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# Individual and population energy budgets of *Abax ater* (Coleoptera, Carabidae)

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For the first time, complete energy budgets were established in a ground-beetle species, *Abax ater*, for both a “standard” individual (defined as an individual that shows complete development from egg to reproductive adult) under semi-natural conditions and a natural population. A female standard individual consumed 26.7 kJ during its lifetime. Gross ($P/C$) and net ($P/A$) production efficiencies decreased with age from 30% and 33%, respectively, in the first larval stage to 9% and 11%, respectively, during the second year in the adult stage. The adult accounted for most of the total individual energy budget (81% of consumption and 75% of production). From data on age-dependent survival and adult population density, the energy flow through a natural population of this species in a near-climax beechwood in Belgium was estimated at 8.1 kJ/m$^2$/year. Larvae predominated in the total population energy budget (51% of consumption and 67% of production). Gross and net production efficiencies, however, remained low (15% and 17%, respectively, overall). Thus, *Abax ater* is characterized by a high assimilation efficiency, a low production efficiency and a relatively high adult contribution to the total energy flow. These features are well in keeping with the demographic traits of this species, i.e. a great adult longevity, a continuous reproduction, a low fecundity and a high population stability, and mark it out as a K-strategist.

## 1. Introduction

Carabid beetles have been the subject of numerous studies from both systematic and ecological viewpoints (Thiele 1977), but few of these have addressed the role they play quantitatively in ecosystems. The data regarding their energy flow are still rather fragmentary. It is only during the last two decades that authors have started to investigate this topic (Weidemann 1971, 1972, Manga 1972, Grüm 1975b, 1976, 1978, 1980, 1986, De Ruiter & Ernsting 1987).

Some works have dealt with the influence of abiotic factors (mainly temperature) on elements of the energy budget such as respiration, fecundity and consumption (Kabacik & Steygwillo 1971, Koehler 1976, Könen 1978, Grüm 1984, Ernsting & Isaaks 1987, 1988, Mols 1988). Others have focused on one element of the budget: production due to growth (Grüm 1973b, 1975a, Sota 1984, Ernsting *et al.* 1992), egg production (Murdoch 1966, Löser 1972, van Dijk 1972, 1973, Grüm 1973a, 1976, Heessen 1980), consumption (Scherney 1960, Van Dinther 1966, Hondo 1984, Sota 1984, Ernsting & Isaaks 1987, 1992, Mols 1988, Nelemans 1988), and respiration (Mols 1988). Only the works of Weidemann (1972), Manga (1972), Grüm (1980) and De Ruiter and Ernsting (1987) have addressed the issue of an energy budget as a whole. But even these did not present complete energy budgets: only the adult stage was considered in the last study, while consumption and rejecta were not measured in the first three ones, which results in some of their estimates being very questionable.

Energy budgets constitute a basic tool to quantitatively assess the role of organisms in ecosystems and the way they allocate resources. They describe the distribution of the energy obtained by consumption ($C$) among production ($P$), respiration ($R$), and rejecta or faeces and urine ($FU$) by the equation:

$$C = P + R + FU.$$

Production and respiration together make up assimilation ($A = P + R$). Production can be further broken down into production due to growth ($P_g$), production of larval exuviae ($P_{ex}$), and production due to reproduction ($P_r$).

In this work, we present the first complete energy budgets for a carabid-beetle species, *Abax ater*, based on measurements under semi-natural conditions. Detailed results for the various elements of the budgets have been and will be published elsewhere (Chaabane *et al.* 1993a, and in prep.). *Abax ater* is the dominant species (in terms of biomass and activity) in many temperate forests — in particular in the forest we studied (Loreau 1984b); accordingly it is likely to play an important ecological role on the macro-invertebrate community at the soil surface (Loreau 1984c). Therefore, a quantitative energy budget for this species represents a useful step in the understanding of the forest ecosystem functioning.

A first energy budget was established for a "standard" individual (defined as an average individual that shows complete development from egg to reproductive adult) under semi-natural conditions. A second energy budget was extrapolated to a natural population using data on age-dependent survival in the laboratory and adult population density in a near-climax beechwood in Belgium.

## 2. Material and methods

### 2.1. Collecting and rearing beetles

The beetles were collected in a near-climax beechwood set up as a natural reserve at Lembeek, Belgium, where *Abax ater* is strongly dominant (Loreau 1984b). They were collected by funnel traps used and described in a previous work (Loreau & Nolf 1993). These traps also served to catch some earthworms (*Lumbricus* and *Dendrobaena* spp.) used mainly for feeding *Abax ater* larvae.

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 entering while letting air circulate. Temperature and humidity were recorded continuously using a thermo-hygrograph placed in one of the tubs. Daily average temperatures were calculated from 12 measurements between two successive sunrises. Rearing conditions were the same as in the laboratory study by Chaabane *et al.* (1993a, 1994a), except for climatic conditions and adult food quantity: the beetles were reared individually in vials furnished with moist sieved forest soil; larvae were fed twice a week on pieces of earthworms; adults were fed twice a week on ground beef meat (30–70 mg, which is less than in the laboratory).

Given the length of the life cycle of *Abax ater* (Chaabane *et al.* in prep.), results were combined from three different cohorts reared simultaneously (Fig. 1). The first one was made up of individuals that hatched from eggs obtained in the laboratory and developed to pupation; the second one was made up of 3rd-instar larvae collected in the field and followed until they hibernated as adults; the third one was made up of young adults collected in the field and followed after hibernation until they first laid eggs.

### 2.2. Elements of the energy budget

Consumption and production (including negative production for pupae and hibernating stages) were measured by gravimetry (difference in body weight after feeding for consumption, and at weekly or bi-weekly intervals for production). Rejecta were also measured by weighting. Energy equivalents were measured using a balistic calorimeter (after Phillipson 1964). The samples used were first oven-dried at 70°C during 48 hours and stocked in a dessicator. The calorimetric microbomb was calibrated with benzoic acid of known calorific equivalent.

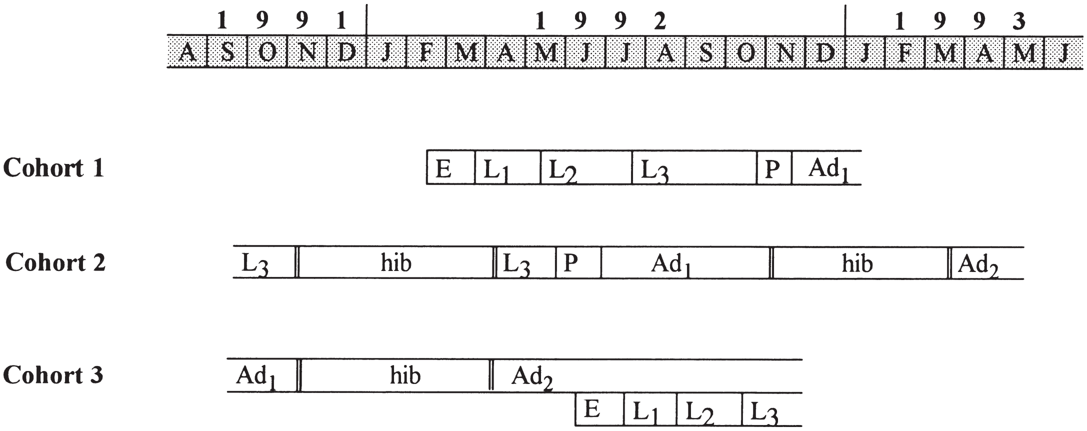

Fig. 1. Diagrammatic representation of the three cohorts reared under semi-natural conditions. E = egg; $L_1$, $L_2$, $L_3$ = 1st, 2nd, 3rd larval instar; P = pupa; $Ad_1$, $Ad_2$ = 1st-, 2nd-year adult; hib = hibernation.

Respiration was measured using a constant-pressure Gilson respirometer (Chaabane *et al.* 1994b). Its energy equivalent was estimated at 19.6 J/ml $O_2$ based on a RQ of 0.715 ± 0.046 (mean ± *S.D.*) obtained from 20 individuals in the laboratory. Respiration was measured for individuals with an empty stomach and at rest. Extra measurements were made on digesting and moving individuals to investigate the effects of digestion and locomotory activity on respiration (Chaabane *et al.* 1994b).

## 2.3. Natural population density

Adult population density was estimated using capture-recapture techniques in previous works (Loreau 1984a, 1990, Loreau & Nolf 1993). The adult population density of *Abax ater* during its seasonal period of maximum activity (mid-May to late July) was found to be extremely constant from year to year, with an average of 0.23 ind./m$^2$. This figure is an underestimate, however, because it does not take account of tenerals, whose soft elytrae prevented them from being marked.

Capture-recapture techniques also showed that adult *Abax ater* can live several years, and that their average survival rate from year to year is 45% (Loreau 1990). Adult density in a cohort should therefore decrease with age according to the relation $N_t = N_0(0.45)^t$ where $t$ is the age in years, and in a stable population this longitudinal structure should be found again in the transversal age structure. It is easy to verify that adults in their first year should then represent 1 – 0.45 = 55% of the adult population, the remaining 45% being made up of adults aged one year or more.

If no individual was marked during its year of imaginal emergence, the total adult population density would be 0.23/0.45 = 0.51 ind./m$^2$. But part of the adults emerging in spring or summer were likely caught and marked later in summer and autumn, although activity decreases progressively in this period. As this part was not known, we used the mean between the two above figures, that is, (0.23 + 0.51)/2 = 0.37 ind./m$^2$, as our best estimate of adult population density during the period of maximum activity. Thus the flow of adults in the population was taken to be 0.37 ind./m$^2$/y, which was distributed into 0.20 ind./m$^2$/y for first-year adults and 0.17 ind./m$^2$/y for adults aged one year or more. This age distinction is important in the energy budget because reproduction only takes place from the second year (see below).

Larval population density was first estimated by quadrat sampling. But these estimates were found to be unreliable

Table 1. Average fresh body weight (FW), average water content, energy equivalent of 1 mg dry weight (DW) with ashes (average ± standard deviation) and number of burnt samples (*N*) for the various developmental stages of *Abax ater* and their food and rejecta.

| Stage or material | FW (mg) | Water content (% FW) | Energy equivalent (J/mg DW) | *N* |
|---|---|---|---|---|
| Egg | 6.9 | 79.4 | 24.9 ± 1.2 | 3 |
| Larva 1 | 7.1 | 81.2 | 23.4 ± 0.8 | 5 |
| Larva 2 | 19.7 | 78.0 | 24.0 ± 0.5 | 9 |
| Larva 3 | 54.0 | 80.4 | 23.9 ± 0.7 | 13 |
| Larva 3 before pupation | 171.7 | 77.0 | 24.6 ± 0.5 | 8 |
| Pupa | 156.0 | 77.6 | 22.9 ± 1.3 | 7 |
| Adult | 260.0 | 62.0 | 24.3 ± 1.2 | 46 |
| Exuvia | – | – | 21.8 ± 1.1 | 2 |
| Earthworms (food to larvae) | – | 80.2 | 20.3 ± 1.4 | 5 |
| Ground meat (food to adults) | – | 71.0 | 22.7 ± 1.4 | 10 |
| Rejecta (larvae) | – | – | 19.5 ± 1.3 | 2 |
| Rejecta (adults) | – | — | 22.3 ± 2.0 | 3 |

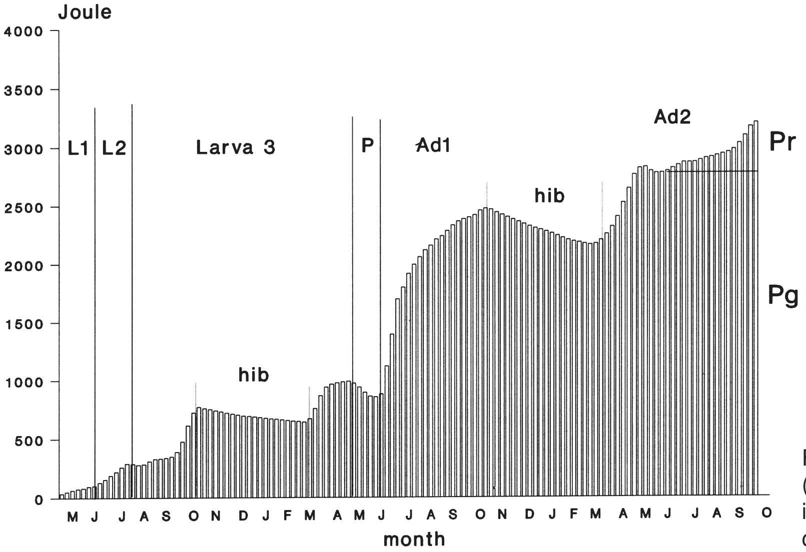

Fig. 2. Cumulated production (in joules) of a female standard individual under semi-natural conditions. Legend as in Fig. 1.

because of the small numbers of larvae collected. Also, every larval instar is not present throughout the year. Therefore the flow of individuals of the various larval stages was finally estimated from the survival rates measured in the first cohort reared under semi-natural conditions (Fig. 1) and the above field estimate of the adult flow. The flow of each stage (*i*) was estimated by dividing the flow of the next stage (*i* + 1) by the survival rate from that stage (*i*) to the next (*i* + 1), starting with the pupal stage and going back gradually to the egg stage.

## 3. Results

### 3.1. Basic data

The basic data required to calculate production in energy units for the various developmental stages are presented in Table 1. The energy equivalent of a unit dry weight was lower in the larval stages than at the egg stage but increased before moulting; it was lowest at the pupal stage and high again in adults. Data for males and females were not significantly different and were combined accordingly.

The respiration rate $\rho$ (in µl $O_2$/mg FW/h) increased exponentially with temperature in the range 5–15°C for all stages, resulting in linear regressions of ln $\rho$ as a function of temperature (Table 2). Cumulated respiration in each stage was calculated as the product of its respiration rate $\rho$ by its average fresh weight FW and its average duration. The result was then converted into joules by multiplying it by the energy equivalent of 19.6 J/ml $O_2$. The respiration obtained with an empty stomach and at rest was finally multiplied by a factor of 2.3 for the active stages to account for digestion and locomotor activity. Respiration was found to increase about twofold during the first day after food ingestion, and up to six-fold during locomotion. This factor of 2.3 was calculated from independent estimates of the frequency of feeding (twice a week) and duration of intense locomotor activity (12 h a week) in the field (Chaabane *et al.* in prep.).

### 3.2. Energy budget of a standard individual

The cumulated production curve (Fig. 2) shows a relatively low production in the larval stages, a slight energy loss at the pupal stage, a high production after imaginal emergence, a slight energy loss during hibernation and a moderate production after hiber-

Table 2. Relation between respiration rate ($\rho$, in µl $O_2$/mg FW/h) and temperature ($T$, in °C), with associated correlation coefficient ($r$) and number of individuals ($N$), for the various developmental stages.

| Stage | Relation between $\rho$ and $T$ | $r$ | $N$ |
|---|---|---|---|
| Larva 1 | $\ln \rho = 0.110\,T - 2.44$ | 0.963 | 8 |
| Larva 2 | $\ln \rho = 0.096\,T - 2.55$ | 0.930 | 12 |
| Larva 3 | $\ln \rho = 0.097\,T - 3.25$ | 0.717 | 22 |
| Pupa | $\ln \rho = 0.076\,T - 3.71$ | 0.897 | 3 |
| Adult female | $\ln \rho = 0.110\,T - 3.48$ | 0.852 | 12 |

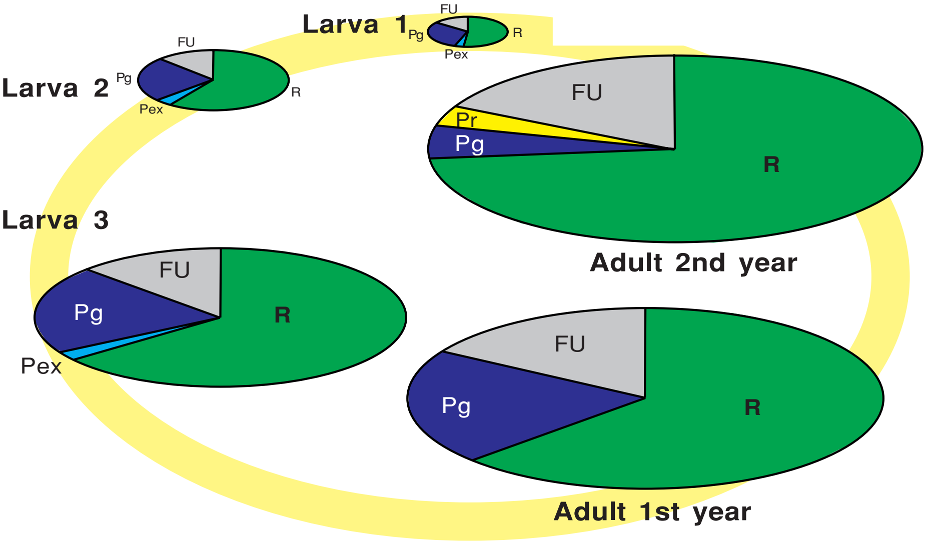

Fig. 3. Energy budgets of a female standard individual under semi-natural conditions in the various developmental stages. Area is proportional to energy.

nation and during reproduction. Adults laid eggs only from their second year, after hibernation. The total life span of our standard individual was about 840 days.

A female standard individual consumed 26.7 kJ during its lifetime (Table 3). Since the ingested energy ($C$) must be equal to the sum of the other elements ($P + R + FU$), a complete budget enables a check. The budgets published in the literature are rarely balanced (unless they are incomplete and the lacking elements are calculated from the measured elements), and most generally res-

Table 3. Energy budget of a standard individual under semi-natural conditions (in joules).

| Stage | Duration (days) | $P_g$ | $P_{ex}$ | $P_r$ | $P$ total | $R_m$ | $R_c$ | $FU$ | $C$ | $R_c/R_m$ |
|---|---|---|---|---|---|---|---|---|---|---|
| Larva 1 | 40 | 81 | 10 | 0 | 91 | 157 | 182 | 35 | 308 | 1.16 |
| Larva 2 | 51 | 201 | 24 | 0 | 225 | 697 | 498 | 94 | 817 | 0.71 |
| Larva 3 | 107 | 707 | **81 | 0 | 788 | 2 659 | 2 787 | 461 | 4 036 | 1.05 |
| Larva 3 hibernation | 140 | – 147 | 0 | 0 | – 147 | – | 147 | 0 | 0 | – |
| Subtotal larvae | 338 | 842 | **115 | 0 | 957 | *3 660 | 3 614 | 590 | 5 161 | 0.99 |
| Pupa | 30 | – 151 | **0 | 0 | – 151 | 154 | 151 | 0 | 0 | 0.98 |
| Adult female 1st year | 133 | 1 678 | 0 | 0 | 1 678 | 5 976 | 6 409 | 1 343 | 9 430 | 1.07 |
| Adult female hibernation | 140 | – 359 | 0 | 0 | – 359 | 378 | 359 | 0 | 0 | 0.95 |
| Adult female 2nd year | 196 | 581 | 0 | 529 | 1 110 | 9 743 | 9 269 | 1 724 | 12 103 | 0.95 |
| Subtotal adult female | 469 | 1 900 | 0 | 529 | 2 429 | 16 097 | 16 037 | 3 067 | 21 533 | 1.00 |
| Total life cycle female | 837 | 2 591 | 115 | 529 | 3 235 | 19 889 | 19 802 | 3 657 | 26 694 | 1.00 |

* Including the 147 J for calculated respiration during hibernation.
** $P_{ex}$ of pupa is included in $P_{ex}$ of larva 3.

piration is considered as being responsible for the flaw (Wightman 1977, 1981). Therefore we compared measured respiration ($R_m$) with respiration as it was calculated from the other elements of the budget:

$$R_c = C - (P + FU)$$

In this study, $R_c/R_m$ was almost exactly 1 over the whole life cycle, although this ratio was somewhat variable when each stage was considered separately (Table 3). Thus our budget was remarkably balanced overall. In what follows, we shall use $R_c$ instead of $R_m$ to satisfy the balance for each stage.

Over the whole life cycle, 74% of ingested energy were lost to respiration and only 12% were devoted to production. The bulk of energy was thus dissipated in respiration, which drained more than 6 times the energy drained by production. The relative importance of respiration increased with age, from 59% in the first larval instar to 77% in the second-year adult (Fig. 3). Conversely, gross production efficiency ($P/C$) and net production efficiency ($P/A$) shrinked from 30% and 33%, respectively, in the first larval instar to 9% and 10.7%, respectively, in the second-year adult (Table 4). Assimilation efficiency ($A/C$) was 88.6% for larvae and 85.7% for adults.

The energetic needs of an individual increased progressively during its development (Fig. 3), because of increases in both body mass and stage duration (from 40 days in the first larval instar to 196 days in the second-year adult: Table 3). The contribution of the adult stage in the total individual energy budget was much higher than that of the larval stages; it accounted for 81% of consumption and 75% of production.

Table 4. Energy efficiency ratios for the various developmental stages under semi-natural conditions.

| Stage | $P/A$ | $P/C$ |
|---|---|---|
| Larva 1 | 33.3 | 29.5 |
| Larva 2 | 31.1 | 27.5 |
| Larva 3* | 22.0 | 19.5 |
| 1st-year female | 20.7 | 17.8 |
| 2nd-year female* | 10.7 | 9.2 |
| Total life cycle | 14.0 | 12.1 |

* excluding hibernation.

### 3.3. Energy budget of a natural population

Temperatures recorded at ground level in the Lembeek beechwood and under our semi-natural conditions were almost identical, with low daily amplitudes. Therefore the energy budget of the natural population was estimated assuming the same temperatures as under semi-natural conditions.

The survival rates of the various stages under semi-natural conditions and the estimated flows of individuals in the natural population are given in Table 5. Survival decreased from the first to the third larval instar, where it was lowest. Although mortality was correlated with stage duration (see Table 3 for data on stage duration), the main period of mortality was observed to be before moulting, when larvae stopped feeding.

The energy budget of a natural population differs from that of a standard individual not only in that mortality is allowed for in each stage, but also in that consumption relies on a more diverse but less abundant food than under rearing conditions. Since it was impossible to assess consumption in the field, we established the budget as if the beetles ingested as much food in the field as was provided in our rearings. All the elements of the budgets were thus calculated for each stage by multiplying the flow of individuals by the corresponding parameters for a standard individual under semi-natural conditions.

The energy budget was established assuming that each year adults aged one year or more lay eggs in spring, the 3rd-instar larvae hibernate, the young adults emerge in summer of next year, and hibernate before reproducing for the first time during their second year. This 2-year basic life

Table 5. Survival rates to the next stage for the various stages in a cohort under semi-natural conditions and estimated flows of individuals in the natural population.

| Stage | No. of indiv. | survival rate (%) | estimated flow (ind./m$^2$/y) |
|---|---|---|---|
| Egg | 50 | 60 | 1.99 |
| Larva 1 | 30 | 87 | 1.19 |
| Larva 2 | 26 | 69 | 1.04 |
| Larva 3 | 18 | 33 | 0.72 |
| Pupa | 6 | 80 | 0.24 |
| Adult 1st year | 5 | | 0.20 |
| Adult ≥ 1 year | | | 0.17 |

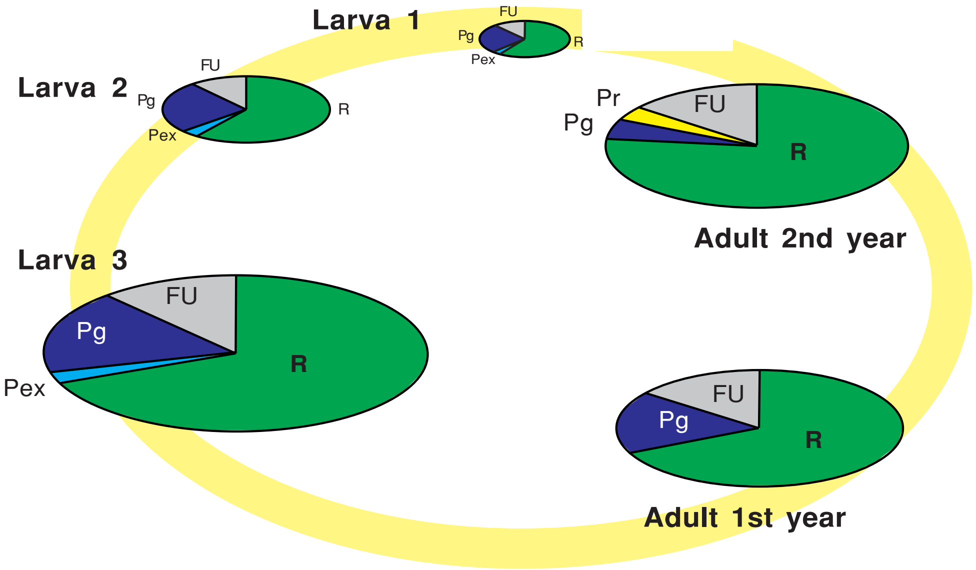

Fig. 4. Energy budgets of the natural population in the developmental stages. Area is proportional to energy.

cycle is only one among several possible ones, but most life cycles under the climate of Belgium are likely to include two hibernation periods (Chaabane *et al*. 1993b, and in prep.), and the budget would be quite similar. Males were assumed to be equivalent to females without egg production, and the sex ratio was assumed to be balanced. Lastly, female fecundity was adjusted to balance mortality; it was thus estimated at about 23 eggs per female (from Table 5). This figure is higher than the average 15 eggs per female recorded under semi-natural conditions, but it is reasonable, for food quality (and diversity) may have been lower in our rearings than in the field.

Table 6. Energy budget of the natural population in the beechwood at Lembeek (in J/m$^2$/y).

| Stage | $P_g$ | $P_{ex}$ | $P_r$ | *P* total | $R_c$ | *FU* | *C* |
|---|---|---|---|---|---|---|---|
| Larva 1 | 96 | 11 | 0 | 107 | 217 | 42 | 366 |
| Larva 2 | 209 | 25 | 0 | 234 | 518 | 97 | 849 |
| Larva 3 | 509 | 59 | 0 | 568 | 2 007 | 332 | 2 907 |
| Larva 3 hibernation | – 106 | 0 | 0 | – 106 | 106 | 0 | 0 |
| Subtotal larvae | 708 | 95 | 0 | 803 | 2 848 | 471 | 4 122 |
| Pupa | – 35 | *0 | 0 | – 35 | 35 | 0 | 0 |
| Adult 1st year | 336 | 0 | 0 | 336 | 1 282 | 269 | 1 887 |
| Adult hibernation | – 72 | 0 | 0 | – 72 | 72 | 0 | 0 |
| Adult ≥ 1 year | 99 | 0 | 69 | 168 | 1 597 | 293 | 2 058 |
| Subtotal adult | 363 | 0 | 69 | 432 | 2 951 | 562 | 3 945 |
| Total life cycle | 1 036 | 95 | 69 | 1 200 | 5 834 | 1 033 | 8 067 |

* $P_{ex}$ of pupa is included in $P_{ex}$ of larva 3.

The total energy flow through the natural population of *Abax ater* in the beechwood at Lembeek was thus estimated at 8.1 kJ/m$^2$/y (Table 6). Energy flow increased from the first to the third larval instar but, because of the high mortality in the 3rd larval instar and the pupal stage, it decreased afterwards (Fig. 4). Therefore, unlike in the budget of a standard individual, the larval contribution to the energy flow of the natural population was higher than that of adults (51% of consumption and 67% of production). As a result, the part of production was slightly higher than for a standard individual: it accounted for 15% of the overall budget, while respiration accounted for 72%. Net production efficiency was 17% (versus 14% for a standard individual). Production was mainly due to growth, which accounted for 86% of total production; the production of exuviae and egg production represented only 8% and 6%, respectively, of total production.

The energy required for an individual to complete its life cycle successfully until reproduction was estimated at 47.5 kJ on average in the natural population (obtained by dividing the total energy flow by the flow of reproductive adults aged one year or more, Table 5), against 26.7 kJ for a standard individual. The difference corresponds to the average energy lost in mortality during the development from the egg to the age of reproduction; about 1 out of 12 individuals produced as eggs is expected to reproduce in turn.

## 4. Discussion

Our energy budgets for a standard individual and a natural population of *Abax ater* are the first complete energy budgets established for a carabid beetle. The detailed measurements of the various elements of the budget over the whole life cycle allowed us to obtain a remarkably balanced budget for a standard individual. Measured respiration corrected for digestion and locomotor activity ($R_m$) was almost exactly equal to respiration as it is calculated from the other elements of the budget ($R_c$) over the whole life cycle, while usually the ratio $R_c/R_m$ ranges from 1.2 to 6.2 (Wightman 1977, 1981). In the inactive stages (pupa and hibernating adult), in which no correction was brought for digestion and locomotor activity, $R_c/R_m$ varied from 0.95 to 0.98, which shows that respirometric measurements were accurate. In the active adult, $R_c/R_m$ varied from 0.95 to 1.07, with an average of 1.00 over the whole adult stage, which shows that our correction for digestion and locomotor activity was successful. The ratio $R_c/R_m$ was more variable in the larval stages (from 0.71 to 1.16), probably because our correction factor derived from adult behaviour was less adequate for larvae. Our energy budget for the natural population is less accurate because of uncertainties regarding actual survival rates and population densities of larval stages and actual consumption in the field. However, errors should be reasonably low, especially on energy efficiency ratios. Thus, even though the relative importance of larvae in the total energy flow was distinctly higher for the natural population than for a standard individual, net production efficiency ($P/A$) was only 3% higher.

Comparison of our results with previous studies is difficult because these either did not cover the whole life cycle or did not measure consumption and rejecta. In Table 7, we compare our individual

Table 7. Energy budget of a standard individual from hatching to reproduction, net production efficiency ($P/A$) and $R/P$ ratio in a few carabid species.

| Species | $P_g + P_{ex}$ (J) | $P_r$ (J) | $P$ total (J) | $R$ (J) | $FU$ (J) | $P/A$ (%) | $R/P$ | Ref. |
|---|---|---|---|---|---|---|---|---|
| *Pterostichus oblongopunctatus* | 546 | 249 | 795 | 808 | – | 50 | 1.0 | (1) |
| *Pterostichus oblongopunctatus* | 530 | 320 | 850 | 5010 | – | 15 | 5.9 | (2) |
| *Pterostichus metallicus* | 1 060 | 254 | 1 314 | 1 155 | – | 53 | 0.9 | (1) |
| *Abax ater* | 2 706 | 529 | 3 235 | 19 803 | 3 656 | 14 | 6.1 | (3) |

(1) Weidemann 1972, (2) Recalculated by Grüm 1980, (3) This work.

energy budget for *Abax ater* with comparable data on production and respiration for two *Pterostichus* species from Weidemann (1972). The figures for production seem consistent, and increase with body mass (*Pterostichus oblongopunctatus* is the smallest, and *Abax ater* the largest of the three species). But Weidemann's (1972) figures for respiration and *R*/*P* ratios are unrealistically low because they are based on metabolism with an empty stomach and at rest. Since consumption and rejecta were not measured, it is impossible to balance the budget. Grüm (1980) recalculated the figures for *Pterostichus oblongopunctatus* using complex indirect methods taking account of locomotor activity, and arrived at a net production efficiency that is very close to the one we found for *Abax ater* (Table 7). However, his estimates of respiration are very likely overestimates; they would implicate that locomotor activity increased total respiration by a factor 6.2. This seems unrealistically high compared with our factor 2.3 for *Abax ater*, which also includes stimulation of respiration by digestion. A factor as high as 6.2 would only be possible in *Abax ater* if all individuals were running almost continuously! One should also reasonably expect *Pterostichus oblongopunctatus*, which is smaller and has a shorter life cycle, to have a higher production efficiency than does *Abax ater*. Probably the truth lies somewhere between Weidemann's and Grüm's estimates.

Similar problems arise when we compare our population energy budget with estimates of production and respiration for natural populations from previous works (Table 8). Manga (1972) again measured metabolism with an empty stomach and at rest; respiration was thus underestimated. Weidemann's (1972) estimates for *Pterostichus oblongopunctatus* and *Pterostichus metallicus* seem obviously incorrect. They are simple extrapolations of his data for a standard individual (Table 7) to natural populations. Since production efficiency is higher in the larval stages than in the adult stage, production efficiency can only increase in the population budget (which takes account of larval mortality before reaching the adult stage) compared with the individual budget. In Weidemann (1972; compare Tables 7 and 8), net production efficiency instead decreases from 53% to 15% in *Pterostichus metallicus*! We cannot conceive of any mechanism to explain such a drop. Lastly, Grüm's (1980) figures for respiration are likely to be overestimates for the same reasons as above.

As an attempt to partly circumvent these problems, we may recalculate the figures for respiration from these studies assuming that digestion and locomotor activity increase respiration by the same estimated factor 2.3 as in *Abax ater*. This amounts to multiplying the figure for respiration from Manga (1972) by 2.3, those from Weidemann (1972) for standard individuals also by 2.3, and those from Grüm (1980) by 2.3/6.2 = 0.37. We then obtain a narrower range of net production efficiencies, from 16% in *Pterostichus niger*, *Carabus glabratus* and *Carabus hortensis* to 33% in *Pterostichus metallicus*, *Abax ater* with 17% now being near the lower end of the range. However, we stress that these corrected figures are hypothetical, for we do not know whether

Table 8. Production, respiration, net production efficiency (*P*/*A*) and *R*/*P* ratio in a few carabid populations.

| Species | Life cycle | *P* (kJ/m²/y) | *R* (kJ/m²/y) | *P*/*A* (%) | *R*/*P* | Ref. |
|---|---|---|---|---|---|---|
| *Nebria brevicollis* | a | 1.63 | 1.73 | 48 | 1.1 | (1) |
| *Pterostichus oblongopunctatus* | s | 1.96 | 2.60 | 43 | 1.3 | (2) |
| *Pterostichus metallicus* | a | 0.53 | 2.97 | 15 | 5.6 | (2) |
| *Pterostichus niger* | a | 1.03 | 14.30 | 7 | 13.9 | (3) |
| *Carabus glabratus* | a | 0.40 | 5.74 | 7 | 14.4 | (3) |
| *Carabus hortensis* | a | 0.23 | 3.18 | 7 | 13.8 | (3) |
| *Carabus arcensis* | s | 0.38 | 2.29 | 14 | 6.0 | (3) |
| *Carabus nemoralis* | s | 0.26 | 1.58 | 14 | 6.1 | (3) |
| *Abax ater* | s–a | 1.20 | 5.83 | 17 | 4.9 | (4) |

(1) Manga 1972, (2) Weidemann 1972, (3) Grüm 1980, (4) This work. s = spring breeder; a = autumn breeder; s–a = breeding from spring to autumn

digestion and locomotor activity have similar quantitative effects on respiration as in *Abax ater*.

Grüm (1980) concluded that spring breeders had higher production efficiencies than did autumn breeders. Although this hypothesis is likely, because autumn breeders require a longer larval development, the available data do not clearly support it (Table 8). Spring or autumn breeding may not be the most important aspect determining production efficiency. We suggest that the length of larval development and of the life cycle as a whole is a more important determinant of production efficiency. Large species with long life cycles such as *Abax ater* or some *Carabus* species are expected to have lower production efficiencies than species with an annual life cycle such as *Pterostichus oblongopunctatus* or *Nebria brevicollis*.

Production efficiencies (*P*/*A* and *P*/*C*) were found to decrease progressively in the course of the life cycle. As the beetle grows, progressively less energy is devoted to further growth and more energy is devoted to locomotion and respiration. However, in *Abax ater*, growth production is still very high in the beginning of the adult stage. It is only during the second year in the adult stage that growth production becomes very low.

Assimilation efficiency (*A*/*C*) was very high in all stages in *Abax ater*, but a little higher in larvae (88.6%) than in adults (85.7%). This difference is probably due to the fact that larvae ingest their food after a pre-oral digestion. High assimilation efficiencies characterize most carnivores which ingest food of high nutritional value. Equivalent efficiencies can be found in spiders, which also have a pre-oral digestion (85–89%: Kajak 1967, Humphreys 1977), and in ants such as *Leptothorax unifasciatus* which feed on eggs and honeydew (94%: Martin 1990). The high assimilation efficiencies of carnivores can also result from a selective ingestion: 1/3 to 2/3 of the energy content of their prey could be rejected and only the most valuable parts ingested (Phillipson 1960). In *Abax ater*, the larval pre-oral digestion is one such mechanism, preventing indigestible parts from being ingested. In our rearings the adults were fed ground meat containing few indigestible elements, but this may not be the case with their natural food: when prey are scarce, they are often swallowed totally, and fragments of prey cuticle and plant material are commonly found in the gut of adults caught in the field (Loreau 1983). Therefore adult assimilation efficiency should be lower in the field and dependent upon the available prey. In adult *Notiophilus biguttatus*, which ingest springtails totally, assimilation efficiency is not higher than 73% (De Ruiter & Ernsting 1987).

The impact of *Abax ater* on its prey populations may be important, especially on earthworms, which seem to be the nearly exclusive food to larvae and the main prey of adults (35% of the number of prey consumed by adults in the Lembeek beechwood, and probably more in biomass: Loreau 1983). Weidemann (1978) suggested that only 50 to 60% of the attacked prey are actually consumed by carabids, and we often observed that *Abax ater* did not consume earthworms totally. This leads to an estimated flow of 15 kJ/m$^2$/y of killed prey in the beechwood at Lembeek, of which 10 kJ/m$^2$/y, or 2.9 g FW/m$^2$/y, would come from earthworms. Unfortunately, we do not have data on earthworm production for comparison. But we expect this to be relatively low given the low soil pH (3.8), and hence the impact of *Abax ater* to be not inconsiderable. Judas (1989) did not find a significant impact of predators (shrews and ground beetles) on earthworms in a field experiment in a beechwood at Solling, Germany, but the soil conditions are more favourable to earthworms at Solling.

In conclusion, *Abax ater* is characterized by a high assimilation efficiency, a low production efficiency, a high energy loss through respiration and a relatively high adult contribution to the total energy flow, which result from its great longevity and its chasing predatory strategy, especially in the adult stage. These characteristics are well in keeping with other physiological and demographic traits of this species, i.e., a continuous reproduction, a low fecundity, a great ability to withstand starvation, and a high population stability. All these features mark it out as a K-strategist, and likely contribute to explain its dominance in many temperate forests with limited and variable food resources.

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