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Growth and egg production in *Abax ater* (Coleoptera, Carabidae)

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Summary

Production over a complete life cycle, from egg to reproductive adult, is investigated in the carabid beetle *Abax ater*, as part of a study on the energy budget of this species. Research was carried out both in the laboratory under controlled conditions of temperature and photoperiod, and under semi-natural outdoor conditions to take into account natural fluctuations in climatic factors.
Growth was considerable in the adult stage: 32 % of a breeding adult's dry body mass were produced during larval development, while 59 and 9 % were produced during the first and second year, respectively, after pupation. In both larvae and adults, growth was slower under semi natural conditions than in the laboratory during early development, but was compensated for by a stronger growth later, suggesting regulation of body mass through compensatory growth. Egg production was possible only after adult hibernation; it accounted for 21 % of total production in the adult stage, with a very low fecundity (12 eggs per female per year on average).
Abax ater is characterised by a body growth that is slow and spread over both the larval and adult stages, a reproductive effort that is very small and spread over several years and over several months in each year, and a great longevity. These demographic and bioenergetic traits are typical for a 'conservation' K strategy.

Key words: Carabidae, *Abax ater*, growth, egg production

Introduction

Production is a key element of the energetics and quantitative ecology of organisms and populations. Production is what allows organisms and populations to grow. In carabid beetles as in other insects, it includes individual body growth, egg production and production of larval exuviae (Manga 1972; Grüm 1975b, 1980; Weidemann 1971). Although it has been studied by a number of authors, most studies have considered only adults (Thiele 1977), leaving the parts taken by larvae and pupae unknown.
Here we investigate production over a complete life cycle, from egg to reproductive adult, in the carabid beetle *Abax ater*, as part of a study on the energy budget of this species (Chaabane et al. 1996). *Abax ater* is a dominant species – in terms of biomass and activity – in many forests of Western and Central Europe, and is thought to play a significant role in the regula-

tion of the invertebrate fauna at the soil surface (Loreau 1984b). It also has a peculiar life cycle, with a very wide period of activity, a continuous reproduction and a flexible hibernation at either the adult or the larval stage (Loreau 1985). Therefore understanding its energetics and resource allocation is of special interest.
Measuring production in the field is difficult for carabid beetles because of their mobility and relatively low population densities; accordingly previous studies on production were made in the laboratory. We carried out our research both in the laboratory under controlled conditions of temperature and photoperiod, and under semi-natural outdoor conditions to take into account natural fluctuations in climatic factors.

Materials and Methods

Collecting the beetles

Adult *Abax ater* were collected using funnel traps in a near-climax beechwood at Lembeek, 15 km south of Brussels, Belgium (described in Loreau 1984a).

Laboratory rearing conditions

Insects were reared in the laboratory in climatic chambers equipped with an automatic system controlling temperature and photoperiod and ensuring a continuous ventilation. Standard (summer) conditions were set at 18 °C by daytime 16 h per day, 15 °C by night-time 8 h per day, and humidity always near saturation. These conditions are very close to those that can be experienced in the top layer of the beechwood soil in July (Loreau 1984a). Winter conditions for hibernation were set at 3 °C by daytime 8 h per day and 1 °C by night-time 16 h per day. These conditions are close to those which can be experienced in the top layer of the beechwood soil in January. An accidental cooling close to freezing point occurred due to a power failure during the 18th week of the larval rearings. It lasted for about 6 hours before summer conditions were restored.
Larvae were reared separately in glass vials 5 cm in diameter, 3 cm high and furnished with 1 cm of sieved soil. Adults were kept separately in PVC vials, 8 cm in diameter, 12 cm high and furnished with 7 cm of moist sieved forest soil. Every month, each female was placed in the presence of a male, which was withdrawn after copulation. The individuals were fed twice a week on pieces of earthworms of the species *Dendrobaena subrubicutda* and *Lumbricus eiseni* for the larvae and on ground beef meat for the adults (Thiele 1968).
Cohorts of 10 first-instar, 5 second-instar and 5 third-instar larvae were followed from eggs produced in the laboratory. A cohort of 3 males and 5 females that emerged from pupae produced in the laboratory was followed during 32 weeks after emergence, and again during 37 weeks after a 10-week hibernation.
In addition, a group of 35 females caught in the Lembeek beechwood in October 1990 was kept under winter conditions for 10 weeks and checked for egg production from February until late October 1991. Another group of 15 males and 15 females caught in the field in August 1991 was maintained under summer conditions until late November and checked for egg production during 20 weeks after a 10-week hibernation.

Outdoor rearing conditions

The beetles were reared under semi-natural conditions in four outdoor tubs sunk into the soil under a bush on the Solbosch campus of the Free University of Brussels. The tubs were covered by a glass sheet preventing rain from coming in while letting air circulate. Temperature and humidity were recorded continuously using a thermohygrograph placed in one of the tubs. Daily average temperatures were calculated from 12 measurements between two successive sunrises.
Given the length of the life cycle of *Abax ater*, production was studied from three different cohorts. The first one was made up of 26 larvae that hatched from eggs obtained in the laboratory and developed to pupation from March to October 1992. The second one was made up of 20 3rd-instar larvae collected in the field in September 1991; the 3 adult males and 2 adult females that emerged after pupation in June 1992 were followed until October 1992. The third one was made up of 6 adult males and 5 adult females collected in the field in October 1991; these were followed during a full year. In addition, 5 teneral females were caught in the field in September 1991 and checked for egg production after hibernation.

Growth production

The fresh body mass of individuals was measured (±0.1 mg) every week during the first two larval stages and every two weeks later on. It is difficult to obtain a reliable estimate of body mass of predatory animals under homogenous conditions: their meals can be very large and influence their weight to a large extent. We therefore weighed them before feeding, i.e., 3 days after their last meal.
Their daily growth was measured as $(M_t - M_0)/t$ where M_t = body mass at the end of the period, M_0 = initial body mass, t = duration of the period.
The dry body mass was measured at the beginning and at the end of each larval and pupal stage on individuals reared separately for that purpose, starved for three days and then oven-dried at 70 °C for 48 hours. For adults, measurements of dry body mass were taken immediately after imaginal emergence and three months later.

Production of exuviae

After each larval moulting, exuviae were collected, then oven-dried at 70 °C for 48 hours and weighed.

Egg production

The eggs of *Abax ater* are protected by a thin clay cover (Löser 1972). In freshly laid eggs, this cover is fragile. Therefore we searched for eggs manually; we then washed the soil on a 2 mm-mesh sieve to ensure that no eggs were missed. Eggs were collected throughout the breeding period and placed in Petri dishes on a sterilised moist filter paper.

Results

Larval growth

In the laboratory, the fresh body mass of larvae increased steadily until the 12th week with a small plateau at each moulting (Fig. 1A). Growth was more irregular subsequently; in particular, a significant weight loss occurred in the 19th week. This was due to the accidental drop in temperature in the previous week, which also resulted in a decreased food consumption (Chaabane et al. 1994). Body mass again increased later slightly to reach 180 ± 8 mg (mean ± standard deviation) before pupation. The drop during the pupal stage was quite small, since the young teneral imago weighed 164 ± 8 mg, that is to say a mass loss of 9 % only.
Growth under semi-natural conditions was slower than in the laboratory during the first two larval instars, but more rapid during the third instar (Fig. 1 B and Table 1). There was a slight decrease in body mass during the month preceding pupation due to an interruption of food consumption. The mass loss during the pupal stage was here also quite small (10 %).
Comparison between the laboratory and semi-natural conditions (Table 1) shows that the slower growth during the first two larval instars resulted in a significantly lower body mass at the beginning of the third larval instar under semi-natural conditions ($t = 3.90$; 15 df; $P < 0.05$), but this difference had virtually vanished by the end of the third instar ($t = 1.68$; 15 df; $P = 0.11$) despite unequal temperatures and instar durations (Table 1).

Table 1. Comparison of larval growth under laboratory and semi-natural conditions: numbers of individuals (n), mean ambient temperatures, body masses (mean ± standard deviation) at the beginning and at the end of each larval instar and instar durations

In-star	*Laboratory conditions*					*Semi-natural conditions*				
	n	Mean temp. (°C)	Initial mass (mg)	Final mass (mg)	dura-tion (days)		Mean temp. (°C)	Initial mass (mg)	Final mass (mg)	dura-tion (days)
	10	17.0	7.46±0.6	22.5±2.7	25	*26*	9.0±1.5	7.1±0.9	20.8±3.0	40
2	*5*	17.0	20.4±2.3	64.0±6.6	35	*17*	13.0±2.9	19.7±1.7	55.6±3.3	51
3	*5*	17.0	63.2±5.6	180.2±8.2	143	*12*	15.9±1.9	54.0±3.9	171.7±8.4	107

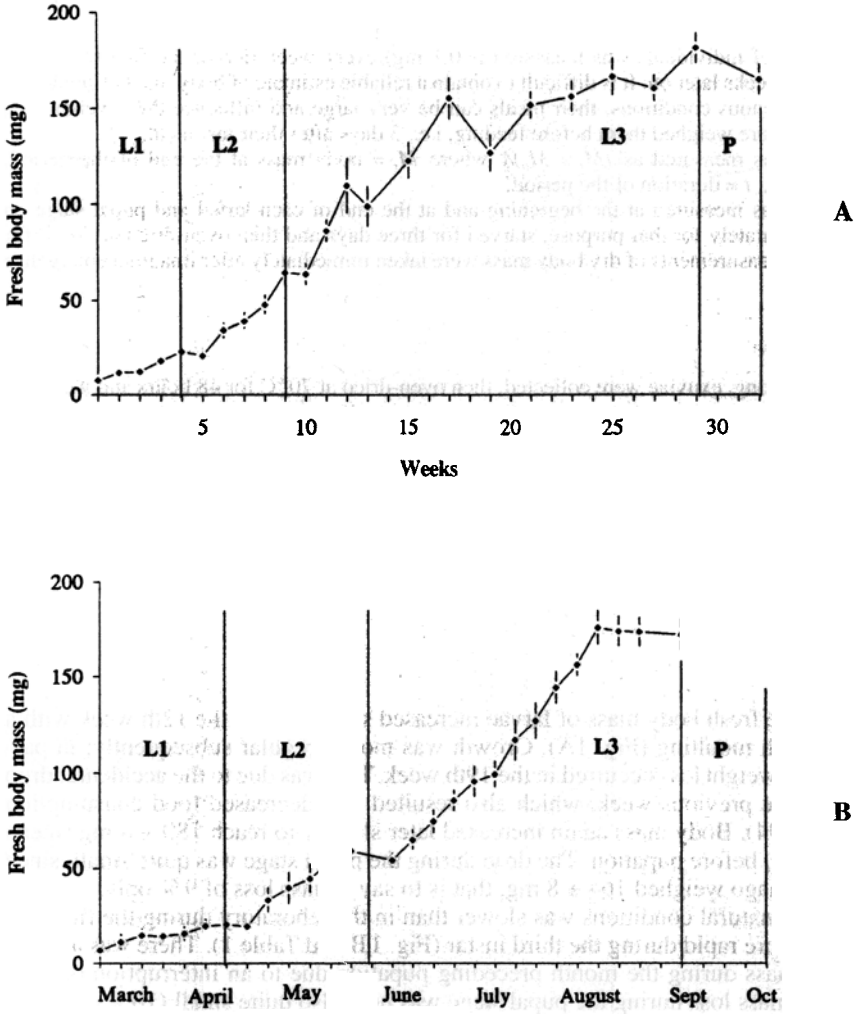


Fig. 1. Pre-imaginal body growth (in mg fresh mass; mean ± standard deviation) under (A) laboratory and (B) semi-natural conditions. L1, L2 and L3: first-, second- and third-instar larva; P: pupa

Adult growth

In the laboratory (Figs. 2A and 2B), body growth was rapid during the first month after imaginal emergence (1.6 and 1.8 mg/day in males and females, respectively). It slowed down during the second month (0.8 and 0.9 mg/day, respectively), and became almost zero during the rest of the first year (0.07 and 0.01 mg/day, respectively). Body mass then stabilised at 234 ± 14 mg in males and 251 ± 7 mg in females. A small mass loss of 15 ± 6 mg (two sexes combined), that is to say 6%, occurred during hibernation. The beetles gained weight again during the month that followed the end of hibernation, especially females, which started soon to lay eggs. Body mass then fluctuated around 249 ± 14 mg in males and 278 ± 8 mg in females.

Under semi-natural conditions (Fig. 2C), body growth was rather rapid during the first two months after imaginal emergence (1.3 mg/day during the first month and 1.0 mg/day during

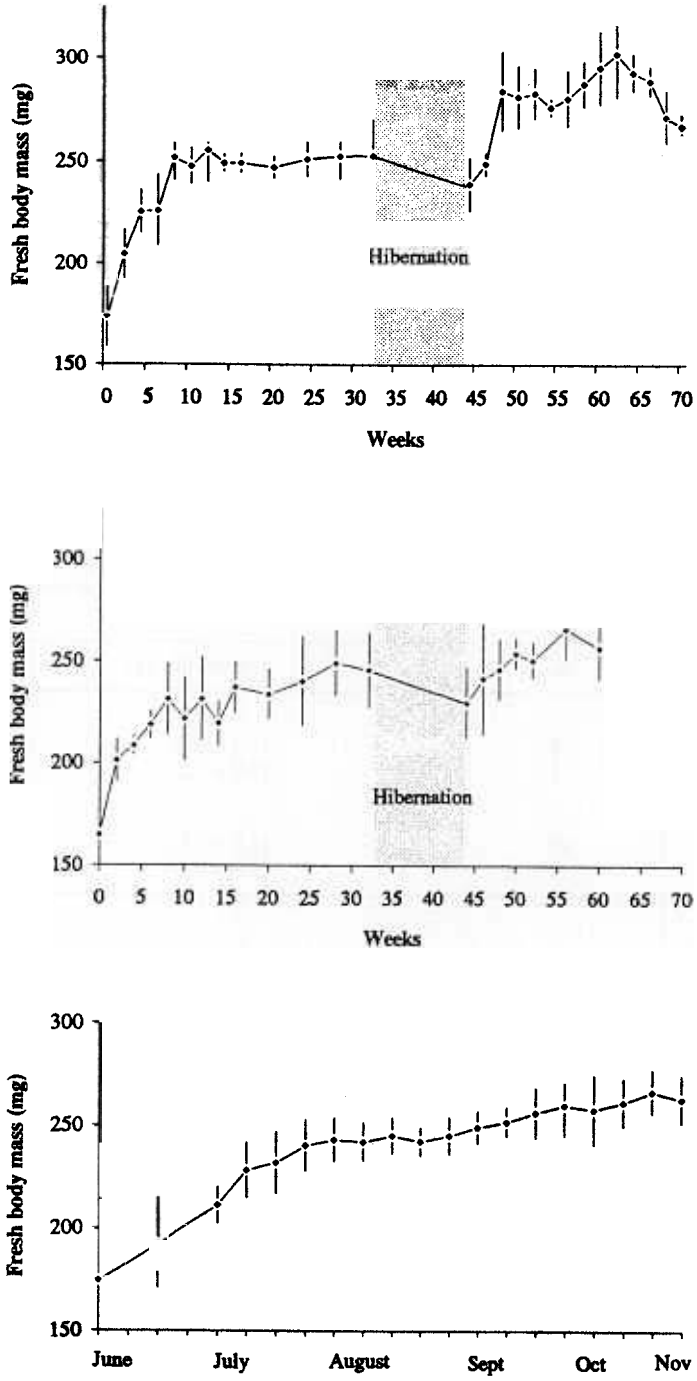


Fig. 2. Adult body growth (in mg fresh mass; mean ± standard deviation): (A) females during the first two years after imaginal emergence under laboratory conditions; (B) males during the first two years after imaginal emergence under laboratory conditions; (C) adults (males and females combined) during the first year after imaginal emergence under semi-natural conditions

the second, two sexes combined). It was slower but persisted during the following months (0.13 mg/day). By the end of the first year, the average body mass was identical to that in the laboratory (244 ± 10 mg, two sexes combined).

Egg production

The five adult females reared since their imaginal emergence in the laboratory all laid eggs after hibernation, whereas no egg production had been observed before hibernation. Egg laying started 3 weeks after the end of hibernation and was spread irregularly over 23 weeks, depending on the individuals. Usually egg production was highest at the beginning of each female's egg-laying period, then declined progressively (Fig. 3). But it was fairly low overall: 12 ± 3 eggs per female during the second year in the adult stage (Table 2). Among the 49 females of unknown age collected in the field in October 1990 and August 1991 and reared in the laboratory, 34 laid variable numbers of eggs, mainly in March and from mid-August to mid-September, with an average of 11 ± 7 eggs per female per breeding season (Table 2). Under semi-natural conditions, similar results were obtained. No egg laying was observed after imaginal emergence in September, but 4 out of 5 females laid 15 ± 3 eggs in June and

Table 2. Egg production in a breeding season after hibernation, in cohorts of females reared since their imaginal emergence and in groups of females of mixed ages collected in the field. n_0 = number of observed females; n_1 = number of females that laid eggs; number eggs: mean ± standard deviation (per female that laid eggs)

	n_0	n_1	number of eggs
Cohorts			
Laboratory conditions	5	5	12.2 ± 3.4
Semi-natural conditions	5	4	15.0 ± 3.2
Groups collected in the field			
Laboratory conditions	49	34	11.1 ± 7.0
Semi-natural conditions	5	3	12.0 ± 5.0

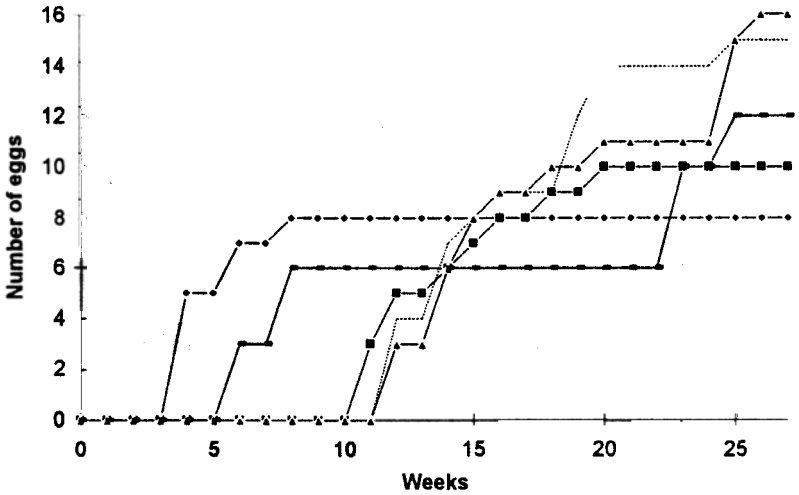


Fig. 3. Cumulative egg production for 5 females after hibernation

July in the following year (Table 2). Three out of 5 young females collected in the field in September 1991 laid 12 ± 5 eggs after hibernation, from late May to mid-July (Table 2).
There was no significant difference between egg production in the laboratory and under semi-natural conditions, either for the cohorts reared since imaginal emergence (t = 1.28; 7 df; P = 0.24) or for the females captured in the field (t = 0.23; 35 df; P = 0.82). There was also no significant difference in egg production between the cohorts reared since imaginal emergence and the females captured in the field, when females that did not lay any eggs were excluded (t = 0.98; 44 df; P = 0.33). Lastly, the average mass of an egg was 6.88 ± 0.72 mg (n = 31).

Dry mass production

The following linear regressions were obtained between dry mass (D) and fresh mass (F):

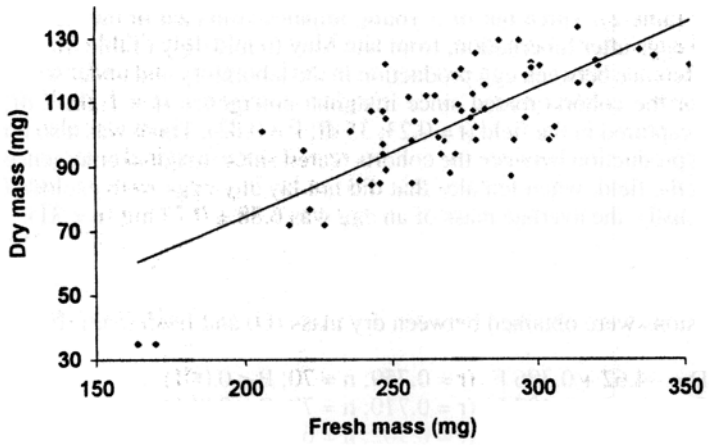
Adult females (Fig. 4A): $D = -4.62 + 0.396\ F$ ($r = 0.759$; $n = 70$; $P < 0.001$)
Adult males (Fig. 4B): $D = -8.43 + 0.407\ F$ ($r = 0.710$; $n = 79$; $P < 0.001$)
Larvae (Fig. 4C): $D = 1.78 + 0.396\ F$ ($r = 0.902$; $n = 60$; $P < 0.001$)

In adults after the teneral stage, the ratio of dry mass to fresh mass was roughly constant around 37 % in both sexes. In larvae, the relation between dry mass and fresh mass was distinctly nonlinear despite the high linear correlation coefficient (Fig. 4C). The ratio of dry mass to fresh mass was roughly constant up to a fresh mass of about 75 mg (beginning of third instar), then decreased up to a fresh mass of about 150 mg, and increased again for larger masses corresponding to the end of the third larval instar.
The changes in the percentage of dry mass during the course of a life cycle are summarised in Fig. 5. This percentage was relatively constant around 20 % during the first two larval instars. It decreased to 12 % during the third larval instar, then increased up to 23 % at the end of this instar. It further increased strongly after imaginal emergence during the teneral stage to stabilise around 37 % in the adult stage.
The above regressions were used to convert our data on fresh mass into dry mass. Table 3 summarises the various elements of production over a complete life cycle. To increase the number of data, we used in this table the combined data from our cohorts reared in the laboratory and under semi-natural conditions as well as some additional data from individuals

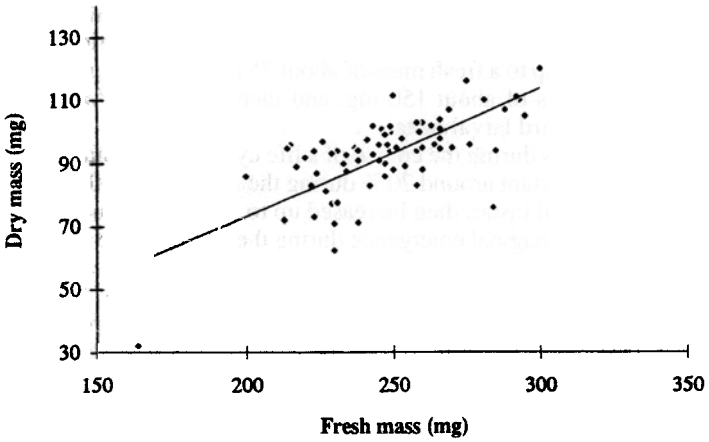
Table 3. Dry mass production (in mg) over a complete life cycle. n = number of individuals; D = dry mass; P_{g+ex} = production due to growth, including exuviae; P_{ex} = production of exuviae; P_r = production due to reproduction (egg production). Mean ± standard deviation

Stage		*Initial D*	*Final D*	P_{g+ex}	P_{ex}	P_r
Larva	41	1.28 ±0.21	4.15 ±0.94	2.86 ±0.99	0.44 ±0.12	
Larva 2	34	3.81 ±0.65	12.20 ±1.51	8.40 ±1.79	1.11 ±0.14	
Larva 3	30	12.10 ±1.34	38.55 ±2.31	26.50 ±3.16	3.73* ±0.91	
Adult 1st year	13	37.47 ±2.04	96.98 ±4.97	59.52 ±5.57		
Adult female 2nd year	25	94.41 ±6.74	102.60 ±9.03	8.20 ±2.50		18.0 ±4.4
Adult male 2nd year	24	96.95 ±6.30	101.29 ±7.79	4.3 ±1.9		

* Exuviae of both the third larval instar and the pupa



A



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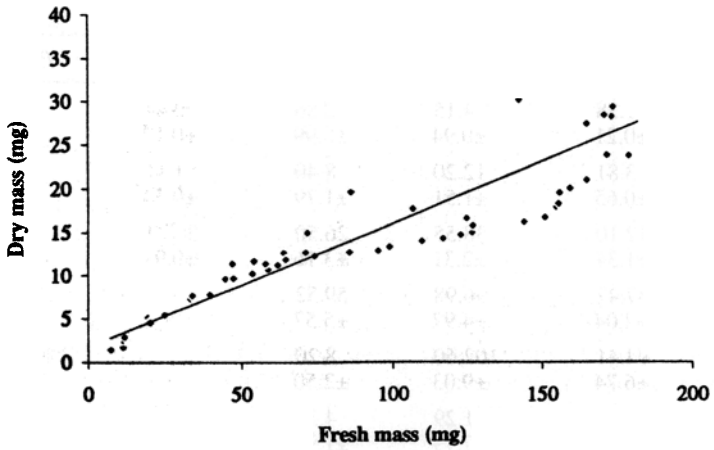

C

Fig. 4. Relation between dry and fresh mass (in mg) in (A) adult females; (B) adult males; and (C) larvae

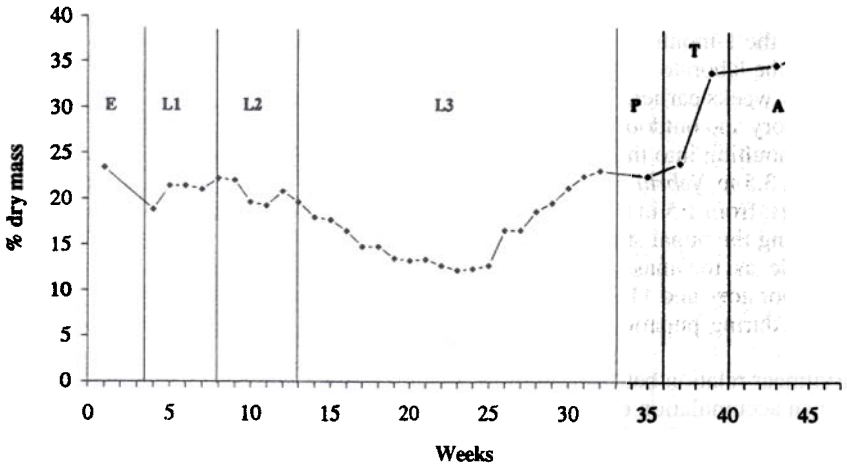

Fig. 5. Changes in the ratio of dry mass to fresh mass (expressed as a percentage) during the course of the life cycle. E: egg; L1, L2 and L3: first-, second- and third-instar larva; P: pupa; T: teneral imago; A: adult

followed during each developmental stage – some of the larvae sacrificed to establish the regression of dry mass on fresh mass and some adults checked for egg production. In the same way, we combined males and females in the first year of the adult stage, since their productions were not significantly different (60.7 ± 5.6 mg dry mass for females; 58.1 ± 5.7 mg for males).

Table 3 shows that growth made up 86 % of total production in the larval stages, versus 14 % for exuviae. Growth was also considerable in the adult stage; it accounted for 79 % of total production over two years in females, versus 21 % for egg production. Growth production was even distinctly higher in the adult than in the larval stages.

Discussion

Larval growth

The larval growth curves under laboratory and semi-natural conditions were roughly of the same logistic-like form which was found in other invertebrate species when they are reared under constant conditions (Wightman & Rogers 1978). However, several features differentiate the two curves:

(1) The mass gain during the first and second larval instars was lower under semi-natural conditions. This probably resulted from the lower temperatures during those stages (9 and 13 °C, respectively, on average, versus 17 °C in the laboratory). Temperature was also found to affect the duration of development and the adult body mass and size in *Notiophilus biguttatus* (Ernsting et al. 1992).

(2) Body growth in the third larval instar was more rapid, and instar duration was shorter, under semi-natural conditions, although average temperature was lower (15.9 °C versus 17 °C in the laboratory). This was partly explained by the thermal accident in the laboratory. Under the same laboratory conditions, we obtained an instar duration of 105 days (versus 143 days) in another experiment without that accident (personal observations). However, the fact that the significant difference in body mass at the beginning at the third instar had vanished by the end of larval development also suggests that a compensatory process may be operating so as to reduce differences in body mass before pupation.

(3) The period of arrested growth before each moulting was longer under semi-natural conditions. In particular, the 1-month resting period before pupation under outdoor conditions was virtually absent in the laboratory. Again, this difference might be due to the thermal accident that occurred a few weeks earlier.
Under both laboratory and outdoor conditions, the larva increased its body mass by roughly a factor 3.2 before moulting into the next instar. Under very favourable conditions, this factor was found to reach 3.5 in *Nebria brevicollis* (Nelemans 1988), while it seemed very variable in *Carabus arvensis*: from 1.5 in the first two instars to 4.9 in the third (Grüm 1975a).
The mass loss during the pupal stage was very low: from 9 to 10 % only. It was of the same order of magnitude as the mass loss during hibernation, which varied between 6 % in 10 weeks in the laboratory and 11 % in 20 weeks under outdoor conditions. In comparison, a mass loss of 50 % during pupation is not uncommon among other holometabolous insects (Ikeda 1979).
Lastly, the curvilinear relation between dry mass and fresh mass in 3rd-instar larvae is likely to be caused by an accumulation of lipidic reserves before pupation. Such a curvilinear relation was also found in adult *Pterostichus coerulescens* (Mols 1988), where it was caused by the development of ovaries and the accumulation of mature eggs in the oviducts.

Adult growth

Growth is still considerable in the adult stage, more considerable even than in the larval stages. 32 % of a breeding adult's dry body mass was produced during larval development, while 59 % was produced during the first year after pupation. In *Carabus* species, only 14 to 24 % of dry body mass was found to be gained during larval development, the strongest growth occurring at the teneral stage, during the first 17 days after imaginal emergence (Grüm 1975a). In *Abax ater*, growth production was also strongest just after imaginal emergence, especially in the laboratory: about 60 % of growth production in the first year of the adult stage occurred during the first month after emergence, 31 % during the second month, and only 9 % during the next 5 months. Under semi-natural conditions, these proportions were 42 %, 33 % and 25 %, respectively. The slower growth under semi-natural conditions can be explained by a lower average temperature and a lower food consumption.
As in the larval development, the slower growth of adults during the first two months after imaginal emergence under semi-natural conditions was compensated for by a stronger growth in the following months, so that body mass was independent of climatic conditions before hibernation. This again suggests regulation of body mass through compensatory growth. In October, when temperature was declining (average temperature: 13.6 °C), the beetles gained weight under semi-natural, but not laboratory, conditions. This increase in body mass probably corresponds to an accumulation of lipidic reserves before hibernation.

Egg production

No egg laying was observed in first-year adults, although copulations did take place. Thus a hibernation seems necessary before egg laying, which started a few weeks later and is spread over almost the whole activity season (about 25 weeks in the laboratory) during the second year in the adult stage. Accordingly, *Abax ater* does not seem to have an annual life cycle, contrary to what has been assumed so far; the minimum length of a complete life cycle probably varies between 1½ and 2½ years (Chaabane et al. in prep.).
Among the 54 females that were collected in the field and checked for egg production, 17 did not lay eggs. Some may have been too young, some may have already laid eggs before being caught, some may also have been too old. More than half of them (10) died at the end of the season or during hibernation. If only females that did lay eggs are taken into account, there was no significant difference in egg production between them and the young females followed since their imaginal emergence. Similar results were obtained by Sota (1984) for *Carabus kumagai*.

Löser (1972) recorded an egg production in *Abax ater* that was twice lower than in our work: 6 eggs per female per breeding season on average. However, he did not take into account the problem of females that laid no eggs, which may explain at least part of the discrepancy. Our figures may even be underestimated because food quality and diversity was lower in our rearings than in the field. Food ration is known to affect egg production (Ernsting & Isaaks 1987), but food quality and diversity may be as important. A higher fecundity is necessary to balance mortality and achieve the observed stability of the natural population (Chaabane et al. 1996).

In any case, *Abax ater* stands out as one of the least fertile carabid species, and *Abax* as one of the least fertile carabid genera. Whereas *Pterostichus* and *Calosoma* species were found to lay 45 to 350 eggs per female per breeding season (Burgess 1911; Kirk 1975) and *Carabus* species, 22 to 56 eggs (Scherney 1959), the fecundities of *Abax ovalis* and *Abax parallelus* were estimated at 15 and 16 eggs per female, respectively (Lampe 1975; Löser 1970). Low fecundities are characteristic for species with a pre-social behaviour (Brandmayr 1979). Females of *Abax* and *Molops* species take care of their eggs, sometimes even of their brood after hatching.

Conclusions

Production due to body growth and exuviae overall varied little between experimental conditions and its estimation using gravimetric measurements can be regarded as very reliable. On the other hand, egg production is likely to be affected by uncontrolled food factors and therefore to be somewhat less reliable.

Abax ater is characterised by a body growth that is slow and spread over both the larval and adult stages, a reproductive effort that is very small and spread over several years and over several months in each year, and a great longevity. These as well as other demographic and bioenergetic traits (Chaabane et al. 1996) are typical for a 'conservation' K strategy.

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