

## SEASONAL DYNAMICS, AGE STRUCTURE AND REPRODUCTION OF FOUR CARABUS SPECIES (COLEOPTERA: CARABIDAE) LIVING IN FORESTED LANDSCAPES IN HUNGARY

FERENC KÁDÁR<sup>1,2</sup>, JUDIT P. FAZEKAS<sup>1,3</sup>, MIKLÓS SÁROSPATAKI<sup>4</sup> and GÁBOR L. LÖVEI<sup>5</sup>

<sup>1</sup>Plant Protection Institute, Centre for Agricultural Research, Hungarian Academy of Sciences  
H-1022 Budapest, Herman Ottó út 15, Hungary

<sup>2</sup>Present address: H-2241 Süllyás, Széchenyi u. 1., Hungary; E-mail: ferenc.kadar47@freemail.hu

<sup>3</sup>Present address: Oak Association for Nature Protection

H-2100 Gödöllő, Páter Károly utca 1, Hungary; E-mail: fjpicur@gmail.com

<sup>4</sup>Department of Zoology and Ecology, Szent István University

H-2100 Gödöllő, Páter Károly utca 1, Hungary; E-mail: Sarospataki.Miklos@mkk.szie.hu

<sup>5</sup>Department of Agroecology, Aarhus University, Flakkebjerg Research Centre  
DK-4200 Slagelse, Denmark; E-mail: gabor.lovei@agro.au.dk

Seasonal dynamics and reproductive phenological parameters of four *Carabus* species (*C. convexus*, *C. coriaceus*, *C. germarii* and *C. hortensis*) common in Hungary were studied by pitfall trapping and dissection. Beetles were collected in an abandoned apple orchard and in the bordering oak forest near Budapest (Central Hungary), in 1988–1991.

The sex ratio was male-dominated, but this was significant only for *C. coriaceus*.

The catch of *C. germarii* adults showed relatively short activity period with unimodal curve, but activity was longer and bimodal for the other three species. Adults of *C. germarii* and *C. hortensis* reached sexual maturity in July, and *C. coriaceus* adults were matured by early August. We did not find newly hatched individuals of *C. coriaceus* or *C. germarii*.

The reproductive period was approximately four weeks in *C. hortensis*, five weeks for *C. coriaceus* and six weeks for *C. germarii*. Reproduction lasted much longer, for about four months, in *C. convexus*. The mean number of ripe eggs per female were 4.2 in *C. convexus*, 5.4 in *C. coriaceus*, 6.6 in *C. germarii*, and 7.4 in *C. hortensis*. The maximum number found was about three times the average in all studied species. The reproductive allocation (ratio of egg complement mass/body mass) was lowest in *C. germarii* (0.133) and highest in *C. hortensis* (0.196), and did not depend on body size.

There was minimal overlap of the activity and reproductive periods of the four species.

Key words: activity period, egg production, dissecting, reproductive allocation.

### INTRODUCTION

Ground beetles (Carabidae) are one of the most species-rich families of beetles (CROWSON 1981). They are frequently studied because are easy to collect, have high densities, and have important roles as natural enemies of pests (LÖVEI & SUNDERLAND 1996) and weeds (SASKA *et al.* 2010). Many of them have complex age structures, surviving and reproducing over several years (SCHJØTZ-CHRISTENSEN 1965, LÖVEI & SUNDERLAND 1996).

Because of the categorisation uncertainties of the reproduction (LINDROTH 1949, PAARMAN 1979), the high variability in the reproductive rhythms (MATALIN 2007), and the regional differences life history characteristics (BUTTERFIELD 1986, MAKAROV 1994, SOTA 1994, MATALIN 2006), local data are necessary to cross-validate generalisations concerning life history features (HŰRKA 1973, SOTA 1994), as well as to develop effective biodiversity management strategies.

In most European countries, several *Carabus* species are on the Red List, legally protected, and often endangered (NIEMELÄ 2001). Six *Carabus* species are protected at the European Community level (Annexes II and IV of the Habitat Directive 92/43/EEC: EUROPEAN COMMISSION 1992). In Hungary, 42 of the total of ca. 540 carabid species are protected, and the maintenance of their populations is a legal requirement (MERKL & VIG 2009). Twenty-eight species of the genus *Carabus* occur in Hungary (SZÉL *et al.* 2007). Their occurrence and habitat preference are reasonably well documented (SZÉL *et al.* 2007), but only a few papers (FAZEKAS *et al.* 1997, 1999, ANDORKÓ & KÁDÁR 2009) present data on the life history traits and reproduction of Hungarian carabids. From Hungary, we have data on reproduction and seasonal activity from only three *Carabus* species: *C. ullrichi* (ANDORKÓ *et al.* 2009), *C. hungaricus* (BÉRCES & ELEK 2013, SZÉL *et al.* 2006), and *C. scheidleri* (ANDORKÓ & KÁDÁR 2009). The life history characteristics of other *Carabus* species common in Europe, such as *C. convexus*, *C. coriaceus*, *C. germarii* and *C. hortensis* can only be surmised from literature data in other regions of Europe (TURIN *et al.* 2003).

We studied four species: *Carabus convexus* F., 1775, *C. coriaceus* L., 1758, *C. germarii* Sturm, 1815 and *C. hortensis* L., 1758. Earlier, *C. germarii* was considered a subspecies of *C. violaceus*, and it appears as *C. violaceus* in FAZEKAS (1997). Today it has a status of an independent species (TURIN *et al.* 2003, SZÉL *et al.* 2007). Its reproduction and life cycle is probably similar to that of *C. violaceus*, thus most of the earlier data can apply to this species (TURIN *et al.* 2003).

These four *Carabus* species are common and widespread in Europe. According to literature data (TURIN *et al.* 2003), *C. hortensis*, a 22–30 mm large species prefers forest interiors, reproduces mainly in August–September. The larvae and a large proportion of adults hibernate. *C. convexus* (14–20 mm) lives in both forests and their edges, preferring sun-exposed hillsides and lowland forests. It reproduces in spring, teneral adults appear in August–September. *C. germarii* (20–35 mm) prefers forest edges, and is a eurytopic forest species, with newly emerged adults in summer and reproduction mainly in August. Some adults hibernate and enter a second breeding in the following summer. *C. coriaceus* is the biggest (32–40 mm) species, occurs in many habitats, including cultivated ones (SZÉL *et al.* 2007, TURIN *et al.* 2003). Newly emerged beetles occur in late summer and reproduce in the autumn. A number of adults hi-

bernate and become active in following spring, later entering an aestivation dormancy. At higher altitudes and northern regions the individual development may last 2–3 years (LINDROTH 1985). All four species are zoophagous, mostly predatory, feeding on earthworms, slugs and snails, but also carrion and sometimes even on vegetable matter (LAROCHELLE 1990).

In this paper, we provide data on the seasonal activity, sex ratio, and comparative reproductive characteristics and dynamics of these four *Carabus* species. Our further aim is to place them in the reproductive spectrum of the Hungarian *Carabus* species, and determine their reproductive allocation. Carabids are not capital breeders – they need resources to develop their eggs. However, the relationship between instantaneous reproductive allocation (i.e. the number of eggs found at anyone time in a female) and total reproductive effort and its dynamics is not known in many species, or only partial data are available (FAZEKAS 1997).

Specifically, we sought to examine the following questions/hypotheses:

- Are there any regional differences in reproductive rhythms, seasonal dynamics, and egg production?
- What is the ratio of males vs. females, and does this differ from unity?
- What is the age structure of the populations, and how is it related to their reproduction?
- We assumed species-specific differences in reproductive allocation that was related to body size: small species should have a higher reproductive investment, as predicted by life history theory (KOTZE *et al.* 2011).
- How do they fit into the reproductive seasonal dynamics of the Hungarian *Carabus* species?

## MATERIAL AND METHODS

### *Study area and trapping*

The habitats examined included a small (2.5 ha), abandoned apple orchard, and the bordering oak forest at Nagykovácsi, Juliannamajor, in the north-western vicinity of Budapest, Hungary. The apple orchard has not been sprayed since 1987; even before that, it was only sprayed with fungicides. In the spring, the soil was disc-tilled between the tree rows, but not under the trees. This is one of the sites of an earlier agro-biodiversity survey (MÉSZÁROS *et al.* 1984).

Ten pitfall traps were placed in the orchard (in the corner near the forest) in the weedy patch under the trees, and 5 in the forest (at least 25 m away from the orchard). The traps were glass jars with 100 mm diameter, with a galvanised iron cover to protect the catch from rain and to decrease by-catch. The killing and preservation agent was a 4% formaldehyde solution. Traps were emptied weekly from April to November in 1988, and between March and November in 1989–1991. For further details, see FAZEKAS *et al.* (1999).

### *Seasonal activity*

We evaluated the seasonal activity of the species based on the number of specimens during the four years. Since the number of traps was different, we standardised the catch as the number of specimens per trap. Seasonal activity in *C. germarii* was described using the quartile method (FAZEKAS *et al.* 1997). This method divides the whole activity period into four quartiles, based on the cumulative numbers caught. The peak of the activity is the date when 50% of the cumulative catch is reached. The main activity period is defined as the period between the dates when 25% and 75% of the cumulative catch is obtained. The early activity period is before the start, and the late activity period is after the end of the main activity period. We could not apply this method to the other three species because their activity was bimodal.

### *Ageing and dissection*

We estimated the age of the beetles based on the coloration and softness of the cuticle, mandible wear, and the condition of the bristles (VAN DIJK 1972). We created the following categories:

- teneral: newly hatched specimen, with soft or yellowish, uncoloured or partially hardened, pale brown cuticle
- young: completely hardened cuticle, sharp mandibles, intact, long bristles on the head
- 1y old: in its first year; like a young individual, but started to show signs of wear on the mandible; bristles mostly intact
- old: past its first year/season, with a hardened cuticle, worn mandibles, shorter, broken bristles on the head.

Adults were dissected to determine the developmental stage of testes and ovaries and the number of eggs (VAN DIJK 1972). Three categories of females were distinguished according to the state of development of their ovaries:

- a) virgin female, undeveloped ovaries;
- b) gravid female in reproductive condition, with ripening eggs in the ovaries;
- c) spent female, in post-reproductive state, with corpora lutea in the ovaries;

The size of the eggs (width × length, measured to 0.1 mm) was measured with an ocular micrometer mounted on a stereomicroscope.

### *Estimation of fecundity*

We characterised the minimum theoretical fecundity as the maximum number of ripe eggs found in one female. If the females of the species lay all their eggs at once, and they succeed to develop their potential number of eggs, this number constitutes the actual realised (maximum) reproduction. If the eggs are laid in several batches, the female, after laying all the ripe eggs in her abdomen (this is the number that dissection reveals), may develop further batches. In this case, the maximum number found constitutes the minimum realised reproduction. In general, the number of eggs laid is higher than found by dissection (KIRK 1971), therefore our estimate was conservative. The four studied species belonged to the second group, because in the dissected females, apart from fully ripe eggs, eggs in various stages of development were found. These eggs, under appropriate conditions, may develop into fully ripe eggs that could have been laid later.

### Reproductive allocation

We calculated reproductive allocation indexes as: egg complement mass/body mass, and egg complement volume/body mass. The size of the egg complement was equal to the mean number of eggs found in a reproductive female. This value is a good indicator for showing the actual, instantaneous reproductive effort, and can be used for comparing different species (HART & BEGON 1982). We measured the dry mass of the ripe eggs (after drying them at 60°C for 24 h). The volume of eggs was calculated using the formula of a rotating ellipsoid (JULIANO 1985). Body mass calculation was based on JAROSIK'S (1989) formula:

$$\text{Body mass} = 0.03069 (\text{body length})^{2.63885}$$

Sex ratio inequality was tested by Yates' corrected  $\chi^2$  test (SOKAL & ROHLF 2012).

## RESULTS

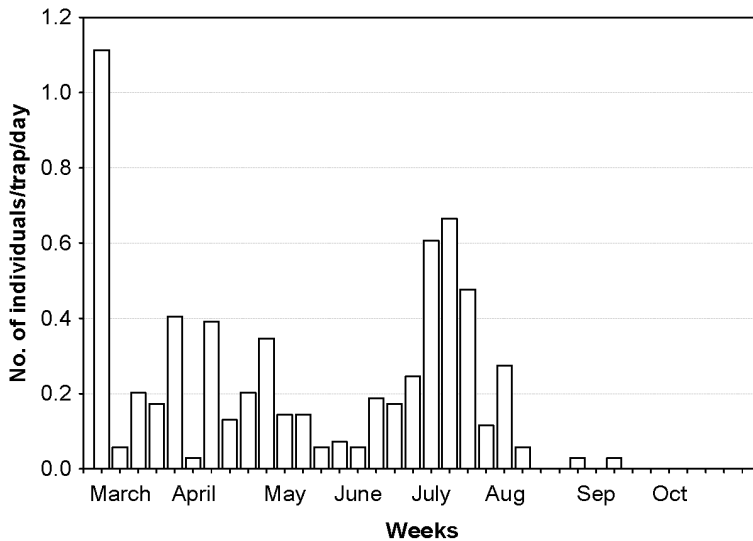
### *C. convexus*

*C. convexus* was the second most numerous species in the forest (Table 1). The proportion of females to males (106 : 90) was not significantly different from equality (Yates' corrected  $\chi^2 = 0.50$ ,  $df = 1$ ,  $p = 0.48$ ). Adults were captured from the very start of the trapping period every year. The activity density was the highest in early spring and in July (Fig. 1). The start of the reproduction could not be determined, because gravid females with ripe eggs in their ovaries were already present at the start of the trapping period. We found ripe eggs until the beginning of June (1990) – July (1988). In the three years, we

**Table 1.** Population characteristics of four *Carabus* species investigated at Nagykovácsi, Central Hungary, 1988–1990.

Population parameter	<i>C. convexus</i>	<i>C. coriaceus</i>	<i>C. germarii</i>	<i>C. hortensis</i>
Total no. of individuals caught*	233	193	198	382
No. of females/no. of males	106/90	57/99	64/95	153/158
No. of females per age class (young/1y/old)	35/56/15	34/18/5	51/10/3	81/59/13
No. of males per age class (young/1y/old)	48/32/10	61/34/4	71/20/4	93/55/10
Number of females with ripe eggs	44	20	25	26
Total number of ripe eggs	183	102	164	193
Maximum number of ripe eggs/female	10	17	18	25
Mean number of ripe eggs ( $\pm$ SD)	4.16 $\pm$ 2.09	5.37 $\pm$ 4.70	6.56 $\pm$ 4.40	7.42 $\pm$ 7.17
Body mass (mg)	74.51	540.48	269.06	223.87
Reproductive allocation (by volume)	0.312	0.339	0.231	0.363
Reproductive allocation (by mass)	0.193	0.176	0.133	0.196

\* no. of individuals caught over 1988–1991



**Fig. 1.** Seasonal (weekly) catch data of *C. convexus* at Nagykovácsi, Hungary in 1988–1991 (N = 233).

captured 14, 4, and 26 gravid females, respectively. The mean egg size was 3.92 mm × 1.65 mm; the female mass was 74.51 mg. There was little between-year variation in the mean egg number/female over the three study years (4.7, 4.5 and 3.8, respectively, see Table 1), but the number of females containing ripe eggs varied considerably (15, 4, and 26, respectively), and the period of reproduction was long. Each year, teneral appeared in July. About 14% of females and 11% of males caught were older than 1y (Table 1).

### *C. coriaceus*

This species was very numerous, more so in the apple orchard than in the forest: 150 specimens were collected in the orchard, while only 43 individuals in the forest (Table 1). The sex ratio (57 females : 99 males) was significantly different from equality (Yates' corrected  $\chi^2 = 5.22$ ,  $df = 1$ ,  $p = 0.022$ ). In 1988–89, the activity period lasted from the end of May/early June to the end of September, shorter than in 1990–1991, when it lasted from early May until the end of October (Fig. 2). We collected 21, 17 and 19 females in 1988–1990, respectively, out of which 8, 10 and 2 were in reproductive condition. Judging from the development of the testes, males reached reproductive condition by early August. The ovaries of females were also underdeveloped until this time. Ripe eggs were found between mid-August and mid-September, with a peak at the end of August. The average egg size was 7.55 mm × 2.94 mm,

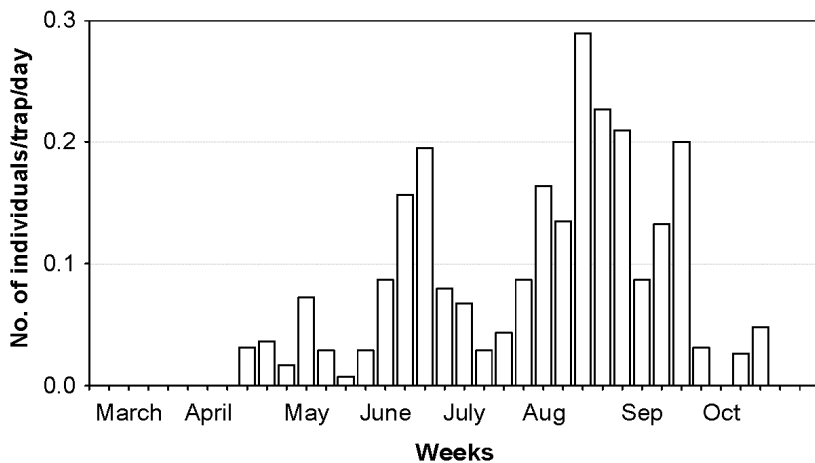
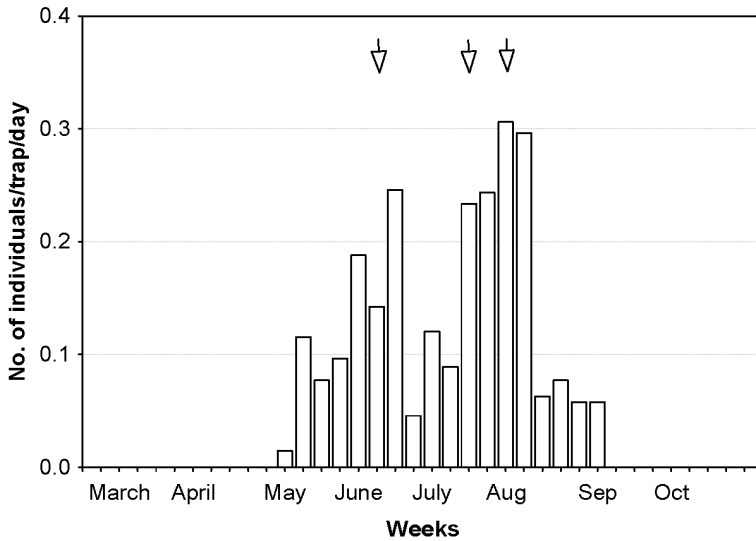


Fig. 2. Seasonal catch data of *C. coriaceus* at Nagykovácsi, Hungary in 1988–1991 (N = 193).

a reproductive female had a mass of 540.48 mg (Table 1). There were large between-year differences in the number of eggs in gravid females: in 1989, the mean was 6.2 eggs per female but in 1990, only 2 gravid females were caught, with 3 and 1 eggs, respectively. The reproductive period lasted approximately 5 weeks. Teneral specimens were not caught. Older individuals made up 8.8% of females and 4.0% of males.

### *C. germarii*

During the four years, 173 specimens were captured in the apple orchard and 25 in the forest (Table 1). Although there were more males (95 vs. 64 females), the sex ratio was not significantly different from unity (Yates' corrected  $\chi^2 = 2.68$ ,  $df = 1$ ,  $p = 0.10$ ). The main activity period started on 26 June, peaked on 29 July and ended on 15 August (Fig. 3). Sixty-four sexually mature females were captured (22, 24 and 18, respectively), with 10, 14 and 1 of them containing ripe eggs. In June, males had underdeveloped testes; but they were mature by July. The reproduction period lasted approximately 6 weeks. Ripe eggs were found from the beginning of July until the end of August, with a peak in mid-August; a single gravid female was captured on 12 September. The average egg size was 4.96 mm  $\times$  1.91 mm, and the body mass of a reproductive female was 269.06 mg. The average number of eggs/female was 6.56 (Table 1; but only 1 gravid female with 2 eggs in 1990). Teneral specimens were not caught. Old individuals accounted for a small percentage of the population (4.7% of females, 4.2% of males).



**Fig. 3.** Seasonal catch data of *C. germarii* at Nagykovácsi, Hungary in 1988–1991. (The left and right arrows mark the main activity period, the central one indicates the activity peak according to FAZEKAS *et al.* (1997) (N = 198).

### *C. hortensis*

This species was present practically only in the forest, with a total number of 382 specimens. The number of females and males (153 : 158) was not different (Yates' corrected  $\chi^2 = 0.01$ ,  $df = 1$ ,  $p = 0.90$ ). The activity period lasted from mid-April until the end of October (Fig. 4). The peak of its activity was influenced by variations in the numbers of different age categories every year. In 1988, the peak was in July because of the high number of sexually mature females (but without eggs). In September 1989, as a result of the high proportion of sexually mature males and females containing ripe eggs, the activity and reproductive peaks coincided. In June 1990, the annual activity peak was caused by reproductively inactive adults. The proportion of sexes also changed annually; the proportion of males was the highest in the year when the reproductive activity was the highest. The total number of females as well as the number of females containing ripe eggs varied by an order of magnitude (Table 1). Immature females reached sexual maturity by July. Ripe eggs could be found in the females from the middle (1989) or late (1988, 1990) September until mid-October, a reproduction period of about 4 weeks. The number of reproducing females (or eggs) was the highest during the third week of September. When the number of captured females was low, the reproduction rate was higher and vice versa. The number of females containing ripe eggs changed little: it was 12 in 1989 and 13 the year after. The average egg



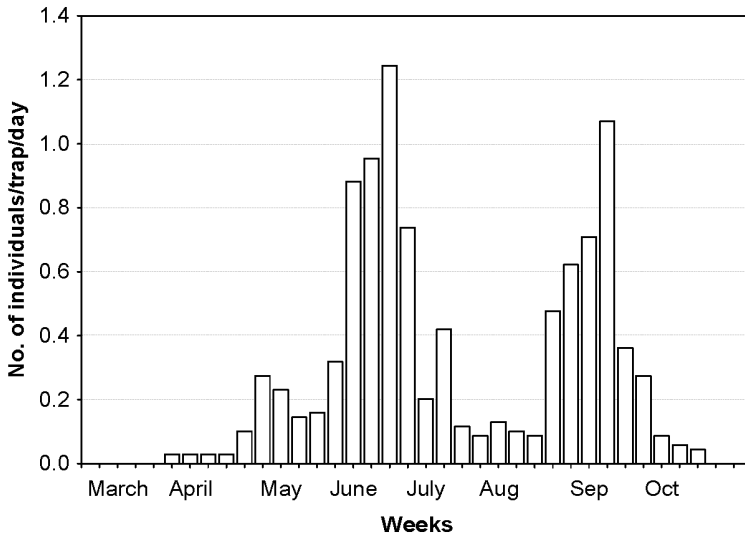


Fig. 4. Seasonal catch data of *C. hortensis* at Nagykovács, Hungary in 1988–1991 (N = 382).

number/female showed significant differences (13.6 vs 1.6 eggs/female, Student's *t*-test,  $t = 7.28$ ,  $df = 23$ ,  $p < 0.001$ ). The mean egg size was 4.98 mm × 2.05 mm, and the calculated body mass of a reproductive female was 223.87 mg. The average egg number per female was 7.42 (Table 1), again masking large between-year variation: in 1989, 12 females had a total of 163 eggs (mean = 13.58 eggs/female), but in 1990, the 13 gravid females had a total of 21 eggs (mean = 1.6 eggs/female). Many older females participated in the reproduction process: 33% in 1989, and 69% in 1990. The share of old individuals was higher (8.5%) for females than males (6.3%).

Overall, the proportion of females containing eggs varied not only by species but by year as well, with no obvious trends. The reproductive allocation, calculated from the ratio of egg complement mass and body mass, was highest in *C. hortensis*, nearly equalled by *C. convexus*, followed by *C. coriaceus*, and *C. germari*. When the ratio of egg volume and body mass was considered, *C. coriaceus* invested more in reproduction than *C. convexus* (Table 1).

In 1990, the egg production decreased in the case of the autumn species compared to the previous years, both in terms of the ratio of females containing ripe eggs as well as the average number of eggs/female.

## DISCUSSION

Our data originated from two different habitats (an abandoned orchard and a neighbouring forest), but they were very close to each other, and their

disturbance during the preceding decade was not different. Therefore we think that there were no spatial differences between these two areas that could influence the parameters studied. Further, the large between-year variations would have masked any smaller variation that could exist within such a small distance.

The sex ratio was male-dominated, but this was significant only in the case of *C. coriaceus*. Male surplus was also found in *C. granulatus* (DREES & HUK 2000), *C. auronitens* and *C. nemoralis* (WEBER & HEIMBACH 2001). The higher number of trapped males is frequently attributed to males looking for mating partners (BAUMGARTNER 2000). The females are much less mobile during the egg laying period than the males. Feeding condition can also play a role: when hungry, equal numbers of *C. hortensis* females and males were caught, but when well-fed, males outnumbered females by 50% (SZYSZKO *et al.* 2004). This would indicate suboptimal feeding conditions in this habitat.

Our results underline that a species does not have the same dynamics in all of its range (MATALIN 2007). The activity peak of *C. coriaceus* in the north-western forests of Germany occurs at the end of September (DÜLGE 1994), a month later than in central Hungary, but the reproductive period coincides with what HŪRKA (1973) found in the Czech Republic. In our study, the activity period of *C. germarii* (earlier considered a subspecies of *C. violaceus*) began two months earlier than that of *C. violaceus* in Austria (PAILL 2000) but ended earlier than in northern Germany (STUBBE 1983). In Italian vineyards, *C. germarii* has two activity peaks (ZANDIGIACOMO *et al.* 1987).

In the present study, we did not find newly hatched *C. coriaceus* nor *C. germarii* specimens. This could be a population-specific phenomenon, because during other studies in Hungary, several teneral were captured (KÁDÁR *et al.* unpubl. data).

The registered start of the activity period for *C. convexus* was in synchrony with literature data, but its reproduction in Hungary started earlier (in mid-March), than elsewhere in Europe (TURIN *et al.* 2003).

*C. hortensis* females can contain ripe eggs from August onwards (HŪRKA 1973), while in our study site, this occurred a month later, coinciding with the findings from Norway (REFSETH 1988). This difference can be caused by study conditions, or indicates suboptimal food conditions in the given year. Carabids only start developing eggs once their metabolic needs are met and eggs are even resorbed under food shortage (LÖVEI & SUNDERLAND 1996).

The reproductive allocation of the four studied species did not differ significantly. A general relationship was not found: while the much smaller *Agonum dorsale* and *Brachinus eximius* have a parameter of 0.09 (FAZEKAS 1997, FAZEKAS *et al.* 1999), the medium-sized *Pterostichus melas* has 0.6 (FAZEKAS 1997). The four species studied here are bigger, yet their reproductive

allocations were between the above two values (Table 1). Using a comparable method, FILIPOV (2007) measured a ratio of female body length: egg length for *Carabus nitens*, which is related (in an inverse way) to reproductive allocation. According to this, the reproductive allocation in *C. nitens* (0.21) is between our calculated data for *C. hortensis* and *C. coriaceus* (0.17–0.24), while the actual instantaneous allocation (considering the mean no. of eggs/female), it is close to our values for *C. convexus* (0.99, for the other species, 1.12–1.48). Further studies are needed to validate these calculations. For now, we can only conclude that in carabids, this parameter is probably not size-dependent, unlike body mass or mean egg numbers; it did not seem to depend on the number reproducing females, either.

The density-dependent differences in reproduction at the population level seemed to be reached in different ways. In *C. hortensis*, this may be achieved by changes in egg numbers/reproducing female (as neither the number of reproductive females nor their mean body mass showed between-year differences, Table 1). However, in *C. convexus* the overall reproductive success may be regulated by the changing number of reproducing females, while the other two parameters (body mass, mean egg number/female) did not vary.

Our results concerning the three autumn breeding species agree with those of GRÜM (1984) and HUK and KÜHNE (2000), who described a negative correlation between the mean number of ripe eggs in the ovaries and the body mass of the species. This did not apply to *C. convexus*. This spring breeder in our study area had five times higher mean egg numbers than conspecifics from a forested area in Eastern Hungary (mean no./female = 0.8, MAGURA *et al.* 2013). We also found mature eggs a month earlier than MAGURA *et al.* (2013). The two regions may host populations with different reproductive potential, similar to the case of an eastern Hungarian population of *Anisodactylus signatus* (FAZEKAS *et al.* 1997). It is also possible that the eastern Hungarian habitat is rather unfavourable.

We conclude that in Hungary, *C. convexus* probably is the one of the earliest, while *C. hortensis* is one of the latest reproducing *Carabus* species. Reproduction in *C. convexus* occurs before that of *C. nemoralis*, which was formerly thought one of the earliest reproducing species (TURIN *et al.* 2003). The activity of *C. nemoralis* in Central Europe begins in March, and is high in April (WEBER & HEIMBACH 2001).

The time between the first ripe eggs in *C. hortensis* females and the appearance of the first tenerals indicate an individual development time of approximately 9 months, less than the 10 months in TURIN *et al.* (2003). This is a long period, making the population rather vulnerable to random events. Reproduction of old females would lessen this vulnerability, and large numbers of young individuals can delay their reproduction until the following

year. This way the risk of reproduction can be spread among the different age categories. Most *C. hortensis* specimens can live for up to 3 years (GRÜM 1975), possibly reproducing more than once. We found a higher proportion (50%) of older, reproducing females than SCHJØTZ-CRISTENSEN (1968) did in Denmark (33.5%). The egg production in *C. hortensis* was the lowest in the year when its number was the highest. Several species show such a negative correlation between the number of individuals caught and the number of eggs in the ovaries, including *P. oblongopunctatus* (HEESSEN 1980), *C. melanocephalus* (BAARS & VAN DIJK 1984), and *Anisodactylus signatus* (FAZEKAS *et al.* 1997). Unlike *C. hortensis*, *C. convexus* seems to spread the risk of reproduction within season, extending it to approximately four months (Fig. 5).

We found spatial (two species were found mostly in the forest, the other two mostly in the orchard) and temporal (shift in the reproductive period of species at the two sites: *C. convexus* vs. *C. hortensis* and *C. coriaceus* vs. *C. germarii*, see Fig. 5) separation between the examined species. Similar relation exists between teneral of *C. coriaceus* and *C. nemoralis* (MÜLLER & KASHUBA 1986). In Germany, the activity peak of *C. violaceus* occurred three weeks earlier when it was sympatric with *C. hortensis* than in an allopatric situation (GÜNTHER & ASSMANN 2000). Competition is often invoked to explain spatial and/or temporal separation of reproductive periods (LOREAU 1989) although experimental evidence for such competition is not conclusive (LÖVEI & SUNDERLAND 1996). The reproduction dynamics of the four examined *Carabus* species (Fig. 5) was arranged along the spring-autumn continuum. Considering the position of other *Carabus* species such as *C. ullrichi* (ANDORKÓ *et al.* 2009), *C. scheidleri* (ANDORKÓ & KÁDÁR 2009), *C. scabriusculus* (KÁDÁR & BUJÁKI, unpubl. data), and *C. hungaricus* (SZÉL *et al.* 2006) along this continuum supports and refines this non-overlap. Such temporal separation exists among 68 species in the Netherlands (DEN BOER & DEN BOER-DAANJE 1990) and ten coexisting *Carabus* species in the Bielowieza Forest, Poland (SKŁODOWSKI 2005). Most of such studies involved adults, while the larvae are more sensitive and may

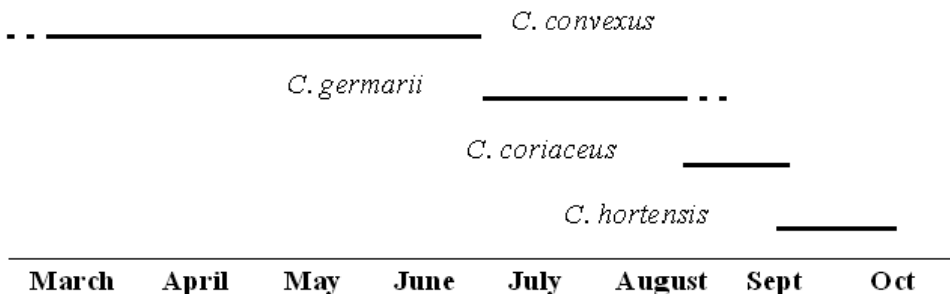


Fig. 5. Reproductive activity of four *Carabus* species collected at Nagykovácsi, Hungary in 1988–1990.

require synchronisation with their key preys which could lead to such a clear-cut separation in activity. It is plausible to assume that the difference can be explained by the bionomics and ecology of the larvae (LÖVEI & SUNDERLAND 1996) which should be tested in further experiments.

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