Risk spreading in the voltinism of *Scolitantides orion orion* (Pallas, 1771) (Lycaenidae)

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Abstract. As far as known the Chequered Blue (*Scolitantides orion* (Pallas, 1771)) develops either one or two generations per year. To clarify the voltinism strategy adopted by a population of this species in eastern Germany, we continuously monitored them under natural conditions in 2004. In parallel, breeding-experiments were undertaken in four cages placed within the habitat. Both sets of observations revealed three distinct generations of adults, but only two generations of preimaginal stages were detected per year. The first adults emerged from diapausing pupae in spring. This first generation of adults produced a second generation (the first preimaginals of this season) which developed diapausing as well as non-diapausing pupae. Adults of this second generation again produced diapausing and non-diapausing pupae (the second generation of preimaginals of this season). From the non-diapausing pupae emerged a third generation of adults, which however did not reproduce. The first generation of every year is recruited from all diapausing pupae of the two preimaginal generations of the preceding year. This voltinism is interpreted as a risk-spreading strategy that allows the plastic development of a maximum number of generations during one season. In the study area, the larvae of *S. orion orion* feed exclusively on *Sedum maximum* and the facultatively myrmecophilous larvae were associated with ant species of Formicinae as well as Myrmicinae, but also developed without such an association. Five ant species were identified in these associations, *Formica* (*Serviformica*) *glauca* Ruzsky, 1895, *Lasius* (*Lasius*) *emarginatus* Olivier, 1791, *Tetramorium impurum* (Förster, 1850), *Formica* (*Serviformica*) *fusca* Linnaeus, 1758, and *Camponotus ligniperda* Latreille, 1802, and the first three species are recorded for the first time to be associated with this lycaenid species.

Key words. diapause, plastic voltinism, risk spreading, *Scolitantides orion*, Lycaenidae, facultative myrmecophily, ant species, host plant, *Sedum maximum*.

Introduction

The Chequered Blue (*Scolitantides orion* (Pallas, 1771)) is a Palaearctic species occurring from the Atlantic coast to Japan (Coulondre 1994; Tolman & Lewington 1998). Within this region, the distribution of *S. orion* is a patchy pattern of several disjunct areals, for which six subspecies are recognised: *S. o. orion* from Central and southeastern Europe and Turkey; *S. o. parvula* de Sagarra, 1926 from the Pyrénées and the Iberian Peninsula; *S. o. ultraornata* Verity, 1937 from southern Fenno-Scandia; *S. o. tytleri* Evans, 1924 from Tibet; *S. o. ornata* Staudinger, 1892 from Central Asia to the Far East, and *S. o. jezoensis* Matsumura, 1919 from Japan (Coulondre 1994). In Germany several populations occur in Hesse, Rhineland-Palatinate, Baden-Wuertemberg, Bavaria, Thuringia, and Saxony (Gaedike & Heinicke 1999). *S. orion* is a xerothermophilous species. Populations usually occur in sunny places within mountainous areas, often in river valleys (Settele et al. 1999; Huemer 2004). Despite the fact that *S. orion* is generally well known to lepidopterists certain features of its life history are still insufficiently studied. One controversial issue is the number and phenology of generations per year and these are the main foci of the study presented here. The data available for *S. o. orion* suggest that there are different numbers of generations per year. One generation is stated for populations from Central Europe (Tolman & Lewington 1998), but two are reported for several areas in Switzerland (Tolman & Lewington 1998; Lepidopterologen-Arbeitsgruppe 1994). Forster & Wohlfahrt (1955) generally mentioned two generations for Central Europe but only one at the upper altitudinal limit of the species' distribution in the Alps. Within the Czech Republic two generations were reported from Central Bohemia (Srdinko 1912), but only one from Moravia (Kudla 1951). Two generations are also mentioned from South Tyrol (Huemer 2004). Even within Germany, different numbers of generations per year have been recorded for various regions. While in Rhineland-Palatinate there appears to be only one generation (Reinhardt & Kinkler 2004), a partial second generation occurs in Thuringia (Bergmann 1952), and two generations are recorded from Saxony (Reinhardt 2003). According to Coulondre (1994), voucher specimens of the second generation of *S. o. orion* in insect collections represent only 0–10% of the quantity of the first generation. As many of these data are based on voucher specimens collected in different years, we investigated the phenology in one population in eastern Germany in order to obtain reliable data for an entire season. Observations made on larval host plant use and on their associated ants are mentioned as well.

Methods

The study site is situated to the north-west of Meissen (Germany: Saxony) in a south-facing granite-quarry that is extremely xerothermic on most of its surface. Here large stands of *Sedum maximum* are growing. However, plants like *Humulus lupulus, Rosa canina*, and *Rubus* sp. are encroaching this area and three more *Sedum* species, viz. *Sedum acre*, *S. sexangulare*, and *S. rupestre,* are also present.
Usually, our observations of *S. orion* in this habitat took place every second day, but every day during periods when butterflies were emerging or when a generation was about to be completed. Thus, observations were made on the following days: April 21, 23, 27, 28, 29; May 03, 04, 11, 14, 18, 19, 24, 27, 28; June 01, 03, 04, 07, 09, 11, 14, 15, 21, 22, 23, 24, 25, 26, 28, 30; July 01, 02, 04, 05, 06, 07, 08, 10, 12, 13, 14, 15, 16, 17, 19, 20, 21, 23, 25, 27, 29, 30; August 02, 03, 04, 05, 06, 08, 09, 11, 12, 14, 16, 18, 19, 21, 22, 24, 26, 30; and September 02, 03, 04, 06, 07, 08, 10, 13, 14, 17, 19, 20, 22, 23 2004. No observations were undertaken during strong rains or thunderstorms. At the end of April and the beginning of June the stands of *S. acre*, *S. sexangulare*, and *S. rupestre* were intensively investigated for the presence of eggs and larvae of *S. orion*.
Four cages were installed in the habitat to observe the development of *S. orion* under somewhat controlled conditions. Each cage was composed of two plastic dishes covered by a mosquito net held by willow rods. The measurements for each cage were 60×40×30 cm. The plastic dishes were filled with a mixture of sterilised soil from the quarry habitat and commercial potting soil. One dish of each cage was planted with *S. maximum* from the quarry habitat after the plants had been checked to be free of aphids, thrips, hover fly larvae, and immatures of *S. orion*. The second dish contained different plants: cage 1, 2 and 2a were planted with *Sedum album* from the Dresden

Botanical Garden, cage 3 received only a large stone, and cage 4 a mixture of *S. maximum* and *S. rupestre* from the Dresden Botanical Garden. Between all plants we placed stones of about 8 cm in diameter. The cages were controlled during each visit to the site and were moisturised if necessary. Cages 1, 2 and 3 were installed on April 23. Cages 1 and 2 were covered immediately. Cage 3 was left uncovered until the first eggs were laid on its *S. maximum* plants, which happened until April 27. On April 29 two females of *S. orion* were placed in cage 1 and one in cage 2 for oviposition. In cage 1 all fully developed larvae pupated in places where they could be controlled easily. Thus, all pupal shells could be removed after the adults emerged while generation 3 started to develop. In cage 2 pupation often took place in hidden places. Therefore, after the emergence, copulation, oviposition, and death of the adults of the second generation their eggs were transferred to a new cage called cage 2a, while the pupae of the second generation that had not yet emerged were left in cage 2. Cage 4 was installed on May 19 and one *S. orion* female was put inside the same day. On September 20 all cages were removed and inspected in detail. The remaining pupae were placed in a plastic container on mosses and left outdoor.

Results

Field observations

Flight times in the field (Fig. 1)**.** First generation. Butterflies of the first generation were noted during two months from April 21 to June 21. The first eggs on *Sedum maximum* were found on April 27. No *S. orion* of this first generation flew after June 21, though the weather was sunny, warm, and dry.
Second generation. On July 4 an obviously freshly-emerged adult of *S. orion* was detected. Two butterflies were observed on each of the following four days. The main flight activity lasted between July 12 and August 6. After August 6 the number of observed specimens decreased until August 12, when the last two adults of the second generation were seen, even though the weather was warm and dry afterwards.
Third generation. An obviously freshly-emerged adult of *S. orion* was detected on August 21 and also on August 22. During the following days, the weather was cold and rainy and thus it was impossible to observe any butterfly. At the beginning of September the weather became warm and sunny again and during the hot day of September 4 another adult *S. orion* was seen. This summer-like weather continued until September 17. During this period, three butterflies were observed on September 8 and 10, two butterflies on September 14 and 17, and the last one on September 19.
Host plants of the larvae. The larvae were found exclusively on *Sedum maximum*, though congeneric *S. acre*, *S. rupestre*, and *S. sexangulare* were also present in the study area.
Association with ants. *S. orion* larvae were observed in association with four species of Formicinae ants: *Camponotus ligniperda* Latreille, 1802, *Formica* (*Serviformica*) *fusca* Linnaeus, 1758, *Formica* (*Serviformica*) *glauca* Ruzsky, 1895, and *Lasius* (*Lasius*) *emarginatus* Olivier, 1791.

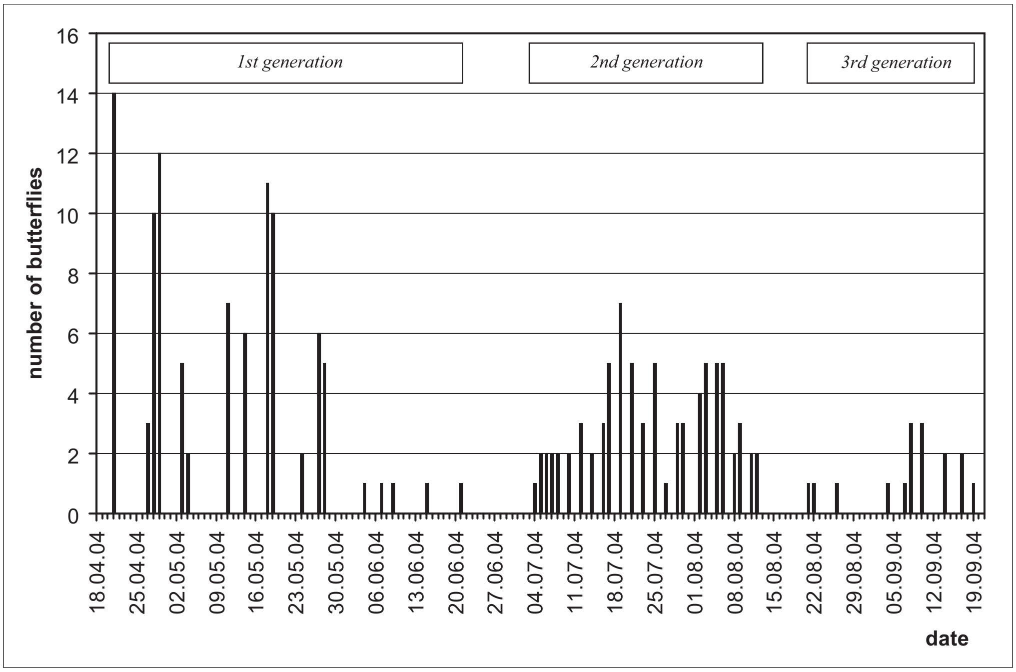

Fig. 1. Number of adult *S. orion* in the study area during 2004. Double counts cannot be excluded because specimens were not marked.

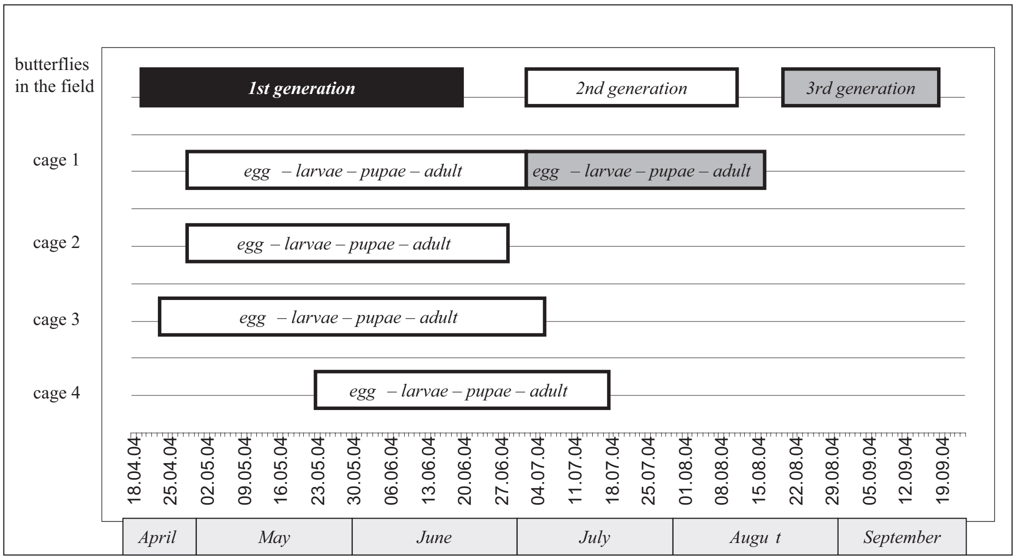

Fig. 2. Phenology of *S. orion* in cages in relation to flight periods in the field. Each bar for each cage starts with oviposition and ends with butterfly emergence. Development until the third generation was completed in cage 1 only (black bar: first generation; white bars: second generation; grey bars: third generation).

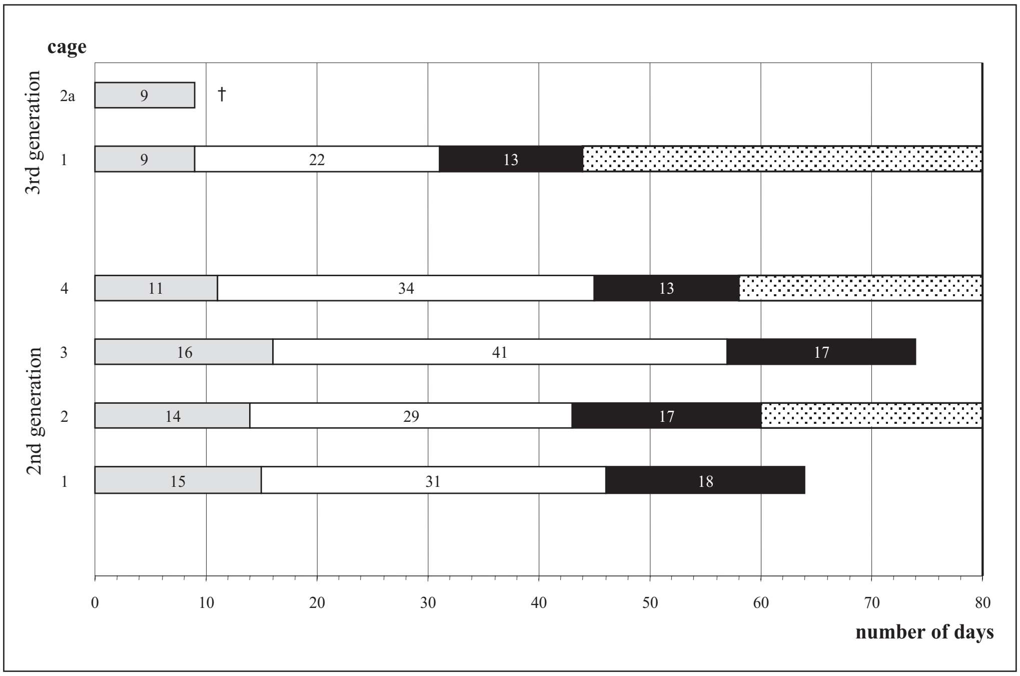

Fig. 3. Duration of development of the preimaginal stages of *S. orion*. Grey bar: egg stage; white bar: larval stages; black bar: non-diapausing pupae; black and dotted bar: diapausing pupae. The right edge of the black bars also indicates the beginning of the emergence of the adults.

Observations in cages **Figs. 2, 3**

Cage 1. Development of the second generation. On May 3 we found the freshly-laid eggs of the two *S. orion* females that had been inside the cage since April 29. All 17 eggs were laid on *Sedum maximum*, though *S. album* was present too. Eight larvae developed to the pupal stage, from which six adults emerged on July 3 and subsequent days. The remaining two pupae did not emerge, but died and were removed later. The development of eggs required about 15 days, whereas the development of larvae took about 31 days and the development of pupae about 16 days. All adults emerged within three days. The entire developmental period of the second generation lasted about nine weeks. After the larvae became seven millimetres long, they were associated with *Lasius emarginatus* until the pupal stage. Since it was possible to find all pupae, cage 1 was used to study the development of the following generation also.

Development of the third generation. The butterflies of the second generation emerged on July 3 and the first copulation was observed on July 4. On July 5 the first eggs were found on *S. maximum*. Again *S. album* was not used for oviposition. Subsequently, nine larvae developed to the final stage. The larvae were first visited by *L. emarginatus* when they were about four millimetres long. Egg development required about nine days whereas the development of larvae took about 22 days and that of pupae about 13 days. At that time it was impossible to detect the pupae without taking apart the entire cage. On August 18 emerged the first adult of the third generation after a development from egg to adult of about 44 days. This butterfly remained alone and finally died between August 27 and 29. When the cage was inspected in autumn two live pupae were found hidden deeply in the plastic dish. However, six other pupae were not found.

Cage 2 and 2a. Development of the second generation. The female placed inside this cage laid eggs that we found on May 3. 40 eggs were attached to *Sedum maximum,* but 17 eggs also on *S. album*. L1-larvae were mining inside the leaves of the latter plant species but all of them died. 15 L1-larvae developed on *S. maximum,* feeding on the youngest leaves at the tip of the plants and after pupating from June 13 onwards. After some of the *S. maximum* plants had been totally defoliated by the feeding larvae three of the full-grown larvae continued feeding on *S. album*. However, after adding two *S. maximum* plants they returned to this food source. Finally, five pupae were detected only, but seven imagines emerged between June 30 and July 4. The inspection of the cage on September 20 revealed only one live pupa. Thus, seven individuals from the original 15 L1-larvae were missing at the end. Egg development required about 14 days whereas the development of larvae took about 29 days and the development of non-diapausing pupae about 16 days. The adults emerged during three days. The entire time of development lasted 8.5 weeks. *Tetramorium impurum* (Förster, 1850) ants were present when L1-larvae emerged, and first associations were observed one day later. Workers of *Formica glauca* were observed for the first time inside the cage and in association with the larvae when these reached 10 millimetres long.

Development of the third generation. On July 2 the first *S. orion* eggs were found on newly added *S. maximum* plants. No eggs were laid on *S. album*. The plants with the eggs were then transferred into cage 2a where larvae emerged after nine days. A thunderstorm destroyed this cage on July 20 and all larvae were lost.

Cage 3. Development of the second generation. On April 27 the first *S. orion* eggs were found on *S. maximum* plants in this still open cage. Eggs were laid between April 23 (day of installation of cage during cold and rainy weather) and April 27. Larvae emerged after 16 days, pupated after 41 additional days, and the pupal stage required about 17 days. Thus, the entire period from egg to adult comprised about 74 days. On June 21 two of the full-grown larvae drowned in a little puddle that formed after three days of rain. On July 8 one imago emerged while a pupae was found dead. 17 days after the emergence of larvae the first ants were detected inside the cage. At that time, the larvae already had a length of nine millimetres. *Formica* (*Serviformica*) *fusca* was the first ant species to be observed in a clear association with the *S. orion* larvae. One week later workers of *Tetramorium impurum* were found also. They were temporarily seen together with workers of *F. fusca* on the same shoot of a *S. maximum* plant but always at different *S. orion* larvae. Breeding was not continued in this cage.

Cage 4. Development of the second generation. The *S. orion*-female placed in this cage lived for 11 days, from 19 until 30 May. Oviposition took place during six days and resulted in 84 eggs, three on one *S. maximum* shoot, 61 eggs on

another, and 20 eggs on a third shoot. No eggs were found on many other available *S. maximum* shoots. Larvae emerged after 10 days, developed for 34 days, and the pupal stage lasted 13 days. The first adult emerged on July 21 and died on July 28. A second adult emerged on July 30 and died on August 2. These two adults died without reproductive success. On August 6 two other dead butterflies with undeveloped wings were detected. There was no more emergence. Developmental time from egg to adult took about 58 days. During the inspection of the cage on September 20, 21 living pupae were found. After all *S. maximum* plants became leafless many full-grown larvae continued feeding on *S. rupestre*, but returned to *S. maximum* when this plant species was provided again. No ants visited this cage.
Spring 2005. Altogether, 24 diapausing pupae survived the winter of 2004/2005. The adults emerged in late April 2005.

Discussion

This study focuses mainly on the phenology and voltinism of *S. o. orion*. It was especially important to have a high rate of field observations to detect the short, but clear breaks in flight activity between generations and to avoid misinterpretations resulting from bad weather conditions with no flight activity. Our continuous observations in the field as well as in cages show clearly that *S. o. orion* developed three generations in the study area during 2004.

So far as we could verify, previous reports of one or two generations per year were derived from single observations or collection specimens, but not from continuous observations of the development of individual specimens in the field. Moreover, Reinhardt (2003), Reinhardt & Hardtke (2003), and Reinhardt & Kinkler (2004) constitute their interpretations on samples of adults from small areas, but amalgamate samples from different years to one hypothetical year. Thus, these authors could not recognise the short interruptions in the flight activity between generations of *S. o. orion* because the phenology varies too much between years. Furthermore, the samples analysed from Saxony by Reinhardt (2003) and Reinhardt & Hardtke (2003) did not comprise voucher specimens from the entire period during which the adults of *S. o. orion* are on the wing.[1]

The development of three generations in the study area might be correlated to local circumstances and thus can not necessarily be generalised. We assume that the variable numbers of generations per year reported in the literature (Kudla 1951; Bergmann 1952; Forster & Wohlfahrt 1955; Henriksen 1982; Koch 1984; Tolman & Lewington 1998; Reinhardt 2003; Huemer 2004; Reinhardt & Kinkler 2004) are related to altitude and latitude of the habitats, and thus to different ecological conditions, i.e. temperature and length of growing season. These abiotic factors are well known to influence the

[1] It is anecdotal that lepidopterists from Dresden and its vicinity traditionally visit the *S. orion* habitats along the right edge of the Elbe during May since decades, combining their excursions with a visit in the nearby restaurants to enjoy the Asparagus season. Thus, voucher specimens from this area well represent the first generation, but significantly less so for subsequent generations.

developmental rate (Fischer & Fiedler 2002) and dormancy (Müller 1992) of insects. Thus, all data available suggest that *S. orion* has a plastic developmental strategy depending on local climatic conditions.

However, our study on *S. o. orion* did not compare the influence of, e.g. temperature in different populations. Instead, one population was investigated at a very restricted location and thus it can be assumed that all specimens observed were influenced by abiotic factors in the same manner. Besides the fact that *S. o. orion* develops three generations the synchronous development of diapausing and non-diapausing pupae in the second as well as the third generations is a phenomenon hitherto not recorded in the literature. The factors influencing the development of these diapausing pupae are still unknown since dormancy-inducing exogenic abiotic factors can be excluded at least for the second generation. Müller (1992) refers to the possibility of endogenic factors inducing dormancy in insects in the absence of exogenic dormancy-inducing factors. He calls such a prospective dormancy parapause. However, a prospective dormancy does not explain the coexistent development of diapausing and non-diapausing pupae. The strategy for a genotype to develop both non-diapausing and diapausing phenotypes in one generation is described by Hopper (1999) as "risk-spreading," though the mechanism underlying this risk-spreading and its genetical basis are still unknown. The discovery of this phenomenon in *S. o. orion* was unexpected. Thus, no statistically relevant numbers of diapausing and non-diapausing pupae were noted. However, the fact that this species has the ability for "risk-spreading" guarantees a maximum number of generations per year under the relevant local conditions – and thereby a higher offspring number. Moreover, the ability for "risk-spreading" may explain why only one or two generations are recorded for *S. orion* from areas with shorter vegetation periods as in mountain hills or at more northerly latitudes. It can also explain why a 'partially second generation' is frequently recorded for *S. o. orion* (Bergmann 1952; Coulondre 1994; Lepidopterologen-Arbeitsgruppe 1994).

All observations made in the study area revealed that larvae of *S. o. orion* developed on *Sedum maximum* while all larvae fed with *S. album* died. In contrast, Weidemann (1995) records that *S. orion* develops on *Sedum album* too, but it is questionable whether this record is just taken from Henriksen (1982) who mentions this host plant for *S. o. ultraornata* from Fenno-Scandia. Host plant quality can influence the development of insects, it can also influence diapause and voltinism under constant photoperiod and temperature as shown for *Choristoneura rosaceana* (Lepidoptera: Tortricidae) by Hunter et al. (1996). Such observations pose the question whether the varying voltinism observed for different *S. orion* populations may also depend on the host plant used by the larvae.

In the Elbe valley west of Dresden *S. o. orion* develops new generations as long as favourable conditions exist. Apparently, the third generation appears so late during the season that the adults do not reproduce successfully, but diapausing pupae of the second and third generations guarantee the survival of the population.

Our observations confirm that *S. orion* larvae are steady, but facultatively myrmecophilous, since larvae developed without ants in cage 4 as well. Until now, ant species associated with *S. orion* have only rarely been recorded (cf. Aigner-Abafi 1899; Malicky 1969; Fiedler 1991). In the present study, *Formica* (*Serviformica*) *glauca*, *Lasius* (*L.*) *emarginatus* (Formicinae), and *Tetramorium impurum* (Myrmicinae) were found in association with *S. orion* larvae for the first time. *Camponotus ligniperda* and *Formica* (*Serviformica*) *fusca* have also been observed in association with *S. orion*, which is already recorded by Fiedler (1991) and Saarinen (1995). Anyhow, the attractiveness of *S. orion* larvae for ants appears to be very high because all larvae in the field were found in association with ants. In fact, *S. orion* was one of the earliest European lycaenid species on which the phenomenon of myrmecophily was studied (Ehrhardt 1914; cf. Malicky 1969; Fiedler 1991).

Acknowledgements

The first author wishes to thank Rolf Entzeroth (Technical University Dresden) for participating in taking care of the diploma thesis. Barbara Ditsch and Ingo Uhlemann (Botanical Institute, Technical University Dresden) kindly provided and identified the *Sedum* plants. We thank Conny Hättasch and Katja Bochnig (Dresden) for their assistance in different technical matters. We appreciate the constructive discussions on *S. orion* and its host plants in the vicinity of Dresden with Hans-Jürgen Hardtke (Possendorf), Michael Kurze (Dresden), and Hanno Voigt (Dresden). Konrad Fiedler (Wien) provided critical and helpful comments on the manuscript, and Bernard Landry (Genève) kindly checked the English text.

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