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LIFE-HISTORY CHARACTERISTICS OF THE GROUND BEETLE *CARABUS SCHEIDLERI* (COLEOPTERA: CARABIDAE) IN HUNGARY

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The aim of this study was to describe patterns of seasonal activity, age structure, and reproductive characteristics of a population of the ground beetle *Carabus scheidleri* inhabiting an abandoned agricultural field in Hungary. Adults used in this investigation were collected by pitfall trapping during the summers of 2000, 2001 and 2002. The activity period overlaps with the reproductive period. Beetles showed two seasonal activity/reproductive peaks: at the end of May, young and immature adults dominated; and the second activity peak occurred in July, when both mature and young adults were caught. Ripe eggs were found in the ovaries from the end of May until the end of August. The mean number of eggs per female was 5.06±4.82 (the maximum number of eggs/gravid female was 22 and the most frequent number of eggs /gravid female was 2). The rate of egg deposition was around 0.067. The seasonal fecundity was 15.79 in 2000, 20.46 in 2001 and 49.06 in 2002. Our results suggest that this species in this area overwinters both as larvae and as adult, it has overlapping generations and several reproductive periods. These characteristics ensure the persistence of the population in human-modified and highly disturbed habitats.

Key words: *Carabus scheidleri*, seasonality, age structure, reproduction, fecundity

INTRODUCTION

One of the cornerstone of conservation planning is the identification of priority areas for biodiversity conservation (MARGULES & PRESSEY 2000, BLADT *et al.* 2008). Many studies have focused on various species indicator groups in identifying area networks for the conservation of biodiversity. Besides, some studies have tested succesfully the usage of species attributes of different indicator groups (BAGUETTE & SCHTICKZELLE 2006, CLEARY *et al.* 2009). Ground beetles are among these good ecological indicators, because their taxonomy and ecology are well documented (LÖVEI & SUNDERLAND 1996) and many studies proved their sensitiveness to habitat alternations/disturbance. Throughout their worldwide distribution and abundance they prove a relaible snapshot about the conservational status of the studied habitat types. However, most of the recent papers concentrate on assemblage level using mechanistic modelling of those in the light of habitat alternations (NIEMELÄ 2001, NIEMELÄ *et al.* 2007, MARTINEZ *et al.* 2009). Only few papers are concerned with the life history traits and reproduction of carabids (BARBARO & VAN HALDEN 2009) although sometimes the classical elements of species attributes provide clues for conservation of biodiversity.

In carabids, reproduction can take place at quite different times of the year. LARSSON (1939) distinguished three different reproductive types in carabids: *autumn-breeders*, which reproduce in autumn or even from the height of summer onwards and usually hibernate as larvae; *spring breeders with autumn activity*, which hibernate as adults and reproduce from spring to early summer, after which most of the beetles die off, and the new generation appears in autumn, becoming fully active althought it only reproduces subsequent to hibernation; and *spring breeders without autumn activity*, which reproduce in the same time as the other spring breeders, but the young beetles exhibit little activity following eclosion in autumn. LINDROTH (1949) suggested the use of the alternative and more general terms *adult hibernator* and *larval hibernator*. However, posterior investigations have shown that not only the larvae, but also the adults of autumn breeders hibernate, after which they can enter a second reproductive period (GILBERT 1956, VLIMJ *et al.* 1968, VAN DIJK 1972). So far, the existence of two populations side by side, the one reproducing in spring and the other in autumn was found by SCHJØTZ-CHRISTENSEN (1965), and by LÖSER (1970). THIELE (1977) distinguished the following types of annual rhythms in carabids: spring breeders with summer larvae, and hibernate as adults; species with winter larvae and reproduce from summer to autumn, without adult dormancy; species with winter larvae and the adults emerge in spring, with dormancy before reproduction; species with flexible reproductive periods; and species which develop over more than one year.

The studied *Carabus scheidleri* PANZER, 1799 is a protected species in Hungary, as are most *Carabus* species. Being a generalist predator, this species can be an important natural enemy in agricultural areas, small gardens, and parks. It occurs in several types of habitats: Arrhenatheretea, Querco-Fagetea and agricultural land (KÁDÁR & SZÉL 1999), fields, meadows and gardens (PAVLÍČEK & HOUŠKOVÁ 1989), Austrian potato fields (KROMP 1990), beach forests, hedges, watersides and various types of forests (KORBEL 1973), *Quercetum* and *Fagetum* mainly, but it is also common in lowlands and hills (KLEINERT 1983). In Hungary, in the Pilis Biosphere Reserve the species is associated with disturbed, human-modified areas (ANDORKÓ & KÁDÁR 2006). We have sparse information about the biology, population dynamics and the ecology of this species in Hungary (ANDORKÓ *et al.* 2005). Thus, because of the lack of adequate knowledge on the life-history characteristics of this species, our objective is to study the patterns of seasonal activity, age structure, and reproductive characteristics, such as different ovarian stages, number of ripe eggs, reproductive output, of a *C. scheidleri* population living in an abandoned agricultural field in Hungary. We also intend to present the classification of this species into one of the breeding categories discussed above.

MATERIALS AND METHODS

Study area, sampling methods

The study area was an abandoned, uncultivated field at Nagykovácsi (Julianna-major), in the northwest vicinity of Budapest, Central Hungary (GPS: N 18°56'3", E 47°32'53"). The study area was bordered by an oak forest (*Quercetum petreae-cerris*), an abandoned apple orchard on a hillside, shrubs, grassy areas near the forest edge, and a mosaic of cultivated fields (lucerne, winter wheat, small vegetable gardens). The surface of the basin is covered by loess, under this layer older waterproof rocks – like sandstone and clay – are situated. All around these basin sod-slopes with limestone are found. The examined plot was an uncultivated field (1 ha) abandoned for more than ten years, where the vegetation contained *Solidago* sp., *Arrhenatherum elatius*, *Agropyron repens*, *Melilotus officinalis*, *Campanula glomerata*, *Carlina vulgaris*, *Picris hierarcioides*, and several shrubs, mainly *Rosa* sp.

Ten pitfall traps (plastic jars of 80 mm diameter, containing 4% formaldehyde as a killing and preserving agent) were installed in two rows. The rows were 10 meters apart and the distance between the traps was 5 meters.

Samples were collected weekly between mid-May and the end of August in 2000 and 2001, and from the end of April until mid-September in 2002.

Collections were sieved and transferred to 4% formaldehyde in the field, sorted under microscope in the laboratory and stored in the same fluid for dissection.

Seasonal activity

Seasonal activity was described using the quartile method (FAZEKAS *et al.* 1997), based on the total number of individuals caught. The peak of activity is the date when 50% of the total number of individuals was caught; while the beginning and the end of the main activity period were defined as the dates when 25% and 75% of the total number of individuals had been captured. The early activity period extended from the start of the activity to the beginning of the main activity period, and late activity period is defined as the time from the end of the main activity period until activity ceased. Since this method is based on the arithmetic mean, which is very sensitive to the extremes in the dataset, we can not apply it in the seasons (i.e. years), where the activity profiles show bimodal shapes.

Age determination

Beetles from each sample were sexed, aged and dissected to assess reproductive status. Ageing was based on the extent of bristle and on mandible wear, elytral hardness and coloration (VAN DIJK 1972, 1979): young beetles, with soft or flexible elytra, sharp mandibles, long and intact bristles; old beetles with hard and fully coloured elytra, severely worn mandibles and bristles; and middle-aged beetles, transition between the two categories, with hardened sclerite, little wear on the mandibles and on the bristles.

Females were dissected to determine the developmental stage of their ovaries and the number of eggs found in their ovaries, following the method of VAN DIJK (1972, 1979), WALLIN (1989) and DIEFENBACH *et al.* (1991). We distinguished three categories: immature beetles without eggs in ovaries, compact, small, long ovaries, narrow and twice as long as the common oviduct lateral oviducts (prereproductive stage); gravid beetles with eggs of different stages of maturation present in the ovaries, lateral oviducts have longer diameter (reproductive stage); spent beetles with lateral oviducts large, ovaries less compact than those of an immature female, beetles that passed at least one reproductive season (postreproductive stage).

Estimating reproductive output

The reproductive output of the population was estimated using Grüm's method (GRÜM 1984). This method requires calculation of the mean number of ripe eggs in ovaries, at weekly intervals, followed by the observed rate of egg deposition:

$$\mu = (\ln N_{k-1} - \ln N_k) / dt$$

where μ is the rate of egg deposition, *dt* = number of days between the estimation of N_{k-1} and N_k (the last two values of N_i), N_i = the number of the ripe eggs found in the ovaries in the *i*th time.

Then the estimated seasonal fecundity, which means that the mean number of eggs laid by a female in the population during the entire breeding period becomes:

$$v = \Sigma\, N_i T_i\, \mu_i$$

where T_i is the number of days in the *i*th period, and μ is the previously estimated rate of egg deposition.

Data analysis

The repeated measured ANOVA test was used to test for differences based on the total number of individuals, the total number of females and males per trap between the years. This test was also used to test for differences between the mean abundances of females and males per trap according to their age and ovarium categories (in females only). Significant difference among the sampling periods was revealed by the post hoc Fisher least significance difference-test. The normal distribution of the dataset was tested by Shapiro-Wilk test. According to the results of this test we transformed the data logarithmically (log(x+1)). The Statistica 6.0 program was used for statistical calculations (STATSOFT 2000).

RESULTS

Seasonal activity

We captured 959 individuals, 591 females and 368 males during the three years (Table 1).

The entire activity period of the three years of sampling lasted from the beginning of May until the beginning of September, with two peaks in the first two years and with one peak in 2002. In 2000 the activity peaks occurred at the end of June and at the end of July, but because of the experimental arrangement, results

Table 1. Characteristics of the *Carabus scheidleri* population investigated at Nagykovácsi, Central Hungary in 2000, 2001 and 2002.

	2000	2001	2002
Total catch (females/males)	342(174/168)	237(172/65)	380(245/135)
No. of females per age class (young, middle-aged, old)	78/45/51	146/17/9	171/56/18
No. of males per age class (young, middle-aged, old)	86/41/41	61/4/0	80/29/26
No. of females per reproductive class (immature, gravid, spent)	20/98/56	38/122/12	48/163/34
Total no. of ripe eggs found	1029	802	1311
Mean number of eggs per female (SD)	5.91 (5.38)	4.66 (4.24)	5.35 (5.13)
Observed rate of egg deposition	0.05	0.07	0.06
Estimated seasonal fecundity	15.79	20.46	49.06

could not be statistically analysed. In 2001 the main activity period occurred from mid-May until mid-July. There were two activity peaks at the beginning of the season, one in mid-May and the other at the beginning of July. There was no early activity period, because the beetles appeared in high number at the beginning of the season. The late activity period occurred from the end of July until the end of the trapping season. In 2002 the main activity period occurred between the end of June and the beginning of August. The activity peak was at the end of July. The seasonal dynamics curve was skewed to the right in 2002 (Fig. 1).

In 2000 we captured more females than males, and their activities were the same. In 2001 there were three times more females caught than males, but the individuals of both sexes showed similar activity curves. In 2002 twice as many females were captured as males, and their activities were the same. The mean number of males showed significant difference between 2001 and 2002 [F (1; 63) = 4.25; p = 0.04]. The mean number of females did not differ significantly between 2001 and 2002 [F (1; 63) = 0.01; p = 0.9].

Age composition

In 2000 young, middle-aged and old males were caught during the whole season, and the young adults dominated. In 2001 almost only young males were found (Fig. 2). In 2002 we captured young males during the whole season, middle-aged males in lower numbers almost during the whole season, and old beetles in July in high number.

All three age categories of females were found in each year. In 2000, the numbers of the females of different age-categories were very similar, but young beetles dominated. In 2001, we captured nearly exclusively young females, but we also found some middle-aged individuals in the middle of the season and some old individuals during the whole season (Fig. 3). In 2002, young females dominated, and we caught middle-ages and old females from the middle to the end of the season.

Reproduction

According to the results from the dissection of the females, we found immature beetles in every year. In 2000, we found few immature individuals. In 2001, the peak of the immature females was at the end of May (Fig. 4), and in 2002 we caught more immature females in the middle of the season. In 2000, the peak of gravid females occurred at the end of June, in 2001 the peaks occurred at the end of May and at the end of June, and in 2002 one peak occurred at the end of July. A high number of spent females were found in 2000 with one peak at the beginning of July. In 2001, we caught just some of these females. And in 2002 we captured some spent females at the end of the season.

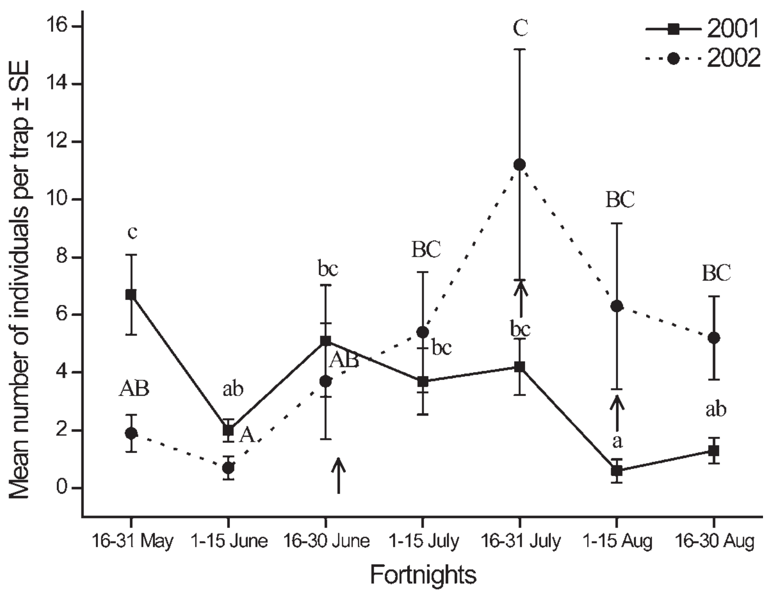

Fig. 1. Seasonal activity of *C. scheidleri* individuals at Nagykovácsi, Central Hungary in 2001 and in 2002. The arrows [narrow arrows in 2002] denote the main activity period (left and right arrows) and activity peak (middle arrow). (Different letters indicate significant (p<0.05) differences within the given years by post-hoc Fisher LSD test.) Repeated measures ANOVA between the years: [F (1; 63) = 0.67; p = 0.41].

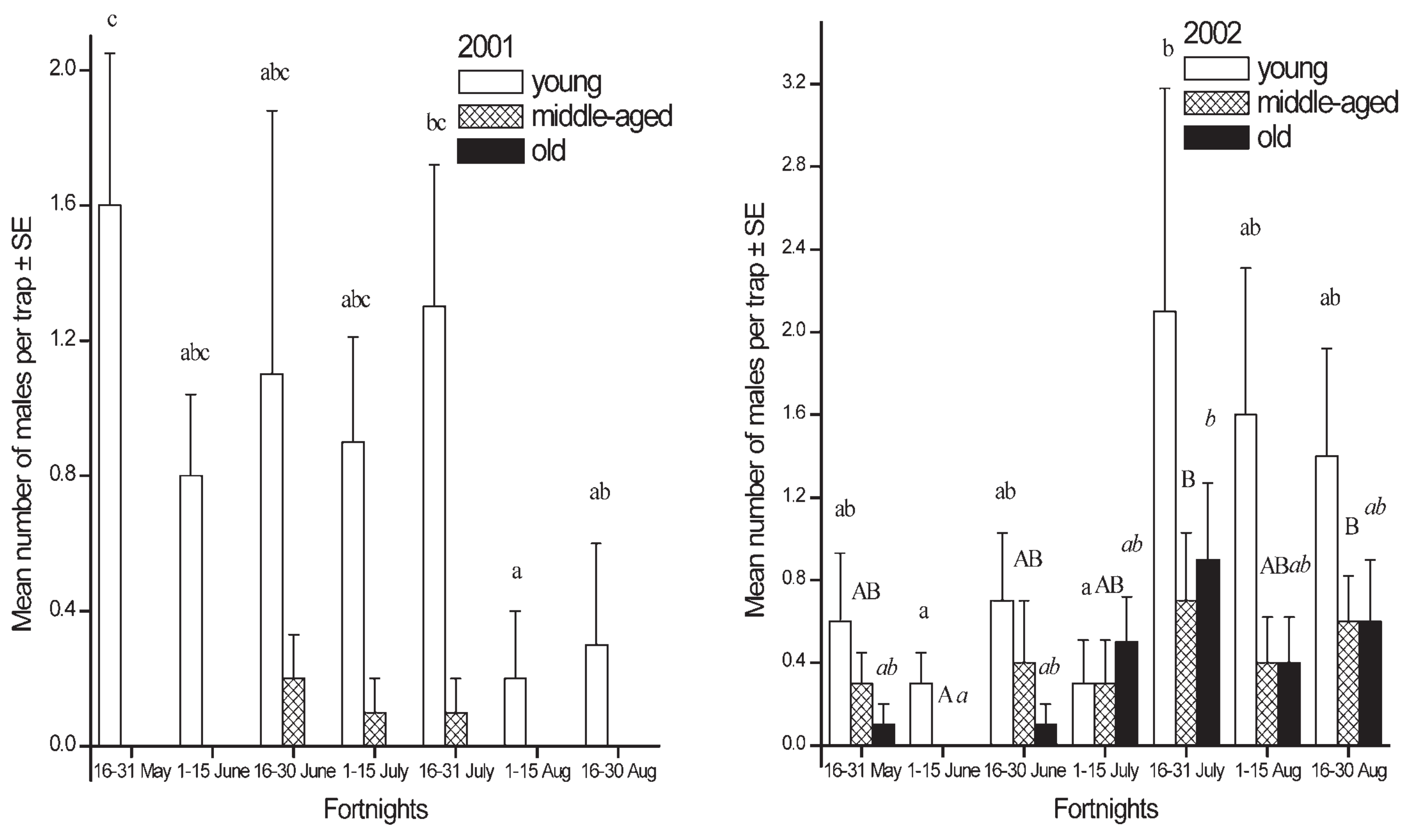

Fig. 2. Different age-categories of *C. scheidleri* males collected by pitfall traps at Nagykovácsi, Central Hungary in 2001 and in 2002. (Different letters indicate significant ($p < 0.05$) differences within the given years by post-hoc Fisher LSD test.) Repeated measures ANOVA between the years: young: [$F (1; 63) = 0.0009$; $p = 0.97$]; middle-aged: [$F (1; 63) = 14.45$; $p < 0.001$]; old: there were no old males in 2001

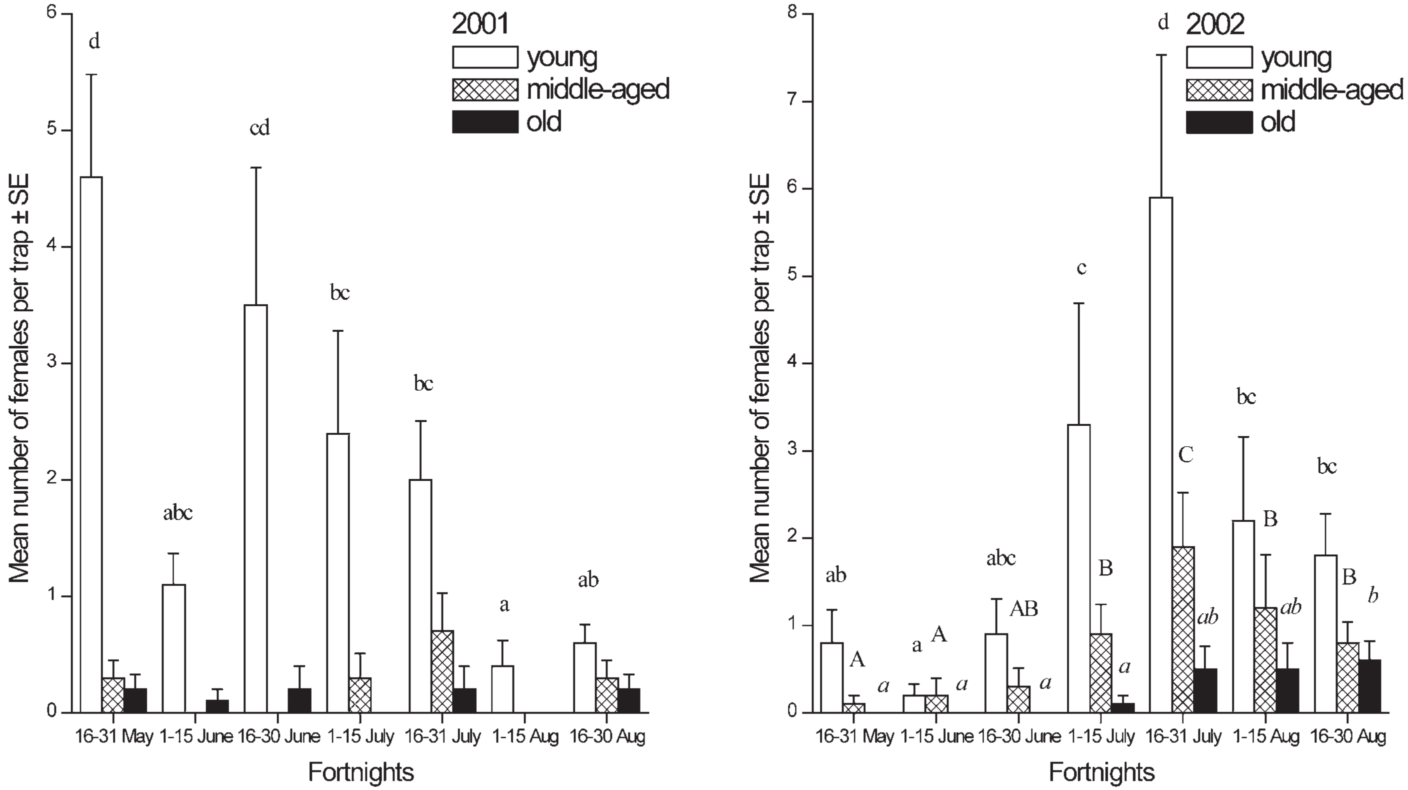

Fig. 3. Different age-categories of *C. scheidleri* females collected by pitfall traps at Nagykovácsi, Central Hungary in 2001 and 2002. (Different letters indicate significant ($p < 0.05$) differences within the given years by post-hoc Fisher LSD test.) Repeated measures ANOVA between the years: young: [$F (1; 63) = 0.46$; $p = 0.49$]; middle-aged: [$F (1; 63) = 9.67$; $p < 0.01$]; old: [$F (1; 63) = 2.15$; $p = 0.14$]

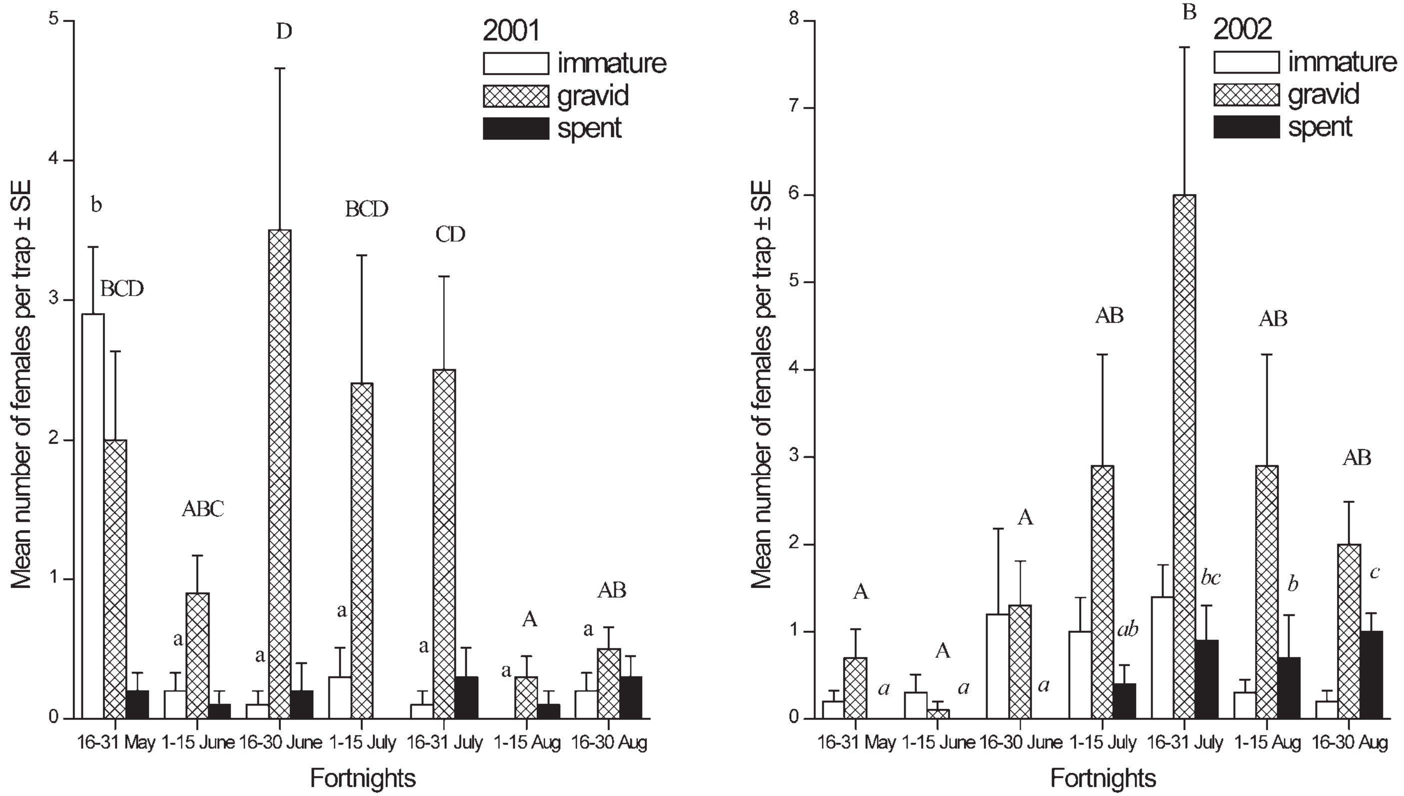

Fig. 4. The mean number of *C. scheidleri* females in each developmental stage captured by pitfall traps at Nagykovácsi, Central Hungary in 2001 and 2002. (Different letters indicate significant ($p < 0.05$) differences within the given years by post-hoc Fisher LSD test.) Repeated measures ANOVA between the years: immature: [F (1; 63) = 0.82; p = 0.36]; gravid: [F (1; 63) = 0.35; p = 0.55]; spent: [F (1; 63) = 5.47; p = 0.02]

Egg production and fecundity

The number of ripe eggs found in the ovaries is given in Table 1.

We found consistent pattern between the activity of females and the number of ripe eggs according to sampling dates. Ripe eggs were found in the ovaries from the end of May until the end of August.

The mean number of ripe eggs was 5.91 in 2000, 4.66 in 2001 and 5.35 in 2002 (Table 1). There was no significant difference in the population's mean egg number between years 2001 and 2002 [$F (1; 63) = 0.24$; $p = 0.62$]. Females had a maximum of 22 ripe eggs. The most frequent egg number during the three years was 2.

The highest observed rate of egg deposition was 0.07 in 2001 (Table 1). The highest estimated seasonal fecundity was 49.06 in 2002.

DISCUSSION

We summarize that *C. scheidleri* develops during one year, overwinters both as larva and as adult, adult females live more than one year, they reproduce more than once, and the different generations overlap during one season, assuring the persistence of the population. Old beetles participate also in the reproduction.

Determination of the mandible wear is the most precise method for age-estimation (FAZEKAS 1997). According to SPARKS *et al.* (1995) this ageing is used for only illustration and not for age-estimation. In the case of *C. scheidleri*, we could estimate the age of the adults and also the type of overwintering, which were supported by the results of the dissection. According to the results of ANDORKÓ *et al.* (2007), age estimation based on mandible wear is a good age estimator when different generations of the species do not overlap, like with *Carabus ullrichi*. When generations overlap, the two age-estimations – like the age estimation based on mandible wear and the age estimation based on the developmental stage of the ovaries – give good results. Because of the absence of middle-aged and old males in the activity in 2001, we suppose that males live for just one year. In carabid beetles it is well-known that in general females live longer than males (KRECKWITZ 1970; HŮRKA 1973). Females live longer also in this case.

Young and immature females appearing at the beginning of the season overwintered probably as adults, but they did not reproduce and this will be their first reproductive period. Mature females appearing at the beginning of the season overwintered also as adults, but this will be their second reproductive period. The spent females have already reproduced. The presence of immature females in the middle and at the end of the season would indicate that the beetle also overwinters as larvae. The activity peaks are similar to the reproductive peaks in the case of *C. scheidleri*, so the reproductive period overlaps with the activity period. This is not obvious in all ground beetles, for example the reproductive peak occurred earlier than the activity peak in the case of *Anisodactylus signatus* in Hungary (FAZEKAS *et al.* 1997).

In the case of *C. scheidleri* more females may reproduce than in other *Carabus* species, for example in *C. convexus, C. hortensis, C. violaceus, C. coriaceus* (FAZEKAS 1997). The presence of old beetles that reproduce increases the chances of the population's survival. The elongation of reproductive period of *C. scheidleri* in the season is similar to those of *Pterostichus melas* and *Harpalus atratus*. Since the species has several reproductive periods in the same season, this phenomenon can also ensure the population's survival. This population of the species live in an abandoned agricultural field, a strongly human-modified, very disturbed habitat, thus it is essential to assure the persistence of the population at different levels and in different ways.

We tried to classify this *Carabus* species according to the already known categorisation (THIELE 1977) based on annual rhythm and reproductive characteristics. *C. scheidleri* is a large, nocturnal species, which is unable to fly. This species can overwinter as adult and also as larva. According to this information only the species with flexible reproductive periods type (THIELE 1977) can include this species. In such species spring and autumn reproduction can occur side by side in the same population, and what is more important is that the larvae can also develop under summer or winter conditions. The reproductive period can occur at very different periods of the year depending on the climate and the weather.

Based on our results, we suggest this species has evolved to persist in unstable environments and it is well preadapted to the human disturbances by its long activity period, by several reproductive periods (high number of ripe eggs in ovaries/female, the presence of old beetles in the reproduction), by the ability of overwintering both as larvae and as adult which can lead to overlapping generations. These generations could cause a relatively high number of individuals as compare to other *Carabus* species, this can lead to a density dependent competitive success. These above mentioned clues might result that this species can buffer the environmental stochasticity and provide a constant seasonality demonstrated less spatio-temporal variation in activity density. Large species are often long-lived, have low densities and probably low reproductive capacity which dampens their year-to-year population fluctuations (LUFF 1982, LÖVEI & SUNDERLAND 1996). However, these attributes could make this species vulnerable also, because its potential to respond to (unfavourable) environmental variation may be diminished by the accelerated habitat fragmentation/alternation within its distribution area.

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