).

All developmental stages selected plots with the lowest portion of woody plants (0-5 %, L ≥ 0.1126), those with woody plants covering more than 5 % of the surface were either avoided or selected randomly (0.0073 ≥ L ≤ -0.1084).

Tab. 7 a-f: *C. italicus*: The habitat selection value L (MORRISSEY & GRUBER 1993) for the five cover categories of three habitat variables for each larval instar and the adults. Values range from +1 to -1; positive values indicate selection, negative values avoidance and values of 0 random selection of that variable. --: L was not calculated, because the corresponding group selected the variable randomly (Tab. 6). Bold: preference, underlined: avoidance.

a) **L1**

category	grass	moss / bare soil	woody plants
0-5 %	-0.0572	--	**0.1894**
5-25 %	-0.0968	--	-0.0305
25-50 %	**0.0895**	--	-0.0793
50-75 %	0.0365	--	-0.0494
75-100 %	0.0280		-0.0271

b) **L2**

category	grass	moss / bare soil	woody plants
0-5 %	-0.0719	--	**0.2143**
5-25 %	-0.0339	--	-0.0406
25-50 %	**0.0519**	--	*-0.0650*
50-75 %	**0.0600**	--	-0.0679
75-100 %	-0.0061		-0.0306

c) **L3**

category	grass	moss / bare soil	woody plants
0-5 %	-0.1020	--	**0.2070**
5-25 %	-0.0918	--	-0.0212
25-50 %	**0.1565**	--	-0.1084
50-75 %	0.0408	--	-0.0367
75-100 %	-0.0034		-0.0306

d) **L4**

category	grass	moss / bare soil	woody plants
0-5 %	-0.1045	--	**0.1126**
5-25 %	-0.0839	--	0.0073
25-50 %	**0.1022**	--	-0.0710
50-75 %	0.0594	--	-0.0140
75-100 %	0.0268		-0.0246

e) **L5**

category	grass	moss / bare soil	woody plants
0-5 %	-0.0676	--	**0.1290**
5-25 %	-0.0477	--	-0.0096
25-50 %	-0.0009	--	-0.0690
50-75 %	**0.0871**	--	-0.0117
75-100 %	0.0291		-0.0285

f) **L6 (females only)**

category	grass	moss / bare soil	woody plants
0-5 %	-0.0516	--	**0.1726**
5-25 %	-0.0628	--	0.0096
25-50 %	-0.0559	--	-0.0869
50-75 %	**0.1616**	--	-0.0545
75-100 %	0.0087		-0.0306

g) **adult**

category	grass	moss / bare soil	woody plants
0-5 %	-0.0651	-0.0089	**0.1565**
5-25 %	-0.0678	-0.0452	-0.0081
25-50 %	0.0438	0.0503	-0.0746
50-75 %	**0.0796**	0.0038	-0.0391
75-100 %	0.0094		-0.0244

O. caerulescens

The preferred habitat on the study site consisted of low grass cover, a high percentage of moss/bare soil and no woody plants.

The larvae and adults showed selectivity respectively avoidance for grass (except L2, L3), moss/bare soil and woody plants (except L2)(Tab. 8). 13 % of the plots showed a percentage of moss/bare soil of 50-75 % (Tab. 4), yet we obtained 22-28 % of all catches on such plots. In total only four (1x L1, 3x L5) individuals were caught on plots with a low cover (0-5 %) of moss/bare soil (= 3.1 % of the plots, Tab. 4).

Tab. 8: Significance of the χ^2-goodness for selectivity of habitat variables (positive or negative) by *O. caerulescens* on 98 plots.

	L1	L2	L3	L4	L5	adult
grass	***	n.s.	n.s.	**	**	***
moss/bare soil	***	**	***	***	***	***
woody plants	***	n.s.	*	***	***	**

An open grass cover (5-50 %) was preferred (except L2 and L3, Tab. 8), whereas one of more than 50 % was either avoided or randomly selected (Tab. 9). L1 (L = 0.1153) and L4 (L = 0.1412) preferred plots with a grass cover of 5 to 25 %. L5 and adults selected plots with grass covering 25-50 % of the surface (L = 0.1063 and 0.1146 respectively).

All developmental stages preferred a 50-75 % cover of moss/bare soil (L ≥ 0.0861). The L-values were highest with high moss/bare soil cover while plots with low cover were avoided.

All developmental stages except L2 (Tab. 8) selected plots with low (0-5 %) woody plants cover (L ≥ 0.0803, Tab. 9) and either avoided or randomly selected such with a higher cover.

Tab. 9 a-f: *O. caerulescens*: The habitat selection value L (MORRISSEY & GRUBER 1993) for the five cover categories of three habitat variables for each larval instar and the adults. Values range from +1 to -1; positive values indicate selection, negative values avoidance and values of 0 random selection of that variable. --: L was not calculated, because the corresponding group selected the variable randomly (Tab. 6). Bold: preference, underlined: avoidance.

a) **L1**

category	grass	moss / bare soil	woody plants
0-5 %	0.0346	-0.0268	**0.0990**
5-25 %	**0.1153**	<u>-0.1657</u>	<u>-0.0917</u>
25-50 %	-0.0174	0.0646	0.0411
50-75 %	<u>-0.0930</u>	**0.1279**	-0.0075
75-100 %	-0.0395		-0.0306

b) **L2**

category	grass	moss / bare soil	woody plants
0-5 %	--	-0.0306	--
5-25 %	--	-0.0918	--
25-50 %	--	0.0319	--
50-75 %	--	**0.0905**	--
75-100 %	--		--

c) **L3**

category	grass	moss / bare soil	woody plants
0-5 %	--	-0.0306	**0.0803**
5-25 %	--	-0.1605	0.0048
25-50 %	--	0.0381	0.0381
50-75 %	--	**0.1531**	<u>-0.0823</u>
75-100 %	--		-0.0306

d) **L4**

category	grass	moss / bare soil	woody plants
0-5 %	<u>-0.0599</u>	-0.0306	**0.2294**
5-25 %	**0.1412**	-0.1403	-0.0476
25-50 %	0.0176	**0.0848**	-0.0595
50-75 %	<u>-0.0582</u>	**0.0861**	<u>-0.0814</u>
75-100 %	-0.0406		-0.0306

e) **L5**

category	grass	moss / bare soil	woody plants
0-5 %	0.0155	-0.0158	**0.1154**
5-25 %	-0.0194	<u>-0.1766</u>	-0.0025
25-50 %	**0.1063**	0.0690	-0.0148
50-75 %	<u>-0.0809</u>	**0.1235**	<u>-0.0574</u>
75-100 %	-0.0215		-0.0306

f) **adult**

category	grass	moss / bare soil	woody plants
0-5 %	**0.0803**	-0.0306	**0.1262**
5-25 %	-0.0517	<u>-0.1604</u>	<u>-0.0674</u>
25-50 %	**0.1146**	0.0789	0.0180
50-75 %	<u>-0.1062</u>	**0.1121**	-0.0359
75-100 %	-0.0370		-0.0306

3.7. The dispersal of larvae and adults

C. italicus

We marked 199 larvae by the cutting technique and 52 adults with colours. The time between capture and recapture remained unknown because an individual marking was impossible. All developmental stages showed low dispersal distances (Fig. 7). 60 % of the recaptured adults (cut-marked as larvae and colour-marked) and more than 80 % of the recaptured larvae had an average dispersal distance (ADD) ≤ 5 m, and no larvae moved farther than 15 m. 8 adults had an ADD bigger than 20 m, and the largest distances recorded were 26 m, 35 m and 38 m.

The dispersal patterns of the two adult-groups were significantly different from that of the larvae (test of independence, ADD-categories > 15 m pooled, d.f. = 4, α = 0.05. Cut adults:cut larvae: χ^2 = 0.0157, colour adults:cut larvae: χ^2 = 0.0089). The adults' ADD's were distributed more regularly than those of the larvae. The latter remained aggregated around the plot where they had been marked (Fig. 7).
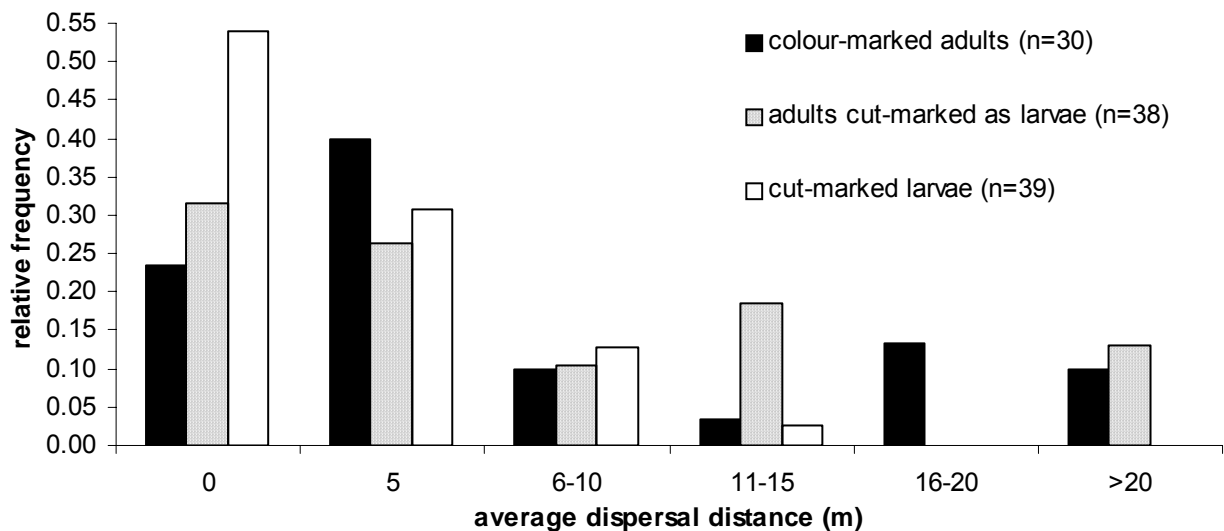
Fig. 7: *C. italicus*: The relative frequencies of the average dispersal distances of the three marking groups, based on recapture data.

The means of the two adult-group ADD's were similar, but they differed from the value of the larvae (Tab. 10), which was more than 5 m smaller.

Tab. 10: *C. italicus*: Average dispersal distances (m) of each group ($\overline{x} \pm$ SD).

marking:	colour	cut-marked	
	adults	adults	larvae
$\overline{x}$	8.17	8.06	2.90
SD	8.64	9.01	3.60

O. caerulescens

We marked 70 larvae with a cut and 20 adults with colour. All developmental stages showed low dispersal distances. The time between capture and recapture remained unknown because an individual marking was impossible. About 70 % of the cut-marked recaptured adults had an ADD ≤ 5 m, whereas 45.5 % of the colour-marked recaptures had an ADD between 6 and 10 m. No larvae moved farther than 10 m (Fig. 8). Only three adults migrated more than 11 m, i.e. 29 m, 32 m and 40 m.

The dispersal patterns of the two adult-groups were not significantly different of that of the larvae (test of independence, ADD-categories > 10 m pooled, d.f. = 3, α = 0.05. Cut adults:cut larvae: χ^2 = 0.7511, colour adults:cut larvae: χ^2 = 0.1923). Individuals of all three groups mainly stayed near the plot where they have been marked.
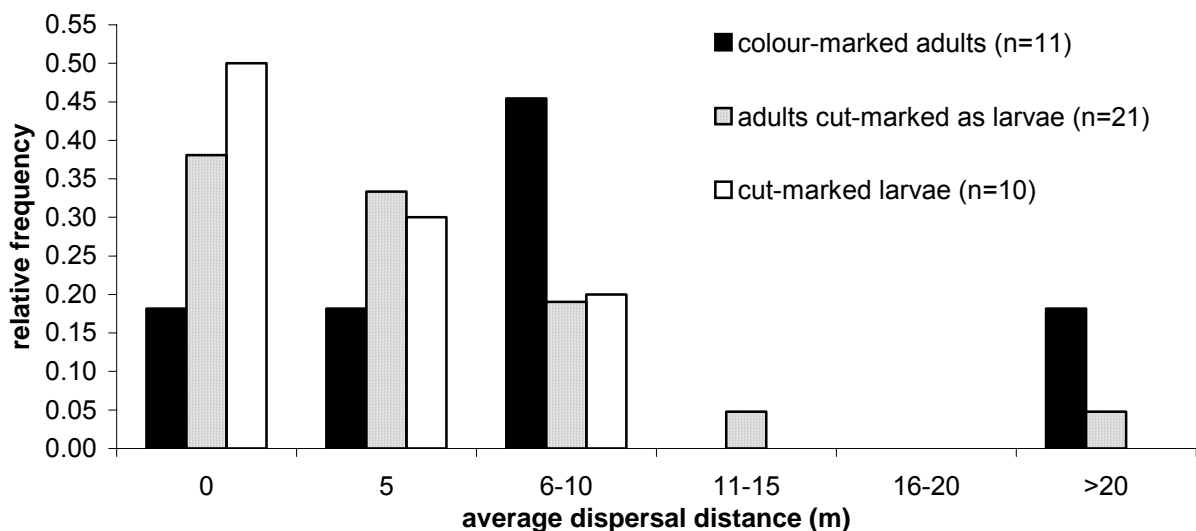
Fig. 8: O*. caerulescens*: The relative frequencies of the average dispersal distances of the three marking groups, based on recapture data.

The mean ADD of the adults being cut-marked as larvae was half the mean of the colour-marked adults (Tab. 11). On average the adults being cut-marked as larvae moved only two meters farther than the larvae (Tab. 11).

Tab. 11: *O. caerulescens*: Average dispersal distances (m) of each group ($\bar{x} \pm$ SD).

marking:	colour	cut-marked	
	adults	adults	larvae
$\bar{x}$	10.68	5.33	3.20
SD	12.51	7.14	3.68

The number of recaptures within each group was small (Fig. 8), therefore the explanatory power was weak.

4. Discussion

4.1. Shadow and its influence on soil and surface temperature

Several statistical values (mean, standard deviation, median, quartiles, maxima, minima and the temperature sum) showed no significant differences between the four measurement spots.

<u>Soil temperature</u>

The soil temperature of an area being shaded in the morning as well as in the evening (M_{me}) was mostly 1-3 °C lower than one of an area with less or no shadow, which is caused by the shorter insolation-times. Plots with morning-, evening- or no shadow had similar soil temperatures. However, we expected the highest temperatures at the shadow-free point (M_{me}) due to the longest insolation, which was not the case. Probably the probe-holes were too small, resulting in an influence by the surrounding soil, the composition of which - influencing heat capacity, heat conductivity and evaporation rate - might have lead to different temperature patterns.

<u>Surface temperature</u>

The temperature increased when the shadow disappeared and decreased when it appeared again, as expected. The temperature pattern differed between the four spots, therefore the shadow clearly influenced the surface temperature. From July to October the differences became smaller as a matter of day length and elevation of the sun.

The spot with evening shadow offered more time for oviposition than the spot with morning shadow. With early insolation the temperature reached the threshold earlier than with late insolation, but at shading in the evening the temperature decreased slowly due to the heat accumulated in the soil. Places with no shadow or evening shadow only offer the best oviposition conditions regarding temperature. After hatching the animals need enough insolation for optimal development, which is provided by areas with no (M_0) or little (M_m and M_e) shadow. Therefore areas with the best oviposition conditions - regarding temperature – also offer the best thermal conditions for development. The larger and more mobile the individuals become, the more are they able to select optimal surface temperature within a small spatial scale.

4.2. Larval instars and phenology

Basically, the number of instars is influenced by the body size of a species (CARRON 1994) and therefore sexual size dimorphism results in an additional instar in females (THORENS 1991), becoming gradually distinct during development (CARRON 1994). The number of instars can vary within a species due to several reasons. UVAROV (1966) proposed effects of climate, food, phase and hormonal functions and INGRISCH & KÖHLER (1998) additionally proposed geographical effects. Different instar determination methods might be another reason.

The observed number of instars in *C. italicus* (♀♀: 6, ♂♂: 5) is the same as mentioned by PICHLER (1956) and INGRISCH & KÖHLER (1998), whereas MÜHLHEIM (2002) reported five (♀♀) and four (♂♂) larval instars and DETZEL (1998) five for both sexes. In *O. caerulescens* we found five instars in both sexes, which are the same figures as PICHLER (1956) presented. In contrast, MÜHLHEIM (2002) suggested five (♀♀) and four (♂♂) instars and MERKEL (1980) four in both sexes. The difference between our findings and the data of MÜHLHEIM (2002) is interesting, because both studies took place in the same area and the measurements were carried out with the same method. The suggested explanation is that during our study the weather was less favourable.

The total number of catches varied between the instars within both species. Especially the drop of more than 100 catches from L1 to L2 and the rise from L4 to L5 are conspicuous. One explanation for this decrease between L1 and L2 could be a high mortality of L1 and early L2. The stable number of catches between L2 and L4 supports this idea. Due to the tiny size of early instars, warmth is of crucial importance; a long period of unfavourable weather might reduce the population. Immediately after the first sampling - during which we caught most of the L1 - the temperature fell by 6 °C and a rainy period (176 mm) of five days occurred. Later on there was no similar unfavourable period.

During the occurrence of the L3 and L4 (end May-mid June) the weather conditions were again unfavourable (rainy and cloudy) and therefore it was impossible to catch grasshoppers, because they remain hidden most probably underneath grass or herbs.

The increase of catches between L4 and L5 could be due to two different reasons: immigration from adjacent areas, and better catchability due to size and higher mobility.

In total, we caught twice as much *C. italicus* as *O. caerulescens*, indicating that the study area provides more optimal habitats for *C. italicus* than for *O. caerulescens*. The study site seems to be similar to that used by DETZEL (1998), who observed a *C. italicus* population living syntopic with a small population of *O. caerulescens*.

With the last sampling we found a density of adult *C. italicus* of 0.13 Ind/m^2, which lies within the data range (0.1-0.3 Ind/m^2) of JÜRGENS & REHDING (1992). The density of adult *O. caerulescens* was 0.06 Ind/m^2, which matches the results of several authors (cited in INGRISCH & KÖHLER 1998) who found densities between 0.01 and 0.08 Ind/m^2.

4.3. The distribution of oothecae, larvae and adults

Both species used the study area unequally, thus they preferred or avoided specific habitat variables according to their habitat requirements. The L1-distributions of the two species were alike indicating similar preferences for egg-laying sites. The distribution within one species differed with time; late larval instars and adults were more mobile and had different habitat preferences than earlier larval instars.

On some plots we found only a few L1, this might have been caused by low hatching rates - due to low number of laid eggs, unfavourable oviposition conditions or unfavourable conditions during embryogenesis - or by high predation.

We never caught more than 25 L1 per species on one plot; according to DETZEL (1998; *C. italicus* lays 10-50 and *O. caerulescens* 30 eggs per clutch) this individuals might have originated from one or two oothecae.

4.4. The influence of shadow and temperature on the two species

Influence on the distribution

The occurrence of each developmental stage was negatively correlated with the presence of shadow. On plots with long shading we found no or only few first instars, whereas plots with more L1 had more insolation per day. Early instar larvae were bound to their hatching site due to their low mobility; thus the larval development depends on the females egg-laying site choice. The high mobility enables late instar larvae and adults to move to areas with optimal thermal conditions (high insolation)

and to avoid shadow. Both species showed an avoidance of woody plants, a further proof for the negative correlation between shading and the occurrence of the two species. WUNDER (2002) showed avoidance of woody plants for adult *C. italicus.* Shaded areas cannot provide optimal thermal conditions as the thermal input at the soil surface can be lowered by 50 % due to the shadow of a nearby 5 m tall tree (SCHEFFER & SCHACHTSCHABEL 1989). Furthermore DETZEL (1998) observed that *C. italicus* hardly feeds on shaded plants.

Shadow might also lead to higher soil humidity causing a slower heating of the soil which slows down the development. Therefore investigations on the correlation between shadow and soil humidity might have been helpful.

Influence on oviposition and development

July and August offer the better oviposition conditions than September/October, when surface temperature rose above the threshold only for a few hours per day. But in July/August the temperatures at noon (< 50 °C) might be too high for oviposition. Nevertheless oviposition should take place early in the season, so that females have enough time to search for optimal egg-laying sites. On the other hand late oviposition might enable an egg-laying site choice providing longer insolation during embryo-genesis in spring.

The unfavourable winter climate inhibits embryogenesis and the embryos undergo a diapause (DETZEL 1998). No data are available so far about the shadow influence on temperature in spring when embryogenesis proceeds (data collection is still going on). The temperature optimum for the embryonic development of grasshoppers is approximately 25-30 °C (BRUCKHAUS 1991, 1992), which is higher than the oviposition threshold. However, areas being shaded in the morning and in the evening are expected to provide less favourable conditions for embryogenesis, due to lower soil temperature. We hardly found any L1 on such areas, therefore females avoided these for oviposition. In *Gomphocerus rufus* and *Chorthippus parallelus* BRUCKHAUS (1990) demonstrated a positive correreation between temperature and the developmental speed of embryos. In *Ch. parallelus* shadow caused an average hatching delay of 12.5 days (OSCHMANN 1993), which might result in a delayed mating and to a lower reproduction rate.

Late instar larvae and adults are mobile, therefore their presence is not only determined by their thermal preferences, but also by their habitat preferences.

4.5. Surface cover preferences

Insects choose habitats providing enough food, effective predator protection and, as ectothermic animals, conditions that provide optimal conditions for thermoregulation (DETZEL 1998). The better the conditions, the higher the fitness of an individual (DETZEL 1998) and consequently of a species. MAZEK-FIALLA (1941) found that the body-temperature of grasshoppers being fully exposed to the sun is up to 8 °C higher than the ambient temperature, but only 3 °C when partly shaded in grass. As oviposition depends on temperature, vegetation density may influence oviposition (INGRISCH & BOEKHOLT 1982).

Grass and moss/bare soil

C. italicus stayed on surfaces with a moderate grass cover but showed no preference for bare soil which would be of importance for a xerothermophilic geophilous species. Light grass allows optimal thermoregulation while dense grass cover provides better protection against predators. Thus their habitat choice may be an optimised compromise. Nevertheless the need for bare soil was shown by the avoidance of plots with dense grass cover. This resulting preference for a habitat mosaic is supported by BRANDT's (1996) data showing that a combination of bare soil and dense vegetation is favourable for *C. italicus.*

O. caerulescens showed a strong preference for bare soil being indicated also by the avoidance of dense grass cover and woody plants. Eggs are laid into soils with little vegetation cover (DETZEL 1998). In the Offenburger Rheinebene (D) WANCURA (1996) determined a preference for an average vegetation cover of 50 % for *O. caerulescens* and did not find any individuals on plots with a vegetation cover under 30 %. These data fit more or less with the present data and with those of HOLDEREGGER (1999), who investigated *O. caerulescens* at Pfynwald too. SÄNGER (1977) characterised *O. caerulescens* as the dominating species on rocky steppes with very sparse vegetation; *C. italicus* was also present in these steppes but in smaller numbers and it was also found in the adjacent *Stipa*-steppes.

Both species lay their eggs into the soil and need a temperature above 16 °C for optimal embryogenesis (DETZEL 1998). This can be considered as reason for the preference of places with sparse vegetation for oviposition, where the freshly hatched L1 could be found. The later change into plots with denser vegetation could be due to searching for higher food supply (e.g. from 10.9. to 9.10 and 9.11.). A protection of the vegetation against adverse climate, as suggested by DETZEL (1998) cannot play any role at our site because the vegetation is not dense enough. The fact that larvae prefer denser vegetation than adults, as mentioned by SÄNGER (1977) and TAUSCHER (1982) was not confirmed by our data; this could be due to different climatic conditions.

<u>Woody plants</u>

Beside the thermal effect of shading woody plants have another impact on grasshoppers. Invading trees and shrubs are responsible for a significant fragmentation of the former open steppes. APPELT (1996) and MERKEL (1980) postulated the minimal habitat size for a population of *O. caerulescens* to be 500-600 m^2, which is ⅕ to ¼ of the size of our study area. But this area is one of the largest open steppes in eastern Rottensand, and woody plants increasingly invade most of these. This fact is reflected by the data of MÜLLER & ZETTEL (1999) who found significantly less steppe plots populated by *C. italicus* and *O. caerulescens* in the eastern than in the western part of Rottensand.

<u>Herbs</u>

Herbs had a too low coverage to have any influence on the distribution of the studied species. However, at Pfynwald the food of **O. caerulescens** consisted mainly of *Astragalus onobrychis* and other herbs (HOLDEREGGER 1999); the spectrum of food of **C. italicus** includes *Hieracium, Euphorbia* and *Artemisia* (EBNER 1951, HARZ 1960, SÄNGER 1973 and DETZEL 1991) three genera occurring at Pfynwald.

The investigated habitat variables are not independent from each other, which might explain the low L-values. Furthermore the species have competitors in the study area, which might force them into less optimal habitats. It would be better to study the habitat structure exactly at the spot were the animal was found. Because Grasshopper larvae occur in groups and flee all together, it is impossible to determine the exact location of each individual.

4.6. The dispersal of larvae and adults

Both species showed low dispersal distances assuming that they are philopatric. Earlier studies on the mobility of adult *C. italicus* (HESS & RITSCHEL-KANDEL 1992) and on adult *O. caerulescens* (DETZEL et al. 1993) support the present data.

In *C. italicus* the average dispersal distances (ADD) of the adults differed from those of the larvae. Larger size, the presence of wings and the higher activity (search for mates and food) may be responsible for the higher mobility of adults. The ADD's of the adults in *O. caerulescens* did not differ of those of the larvae, indicating that the mobility of adults remained largely the same as in the larvae in spite of an expected higher mobility due to size and the presence of wings. Despite more time for dispersal – resulting in higher dispersal distances - the adults cut-marked as larvae showed dispersal distances similar to those of the colour-marked adults in both species. This could not be caused by the different marking methods: our observations showed that cut-marked individuals are well able to fly, and this difference was not present in *C. italicus*.

The present data show, that *C. italicus* as well as *O. caerulescens* stayed in the area where they have hatched. Therefore we can assume that the study area provided favourable habitats for larvae as well as for adults of both species. Nevertheless, it is known that the dispersal of *C. italicus* increases significantly in years with high (8-12 Ind/m^2, INGRISCH & KÖHLER 1998) population densities (MAAS et al. 2002). Therefore

a low dispersal could be expected on the study site due to the low population density (0.13 Ind/m^2).

We never observed individuals having moved to parts of the study site separated by woody plants; this fact indicates that clusters of trees and shrubs may represent obstacles for dispersal.

4.7. Conclusions

Coming back to our hypotheses: both species were clumpy distributed, avoided dense grass vegetation and long shaded areas and showed different habitat preferences; but larvae had not the same habitat preferences as the adults and the latter were not more mobile than the former.

In both species oviposition took place in open areas with unimpeded insolation (no shade, low grass and herbage cover). After hatching *O. caerulescens* stayed in such places, while *C. italicus* moved to denser vegetation. Therefore a mosaic of steppe vegetation and bare soil seems to be important for the existence of the two species.

Spreading of woody plants with increasing shading of the steppe reduces the areas suitable for oviposition and residence and can be considered as a cause for the receding of the two species.

An important measure for habitat conservation is to maintain sufficient steppe areas free of trees and shrubs. It can be assumed that many other xerothermophilic invertebrates would profit at the same time from such measures.

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7. APPENDIX

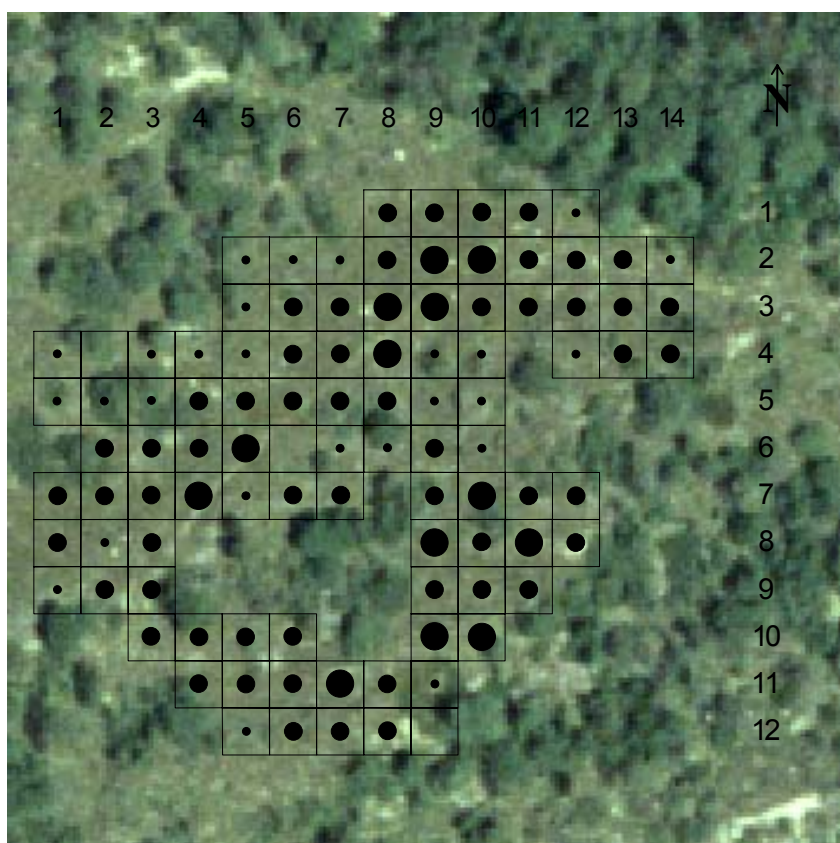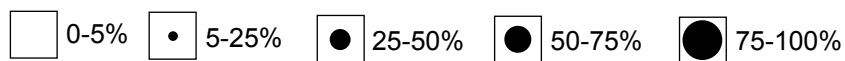Appendix 1: **30.04.2002**, shadow throws on the study site at 7.30 (upper map) and 17.45 (lower map).
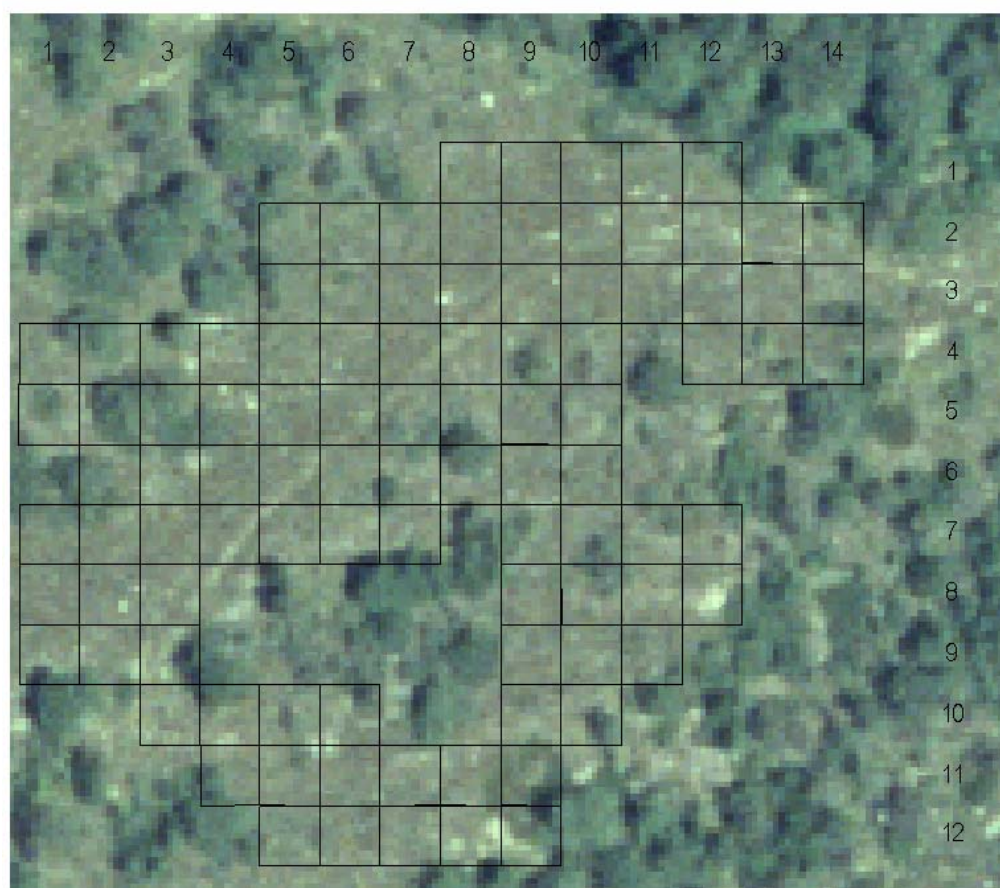
Appendix 2: **30.05.2002**, shadow throws on the study site at 7.30 (upper map) and 17.45 (lower map).

Appendix 3: **04.07.2002**, shadow throws on the study site at 7.30 (upper map) and 17.45 (lower map).

Appendix 4: Grass (upper map) and moss (lower map) coverage on the 98 plots.

Appendix 5: Number of plots with a certain number of caught *C. italicus*, separately for each developmental stage.

L1

Number of catches	number of plots
0	37
1	14
2	7
3	8
4	7
5	5
6	3
7	4
8	2
9	3
10	2
11	1
12	0
13	1
14	2
15	1
16	0
17	0
18	0
19	0
20	0
21	0
22	0
23	0
24	0
25	1

L2

Number of catches	number of plots
0	39
1	18
2	12
3	12
4	7
5	1
6	4
7	1
8	2
9	1
10	0
11	1

L3

Number of catches	number of plots
0	40
1	18
2	17
3	12
4	3
5	3
6	3
7	2

L4

Number of catches	number of plots
0	35
1	19
2	16
3	12
4	6
5	6
6	1
7	2
8	1

L5

Number of catches	number of plots
0	10
1	14
2	9
3	14
4	6
5	10
6	6
7	8
8	3
9	6
10	5
11	0
12	1
13	1
14	1
15	1
16	0
17	2
18	1

L6 (females only)

Number of catches	number of plots
0	24
1	15
2	14
3	12
4	13
5	7
6	5
7	2
8	2
9	2
10	1
11	0
12	1

Adults

Number of catches	number of plots
0	8
1	12
2	8
3	6
4	7
5	5
6	8
7	6
8	9
9	4
10	7
11	2
12	3
13	4
14	2
15	0
16	1
17	2
18	1
19	2
20	0
21	1

Appendix 6: Number of plots with a certain number of caught *O. caerulescens*, separately for each developmental stage.

L1

Number of catches	number of plots
0	31
1	15
2	17
3	11
4	5
5	10
6	1
7	1
8	1
9	2
10	0
11	0
12	2
13	0
14	0
15	0
16	1
17	0
18	0
19	1

L2

Number of catches	number of plots
0	44
1	19
2	21
3	8
4	2
5	1
6	1
7	1
8	0
9	0
10	1

L3

Number of catches	number of plots
0	51
1	23
2	10
3	4
4	5
5	2
6	2
7	0
8	1

L4

Number of catches	number of plots
0	56
1	20
2	8
3	7
4	3
5	2
6	1
7	0
8	0
9	1

L5

Number of catches	number of plots
0	27
1	20
2	16
3	14
4	8
5	2
6	6
7	3
8	1
9	0
10	1

Adults

Number of catches	number of plots
0	40
1	24
2	14
3	7
4	7
5	4
6	0
7	1
8	0
9	1

Appendix 7: All recaptures of marked individuals of both species, separately for the two marking methods.

C. italicus

cut-marked

sampling	sex	instar/ adult	plot	plot of origin
4	f	adult	5.8	5.8
4	f	adult	9.10	9.10
4	f	adult	9.11	9.10
4	m	adult	1.8	2.8
4	m	adult	11.6	11.6
4	m	adult	2.14	3.12
4	m	adult	6.10	3.12
4	m	adult	4.10	4.10
4	m	adult	5.8	5.8
4	m	adult	7.4	6.6
4	m	adult	6.3	6.6
4	m	adult	9.2	9.2
4	m	adult	9.2	9.2
4	m	adult	7.6	9.2
5	f	adult	11.9	12.5
5	f	adult	3.8	2.8
5	f	adult	2.8	4.10
5	f	adult	4.7	4.10
5	f	adult	3.9	4.10
5	f	adult	11.9	9.10
5	f	adult	6.7	9.10
5	f	adult	8.10	9.10
5	m	adult	10.9	10.9
5	m	adult	10.10	10.9
5	m	adult	2.9	2.8
5	m	adult	3.12	3.12
5	m	adult	7.6	3.12
5	m	adult	6.10	4.10
5	m	adult	4.9	4.8
5	m	adult	5.10	5.10
5	m	adult	5.8	5.8
5	m	adult	5.7	5.8
5	m	adult	6.8	5.8
5	m	adult	6.6	6.6
5	m	adult	6.3	6.6
5	m	adult	7.6	6.6
5	m	adult	8.1	9.2
5	m	adult	8.1	9.2
3	f	L6	12.6	11.6
4	f	L6	10.10	10.9
4	f	L6	12.6	11.6
4	f	L6	2.8	2.8
4	f	L6	2.8	2.8
4	f	L6	2.8	2.8
4	f	L6	2.8	2.8
4	f	L6	2.7	2.8
4	f	L6	5.10	4.10
4	f	L6	3.9	4.10
4	f	L6	6.5	5.6
4	f	L6	9.10	9.10
5	f	L6	11.9	10.9
5	f	L6	11.6	11.6
5	f	L6	10.6	11.6
5	f	L6	12.6	11.6
5	f	L6	12.5	12.5
5	f	L6	12.5	12.5
5	f	L6	12.5	12.5
5	f	L6	12.5	12.5
5	f	L6	2.8	2.8
5	f	L6	2.8	2.8
5	f	L6	3.9	4.8
5	f	L6	4.10	5.10
5	f	L6	5.7	5.8
5	f	L6	4.6	6.6
5	f	L6	9.10	9.10
3	f	L5	5.10	4.10
4	f	L5	5.10	5.10
4	f	L5	3.6	6.6
4	m	L5	2.8	2.8
4	m	L5	5.10	5.10
4	m	L5	5.10	5.10
4	m	L5	5.8	5.8
4	m	L5	5.8	5.8
4	m	L5	6.5	6.6
5	m	L5	3.12	3.12
5	m	L5	9.10	9.10
3	m	L4	11.8	10.9

colour-marked

sampling	sex	plot	plot of origin
3	f	12.6	11.6
4	f	11.6	11.6
4	m	11.6	11.6
4	m	2.9	5.10
4	m	5.5	6.6
4	m	11.7	9.10
5	f	4.7	11.6
5	f	2.7	5.8
5	f	4.4	5.8
5	m	8.11	10.9
5	m	11.6	11.6
5	m	11.7	11.6
5	m	11.7	11.6
5	m	2.8	2.8
5	m	3.8	4.8
5	m	3.7	4.8
5	m	5.6	5.6
5	m	9.2	6.6
5	m	7.6	6.6
5	m	5.6	6.6
5	m	9.10	9.10
5	m	9.10	9.10
5	m	8.10	9.10
5	m	9.11	9.10
5	m	9.1	9.2
5	m	8.1	9.2

O. caerulescens

cut-marked

sampling	sex	instar/ adult	plot	plot of origin
4	f	adult	11.5	11.6
4	f	adult	6.10	4.10
4	f	adult	5.7	4.8
4	f	adult	8.10	7.10
4	m	adult	10.9	10.9
4	m	adult	11.7	11.6
5	f	adult	10.9	10.9
5	f	adult	11.6	11.6
5	f	adult	3.12	3.12
5	f	adult	4.9	4.8
5	f	adult	6.8	7.10
5	f	adult	8.10	7.10
5	m	adult	10.10	10.9
5	m	adult	11.8	11.6
5	m	adult	1.9	6.5
5	m	adult	5.6	6.5
5	m	adult	8.3	8.3
5	m	adult	8.3	8.3
5	m	adult	8.3	8.3
5	m	adult	8.3	8.3
5	m	adult	9.3	8.3
4	f	L5	3.12	3.12
4	f	L5	9.10	9.10
4	m	L5	1.8	2.8
4	m	L5	5.6	6.5
4	m	L5	8.11	8.11
3	f	L4	6.10	5.10
4	f	L4	2.8	2.8
4	m	L4	5.6	5.6
5	f	L4	6.10	5.10
4	f	L3	7.10	5.10

colour-marked

sampling	sex	plot	plot of origin
4	m	10.9	10.9
5	f	11.8	10.9
5	f	8.1	4.8
5	f	8.11	9.10
5	m	10.9	10.9
5	m	11.8	10.9
5	m	2.6	2.8
5	m	3.13	3.12
5	m	4.7	4.8
5	m	3.9	4.8
5	m	10.6	9.10