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Seasonal activity, age structure and egg production of the ground beetle *Anisodactylus signatus* (Coleoptera: Carabidae) in Hungary

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Carabidae, *Anisodactylus signatus*, Hungary, seasonal dynamics, age structure, egg production

Abstract. The seasonal activity, age structure and reproduction of the ground beetle *Anisodactylus signatus* were studied in central and eastern Hungary. *A. signatus* is a species with summer as well as winter larvae. Beetles showed two seasonal activity peaks: during mid-June, only "old" (overwintered) individuals were caught and this activity coincided with peak egg production; another activity peak occurred in mid-July, when more than 86% of the collected individuals were "young". The activity period of old beetles was shorter in the eastern population. Egg numbers in the ovaries were low (2–10 eggs/gravid female). No eggs were found in young adults, which suggests that females do not reproduce during their first adult year; in the subsequent season, they lay an estimated total of 15.6 eggs. Adults can live longer than one year.

INTRODUCTION

The ground beetle species *Anisodactylus signatus* (Panzer) is present in most of western and central Europe, reaches as far north as Denmark (Turin et al., 1977; Freude et al., 1976), and extends eastward through Russia and China (Deng et al., 1985). The species is scarce in Western and Central Europe (Freude et al., 1976; Desender, 1985), but is frequent in cultivated fields in Eastern Europe (Lövei & Sárospataki, 1990). *A. signatus* is one of the most common carabids in agricultural fields in Hungary (Horvatovich & Szarukán, 1986), and occurs widely in European Russia (Berim & Novikov, 1983; Matalin, 1992), Central Asia (Saipulaeva, 1986), and Heilongjiang Province, China (Deng & Li, 1981; Deng et al., 1985). The species occurs in fields of sugar beet (Berim & Novikov, 1983; Sekulic & Dedic, 1983), potato (Sorokin, 1981; Prisnyi, 1987), barley (Brunner & Kolesnikov, 1983), spring wheat (Deng et al., 1985), winter wheat (Puchkov & Gnatush, 1981), soybean (Deng et al., 1985), rice (Casale, 1980), and maize (Andriescu et al., 1983; Saipulaeva, 1986; Lövei, 1984).

Species in the genus *Anisodactylus* demonstrate different degrees of mixed feeding. The North American *A. santaecrucis* F. consumes eggs of the carrot weevil *Listronotus oregonensis* in the laboratory (Baines et al., 1990) and in the field (Zhao et al., 1990) as well as lepidopteran pests and weed seeds in apple orchards in Canada (Holliday &

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Hagley, 1984). Records of *A. signatus* document feeding on arthropods such as the Colorado potato beetle *Leptinotarsa decemlineata* (Sorokin, 1981; Prisnyi, 1987), other beetles, aphids, lepidopteran larvae, and pupae (Berim & Novikov, 1983; Deng et al., 1985). However, both larvae and adults of this species also consume plant material, mainly germinating seeds (Ponomarenko, 1969; Horvatovich & Szarukán, 1981; Berim & Novikov, 1983; Deng et al., 1985), and there are indications that *A. signatus* may be a reluctant predator, preferring plant material to animal prey (Berim & Novikov, 1983). Seasonal activity is unevenly documented within this species' wide distribution range (e.g. Kasandrova & Sharova, 1971; Horvatovich & Szarukán, 1981; Berim & Novikov, 1983); other aspects of its population biology, such as dispersal (but see Matalin, 1992), age structure and egg production remain little studied.

The aim of the present paper is to describe patterns of seasonal activity, age structure, and reproductive phenology of *A. signatus* populations living in agricultural fields in two regions of Hungary.

MATERIAL AND METHODS

Study sites and collection methods

Beetles were collected from three sites:

Site 1: a 400 ha maize field at Tükröspuszta, near Kápolnásnyék (47°11´N, 18°36´E), central Hungary. Ten pitfall traps (glass jam jars of 10 cm diameter that contained 70% ethylene glycol as preservative) were deployed in a row. The traps were placed 10 m apart, within the outer 300 m of the field and were emptied weekly, from the time of maize planting in early May to harvest in late October 1978. During this year, *A. signatus* was the most common ground beetle species found (Lövei, 1984) and was trapped in large numbers (N = 679). Aside from a single treatment at the time of sowing, no insecticide was applied.

Site 2: a 5 ha apple orchard in a mosaic of mixed cropland near Újfehértó (47°48´N, 21°40´E), eastern Hungary. This orchard was subjected to regular, "insurance" type insecticide treatments on 8–10 occasions per growing season, between April and July (Mészáros, 1984a). Ten pitfall traps (square plastic cups, 7 x 7 cm in size) that contained ethylene glycol as a preservative were operated from April to October 1984. Trap catches were collected weekly.

Site 3: a large, intensively managed apple orchard (100 ha) at Ilonatanya, near Nyíregyháza (47°57´N, 21°43´E), eastern Hungary. This orchard typically received 11–19 pesticide treatments per year, including 7–11 insecticide treatments during the trapping period (Mészáros, 1984a). Trap design and collection methods were similar to those described for Site 2. Samples were only collected from this site between early May and late July, 1984. (For a more detailed description of the sites, refer to Mészáros, 1984a, b).

Collections were sieved and transferred to 70% ethylalcohol in the field, sorted under microscope in the laboratory and stored in 4% formaldehyde solution for dissection.

Dissection and ageing

From Site 1, beetles from one sub-sample, were sexed, aged, and dissected to assess reproductive status on all but three sampling occasions. This sub-sample comprised >70% of all beetles collected. From site 2, all beetles trapped were dissected. Too few gravid beetles were collected at Site 3; only sex and age distribution results are presented.

Ageing was based on the extent of bristle and mandible wear, elytral hardness and coloration (van Dijk, 1972, 1979). Three age categories were distinguished: tenerals, young adults and old adults. Beetles classified as "teneral" adults were recently hatched individuals that had weak chitinisation and brownish elytral coloration. Beetles classified as "young" had hardened and black elytra, sharp mandibles, and long, intact bristles. These were adults that had not yet overwintered and were easily distinguished until the end of their first season. Beetles classified as "old" had hard and fully coloured elytra, blunt-tipped mandibles and broken or worn bristles. These were overwintered adults that were at least in their second year of life. We could not distinguish between second-year and older beetles.

Seasonal activity definitions

The period of activity was divided into four quartiles that were based on the total number of individuals caught. We defined the peak of activity as the date when 50% of the total number of individuals was caught; this was established from the activity curve. 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, respectively. The "early activity period" extended from the start of the activity to the beginning of the main activity period, and "late activity period" extended from the end of the main activity period until activity had ceased.

Estimating reproductive output

The reproductive output of the population at Tükröspuszta in 1978 was estimated by Grüm's method (Grüm, 1984). This method requires calculation of the mean number of ripe eggs in the ovaries, at weekly intervals, followed by the observed rate of egg deposition:

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

where dt = number of days between the estimation of N_{k-1} and N_k (the last two values of N_i).

Then the mean number of eggs laid by a female in the population during the entire breeding period becomes:

$$v = \sum_{i=0}^{k} N_i \mu_i T_i$$

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

RESULTS

Seasonal activity by site

In Central Hungary, Tükröspuszta (Site 1), adults were captured throughout the 8 May to 31 October trapping period (Fig. 1). The mean activity period occurred during the last three weeks of July, with the peak in mid-July (Table 1). The seasonal activity curve was skewed to the right (Fig. 1).

TABLE 1. Main activity periods and peak activity dates of the different age classes of *Anisodactylus signatus* at two localities in Hungary.

Age classes	Tükröspuszta		Ujfehértó	
	Main activity period	Activity peak	Main activity period	Activity peak
All beetles				
Old	6 June– 9 July	23 June	10–29 June	17 June
Teneral	8–18 July	13 July	20 July–18 August	1 August
Young	7–28 July	13 July	31 July–8 September	19 August
Total	7–29 July	14 July	11 July–22 August	1 August
Females				
Old	9 June–15 July	25 June	11–27 June	19 June
Teneral	6–16 July	10 July	20 July–17 August	5 August
Young	10 July–3 August	16 July	7 August–2 September	24 August
Total	6–24 July	12 July	1 July–24 August	1 August
Males				
Old	9 June–10 July	25 June	1–29 June	15 June
Teneral	9 July–2 August	15 July	20 July–17 August	30 July
Young	8–25 July	14 July	29 July–1 September	16 August
Total	2–21 July	10 July	15 July–21 August	31 July

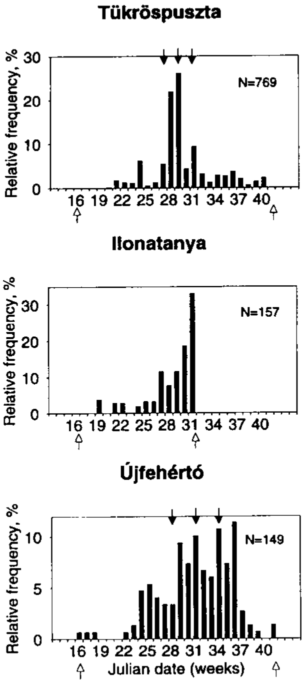

Fig. 1. Seasonal dynamics of adult *Anisodactylus signatus* at three locations in central (Tükröspuszta) and eastern (Ilonatanya and Ujfehértó) Hungary. The white arrows indicate the start and the end of the trapping period. Black arrows above panels denote the main activity period (left and right arrows) and activity peak (middle arrow). The trapping period at Ilonatanya did not cover the whole activity period.

In eastern Hungary, at Ilonatanya (Site 2), trapping did not occur throughout the entire activity period (Fig. 1). Beetles were first caught during the week preceding May 28th, and a steady increase was observed until trapping was discontinued at the end of July (Fig. 1). At the other eastern site, Újfehértó (Site 3), beetles were caught and remained active from the first week of trapping until trapping was discontinued in late September. The main activity period took place between mid-July and late August, and was almost three weeks longer than at Tükröspuszta (Table 1). The peak of activity occurred on August 1st (Table 1), also later than in central Hungary. The seasonal dynamics curve was less skewed than that of the population at Tükröspuszta (Fig. 1).

Seasonal activity of the age classes

Central Hungary, Tükröspuszta. Old beetles were captured on all sampling occasions (Fig. 2). The main activity period was about one month long, starting in June (Table 1). Tenerals first appeared on 27 June and peaked on 13 July. Small numbers of tenerals were trapped almost every week until early October. This resulted in an activity curve that was extremely skewed to the right (Fig. 2). Young beetles appeared about two weeks after the first tenerals; the peak occurred on the same day (Table 1). Activity continued until harvest in late September (Fig. 2).

Eastern Hungary, Ilonatanya (Site 2). Only old beetles were captured from the beginning of the trapping on 7 May until early July (Fig. 2). Increasing numbers of tenerals and young beetles were caught from early July until trapping was discontinued at the end of July.

Eastern Hungary, Újfehértó (Site 3). Old beetles were captured from the first week of trapping, 14–21 April, until late July; one was captured in late August. The mean activity period was shorter than at Tükröspuszta, but peaked one week earlier (Table 1). Tenerals appeared during the week of 7–14 July and were captured until late September (Fig. 2). The main activity period took place one month later than the main activity of the same age class at Tükröspuszta (Table 1). The activity of young beetles peaked later and lasted longer than that of the tenerals (Table 1). The cardinal dates of activity of the tenerals and young beetles completely overlapped at Tükröspuszta but not at Újfehértó (Table 1).

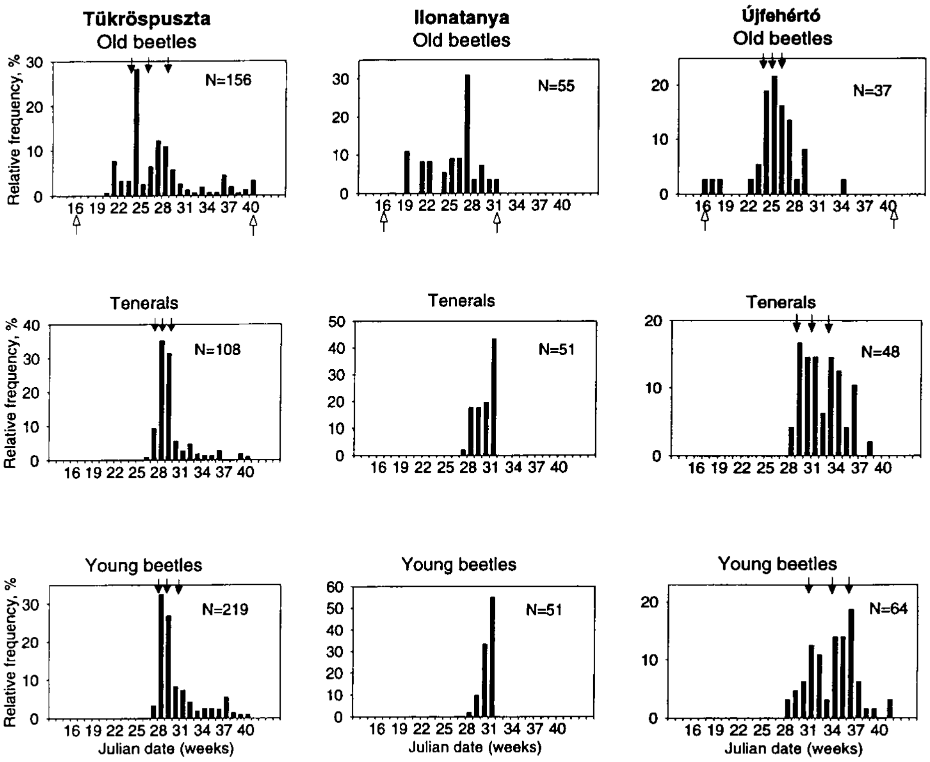

Fig. 2. Seasonal dynamics of three age classes of *A. signatus* at three sites in Hungary. Arrows denote trapping and beetle activity dates as on Fig. 1.

Activity of females vs. males

Tükröspuszta. We captured about twice as many old males (N = 105) as females (N = 51); no such difference occurred for the other two age groups (Fig. 3). Old individuals of both sexes showed similar seasonal activity curves (Fig. 3, Table 1). Old females at this site had a longer mean activity period (36 days) than either tenerals (10 days) or young females (23 days, Table 1). The main activity of old males hardly coincided with that of younger age classes, which nearly completely overlapped. Both young and teneral males continued to be active until the end of the study period while teneral females did not (Fig. 3). Peak activity periods for males were a few days earlier than the respective periods for females (Table 1, Fig. 3).

Újfehértó. We captured more old females than males, the opposite of the results from Tükröspuszta (Fig. 4). Main activity periods of the age groups showed less overlap at this site (Table 1). Female activity periods and peaks were later than the respective dates for males (Table 1). The main activity period for old females (16 days) was shorter than any other female age class, and considerably less than that of the same male age class (28 days, Table 1). The lack of overlap between old and younger beetles resulted in a female

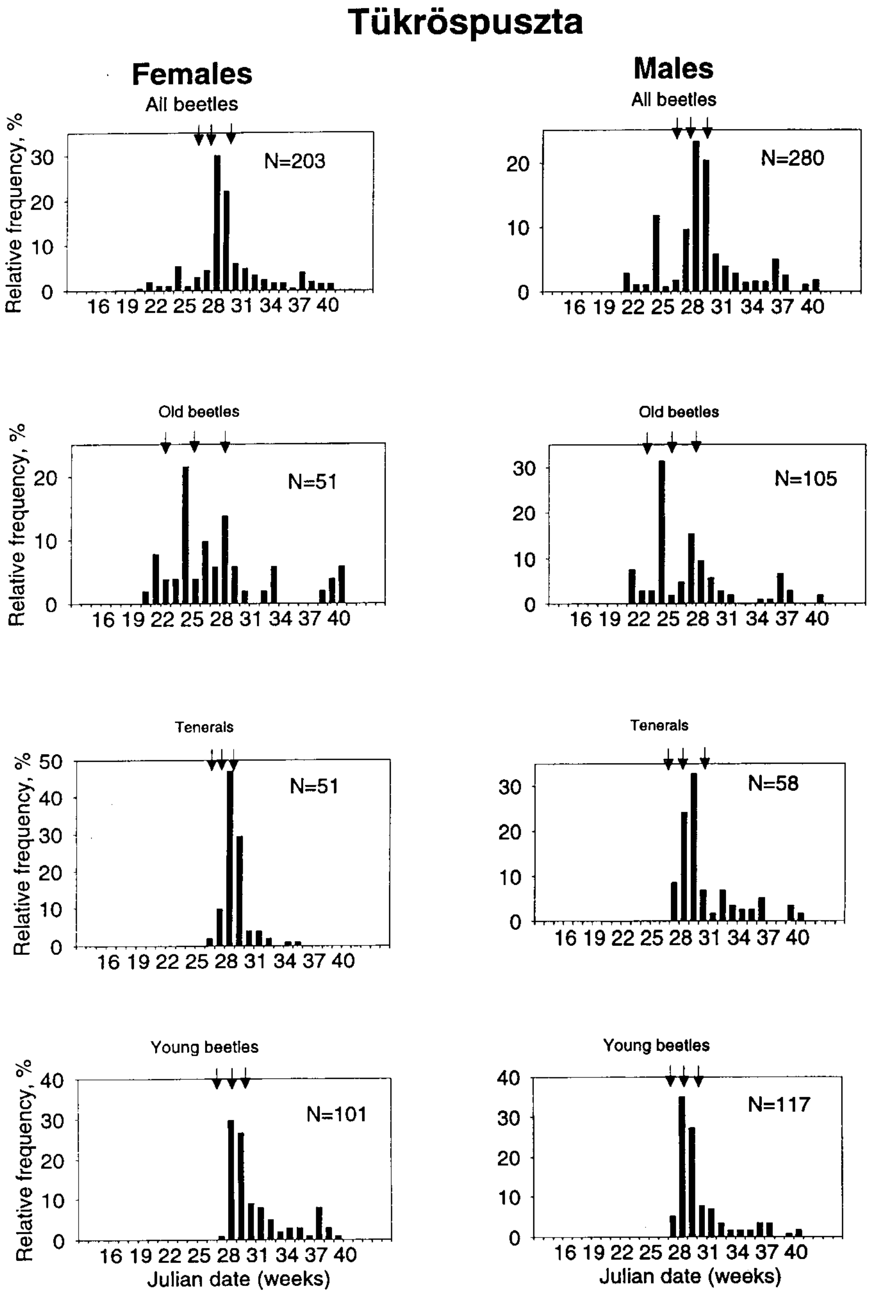

Fig. 3. Seasonal dynamics of different age classes of male and female *A. signatus* at Tükröspuszta, central Hungary. Arrows at the top indicate the main activity period and time of peak activity as on Fig. 1.

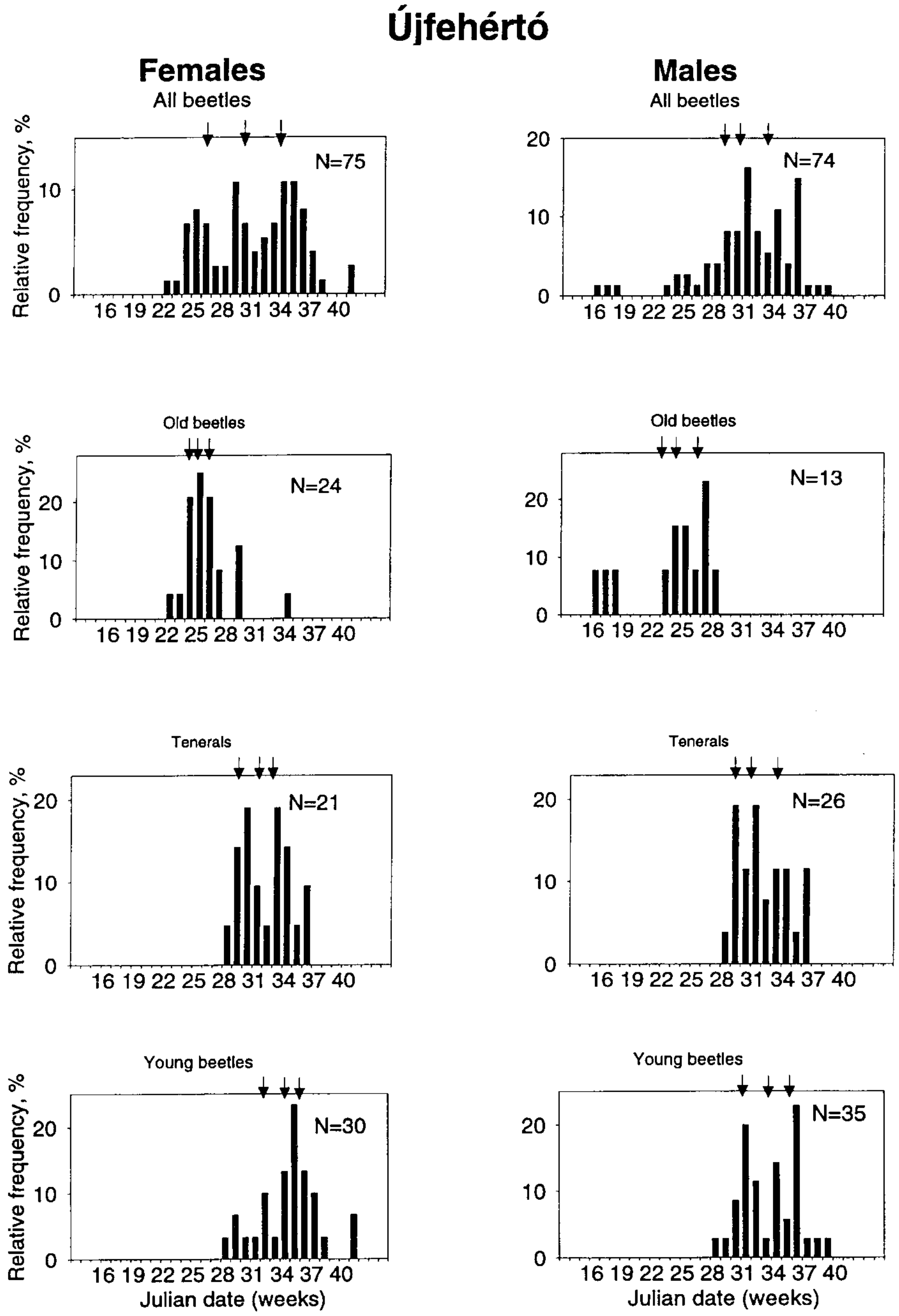

Fig. 4. Seasonal dynamics of different age classes of male and female *A. signatus* at Ujfehértó, eastern Hungary. Arrows at the top indicate the main activity period and time of peak activity as on Fig. 1.

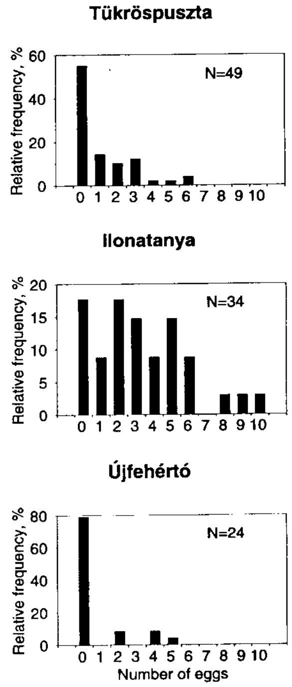

Fig. 5. Relative frequency of different egg numbers per old female *A. signatus* collected in central and eastern Hungary.

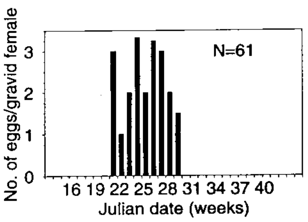

Fig. 6. Seasonal dynamics of mean egg numbers found in gravid *A. signatus* females at Tükröspuszta, central Hungary.

mean activity period of 55 days, the longest of any group at either site. Males at Újfehértó displayed similar activity characteristics (Table 1). The main activity period lasted about four weeks (Table 1).

Inter-site comparisons. The mean activity period of all females combined was less than three weeks at Tükröspuszta vs. almost two months at Újfehértó. Males showed a similar but less pronounced trend (5 weeks vs. 8 weeks, Table 1). A number of further differences were also observed when the age classes were considered separately: (1) a short mean activity period for old Újfehértó females (16 days) vs. a long one at Tükröspuszta (36 days) but no such difference for old males; (2) a very short mean activity period for teneral Tükröspuszta females, 20 days longer for Újfehértó females (Table 1); (3) similar mean activity periods for young females at the two sites, but twice as long for young males at Újfehértó (34 days) vs. Tükröspuszta (17 days). In general, activity curves were more tightly synchronized at Tükröspuszta (shorter mean activity periods) except for old beetles (Table 1). The span of the peak activity dates indicates the same; they all occur within three weeks at Tükröspuszta while they span two months at Újfehértó (Table 1).

Age structure and sex ratio

"Old" adults occurred as 32%, 35% and 25% of individuals collected at the three sites, respectively. At Tükröspuszta, 69% of all beetles captured were males. In the apple orchards in eastern Hungary (sites 2 and 3), females outnumbered males (62% of all beetles at Újfehértó and 65% at Ilonatanya were females). The sex ratio of "young" adults was more even, with 69% females at both Tükröspuszta and Újfehértó, 46% at Ilonatanya (but note the shorter trapping period there).

Egg production

None of the young females had eggs in their ovaries. Gravid females had a maximum of 6 eggs at Tükröspuszta, 10 eggs at Ilonatanya, and 5 eggs at Újfehértó. The relative frequency of different egg numbers per female is shown on Fig. 5. At Tükröspuszta, Ilonatanya, and Újfehértó, respectively, 44%, 82% and 21% of the old females were gravid. At Tükröspuszta, the earliest collection of a gravid female occurred on 23 May (with 3 eggs) and the last one was collected on 18 July (2 eggs); females with the maximum number of eggs were collected in early June (Fig. 6). Similar dates cannot be reliably established for the two other locations due to the short trapping period at Ilonatanya, and the low number of gravid females (5 only) captured at Újfehértó. The mean number of eggs per gravid female was 2.67 (S.D. = 1.68, N = 18) at Tükröspuszta and 4.0 (S.D. = 2.36, N = 28) at Ilonatanya. This difference is significant (Student's two-sample t-test, $t = 2.08$, d.f. = 44, p = 0.043). The difference in the populations' mean egg number was even greater (Tükröspuszta: mean = 1.17, S.D. = 1.73, N = 41; Ilonatanya: mean = 3.29, S.D. = 2.63, N = 34, Student's $t = 4.19$ d.f. = 73, p = 0.001).

The estimated seasonal egg production per female at Tükröspuszta, according to Grüm's method, was between 20.9 and 10.3 (Table 2). The most realistic estimate, based on the longest period for the estimation of egg deposition rate is 15.6 eggs/ female.

TABLE 2. Estimates of mean total seasonal fecundity, according to Grüm's method, for *Anisodactylus signatus* females in the population at Tükröspuszta, Hungary, 1978. Three periods were used to determine egg laying rate.

Period	N_{k-1}	N_k	Egg laying rate	Total fecundity
3–10 July	2.6	1.00	0.14	10.3
11–18 July	1.0	0.14	0.28	20.9
3–18 July	2.6	0.14	0.21	15.6

DISCUSSION

At all sites, the "old" beetles were already active at the start of the trapping. These individuals evidently overwintered as adults. Adult overwintering is also suggested by the appearance of tenerals during autumn (late September–early October). These overwintered adults probably represented the first, smaller peak of the seasonal activity curves in mid-June, which coincided with the peak of egg production. The second, larger activity peak signalled the emergence of "young" individuals; teneral beetles continued to emerge until early October. The time period between the start of reproductive activity in May and the appearance of teneral beetles in June is too short for these to have been the offspring of adults reproducing within the same season; the emerging teneral adults overwintered in larval or pupal stage. If the thermal developmental threshold of pupae were similar to the thermal threshold of the adult activity in spring, overwintered pupae would moult into teneral adults earlier. The fact that this did not happen suggests that at least some individuals overwintered as larvae.

The survival pattern of the old beetles varied across regions. The sudden and complete disappearance of old beetles at Újfehértó and the continued presence of this age class at Tükröspuszta until October suggests that eastern adults may die after one year, while those in central Hungary may live longer. The extent of overlap between "old" and "young" beetles was also different, with less overlap in the east. Although our material was collected in different years, a similar phenomenon was noted by Kasandrova & Sharova (1971) in Russia. Near Ohrenburg, Russia, Lapshin (1971) found old adults from the middle of May to the middle of July; young beetles did not occur during this time.

This long activity period with the presence of more generations is similar to the seasonal activity of autumn-breeding carabid species like *Harpalus rufipes* (Luff, 1980), as opposed to the activity of other spring breeders, e.g. *Agonum dorsale* (Fazekas & Kádár, 1991) or *Clivina fossor* (Desender, 1983), which have no surface-active adults after early August.

Although egg numbers in the ovaries cannot always be taken as true representation of the reproductive effort (Lövei & Sunderland, 1996), the number of eggs found in *A. signatus* females is very low, even as compared with other European species characterized by a low reproductive output. For example, *H. rufipes* is a low-reproducing species (Luff, 1980), yet frequently has up to three times more eggs in its ovaries than *A. signatus* had during our study. Grüm's (1984) estimate also indicates a low level of reproduction.

The congener *A. binotatus* has a similar reproductive pattern to *A. signatus* (Den Boer & Den Boer-Danje, 1990); other species of *Anisodactylus* share some but not all reproductive characteristics. The North American congener *A. sanctaecrucis* can lay up to 142 eggs in the laboratory during a 2.5 month period (Kirk, 1977). The female of this species, like *A. signatus*, remains sexually immature in the first year, lays eggs during May-June the following year, and may also lay eggs in July of the year after.

Our estimate of seasonal reproductive output is based on a study conducted during a year when *A. signatus* was more abundant than usual, thus the estimate may be biased. In the year of study we caught 769 adults of *A. signatus*; conversely, four other years (1977–1981, excluding 1978) with the same yearly trapping effort at the same site yielded a total of 112 individuals (Lövei, unpublished). The mean egg number per gravid female in the maize field was lower than the mean egg numbers in the orchards and also lower than found in Russia (Kasandrova & Sharova, 1971). One possible explanation for this is an inverse density-dependent egg production, which was described by Baars & van Dijk (1984) for *Calathus melanocephalus* L. and by Heessen (1980) for *Pterostichus oblongopunctatus*. We have no dissection data from other years to elucidate such a difference. According to pitfall trap catches from the same field in 1979, the population returned to the lower level of the previous years. Most of the captures from 1979 occurred during the spring activity peak, which is in agreement with the hypothesis that adult numbers in a given year are influenced by the previous year's egg laying conditions.

From our data, we conclude that *A. signatus* has both summer and winter larvae in central Hungary, and adults may live for more than one year, perhaps reproducing more than once. The eastern Hungarian populations seemed to demonstrate a different life history pattern, with less overlap between age classes and a shorter adult life span. Further studies on year-to-year fluctuations in density, laboratory studies of egg laying and more extensive field collections and dissections are necessary before we can assess the flexibility of the reproductive strategy in *A. signatus*.

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