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## Reproductive biology and strategies of nine meloid beetles from Central Europe (Coleoptera: Meloidae)

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### Abstract

The reproductive biology of meloid species from Central Europe is investigated by means of laboratory breeding experiments. They show that the total reproductive potential of meloids, with up to 40,000 eggs, largely exceeds prior data. Furthermore, the number of laid eggs strongly relates to the way by which the triungulins find their host. Clutch size correlates significantly with the size of the beetle, while egg size is independent of this. Both clutch size and egg size decrease with each oviposition. For some species, reproductive data are used to demonstrate how they have adapted to their habitat and to point out existing trade-offs. Based on the obtained results and on an evaluation of the relevant literature, three types of reproductive strategy can be distinguished within the meloids: (1) very high reproductive rates of open field species with phoretic larvae; (2) average reproductive rates of forest populations of species with phoretic larvae and of species the larvae of which search the nests of their hosts actively; and (3) small to average reproductive rates of those species depositing their clutches in the immediate proximity of their hosts' nests.

**Keywords:** *Coleoptera*, *host finding*, *life history*, *Meloidae*, *reproductive strategies*, *trade-off*, *triungulins*

### Introduction

Meloids, also known as oil beetles or blister beetles, are a globally distributed beetle family with about 2,500 species in approximately 120 genera (Bologna and Pinto 2002). They are characterized by the following traits distinguishing them from all other beetle families (cf. Bologna 1991; Pinto et al. 1996). (1) In most of the taxa the first, very mobile larval instar is a triungulin larva (Beauregard 1890; Böving 1924; MacSwain 1956; Selander 1991) that is responsible for the spreading and for finding the source of food. (2) With very few exceptions, the meloid larvae are parasites. Depending on the taxonomic position, the larvae feed on the clutches of common field grasshoppers or on the supplies and larvae of solitary bees (Paoli 1932; MacSwain 1956; Greathead 1962). (3) The larvae develop in a hypermetamorphosis (Fabre 1857, 1858). The development includes a quiescent stage

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resembling a pupa (coarctate phase) (Selander 1991). (4) According to the present state of knowledge, besides false blister beetles (Oedemeridae), meloids are the only animal group capable of producing the highly toxic substance cantharidin (Dettner 1997).

The unusual development of the meloids has been clarified mainly by the work of Siebold (1841), Newport (1851a, 1851b), Fabre (1857, 1858), Beauregard (1890) and Paoli (1932) (cf. also Bologna 1991). After a first triungulin larval stage (=primary larva), appearing in almost all taxa, except in the primitive Eleticinae subfamily, which probably includes non-parasitoid species (Pinto et al. 1996; Bologna and Pinto 2001), four grub-like stages follow (=secondary larva, first grub stage) representing the actual growth and feeding stages. A pseudonymph follows (larva coarctata), which is thought to be a resting stage. From this, again, a grub-like but inactive larva emerges (second grub stage), which moults to the final pupa, from which the imago will emerge. After the maturation stage of the imago, depending on the taxon, the eggs are laid in self-dug subterranean tubes, on a food plant, in the entrances of the nests of wild bees or directly in the nests of wild bees (Linsley and MacSwain 1942; Bologna 1991). The triungulins reach the sources of food by actively looking or by being phoretically carried to them.

Next to these characteristics some taxa exhibit very high ovipositing rates that largely exceed those recorded for other non-social insects. This applies, for example, for *Wagneronota aratae* (Berg) (Selander 1984), *Berberomeloe majalis* Linné (Cros 1912; Bologna 1989) as well as the *Meloe* species (e.g. Newport 1851a; Pinto and Selander 1970; Kifune et al. 1973), which are capable of laying several thousand eggs during their reproductive phase. Although the meloid's high reproductive potential confers them a remarkable position among non-social insects, up until now only very few comprehensive studies exist that deal with parameters relevant to reproduction. So far, no comprehensive survey has tried to clarify if and how meloids differ in their reproductive strategies. The reason for this lack resides, on the one hand, on the fact that until now, the emphasis of meloid research has been on taxonomic, systematic and behavioural studies, as well as on applied problems concerning pharmacological, agricultural, and veterinary medicine questions (Bologna and Pinto 2002). On the other hand, there is little knowledge about their ecology and for many regions of Central Europe the availability of experimental animals is very restricted.

The only comparative, systematic study about the reproductive biology of meloids deals with the species of the *Epicauta vittata* Dejean group (Adams and Selander 1979). Pinto and Selander (1970) studied several aspects of the oviposition and development of North American *Meloe*, and further modest studies of particular species or small groups of species shed light upon diverse aspects related to the reproductive biology, such as the number of eggs and the ovipositing frequency (e.g. Bianchi 1962; Selander and Mathieu 1964; Kifune et al. 1973, Church and Gerber 1977; Krishnan et al. 1996). In most cases, however, the known data are merely aspects of surveys concerning behavioural (e.g. Selander and Mathieu 1969) and developmental biology (e.g. Erickson and Werner 1974a, 1974b), taxonomy (e.g. Selander 1960; Pinto 1972, 1980a; Pinto and Bologna 1993; Bologna and Pinto 1995), faunistics (e.g. Vrabec 1993; Lückmann 1996), or summarizing papers about the biology (e.g. Newport 1851a, 1851b, 1852; Fabre 1857; Katter 1883; Beauregard 1890) or bionomy (e.g. Pinto 1980b; Selander 1984).

The present paper attempts to fill this gap for some species and presents the results of a comparative study of the reproductive biology of the Central European populations of nine meloid species belonging to three genera. For these species, information about clutch size, development time of the eggs, the relationship between reproductive parameters and the

habitat binding etc. is lacking almost completely. In what follows, the obtained distinguishing features of the reproductive biology of the studied species are presented, and the similarities and differences between the species' reproductive biology are pointed out and discussed against the backdrop of biology and ecology. Furthermore, it is considered if and how meloids can be classified according to criteria of reproductive biology.

## Material and methods

### *Investigated species*

The following species were investigated: *Meloe violaceus* Marsham, *M. proscarabaeus* Linné, *M. rufiventris* Germar, *M. scabriusculus* Brandt and Erichson, *M. rugosus* Marsham, *M. uralensis* Pallas, *M. decorus* Brandt and Erichson, and *Lytta vesicatoria* Linné and *Sitaris muralis* Foerster.

The beetles were collected in the field at the beginning of their activity period at different sites in Germany and Austria (for details see Table I).

Most of the species are very rare in Central Europe. Therefore, the number of investigated specimens of the various species differed considerably.

### *Rearing methods*

The rearing, based on the method described by Selander (1986) but adapted to our own requirements, was carried out as follows: the beetles were kept individually in labelled transparent plastic boxes (20 cm × 13 cm × 13 cm) with a slitted lid. Except for *M. decorus* and *S. muralis*, the bottom was filled up with 3 cm of moist sand serving as oviposition substrate, which was moistened regularly. Since breeding experiments carried out in 1998 showed that moist sand is not an adequate ovipositing substrate for *M. decorus*, dry soil was used. For *S. muralis*, a tube made of emery paper (height 15 cm, diameter 10 cm; granulation K 100) was used as substrate, as the literature has reported oviposition on house walls (e.g. Fabre 1857; Friese 1898) in which mason bees had set up their brood chambers. The beetles were kept under natural day–night light conditions at temperatures between 21 and 25°C during the day and between 15 and 18°C during the night. Because, on the one hand, the mating history of the female beetles was not known, and on the other hand, there is likely to be a correlation between mating and oviposition frequency and egg production, females regularly had the opportunity to mate.

Each beetle was weighed in the morning and in the late afternoon on a Sartorius MC1 laboratory balance (precision ± 1 mg).

A good food supply was achieved by feeding a surplus of fresh cleavers (*Galium aparine* Linné) and flowers of dandelion (*Taraxacum officinale* Weber) or the lesser celandine (*Ranunculus ficaria* Linné) for spring species, and with a mixed supply of blades of grass and flowers of dandelion for the autumn species *M. rugosus*. Specimens of *L. vesicatoria* were fed with common privet (*Ligustrum vulgare* Linné). The food for *Meloe* was replaced every morning and evening and was moistened with tap water from a laundry sprayer. The food for *L. vesicatoria* was renewed every second day. Faeces were removed daily. *Sitaris muralis* were not fed, since in previous investigations it was found that this species does not take up any food, except droplets of water (J. Lückmann, unpublished data). This finding is in contrast to Bologna (1991) who reported *S. muralis* as a phytophagous species and who summarized the scarce information on host plants.

*Parameters and procedure*

The following parameters were examined for each species:

- maximum frequency of ovipositions ( $FO_{\max}$ );
- mean interval between two successive ovipositions (IBO);
- mean egg clutch weight (ECW);
- mean egg clutch portion relative to the body weight before oviposition (ECP);
- mean egg length (EL) and mean egg width (EWI);
- mean egg weight (EWE) and mean egg weight per mm pronotum length;
- mean egg number per oviposition (EN) and mean egg number per oviposition per mm pronotum length;
- mean development time of the larvae until hatch (DT);
- maximum total egg number of a species ( $TEN_{\max}$ ).

The following parameters were examined with successive oviposition for each specimen of those species for which the number of ovipositions exceeded half of the maximum number of ovipositions of a current species:

- egg clutch weight per mm pronotum length.
- egg weight per mm pronotum length.
- egg number per oviposition per mm pronotum length.

Table I. Source and number of investigated species. Investigated species (with subgenera and abbreviations), their sampling dates and origins, and numbers of investigated females.

Species (subgenera and abbreviation)	Sampling date	Site	No. of females
<i>Meloe (Meloe) violaceus</i> Marsh. ( <i>M. vio.</i> )	10 April 2000	Stopfenreuth near Vienna (Austria), fertile plain of the Danube	17
<i>Meloe (Meloe) proscarabaeus</i> L. ( <i>M. pro.</i> )	25 March 2000	Warburg near Kassel (Germany), valley of the Diemel river	10
<i>Meloe (Meloe) rufiventris</i> Germ. ( <i>M. ruf.</i> )	31 March 2001		26
<i>Meloe (Meloe) rufiventris</i> Germ. ( <i>M. ruf.</i> )	27 April 2002	Mallnow near Lebus (Germany), valley of the Oder river	4
<i>Meloe (Eurymeloe) scabriusculus</i> Br. and Er. ( <i>M. sca.</i> )	30 April 2003		2
<i>Meloe (Eurymeloe) rugosus</i> Marsh. ( <i>M. rug.</i> )	13 April 2000	Surroundings of the Neusiedlersee (Austria)	4
	16 April 2004		6
<i>Meloe (Micromeloe) decorus</i> Br. and Er. ( <i>M. dec.</i> )	8 October 2001	Magdeburg (Germany), fertile plain of the Elbe river	13
	14 April 2004	Surroundings of the Neusiedlersee (Austria)	2
	11 April 2000	Surroundings of the Neusiedlersee (Austria)	2
	17 March 2002	Phillipsburg near Karlsruhe (Baden- Württemberg, Germany), Rhine dike	13
<i>Meloe (Micromeloe) uralensis</i> Pall. ( <i>M. ura.</i> )	11 April 2000	Surroundings of the Neusiedlersee (Austria)	7
	16 April 2004		3
<i>Lytta vesicatoria</i> (L.) ( <i>L. vesi.</i> )	27 June 2002	Flörsheim-Dahlsheim near Worms (Germany), railway embankment	28
<i>Sitaris muralis</i> (Foerst.) ( <i>S. mur.</i> )	24 August 1986	Landau near Karlsruhe (Germany), house garden (not available in 2003)	34 <sup>a</sup>
	10 August 2002	Frankfurt (Germany), house wall	2
	30 July 2003	Bonn (Germany), house wall	2
	1 August 2003	Frankfurt (Germany), house wall	2

<sup>a</sup>Received dead and preserved in ethanol.

The elytrae of the *Meloe* species are much shorter than the abdomen and based on personal observations, until oviposition their abdominal size increases with increasing size of the developing eggs. Therefore, the pronotum length of all investigated species was determined as a measure of body size.

Egg clutches were carefully dug out of the soil (except for the eggs of *S. muralis*, which were deposited on the surface of the emery paper tube), cleaned of sand grains and soil particles, and weighed. Shortly after oviposition, length and width of 30 eggs from each egg clutch was determined using a stereo light microscope (magnification  $32\times$ ) with a measurement eyepiece. This was followed by the determination of the number of eggs. For *M. violaceus*, *M. rufiventris*, *M. uralensis*, *M. decorus*, and *L. vesicatoria*, all eggs of an egg clutch were counted. For *M. proscarabaeus*, *M. scabriusculus*, and *M. rugosus*, the egg number was estimated by extrapolation: from each egg clutch a sample of eggs was weighed and counted, the total number of eggs in each clutch being estimated from its total weight. Counting the eggs in water-filled Petri dishes prevented the eggs from being damaged. After the egg surfaces had dried, the eggs (except those of *S. muralis*, which were left on the tube) were transferred into small, sand-filled plastic tubes (height and diameter: 6.5 cm), approximately 2 cm deep. The eggs of *S. muralis* were covered by a sticky substance, which made it impossible to separate them without destruction. Therefore the egg numbers of this species were determined by counting the larvae after hatch. All eggs were incubated in a climatic chamber at 20°C. Triungulin hatch from eggs and their emergence on the sand surface (except for *S. muralis*) was recorded daily. In order to simulate the natural soil conditions to which *M. violaceus* is exposed, the plastic tubes were transferred into a climatic chamber with a temperature of 12°C after larval hatch but preceding their emergence at the surface. After five months, the tubes were transferred back to the climatic chamber set at 20°C.

All female beetles were dissected to evaluate the presence of chorionized eggs in the ovarioles, such a presence indicating that an additional oviposition would have been possible. The number, length, and width of such eggs was determined as described above.

### Calculations

Egg weight (EWE) [ $\mu\text{g}$ ] = Egg clutch weight [mg]/Number of eggs [ $n$ ]  $\times$  1000.

Egg clutch proportion relative to the body weight before the oviposition (ECP) [%] = egg clutch weight [mg]/beetle's body weight determined last before oviposition [mg]  $\times$  100.

Means and standard deviations were calculated for the following parameters: interval between two ovipositions, egg clutch weight, weight proportion of the egg clutch relative to the body weight before oviposition, egg weight, egg length, egg width, number of eggs per clutch and larval development time from oviposition to larval hatch.

Based on all means of the individual beetles, the total average and the respective standard deviation were calculated for each species. For all parameters and each species, the minimum and maximum values were determined.

### Statistics

If data followed a normal distribution and the variances were homogeneous, mean values were compared using a unifactorial ANOVA, followed by multiple comparisons with LSD

post hoc tests. If assumptions for a unifactorial ANOVA were not met, a Kruskal–Wallis ANOVA was carried out, followed by a Mann–Whitney *U* test.

The following correlations were analysed:

1. Beetle size (expressed as pronotum length) against the species' mean egg clutch weight, mean egg number, or mean egg weight per female.
2. Oviposition number against egg clutch weight per mm pronotum length, egg number per mm pronotum length or mean egg weight per mm pronotum length; in order to eliminate the influence of females with low oviposition frequency, only females with an oviposition abundance exceeding half of the maximum number of observed ovipositions of a current species were taken into consideration. Such species were considered with samples of at least seven females.

For the relationships in (1) Pearson's product moment correlation and for those in (2) Spearman's rank correlation coefficient were calculated, with  $r$ =coefficient of correlation and  $b$ =regression coefficient (slope of the regression line).

Results of statistical analysis with an error probability  $P \leq 0.05$  were considered as relevant. The software used to perform statistical analyses was SPSS Windows 10.1.3 (SPSS Inc., Chicago, IL, USA).

Due to regular oviposition by *M. proscarabaeus*, *M. scabriusculus*, *M. rugosus*, *M. decorus*, *Lytta vesicatoria*, and *Sitaris muralis*, it can be assumed that the breeding conditions used were adequate. However, for *M. violaceus*, *M. rufiventris*, and *M. uralensis* no optimal breeding conditions could be established.

## Results

### *Number of studied animals and egg clutches*

Out of the 141 individuals used for rearing, 126 oviposited and laid a total of 391 egg clutches. Eleven out of the 15 *M. violaceus* individuals and two out of the six *M. rufiventris* individuals did not lay any eggs; by dissecting the ovaries, however, the numbers of eggs and their proportions (see above) were determined. For 19 out of the 34 females from Landau, which were conserved in ethanol and received in 2003, the egg numbers and their proportions were determined (Table II). Thus, on the whole, 423 clutches were used for the analysis of the parameters described as relevant to reproduction. The results are summarized up in Table II.

### *Oviposition*

The following differences concerning oviposition were determined between the various species:

- The *Meloe* species preferred the hours of the night for oviposition, while *L. vesicatoria* laid its eggs mainly during the day. Thus, for *M. proscarabaeus*, *M. rugosus*, and *M. decorus*, 76%, 53%, and 54% respectively, of ovipositions took place at dusk or night, while for *L. vesicatoria*, 64% of ovipositions took place during the day.
- Except for *M. decorus*, the soil tubes were at least as deep as the body length of the ovipositing female, thus completely hiding the animals during oviposition. *Meloe decorus*, however, dug small hollows with a maximum depth of 1 cm, so usually only the female's

Table II. Parameters of reproduction.

Species	N	EC	FO <sub>max</sub>	EN <sup>a</sup> ± SD (range) <sup>b</sup>	TEN <sub>m-ax</sub>	IBO <sup>a</sup> ± SD (range) <sup>b</sup> (d)	DT <sup>a</sup> ± SD (range) <sup>b</sup> (d)	EL <sup>a</sup> ± SD (range) <sup>b</sup> (mm)	EWI <sup>a</sup> ± SD (range) <sup>b</sup> (mm)	ECW <sup>a</sup> ± SD (range) <sup>b</sup> (mg)	ECP <sup>a</sup> ± SD (range) <sup>b</sup> (%)	EWE <sup>a</sup> ± SD (range) <sup>b</sup> (µg)
<i>Meloe violaceus</i>	15 <sup>c</sup>	15	1 <sup>d</sup>	1903 ± 782 AD (400–3800)	n.a.	n.a.	124.2 ± 1.7 A (123–127)	1.76 ± 0.10 A (1.60–1.95)	0.50 ± 0.03 A (0.40–0.60)	605.4 ± 111.9 A (510–740)	39.9 ± 4.6 A (33.1–43.3)	253.3 ± 54.5 A (172.4–287.8)
<i>Meloe proscarabaeus</i>	34	76	6	6194 ± 1664 B (3100–9700)	39,950	7.7 ± 1.3 A (5–11)	21.4 ± 0.8 B (20–23)	1.13 ± 0.04 B (0.95–1.30)	0.36 ± 0.01 B (0.32–0.40)	565.8 ± 165.5 A (170–930)	39.9 ± 5.0 A (21.4–52.5)	92.4 ± 5.6 B (76.3–109.0)
<i>Meloe rufiventris</i>	6 <sup>c</sup>	7	2 <sup>d</sup>	2960 ± 500 CG (2570–3685)	n.a.	7	19.8 ± 0.5 C (19–20)	1.24 ± 0.07 C (1.08–1.40)	0.40 ± 0.04 C (0.35–0.48)	387.8 ± 21.6 B (363–411)	31.9 ± 4.4 B (25.7–35.7)	124.2 ± 20.6 C (108.9–153.8)
<i>Meloe scabriusculus</i>	10	53	11	3433 ± 1605 C (1500–6200)	39,733	3.6 ± 0.9 B (2–9)	22.8 ± 0.6 D (21–24)	0.71 ± 0.02 D (0.55–0.78)	0.26 ± 0.01 D (0.23–0.30)	112.5 ± 57.8 D (27–220)	18.7 ± 2.4 C (6.1–26.7)	32.1 ± 2.9 D (25.5–37.7)
<i>Meloe rugosus</i>	15	80	10	2404 ± 646 DG (1100–3850)	25,175	4.6 ± 1.0 B (3–10)	18.5 ± 0.9 E (17–21)	0.61 ± 0.03 E (0.50–0.85)	0.23 ± 0.01 E (0.20–0.28)	46.9 ± 14.7 C (21–76)	18.6 ± 2.4 C (6.8–23.1)	19.2 ± 1.8 E (12.8–22.2)
<i>Meloe decorus</i>	15	76	8 <sup>d</sup>	1128 ± 234 EF (500–1570)	10,610	2.5 ± 0.7 C (1–5)	12.1 ± 0.7 F (10–15)	0.87 ± 0.04 F (0.53–1.03)	0.32 ± 0.01 F (0.23–0.40)	66.1 ± 16.0 CD (26–97)	18.5 ± 2.4 C (9.1–25.1)	58.3 ± 6.1 F (42.0–76.0)
<i>Meloe uralensis</i>	10	11	2 <sup>d</sup>	1398 ± 273 AEF (1050–1900)	n.a.	2	15.6 ± 1.5 G (12–18)	0.93 ± 0.06 G (0.80–1.00)	0.34 ± 0.02 FG (0.30–0.38)	93.1 ± 23.2 D (60–120)	20.9 ± 4.2 C (13.5–27.4)	66.4 ± 8.3 F (53.3–77.4)
<i>Lytta vesicatoria</i>	28	81	5	941 ± 367 F (72–1500)	5,542	9.2 ± 2.9 A (3–17)	17.8 ± 0.6 E (16–19)	1.13 ± 0.04 B (0.70–1.40)	0.33 ± 0.01 F (0.20–0.40)	85.6 ± 36.7 D (7–157)	27.2 ± 5.6 B (4.5–38.4)	90.3 ± 9.2 B (60.0–132.2)
<i>Sitaris muralis</i>	25 <sup>f</sup>	25	1	1700 ± 472 ADE (427–2660)	2,660	0	29.2 ± 2.0 H (26–32)	0.88 ± 0.02 F (0.75–1.0)	0.30 ± 0.01 G (0.25–0.35)	81.2 ± 43.6 CD (27–152)	57.2 ± 4.3 D (51.0–62.5)	53.4 ± 9.7 F (38.4–63.2)

N, number of ovipositing females; EC, number of investigated egg clutches; FO<sub>max</sub>, maximum observed number of ovipositions; EN, mean egg number per oviposition; TEN<sub>max</sub>, maximum total egg number laid by a female; IBO, mean interval between two successive ovipositions; DT, mean development time of the larvae until egg hatch; EL, mean egg length; EWI, mean egg width; ECW, mean egg clutch weight; ECP, mean egg clutch portion relative to the body weight before oviposition; EWE, mean egg weight per oviposition.

n.a., not applicable.

Mean values within a column followed by different capital letters are significantly different ( $P < 0.05$ ).

<sup>a</sup>Calculated from the means of all females; <sup>b</sup>minimum and maximum values determined from all egg batches; <sup>c</sup>calculation of DT, ECW, ECP, and EWE based on four egg-laying females, calculation of EN, EL, and EWI on additional 11 dissected females; <sup>d</sup>dissection of the ovaries showed that an additional oviposition would have been possible; <sup>e</sup>calculation of DT, ECW, ECP, and EWE based on four egg-laying females; EN, EL, and EWI on additional two dissected females; <sup>f</sup>calculation of DT, ECW, ECP, and EWE based on six egg-laying females; EN, EL, EWI, and TEN<sub>max</sub> on additional 19 dissected females.



abdomen was hidden. Therefore, the laid eggs were directly deposited under the soil surface and sometimes even visible when looking from above.

- Having completed the oviposition and sealing the tube, the females of the *Meloe* species and of *L. vesicatoria* began food intake, while *S. muralis* did not eat anything during the whole activity period.
- After the sealing of the soil tube, the egg clutches of all of the *Meloe* species and of *L. vesicatoria* were surrounded by the substrate. On the other hand, the clutches of *M. rugosus* from the fertile plains of the Elbe river near Magdeburg always had a hollow space surrounding them; the hollow space above the clutch was up to 10 mm high, and up to approximately 3 mm wide. However, such a hollow space was lacking for the clutches laid by *M. rugosus* from the dry location at the Neusiedlersee in Austria.

*Frequency of oviposition, interval between two successive ovipositions, number of eggs, and development time of the larvae*

Between the species, the maximum frequency of oviposition ( $FO_{\max}$ ) varied quite considerably. While for *M. rugosus* and *M. scabriusculus* up to ten or eleven egg clutches per individual were observed respectively, *S. muralis* only laid eggs once. The dissection of the *M. decorus* individuals that had oviposited eight times showed that for one of the animals its ovaries were still filled with ripe, chorionized eggs. Thus, we may assume that a ninth oviposition would still have been possible. For the other species that could be analyzed, five to six ovipositions per female were determined.

With 9.2 days, *L. vesicatoria* showed the highest mean interval between two successive ovipositions (IBO); the shortest was determined for *M. decorus* with 2.5 days. In some cases, females of this species even laid eggs on two successive days. For *M. scabriusculus* and *M. rugosus*, the mean interval amounted to 3.6 and 4.6 days respectively, and did not differ statistically.

The mean number of eggs per clutch (EN) varied both between and among species. This became obvious when observing the large standard deviations and the large differences between minima and maxima. This resulted from the fact that the number of eggs depended on the beetle's size (expressed as length of the pronotum, see below). The highest mean number of eggs per clutch was observed in *M. proscarabaeus*, amounting to 6,194. For some specimens of this species, the number of laid eggs amounted to almost 10,000. The lowest mean number of eggs per clutch amounted to 941 in *L. vesicatoria*, while in one case a clutch consisted of 72 eggs. The relationship between the species *M. proscarabaeus* and *M. violaceus*, which belong to the nominate subgenus was remarkable: in the former species, a clutch on average consisted of more than three times as many eggs as in the latter.

With almost 40,000 eggs, the highest maximum total number of eggs ( $TEN_{\max}$ ) was determined in *M. proscarabaeus* and *M. scabriusculus*, *S. muralis* exhibited the lowest number, with 2660 eggs.

The mean development time of the larvae till the hatch (DT) was longest in *M. violaceus*, amounting to 124.2 days, and thus exceeded 10-fold that of *M. decorus*, which with a development time of 12.1 days, had the fastest developing eggs among the studied species. When compared with *M. proscarabaeus*, the larvae of *M. violaceus* needed about six times as long until they hatched. Apart from that, differences between species of the same subgenus were small. Thus, species of the subgenus *Eurymeloe* on average needed 18.5 (*M. rugosus*) and 22.8 (*M. scabriusculus*) days, those of the subgenus *Micromeloe* between 12.1 (*M.*

*decorus*) and 15.6 (*M. uralensis*) days. Within the species, the development time varied very little. The standard deviation never exceeded 2 days.

After the hatch, while sclerotizing, the *Meloe* and *Lytta* larvae remained for 2–3 days in the substrate, before emerging at the surface. By contrast, the larvae of *M. violaceus* left the substrate after having been kept for 5 months at approximately 12°C and subsequently having been kept at 20°C. The larvae of *S. muralis* remained motionless in a clump under the layer of empty eggshells.

#### *Characteristic features of the eggs and its proportions*

The eggs of the surveyed species were oval, one of the ends being wider and having a blunter rounding off than the other. The eggs of all of the *Meloe* species were between dark and light orange, those belonging to *L. vesicatoria* and *S. muralis* had a whitish colour. In contrast to the other species, the eggs of *S. muralis* were covered by a transparent, oily and sticky substance, which was almost insoluble in water and had the eggs sticking strongly together. At the narrower end of the egg, the substance shaped into a drop that appeared to be part of the egg. Even after the hatch of the larvae, the empty eggshells stuck together, offering shelter to the larvae, which remained motionless under them (see above).

Depending on the species, the eggs were between 0.5 and 2.0 mm long, the width being approximately one-third of the length. The mean egg length (EL) and width (EWI) of the various species in almost all cases significantly differed from one another, respectively (Table II). On average, *M. violaceus* laid the largest eggs. These eggs were almost three times as long and more than twice as wide as those from *M. rugosus*, which laid the smallest eggs. Furthermore, the difference between the mean egg proportions of *M. violaceus* and *M. proscarabaeus* deserves a particular mention: the eggs of the former species were approximately one and a half times longer and wider than those of the latter.

#### *Egg weights*

Also between the mean egg clutch weights (ECW) of the studied species, large differences were found. *Meloe violaceus* and *M. proscarabaeus* laid the heaviest egg clutches, with weights of 605.4 and 565.8 mg, respectively, while *M. rugosus* laid the lightest, weighing 46.9 mg. The mean clutch weights of the species belonging to the subgenus *Eurymeloe* differed significantly from one another (LSD test: mean difference=14.2378,  $P<0.05$ ).

In order to be able to consider the reproductive effort independently of the individual's size, the proportion of the clutch weight relative to the body weight preceding oviposition was determined (ECP). This value was highest for *S. muralis*, with 57.2% (in one case it reached 62.5%), for *M. scabriusculus*, *M. rugosus*, and *M. decorus* it was lowest with about 18.6%. Within any subgenus, this proportion remained roughly invariable, amounting to 39.9% in the subgenus *Meloe*, and varying between 18.6 and 18.7% in the subgenus *Eurymeloe*, and between 18.5 and 20.9% in *Micromeloe*. The reproductive effort of *M. rufiventris* and *L. vesicatoria* was approximately the same, with 31.9 and 27.2% respectively.

The relationships found for the egg weights (EWE) resemble the ones found for the egg proportions. With 253.3 µg, *M. violaceus* laid the heaviest eggs and *M. rugosus*, with 19.2 µg, the lightest. The eggs laid by *M. violaceus* on average were almost 2.7 times as heavy as those of the closely related species *M. proscarabaeus* (LSD test: mean difference=160.7814,  $P<0.001$ ), those of *M. scabriusculus* were significantly heavier than those of *M. rugosus* (LSD test: mean difference=14.2378,  $P<0.05$ ). Those laid by

*M. decorus* and *M. uralensis* did not differ significantly (LSD test: mean difference=6.0590,  $P>0.05$ ).

#### Correlation between parameters relevant to reproduction and the animal's size

For all species that were analyzed, a positive, statistically significant relation between the mean clutch weight (RBCW) or, respectively, the mean clutch size (RBEN) and the beetle's size—expressed as length of the pronotum—was given (Table III; Figures 1, 2). Nevertheless, the egg weight (RBEW) was shown to be independent of the body size for most species. An exception was *M. proscarabaeus* (Pearson correlation:  $r=0.491$ ,  $P=0.003$ ), for which a significant relation was observable.

#### Correlation between parameters relevant to reproduction in the course of the reproductive period

Since this analysis required a minimum sample size of seven animals, it could only be carried out for *M. proscarabaeus*, *M. rugosus*, *M. decorus*, and *L. vesicatoria* (Table IV). For all of these species, the number of eggs (EN) and the egg weight (EWE) decreased with each oviposition, consequently so did the clutch weight (ECW). With the exception of *M. rugosus*, the decrease in egg weight was significant in all of the considered species. For the parameter clutch weight, this reduction was significant for *M. rugosus*, *M. decorus*, and *L. vesicatoria*, for the parameter egg number it was significant for *M. rugosus* and *L. vesicatoria*.

## Discussion

### Reproductive capacity

As shown by the results described here, the reproductive potential of meloids is even larger than previously assumed. Not only the frequency of oviposition, but also the mean and

Table III. Female size and parameter correlation. Correlation between beetle size (expressed as length of the pronotum) and, respectively, one of the following parameters: mean egg clutch weight per female (RBCW), mean egg number per female (RBEN), and mean egg weight per female (RBEW).

Species	N	RBCW		RBEN		RBEW	
		<i>b</i>	<i>r</i>	<i>b</i>	<i>r</i>	<i>b</i>	<i>r</i>
<i>Meloe violaceus</i>	4 <sup>a</sup>	215.4	0.998**	1505	0.815***	-23.08	-0.220
<i>Meloe proscarabaeus</i>	34	367.3	0.805***	3322	0.768***	7.63	0.491**
<i>Meloe rufiventris</i>	41		n.a.		n.a.		n.a.
<i>Meloe scabriusculus</i>	10	145.1	0.890**	4159	0.918***	1.88	0.232
<i>Meloe rugosus</i>	15	43.6	0.732**	1962	0.747**	3.00	0.391
<i>Meloe decorus</i>	15	66.4	0.895***	1023	0.942***	6.34	0.224
<i>Meloe uralensis</i>	10	67.0	0.687*	1223	0.776**	2.19	0.063
<i>Lytta vesicatoria</i>	28	89.5	0.881***	911	0.897***	7.06	0.278
<i>Sitaris muralis</i>	6 <sup>b</sup>	157.7	0.837*	3229	0.872***	-27.73	-0.647

N, number of females; *b*, regression coefficient; *r*, Pearson's product moment correlation coefficient.

n.a., not applicable, since three out of four females at RBCW and RBEW and four out of seven females at RBEN had the same pronotum length.

\* $P<0.05$ , \*\* $P<0.01$ , \*\*\* $P<0.001$ .

<sup>a</sup>Calculation of RBCW and RBEW based on four ovipositing females, RBEN on an additional 11 dissected females; <sup>b</sup>calculation of RBCW and RBEW based on six ovipositing females, RBEN on an additional 19 dissected females.

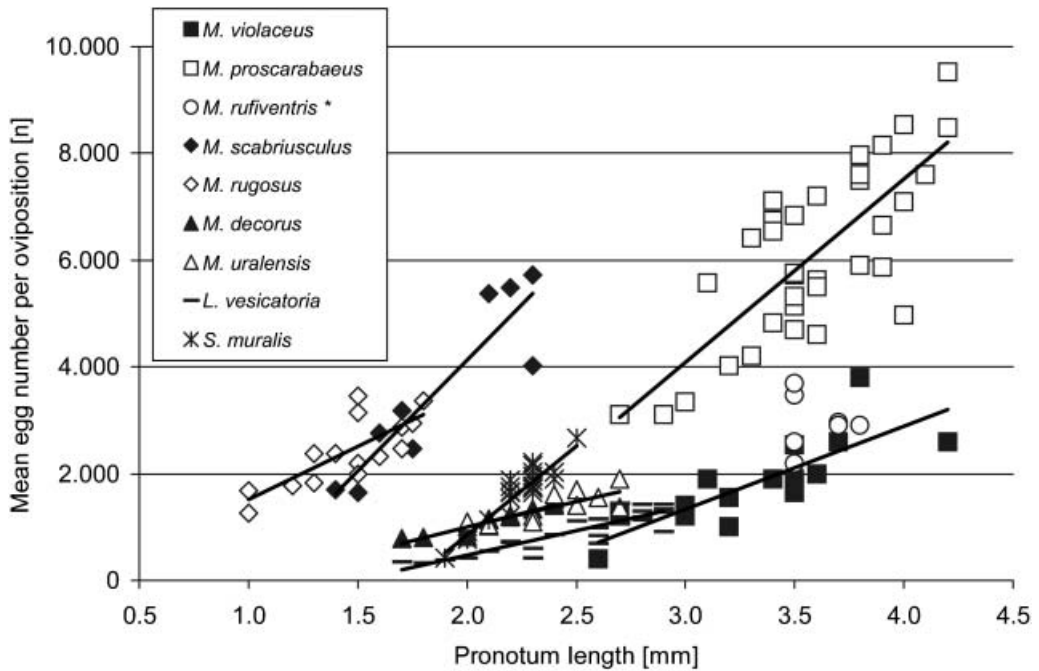


Figure 1. Correlation between mean egg number per oviposition and female and the beetle's size (expressed as pronotum length), determined separately for each species (\*not applicable for *Meloe rufiventris*, since four out of seven females had the same pronotum length).

maximum clutch size as well as the total reproductive rate of the surveyed species exceed, in some cases considerably, the correspondent available values of other species (a summary of the data about the reproductive biology, as found in the available literature, can be found in Table V). Up to now, in the genus *Meloe*, the maximum frequency of reported ovipositions amounted to six in *M. dianella* Pinto and Selander (Pinto and Selander 1970), whereas in this survey 11 ovipositions were observed in *M. scabriusculus*. Higher frequencies of oviposition are only known for species of the *Epicauta vittata* group, with a maximum of 22 ovipositions (Adams and Selander 1979).

With up to 10,000 eggs per clutch, *M. proscarabaeus* largely exceeds the former maximum number of 6,572 eggs reported for *M. menoko* Kono (Kifune et al. 1973). Due to the dependence between the mean egg number per clutch and the size of the females (Figure 1; Table III; note that size depends on the amount of food available for the larvae in the bee nests), between the individuals of a species a strong variation in clutch size results (Table II); this is illustrated by the often large standard deviation.

With 25,175 eggs for *M. rugosus* and almost 40,000 eggs for *M. scabriusculus* and *M. proscarabaeus*, their total reproductive performances also considerably surpass the highest numbers formerly observed in meloids, with 17,200 eggs for *M. menoko* (Kifune et al. 1973). Very large clutches were also observed in *Cissites auriculata* Champion. Bianchi (1962) estimated that a clutch he had found in the field comprised about 22,800 eggs. However, he stresses that the clutch should very likely belong to several animals that had successively added to it. When considering data about reproductive performance, one must always take into account that the individual total egg number (as well as the number of ovipositions) will obviously always depend on the females' life expectancy and on the

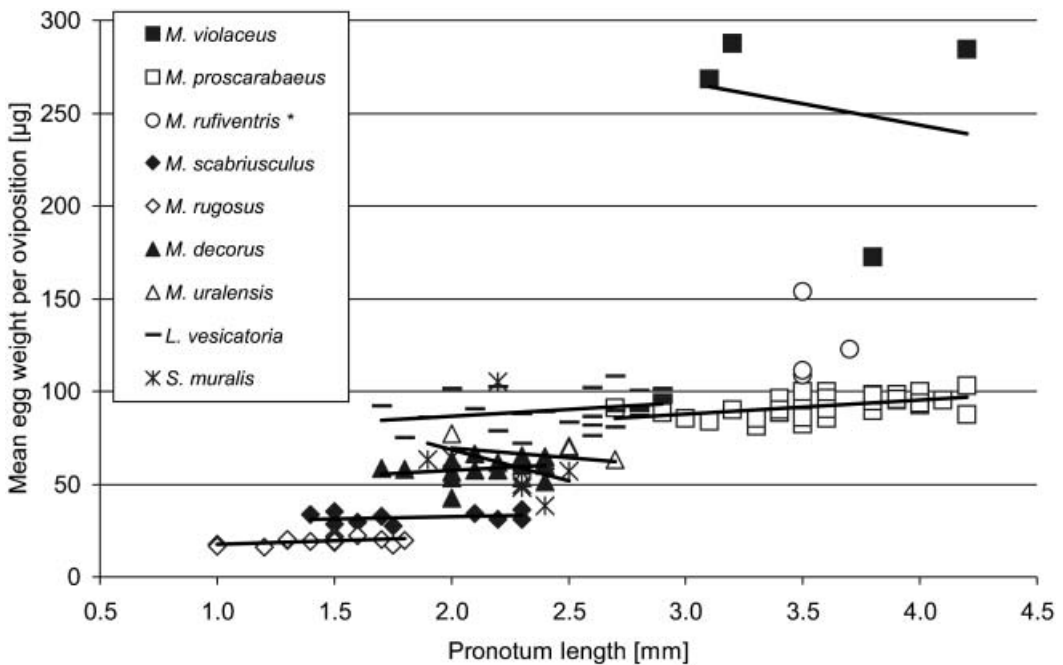


Figure 2. Correlation between mean egg weight per oviposition and female and the beetle's size (expressed as pronotum length), determined separately for each species (\*not applicable for *Meloe rufiventris*, since three out of four females had the same pronotum length).

Table IV. Modification of the standardized reproduction parameters with each further oviposition. Correlation between oviposition number and, respectively, one of the following parameters: egg clutch weight (ECW) per mm pronotum length, egg number (EN) per mm pronotum length, and egg weight (EWE) per mm pronotum length, calculated for females with oviposition abundance exceeding one half of the maximum observed number of ovipositions of the respective species.

Species	N	ECW		EN		EWE	
		<i>b</i>	<i>r</i>	<i>b</i>	<i>r</i>	<i>b</i>	<i>r</i>
<i>M. pro.</i>	21	-6.18	-0.202	-43.3	-0.140	-0.55	-0.295**
<i>M. rug.</i>	7	-1.57	-0.478***	-37.1	-0.309**	-0.17	-0.158
<i>M. dec.</i>	7	-1.89	-0.552***	-11.0	-0.187	-1.23	-0.548***
<i>L. vesi.</i>	15	-5.31	-0.503***	-27.8	-0.230*	-2.63	-0.461***

N, number of females; *b*, regression coefficient; *r*, Spearman's rank correlation coefficient.

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .

interval between two ovipositions. Therefore, it is to be expected that for some of the species, the data supplied by the literature will be subject to some corrections.

In some cases, the egg-laying performances of the meloids surpass those of other beetle and non-social insect species many times over. Depending on the considered taxonomic group, between one and several dozen (compare Table V) (e.g. species of the genera *Eletica*, *Hycleus*, *Linsleya*, *Epicauta*, and *Gnathium*), several hundred (e.g. species of the genera *Pyrota*, *Pseudopyrota*, *Lytta*, *Meloe*, and *Zonitis*), or a few thousand eggs (e.g. species of the genera *Wagneronota*, *Berberomeloe*, *Cissites*, and *Meloe*) are laid.

For the carabids *Carabus granulatus* Linné and *Pterostichus quadrifoveolatus* Letzner, Thiele (1977) mentions mean total egg numbers that amount to 41 and 136, respectively. According to Klausnitzer (2002), e.g. *Melolontha hippocastani* Linné lays a total of 60–80 eggs, *Dytiscus marginalis* Linné up to 1000, and *Leptinotarsa decemlineata* (Say) up to 2,500. The clutches of the females belonging to butterfly *Lymantria dispar* Linné comprise approximately 800 eggs (Dettner and Peters 1999). For the dragonfly *Pyrhosoma nymphula* Sulzer, Corbet (1999) estimates the possible total number of laid eggs at about 8,500.

### Reproduction investments

Usually, within a given species, large individuals produce more offspring (Fox and Czesak 2000). This relationship was observed in all of the studied species (Figure 1), confirming also the results found for the species of the *E. vittata* group (Adams and Selander 1979). Except for *M. proscarabaeus*, for which a significant positive correlation between egg weight and animal size was found (Table III; Figure 2), the egg weight was independent of the ovipositing female's size. This could have a positive effect on the larvae, since the larger offspring of many insects (note that egg weight here is used synonymously to offspring size) grow faster, are more robust in the face of environmental influences, become larger, and their developing juveniles also have a higher survival probability (Fox and Czesak 2000).

During the reproductive period, the egg number and weight decreased with each oviposition for *M. proscarabaeus*, *M. rugosus*, *M. decorus*, and *L. vesicatoria*. For the egg weight of *M. proscarabaeus*, *M. decorus*, and *L. vesicatoria* this relationship was significant, for the egg number a significance was found in *M. rugosus* and *L. vesicatoria* (Table IV). Thus, these results are in contrast with the results of Adams and Selander (1979), who for the species of the *E. vittata* group reported a constancy of clutch sizes over time (changes in egg volume were not considered). Therefore, larvae, as for *M. proscarabaeus*, may not only profit from having larger mothers (see above), but also from hatching from eggs that have been laid sooner in the reproductive period. However, it is unclear if the reduction in the larvae's size, as observed with each oviposition, is somehow biologically relevant.

### Trade-offs

Nevertheless, larger species do not necessarily produce more offspring. On the contrary, a female's reproductive resources are always limited, thus leading to a negative correlation between number and size of the offspring. Therefore, the division of the available resources between number and size of the offspring is a characteristic compromise for each species and has to be interpreted as an adaptation of the life cycles to the respective living conditions (Stearns 2000). The reproductive effort, having been determined as the proportion of the clutch weight relative to the body weight preceding the oviposition, does not vary statistically within any one *Meloe* subgenus. However, the division of resources into number and size of the offspring can in some cases differ quite strongly. Thus, while *M. proscarabaeus* invests mainly into the number of offspring, *M. violaceus* invests mostly into their size.

A different relationship exists between *M. proscarabaeus* and *M. scabriusculus* and *M. rugosus*. The lower mean clutch size of the two latter species is compensated for with a higher ovipositioning frequency, thus levelling out the total reproductive output of the three species.

No differences in the reproductive biology were found between *M. decorus* and *M. uralensis*. Exhibiting a similar reproductive effort, both species on average lay similar numbers of similarly weighing eggs. When compared with *M. scabriusculus* and *M. rugosus*, however, they invest their similar relative reproductive effort mainly into offspring size, while *M. scabriusculus* and *M. rugosus* invest into their number. The different trade-offs in the two groups of species are probably due to differences in their host-finding strategies. Since the phoretic host-finding of *M. rugosus* and *M. scabriusculus* implies that their larvae have a reduced probability to reach a suitable host, by comparison to those of *M. decorus* and *M. uralensis*, a compensation with high numbers of offspring is mandatory. On the other hand, it is understandable that *M. decorus* and *M. uralensis* generate larger and thus probably fitter larvae, since their hosts are actively searched for (see below).

#### *How to find a host and risk of mortality*

The high reproductive rates of the *Meloe* species are probably due to high larval losses. The triungulins of the *Meloe* species, while waiting on flowers for a suitable host, attach themselves to all hairy insects visiting these flowers (Fabre 1858; Precht 1940), resulting in larvae being repeatedly found e.g. on honeybees, dipterans, coleopterans, and lepidopterans (Cros 1931; Lückmann and Kuhlmann 1997). However, Harrington (1895) (quoted by Pinto and Selander 1970) showed that the larvae are at least partially capable of choosing. Though the larvae of an unknown *Meloe* species were repeatedly found on *Lasioglossum discus* (Smith) (= *Halictus discus* Smith), *Prosopis modestus* Say (= *P. affinis* Cresson), and *Ceratina dupla* Say, they were not observed on honeybees or *Andrena nivalis* Smith, also frequent in the area. A similar observation is reported by Pinto and Selander (1970) for larvae of *M. angusticollis* Say. This leads to the assumption that the phenomenon of phoresy on insects other than hosts is probably not fortuitous, but could represent a dispersion event from the hatching point, as a specialization to reduce the competition for hosts and increase the possibility to find an available bee nest (Pinto and Selander 1970), but also connected with a high larval loss due to unsuccessful larvae.

However, under given circumstances, phoresy is also likely to be subject to relatively low larval losses. Species of the genus *Stenoria* and *Hornia* as well as *Apalus bimaculatus* (Linné), *S. muralis*, and *C. auriculata* pursue brood care by laying their clutches into the entrances of their hosts' nests or in the immediate proximity of their hosts (*Stenoria* spp., *A. bimaculatus*, *S. muralis*, *C. auriculata*) or alternatively, by laying them in the cells where they hatched (*Hornia* spp.).

Besides the species of the Lyttini, Pyrotini, Cerocomini, Epicautini, and Mylabrini, also *M. decorus* and *M. uralensis* appear to actively reach their hosts' nests. Thus, studies have shown (J. Lückmann, unpublished data) that triungulins belonging to these species, having been placed on or at the side of dead bees, quickly left the bees or avoided them, instead of attaching to their hairs, as for example, observed in our experiments for *M. proscarabaeus*, *M. violaceus*, *M. scabriusculus*, or *M. rugosus*. Alternatively, on the ground the larvae exhibit a distinct searching behaviour, as observed for the larvae of *L. vesicatoria*. This hypothesis is supported by Vrabec et al. (2002), who during their studies never found larvae of *M. decorus* on bees which had been captured in colonies in which the females had laid their eggs. Nevertheless, both host-finding strategies may be used, since G. Schumann (unpublished data) provides reports of triungulins of *M. decorus* (det. Lückmann) that were observed on flowers of *Potentilla verna* Linné. In order to shed some light on this problem, further studies are planned.

Differing from that of the other *Meloe* species, the host-finding behaviour of *M. decorus* and *M. uralensis* would also explain the fact that when compared with *M. scabriusculus* and *M. rugosus*, they exhibit different trade-offs concerning the mean clutch size and the size of the offspring (=egg weight; Table II). Larger offspring may have a higher fitness and higher survival probability than smaller offspring (review in Fox and Czesak 2000). That is why it is beneficial for *M. decorus* and *M. uralensis* to invest more into each offspring, while *M. scabriusculus* and *M. rugosus* produce a larger number of offspring. A compromise favouring the size of the offspring, as found for *M. decorus* and *M. uralensis*, can also be observed for the non-phoretic larvae of *L. vesicatoria*.

#### *Reproduction and habitat selection*

The significance arising from the resemblances and differences in the parameters relevant for reproduction can only be understood in the light of the species' ecology and habitats (Stearns 2000). Thus they should be considered as an adaptation of the meloids to the phenology of their hosts as well as to the peculiarities typical of their habitat. For the surveyed species, only in a few cases does knowledge about the habitat requirements of populations from Central Europe exist, which might be different from populations existing in for example, Southern Europe. In what follows, the presented results will be discussed keeping this knowledge in mind.

#### *Meloe violaceus and Meloe proscarabaeus*

The species *M. violaceus* and *M. proscarabaeus* have roughly the same geographic distribution (Bologna 1991). In Central Europe the adults of both species have the same activity period and can be found between approximately mid-March and the beginning of June. But there is a great difference in the larval phenology. Whereas in Central Europe the larvae of *M. proscarabaeus* can be found between mid-May and mid-July, those of *M. violaceus* are active between mid-April and the beginning of May (J. Lückmann, in preparation), i.e. at the same time as the imagines (also cf. Havelka 1980). In *M. violaceus*, the overlapping of the activity periods of adults and larvae on the one hand, and the prolonged development time and the stay in the soil during the next months on the other hand, suggests that the larvae found during the spring have hatched from eggs laid during the previous spring (also cf. Pinto and Selander 1970).

The differences in the activity periods of the larvae of *M. proscarabaeus* and *M. violaceus* is founded in the populated habitats. While in the plains of Central Europe *M. proscarabaeus* populates open and warm habitats, *M. violaceus* is a stenotopic species in the plains which populates river hardwood forests. For the latter, only during the brief time window of early spring, thanks to the sparse foliage of the trees, is the forest still light and the light intensity on the forest floor reaches its maximum (Hofmeister 1997). This short period, during which the early-flowering plants, e.g. *Anemone nemorosa* Linné and *Ranunculus ficaria* Linné, blossom, is the only time of the year during which the mostly light- and warmth-loving solitary bees can use the forest as a feeding and nesting habitat (Westrich 1990), and during which the triungulins have the only chance to meet a potential host.

Both species invest the same amount of biomass into their offspring. However, while *M. proscarabaeus* invests this amount into many, smaller offspring, *M. violaceus* divides it between fewer but larger eggs. The differences in the reproductive biology of these two species can be explained by the different length of stay of eggs or larvae in the soil and by



their phenology. The fact that the eggs or larvae of *M. violaceus* remain in the soil for almost a year and that the fitness and survival probability of larger offspring is higher than those of smaller ones (Fox and Czesak 2000) is probably why fewer but larger offspring are produced by *M. violaceus*.

### *Meloe rugosus*

Primarily, *M. rugosus* from Central European populations is a river meadow species that appears to find optimum conditions in the direct flooding area, on sandy, lightly elevated, moderately grassy areas that are sparsely covered with shrubs and trees. Secondly, however, it can also be found, for example, in sand, gravel and clay pits as well as on arid grasslands. Basically, *M. rugosus* is an autumn species with its main activity period in October and November (own data; Vrabec and Hess 2001; also cf. Vrabec 2003), and sometimes also being found in the following months (own data; Bologna 1988).

Its characteristic reproductive biology should be considered an adaptation to the dynamic conditions in the river meadows. Thus, compared with other *Meloe* species, the females lay their eggs in short intervals, by means of which good and possibly only short lasting weather conditions are efficiently made use of. The relatively small mean clutch size, as compared with *M. proscarabaeus*, is compensated for with a larger ovipositioning frequency. The hollow space, which is up to 10 mm high above the clutch and approximately 3 mm wide to its side, surrounds the clutch and is characteristic of animals inhabiting river meadows, whereas it is lacking in animals from dry locations. Filled with air, it probably serves the purpose of allowing a quick seeping away of the water after a flooding.

### *Meloe decorus*

*Meloe decorus* is a typical spring species, active from mid-March to about the end of April. Quite characteristic for the reproductive biology of *M. decorus*, with a time interval of 2.5 days, their females, among all known *Meloe* species, exhibit the shortest time interval between two ovipositions (also cf. Vrabec 1993), the eggs being laid next to the soil surface and developing very quickly (cf. Vrabec et al. 2002). According to our own observations, most of the time the eggs are laid directly into the wild bee colonies (also cf. Vrabec et al. 2002). All of this can be interpreted as an adaptation to the early and short activity period. As for *M. rugosus*, favourable weather conditions can be made the best possible use of thanks to short intervals between the ovipositions. The low depths at which the clutches are laid make it possible for the intense solar radiation to heat up the upper soil layer fast enough, thus accelerating the hatching of the larvae and shortening the development time. By ovipositing within the bee colonies and the ability to enter the host's nest actively, the probability of finding a suitable host is relatively high. This explains why *M. decorus* manages with drastically lower egg numbers than, for example, *M. proscarabaeus* and *M. rugosus*.

### *Sitaris muralis*

*Sitaris muralis* is a typical summer species, the larvae of which spend the time after the hatch, lasting from late summer till next spring, under the layer of dried eggshells (Fabre 1858; Friese 1898; Cros 1910). Its reproductive biology in Central Europe is characterized

by the females ovipositing only once, the clutch comprising a mean number of 1,700 eggs and the clutch weight amounting to 57.2% of the body weight, more than for any other of the surveyed species. Since the adults do not take up food during their entire lifespan, the resources for oogenesis are obtained by the complete reduction of the flight muscles (J. Lückmann, in preparation), a phenomenon similar to the oogenesis-flight syndrome (van Huizen 1977; Nelemans 1987; Rankin et al. 1994). The egg clutches are then laid directly into the passages of the mason bees or deposited in their proximity. Due to the vicinity between the clutch or larvae and their potential hosts, the probability of attaching to a bee is relatively high, which is why this species presumably only invests into a relatively low number of eggs, the total number of eggs being very low by comparison with all other species.

#### *Reproductive strategies within meloid beetles*

Based on the obtained results and the evaluation of the existing published reproduction data, which are summarized in Table V, the following general reproductive strategies can be postulated on the criteria “total number of laid eggs”, “host finding strategy”, and “site of oviposition”:

- Group 1: here belong many *Meloe* species, e.g. *M. proscarabaeus*, *M. scabriusculus*, *M. rugosus*, the larvae of which let themselves be carried phoretically from flowers in open land biotopes into their hosts' nests, thereby being exposed to a high risk of not coming into development. Larval losses are compensated for with very high reproductive rates (total egg numbers >20,000). According to the habitat, a few large (e.g. *M. proscarabaeus*, *M. menoko*) or many small clutches (e.g. *M. scabriusculus*, *M. rugosus*) are laid.
- Group 2: here belong species such as *M. violaceus*, *M. decorus*, *M. uralensis*, *L. vesicatoria* as well as the species of the Lyttini, Pyrotini, Eupomphini, Cerocomini, Epicautini, and Mylabrini. By actively searching for their hosts' nests as in *M. decorus* and *L. vesicatoria*, or due to specific features found in certain habitats in phoretic species as e.g. *M. violaceus* from Central European populations, the probability of finding a host is considerably increased compared with the first group. The risk of larval losses is compensated for with average reproductive rates.
- Group 3: here belong *C. auriculata* (Horiini), *S. muralis*, *Tricrania sanguinipennis* (Say) as well as species of the genera *Apalus*, *Allendeselazaria*, *Glasunovia*, *Ctenopus*, *Sitarobrachys*, *Stenoria*, *Nyadatus*, and *Hornia* (all Nemognathini). Although their larvae are phoretic, the females deposit their clutches into the entrances of their hosts' nests or into their immediate proximity (*Stenoria* spp., *A. bimaculatus*, *S. muralis*, *C. auriculata*) or, alternatively, into the cells in which they themselves hatched (*Hornia* spp.). This way, the probability of finding a host is relatively high. Therefore, larval losses are made up for either with small to average clutch sizes and low ovipositioning frequencies (e.g. *Hornia* spp., *C. auriculata*) or else with larger individual clutches (e.g. *A. bimaculatus*, *S. muralis*).

Due to the insufficient data basis, it is unclear where the studied species *M. rufiventris* and many other *Meloe* species should be classified. The same can be said for the species of the genus *Tetraonyx* (Tetraonycinae), the remaining *Sitaris* species, as well as the remaining genera of the tribe Nemognathini, especially the genera *Zonitis*, *Pseudozonitis*, *Gnathium*, and *Nemognatha*. The species belonging to these genera lay small to medium-sized egg

Table V. Reproductive data of various meloid species.

Taxon	EN $\pm$ SD (min.–max.) [n]/NO <sub>max</sub> /TEN <sub>max</sub>	EL/EWI (mm)	DT $\pm$ SD (°C) [n]	OP	HF	BR
Subfamily Eleticinae						
<i>Eletica</i> Dejean						
<i>E. rubripennis</i> Pic	53 [3]			B	a	1
<i>E. wahlbergi</i> Fahraeus	app. 100 [1]		40 (a.t.)	B	a	1
Subfamily Meloinae						
Tribus Pyrotini						
<i>Pyrota</i> Dejean						
<i>P. insulata</i> LeConte	884 $\pm$ 261 <sup>a</sup> [14]/6		10.2 $\pm$ 1.1 (24) [50]	SC	a	2
<i>P. nigrovittata</i> (Haag-Ruthen.)	865 $\pm$ 76 <sup>a</sup> [2]		12–8 (a.t.)	SC	a	3
<i>P. palpalis</i> Champion	583 <sup>a</sup> (385–788) [3]		10 (a.t.)	SC	a	3
<i>P. invita</i> Horn	579 [1]			SC	a	3
<i>P. akhurstiana</i> Horn	532 [1]	1.20	14.0 (25) [1]	SC	a	4
<i>P. postica</i> LeConte	496 $\pm$ 8 [2]	1.20	18.0 (25) [2]	SC	a	4
<i>Wagneronota</i> Denier						
<i>W. aratae</i> (Berg)	4000 $\pm$ 220 [2]	1.37/0.37	12 (a.t.) [3]	SC	a	5
<i>Pseudopyrota</i> Kaszab						
<i>P. lyttomeloides</i> Selander	177 $\pm$ 19 <sup>a</sup> (110–274) [7]		19.3 $\pm$ 0.2 (a.t.) [7]	SC	a	6
<i>P. riojanensis</i> (Pic)	620 $\pm$ 105 <sup>a</sup> (415–760) [3]		13.2 $\pm$ 1.5 (a.t.) [3]	SC	a	6
Tribus Eupomphini						
<i>Eupompha</i> LeConte						
<i>E. wenzeli</i> (Skinner)	175 $\pm$ 40 (130–207) [3]		12.7 $\pm$ 1.2 (26) [3]	SC	a	7
<i>Tegrodera</i> LeConte						
<i>T. erosa aloga</i> Skinner	181 $\pm$ 27 (100–252) [4]	1.6	17.0 $\pm$ 1.2 (25) [6]	SC	a	4
<i>Pleurospasta</i> Wellmann						
<i>P. mirabilis</i> (Horn)	142 $\pm$ 35 [2]	1.5	18.0 (25) [2]	SC	a	4
Tribus Mylabrini						
<i>Hycleus</i> Latreille						
<i>H. pustulatus</i> Thunberg	110 $\pm$ 33 (40–160) [72]			SC	a	8
Tribus Epicautini						
<i>Linsleya</i> MacSwain						
<i>L. sphaericollis</i> (Say)	51 (25–70) [31]		29 (20)	SC	a	9
<i>L. convexa</i> (LeConte)	50 (18–138) [44]			SC	a	10

Table V. (Continued.)

Taxon	EN ± SD (min.–max.) [n]/NO <sub>max</sub> /TEN <sub>max</sub>	EL/EWI (mm)	DT ± SD (°C) [n]	OP	HF	BR
<i>Epicauta</i> Dejean						
<i>E. caviceps</i> -group						
<i>E. impressifrons</i> Van Dyke	8 [1]			SC	a	11
<i>E. wheeleri</i> Horn	35 [1]			SC	a	11
<i>E. afoveata</i> Werner	10 [1]			SC	a	11
<i>E. alphonsii</i> Horn	32 ± 11 [1]			SC	a	11
<i>E. californica</i> Werner	45 [1]			SC	a	11
<i>E. maculata</i> -group						
<i>E. magnomaculata</i> Martin	102 ± 10 (76–105) [4]	1.25/0.5	10.5 ± 0.5 (26 ± 1) [2]	SC	a	12
<i>E. ventralis</i> Werner	70 ± 12 (46–132) [5]	1.25/0.5	14.3 ± 1.2 (26 ± 1) [6]	SC	a	12
<i>E. pardalis</i> LeConte	78 ± 16 (52–152) [6]	1.25/0.5	18.4 ± 1.5 (26 ± 1) [5]	SC	a	12
<i>E. andersoni</i> Werner	62 ± 9 (27–111) [9]	1.25/0.5	13.8 ± 0.7 (26 ± 1) [8]	SC	a	12
<i>E. phoenix</i> Werner	46 ± 9 <sup>a</sup> (21–63) [4]	1.25/0.5		SC	a	12
<i>E. normalis</i> Werner	49 ± 9 <sup>a</sup> (35–62) [2]	1.25/0.5	24.0 ± 1.0 (25 ± 4) [2]	SC	a	12
<i>E. jeffersi</i> Pinto	86 ± 7 <sup>a</sup> (43–127) [12]	1.25/0.5	23.9 ± 1.3 (25 ± 4) [10]	SC	a	12
<i>E. apache</i> Pinto	109 ± 6 <sup>a</sup> (89–145) [8]	1.25/0.5	21.6 ± 0.8 (25 ± 4) [5]	SC	a	12
<i>E. maculata</i> (Say)	126 ± 9 <sup>a</sup> (115–146) [4]	1.25/0.5		SC	a	12
<i>E. vittata</i> -group						
<i>E. vittata</i> (Fabricius)	138 ± 20 <sup>a</sup> [5]/8/754		13.1 ± 0.4 (27) [9]	SC	a	13
<i>E. occidentalis</i> Werner	175 ± 13 <sup>a</sup> [4]/9/1900		9.3 ± 0.2 (27) [12]	SC	a	13
<i>E. temexa</i> Adams and Selander	195 ± 5 <sup>a</sup> [7]/19/3625		9.7 ± 0.1 (27) [71]	SC	a	13
<i>E. tamara</i> Adams and Selander	122 ± 22 <sup>a</sup> [3]/21/2074		14.9 ± 0.2 (27) [32]	SC	a	13
<i>E. vitticollis</i> (Haag-Ruten.)	177 ± 20 <sup>a</sup> [5]/15/3639		12.6 ± 0.2 (27) [30]	SC	a	13
<i>E. unilineata</i> Champion	151 ± 20 <sup>a</sup> [4]/14/2664		17.7 ± 0.2 (27) [30]	SC	a	13
<i>E. monachica</i> (Berg)	139 ± 10 <sup>a</sup> [8]/22/2871		12.4 ± 0.1 (27) [78]	SC	a	13
<i>E. luteolineata</i> Pic	196 ± 13 <sup>a</sup> [6]/18/3517		12.1 ± 0.1 (27) [68]	SC	a	13
<i>E. leopardina</i> (Haag-Ruten.)	87 ± 6 <sup>a</sup> [3]/8/631		12.6 ± 0.3 (27) [19]	SC	a	13
Tribus Lyttini						
<i>Lytta</i> Fabricius						
<i>L. cyanipennis</i> Linné	390 (260–570) [25]		14–15 (20)	SC	a	9
<i>L. nuttali</i> Say	320 (180–490) [25]/5		20–21 (20)	SC	a	9
<i>L. magister</i> Horn	416 ± 52 (298–517) [3]	1.6	13.0 ± 0.7 (25) [3]	SC	a	4
<i>L. mutilata</i> (Horn)	636 ± 17 [2]	1.5	14.5 ± 0.5 (25) [2]	SC	a	4
<i>L. viridana</i> LeConte	340 (220–490) [25]		16–17 (20)	SC	a	9
<i>L. vesicatoria</i> Linné	80–250	1.5/0.5		SC	a	14
<i>Berberomeloe</i> Bologna						
<i>B. majalis</i> Linné	1000–2500 [1]/s.t.	1.8–1.9	10–54 (temp.?)	SC	a	15, 16

Table V. (Continued.)

Taxon	EN ± SD (min.–max.) [n]/NO <sub>max</sub> /TEN <sub>max</sub>	EL/EWI (mm)	DT ± SD (°C) [n]	OP	HF	BR
Tribus Meloini						
<i>Meloe</i> Linné						
SG <i>Meloe</i> Linné						
<i>M. proscarabaeus</i> Linné	4218 <sup>b</sup> [1]/4; 3000–4000/3–4		21–47 (RT)	SC	ph	17, 18
<i>M. prosc. sapporensis</i> Kono	5520 [1]/1	1.14/0.4		SC	ph	19
<i>M. campanicollis</i> Pinto and Selander	839 [1]/1			SC	ph	20
<i>M. coarctatus</i> Motschulsky	2277 ± 263 [2]/1	0.79/0.25		SC	ph	19
<i>M. dianella</i> Pinto and Selander	658 ± 113 (337–899) [13]/6			SC	ph	20
<i>M. impressus</i> Kirby	1278 ± 43 <sup>a</sup> (701–1652) [6]/5			SC	ph	20
<i>M. menoko</i> Kono	3785 ± 2621 (525–6572) [6]/3/17200	0.84/0.28	175 (temp.?) [2]	SC	ph	19
SG <i>Eurymeloe</i> Reitter						
<i>M. brevicollis</i> Panzer	1400–1500 <sup>b</sup> [1]	0.65/0.2		SC	ph	21
<i>M. corvinus</i> Marseul	6918 [1]/1	0.73/0.23		SC	ph	19
SG <i>Micromeloe</i> Reitter						
<i>M. decorus</i> Brandt and Erichson	300–400 [3]/5/app. 1000		14–16 (25), 20 (15)	SC	a ?	22
SG <i>Treioidous</i> Dugès						
<i>M. afer</i> Bland	1937 ± 636 (1232–2467) [3]	0.78/0.27	10 (24) [16]	SC	ph	23
<i>M. laevis</i> (Leach)	2256 ± 215 <sup>a</sup> (1353–3854) [12]/4			SC	ph	20
SG <i>Lasiomeloe</i> Reitter						
<i>M. olivieri</i> Chevrolat	233 ± 126 <sup>c</sup> (100–350) [3]	1.25/0.3	20 (20–25) [1]	SC	ph	24
Subfamily Tetraonycinae						
Tribus Tetraonycini						
<i>Tetraonyx</i> Latreille						
<i>T. fulvus</i> LeConte	app. 150 <sup>c</sup> [3]	0.7	9.0 (25) [3]	F	ph	25
Subfamily Nemognathinae						
Tribus Horiini						
<i>Cissites</i> Latreille						
<i>C. auriculata</i> Champion	22800 <sup>d</sup>	0.75/0.25	12 (a.t.)	BT	ph	26
Tribus Nemognathini						
<i>Zonitis</i> Fabricius						
<i>Z. atripennis flavida</i> (LeConte)	414 ± 100 [2]; app. 150 <sup>c</sup> [7]	0.94	10.3 (25) [7]	F	ph	27, 25
<i>Z. bilineata</i> Say	265 [10]			F	ph	28
<i>Z. dunniana</i> Casey	248 ± 64 [2]	1.0	9.0 (25) [1]	LU	ph	25
<i>Z. punctipennis</i> (LeConte)	app. 150 <sup>c</sup> [3]	0.9	11.0 (25) [3]	F	ph	25
<i>Z. japonica</i> Pic	500 ± 280 (150–800) [5]/5	0.5/0.2	8.0 (temp.?) [5]	F	ph	29
<i>Gnathium</i> Kirby						
<i>G. minimum</i> (Say)	58 (87–38) <sup>a</sup> [8]	0.7	8.0 (25) [1]	F	ph	24
<i>G. obscurum</i> MacSwain	11 (6–16) <sup>a</sup> [8]	0.7	8.8 (25) [8]	F	ph	25

Table V. (Continued.)

Taxon	EN $\pm$ SD (min.–max.) [n]/NO <sub>max</sub> /TEN <sub>max</sub>	EL/EWI (mm)	DT $\pm$ SD (°C) [n]	OP	HF	BR
<i>Pseudozonitis</i> Dhillon						
<i>P. brevis</i> Enns	269 (196–328) [4]	0.8	6.7 (25) [4]	P	ph	25
<i>Nemognatha</i> Illiger						
<i>N. apicalis</i> LeConte	165 (47–285) [15]			P	ph	30
<i>N. dubia</i> LeConte	330 (115–510) [5]			P	ph	30
<i>N. lurida</i> LeConte	288 $\pm$ 88 [2]			P	ph	30
<i>N. nemorensis</i> Hentz	app. 25 [4]			P	ph	28
<i>N. nigripennis</i> LeConte	app. 150 <sup>c</sup> [6]	0.7	7.5 (25) [4]	P	ph	25
<i>N. nitidula</i> Enns	app. 150 <sup>c</sup> [5]	1.0	9.8 (25) [5]	P	ph	25
<i>N. lurida apicalis</i> LeConte	app. 150 <sup>c</sup> [1]			P	ph	25
<i>N. lurida lurida</i> LeConte	app. 200 <sup>c</sup> [3]	0.75	7.3 (25) [3]	P	ph	25
<i>N. lueta lueta</i> LeConte	app. 200 <sup>c</sup> [1]	0.75		P	ph	25
<i>Sitaris</i> Latreille						
<i>S. muralis</i> (Foerster)	2160 [1]; 900 [1]	0.75; 0.7		BT	ph	31, 14
<i>Allendeselazaria</i> Escalera						
<i>A. nymphoides</i> Escalera	app. 200/3	0.9		BT	ph	32
<i>Hornia</i> Riley						
<i>H. minutipennis occidentalis</i> Linsl.	/1308		26 (a.t.)	BC	ph	33
<i>H. mexicana neomexicana</i> Cock.	40 $\pm$ 17 (1–235) [20]/12/365 and 700		20–22	BC	ph	34, 35
<i>H. boharti</i> Linsley	/549		42 (a.t.)	BC	ph	33
<i>Tricrania</i> LeConte						
<i>T. sanguinipennis</i> (Say)	/1925			BC	ph	36

EN, mean egg number per oviposition; FO<sub>max</sub>, maximum number of ovipositions; TEN<sub>max</sub>, maximum total egg number laid by a female; EL, mean egg length; EW, mean egg width; DT, mean development time; OP, ovipositing place; HF, host-finding strategy; BR, bibliographical reference (classification based on Bologna and Pinto 2001). Due to heterogeneous data base, not all data are available for all species. a, active searching; a.t., ambient temperature; app., approximately; B, under bark of trees; BC, bee cell in which female beetle developed; BT, ultimate proximity of the bee tunnel; F, flower face; LU, leaf underside; P, phyllaries of buds and flowers; ph, phoretic; SC, soil cavity; SG, subgenus; s.t., several times; ?, not clear.

<sup>a</sup>Rounded values; <sup>b</sup>dissected female; <sup>c</sup>includes data of two dissected females; <sup>d</sup>egg mass based on four or five separate ovipositions of one or more females; <sup>e</sup>due to sticky egg surface the egg number was estimated because counting of eggs was impossible without destroying them. BR: 1, Pinto et al. (1996); 2, Mathieu (1980); 3, Selander and Mathieu (1964); 4, Erickson and Werner (1974a); 5, Selander (1984); 6, Selander (1990); 7, Pinto (1980a); 8, Krishnan et al. (1996); 9, Church and Gerber (1977); 10, Selander and Pinto (1967); 11, Pinto (1972); 12, Pinto (1980b); 13, Adams and Selander (1979); 14, Beauregard (1890); 15, Cros (1912); 16, Bologna (1989); 17, Newport (1851a); 18, Katter (1883); 19, Kifune et al. (1973); 20, Pinto and Selander (1970); 21, Lückmann (1996); 22, Vrabec (1993); 23, Pinto and Bologna (1993); 24, Bologna and Pinto (1995); 25, Erickson and Werner (1974b); 26, Bianchi (1962); 27, Selander and Bohart (1954); 28, Enns (1956); 29, Kifune (1961); 30, Linsley and MacSwain (1952); 31, Fabre (1857); 32, Cros (1913); 33, Linsley and MacSwain (1942); 34, MacSwain (1958); 35, Porter (1951); 36, Parker and Böving (1924).

clutches, comprising a few dozen or a few hundred eggs, on the flowers, young shoots, or leaves of their host plants, larvae phoretically reaching their hosts' nests.

Since Erickson and Werner (1974b) stress that the females of the Nemognathinae in most cases only lay eggs once, in rare cases also twice, further studies should clarify which reproductive strategy is being pursued by the representatives of these groups. Possibly, the results of Erickson and Werner (1974a, 1974b) and of many other authors are, however, based on suboptimum rearing conditions, which implies that with better suited methods one would obtain higher ovipositioning frequencies and therefore higher total egg numbers. For *Meloe* species with relatively low clutch sizes, for example, *M. campanicolis* Pinto and Selander or *M. dianella* Pinto and Selander, it may be guessed that, due to the specific nature of the habitat, the egg numbers were reduced as compared to other species (cf. *M. violaceus* from Central Europe), but that they are compensated for with high ovipositioning frequencies and/or that the larvae are not phoretic.

When referring to life and reproductive strategies it occurs over and over again that the concept of r- and K-strategy (MacArthur and Wilson 1967; Pianka 1970) is discussed. Although a series of examples exists, for which the r/K-pattern appears to fit (Begon et al. 1991), it is not capable of explaining all realized life cycles, therefore a generalization of the assumption of such dichotomous life strategies appears to be poorly suited (Stearns 1977, 1992).

The surveyed meloids, too, cannot be integrated into this concept, since the species are characterized both by r- and K-selecting features, thus making a straightforward classification into one of the two types quite impossible (Table VI).

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Table VI. Meloid beetle properties within the r/K-concept.

Parameter	Species									
	<i>M. vio.</i>	<i>M. pro.</i>	<i>M. ruf.</i>	<i>M. sca.</i>	<i>M. rug.</i>	<i>M. dec.</i>	<i>M. ura.</i>	<i>L. vesi.</i>	<i>S. mur.</i>	
<b>K-strategy</b>										
Predictable/stable habitat		X	?	X		X	X	X	X	
Larger adults	X	X	X					X		
Long-lived adults					X					
Low adult mobility	X	X	X	X	X	X	X		X	
Larger offspring	X									
Few offspring (total)	X		X			X	X	X	X	
Parental care						X	?	?	X	
<b>r-strategy</b>										
Unpredictable/ephemeral habitat	X				X					
Smaller adults				X	X	X	X		X	
Short-lived adults	X	X	X	X		X	X	X	X	
High adult mobility								X		
Smaller offspring		X	X	X	X	X	X	X	X	
Many offspring (total)		X		X	X					

?, not known, but it is to be expected.

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