

Quantitative assessment of consumption by *Abax ater* Villers (Coleoptera, Carabidae)

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Summary. Food ingestion by *Abax ater* was measured in the laboratory under fluctuating summer conditions: day/night = 16 h/8 h, 18 °C/15 °C, humidity at saturation. During their 7 months' development, larvae ingested 2340 mg (FW) of pre-digested earthworm flesh before their pupal moulting. Adult consumption was partly measured and partly estimated. Young emerging imagoes fed on ground beef meat consumed about 5740 mg (FW) during their first year (7 months) of activity. Older hibernated imagoes consumed 3850 to 5350 mg (FW) during the same time lapse. When fed on earthworms, their consumption was about twice higher. Adult consumption was zero at temperatures below 6 °C and reached its maximum value at 15 °C. At this temperature, gut clearance required 4–8 days but more than 50% of gut emptying was attained after 48 hours. These data are a first step towards an energy budget for *Abax ater*. Although the daily consumption rates (7–10% of individual weight) are by far lower than those quoted in the literature for other carabids, they are probably higher than the actual natural consumption rates.

Key words: Consumption, energy budget, larval development – *Abax ater*

Introduction

Carabid beetles are thought to play a regulatory role as generalist predators on the soil macro invertebrate community in forest ecosystems (Weidemann 1972; Thiele 1977; Loreau 1984a) although this role is badly documented in a quantitative way. Some consumption measurements have been performed but on rather short periods (Van Dinther 1966; Scherney 1960; Sota 1984; Ernsting 1987), and some of these published figures are unlikely (see Discussion). Hondo (1984), however, measured the consumption for the whole larval cycle of *Parena perforata*.

The establishment of energy budgets for the dominant carabid beetles would provide the best picture of their actual impact. Such information has been gathered for *Nebria brevicollis* (Manga 1972) and *Pterostichus oblongopunctatus* (Weidemann 1972) but is still lacking for other species. *Abax ater* is one of those species that are quite common and even dominant in many forest ecosystems of Western Europe. Although it has already been studied in some detail by many authors, its quantitative ecological role remains largely unknown. Being a nocturnal litter-dwelling species, *A. ater* is difficult to observe in the field. Therefore the analysis of its natural diet is based mainly on the microscopic observation of the adults' gut content (Loreau 1983). Experiments have also been performed to quantify its food preferences in the laboratory (Loreau 1984c). Adult *A. ater* are thus known as generalist opportunistic feeders, chasing a large variety of worms, molluscs, insects and other

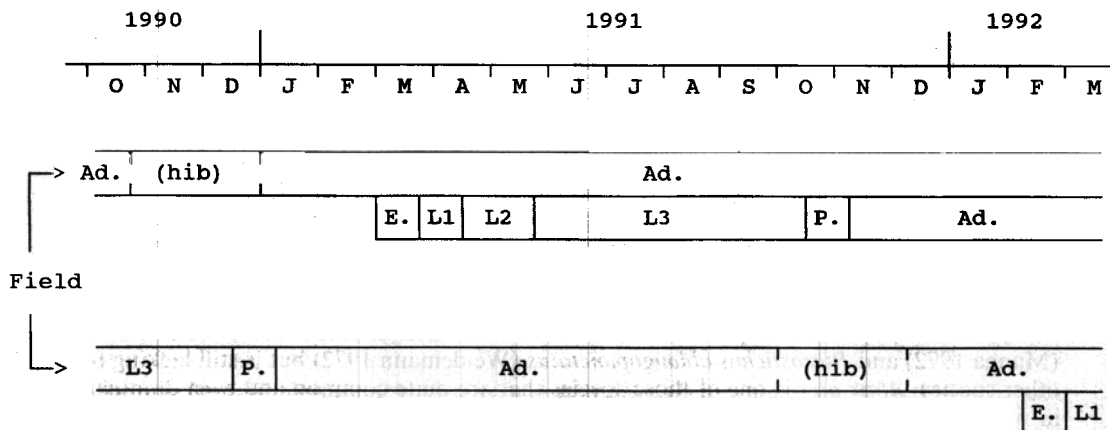
arthropods with dramatic seasonal changes (Loreau 1983). The larval diet is much less documented because larvae carry out a preoral digestion and do not swallow any recognisable piece of prey. However, rearing observations led Löser (1972) to suspect a more or less specialised predation on earthworms. A study of the ecological niches of a carabid beetle community in a beech forest at Lembeek (near Brussels, Belgium) showed that *A. ater* was the dominant species (Loreau 1984a) and suggested that it played an important ecological role on the macro invertebrate community at the soil surface (Loreau 1984b). Therefore a quantitative assessment of the consumption by *A. ater* would be a valuable step in the understanding of the forest ecosystem functioning. This will be the aim of this paper. It is also a first step in the study of the energy budget of this carabid species.

Material and methods

Consumption over a whole life span

All the stages of *A. ater* were reared under "summer laboratory conditions" day/night = 16 h/8 h, 18 °C/15 °C, humidity always at or close to saturation, the insects being isolated in vials furnished with some moist sieved forest soil. In all stages, consumption was measured as the difference in weight between a known amount of food provided to the beetles and the amount remaining one or two days later.

Larvae: Eggs were laid in March 1991 by adults that had been caught in October 1990 in the beech forest of Lembeek and hibernated for 10 weeks in the laboratory. These eggs hatched after about 20 days (Fig. 1). Ten young larvae were put separately in glass vials 5 cm in diameter, 3 cm high and furnished with 1 cm of sieved soil. Five of them died before reaching instar 2; the other five survived and reached the pupal stage. When they became 3d-instar larvae, they were transferred into deeper glass vials furnished with 6 cm of sieved soil. Throughout their life, the larvae were fed on pieces of earthworms of the species *Dendrobaena subrubicunda* and *Lumbricus eiseni*. These species are the commonest worms in the litter layer and under the bark of dead wood in the beech forest where the adult *A. ater* came from. They were maintained in the laboratory on beech bark from fallen logs. To feed the carabid larvae, the worms were cut into pieces and gently pressed, which expelled part of the gut content and some coelomic fluid; when they no longer lost any fluid, they were weighed to the



Ad. = adults, E = eggs, (hib) = hibernating adults,
L1, L2 & L3 = 1st-, 2d- & 3d-instar larvae, P = pupae

Fig. 1. Scheme of development of the animals used in the experiments

nearest mg, put on small aluminium trays and deposited on the soil surface of the carabid rearings. Food was provided twice a week between 4 and 6 p.m. The amount given depended on the larval stage: 20–30 mg for a 1st-instar, 40–60 mg for a 2^d-instar and 60–120 mg for a 3^d-instar larva. The remains of food were collected on the following day between 9 and 10 a.m.; they looked like a small dark meatball, sometimes spoiled with soil particles. After removing these soil particles under the microscope, the remains were weighed. It was assumed that there was no evaporative loss since the atmosphere in the rearings was water-saturated. Control measurements indeed showed no significant weight losses for small and medium pieces of worm, but larger worm pieces lost 9% of their weight. This might result in an overestimation of food consumption by 3^d-instar larvae. An accident happened during the 18th week: a night electrical failure altered the programme of the climatic chamber. During some 6 hours, the temperature was lowered at about 0 °C before we mentioned it and restored the “summer laboratory conditions”. The larvae seemed unaffected by this accidental cooling but their physiology might have been influenced. 5 extra 3^d-instar larvae were caught in October 1990 in the field and their consumption was measured in the same way.

Teneral imagoes: The 5 3^d-instar larvae that had been caught in the field stopped feeding and became pupae under the unchanged “summer laboratory conditions” (Fig. 1); 3 of them succeeded their imaginal moulting and produced 3 teneral females. These females were kept separately in PVC vials, 8 cm in diameter, furnished with 10 cm of moist sieved forest soil. As in Thiele (1968), they were fed twice a week on ground beef meat. A meatball of 70–120 mg, weighed to the nearest, was provided on an aluminium tray between 4 and 6 p.m. The remains were collected 48 hours later, separated from soil particles and weighed. Here also it was assumed that there was no evaporative loss; control weighings showed no more than 3 mg of loss, and in some cases up to 2 mg of increase (hygroscopic water uptake). The consumption by these young imagoes was measured for 7 weeks, including the whole teneral stage (the first 4–5 weeks). The measurements were then interrupted during 8 weeks and performed again during the following 8 weeks.

Hibernated imagoes: Adult *A. ater* were collected by Barber traps in the beech forest of Lembeek. They were kept in the laboratory at 10 °C for 2 weeks and hibernated under “winter laboratory conditions” for 10 weeks: day/night = 8 h/16 h, 3 °C/1 °C, humidity at saturation. After hibernation, the temperature of the climatic room was progressively raised in order to reach the “summer laboratory conditions” in 2 weeks. 5 males and 5 females were kept separately in PVC vials and fed twice a week. Their consumption was measured for 11 weeks; after an interruption of 9 weeks, it was performed again during the following 6 weeks.

Influence of temperature

The effect of temperature on consumption was assessed only for adult *A. ater* about 3 months after their hibernation in the laboratory. In order to avoid the influence of seasonal and/or physiological differences, all the measurements were carried out simultaneously in 5 climatic rooms with these day/night characteristics: a) 24 h/0 h, 4 °C/4 °C; b) 16 h/8 h, 10 °C/10 °C; c) 16 h/8 h, 15 °C/15 °C; d) 16 h/8 h, 18 °C/15 °C and e) 24 h/0 h, 25 °C/25 °C. Humidity was at saturation in all the cases. Each series of measurements concerned 10 males and 10 females. Since this experiment had been designed for measuring both consumption and excretion, the insects were kept separately in Petri dishes furnished with a pre weighed moistened filter paper. Prior to the measurements the animals were acclimatised for 3 weeks; this period enabled us to assess the maximum amount of meat they could eat. Consumption as described previously was measured during 2 weeks.

Speed of gut transit

Most predators are able to swallow large meals but once fed up, they need to digest, at least partly, before feeding again. It was of some interest therefore to assess at which speed *A. ater* clear their gut, measured as in Loreau (1990) by the daily decrease in weight after a large meal. Only adults kept separately in PVC vials were concerned. Measurements were performed about 4 months after their hibernation in the laboratory, under 3 different day/night conditions a) 16 h/8 h, 10 °C/10 °C; b) 16 h/8 h, 18 °C/15 °C and c) 24 h/0 h, 25 °C/25 °C. After 2 weeks of starving, the beetles were fed on ground beef meat and weighed (to the nearest mg) daily for 9 to 10 days. Each series of measurements concerned 5 males and 5 females acclimatised for more than 4 weeks.

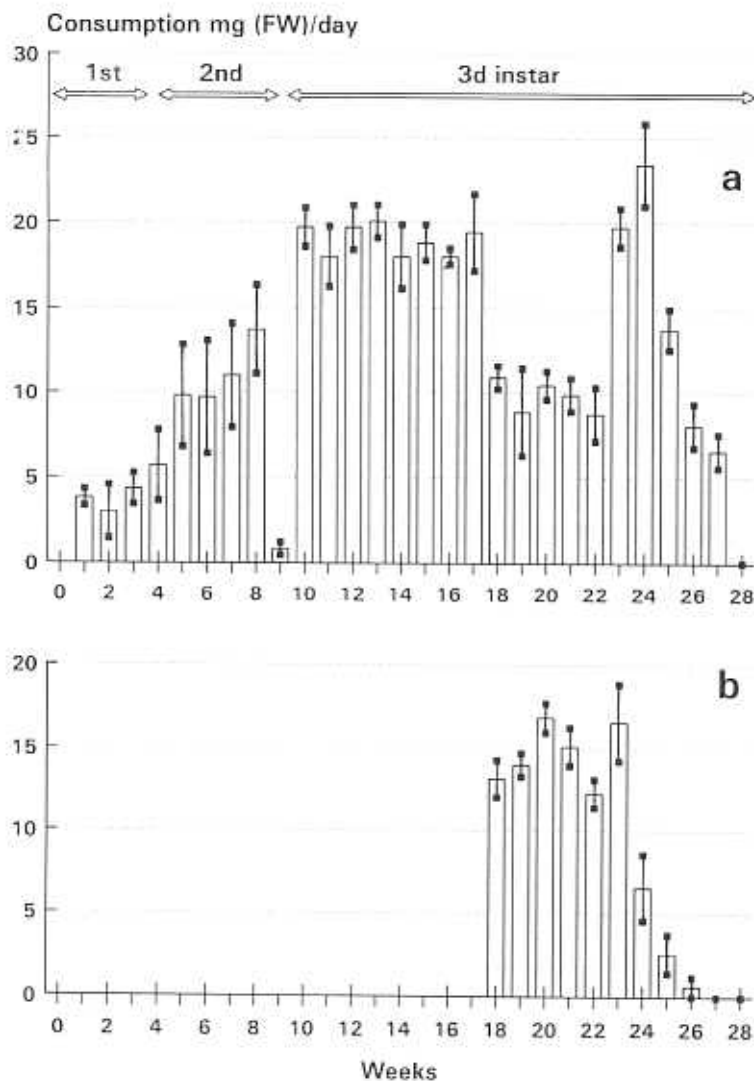


Fig. 2. Daily consumption (mean \pm standard deviation) of earthworms (mg of fresh weight) by *A. ater* larvae a) during the complete development of laboratory-born individuals and b) for 3rd-instar larvae caught in the field

Influence of food nature

Simultaneously with the experiments on the influence of temperature, we tried to assess whether a more natural food would influence consumption quantitatively. 5 males and 5 females, after hibernation, were acclimatised for 3 weeks at day/night = 16 h/8 h, 18 °C/15 °C and fed on pieces of the earthworms *Dendrobaena subrubicunda* and *Lumbricus Eiseni* for 2 weeks.

Results

Consumption over a whole life span

Larvae: Some striking features appear in the changes in the week after week consumption during larval life (Fig. 2): a) Feeding stopped during moulting from the 2nd- to the 3rd-instar

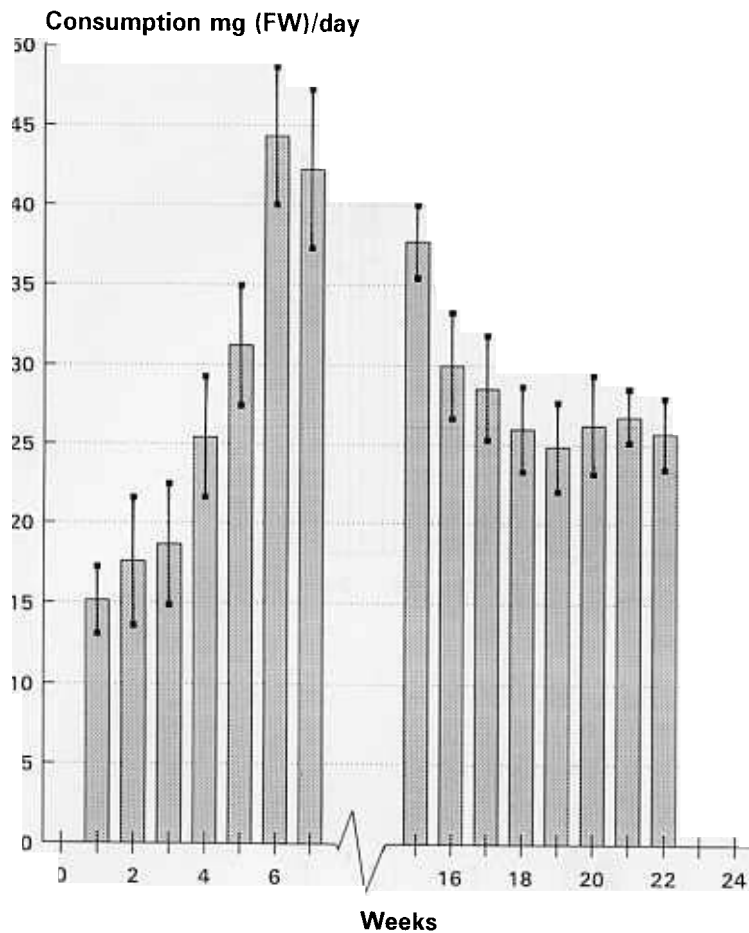


Fig. 3. Daily consumption (mean \pm standard deviation) of ground beef meat (mg of fresh weight) by emerging female adult *A. ater*. Measurements were interrupted from week 8 to week 14

larva. The moulting from the 1st- to the 2^d-instar larva was also accompanied by an interruption in feeding (2–3 days) but this was compensated by an enhanced food uptake after moulting and thus is not visible on the weekly consumption graph. b) Consumption declined sharply in the middle of the third larval instar. This decline immediately followed the accidental cooling mentioned in material and methods. The low consumption rate lasted for about 5 weeks and resumed for 2 weeks before declining again; the latter decrease was the premise of the prepupal stage. c) The 3^d-instar larvae caught in the field (Fig. 2b) exhibited a slightly lower consumption than that of laboratory grown larvae before the accidental cooling. Of course, we did not know their exact age when we collected these larvae, but they showed the same kind of consumption decrease when reaching the prepupal stage. Therefore we have made coincide the end of consumption by the two categories of larvae on the time axis. d) There is a more or less marked increase in food uptake at the end of the 3^d larval instar just before the prepupal consumption decrease. The cumulative consumption during larval life is summarised in Tab. 1: under constant summer conditions, about 2350 mg of fresh pre-digested earthworms are necessary for completing the larval development of *Abax ater*.

Teneral imagoes: The teneral stage lasts about 4 weeks. It is characterised by soft elytra that are progressively sclerotinised. The consumption started at about 15 mg of fresh

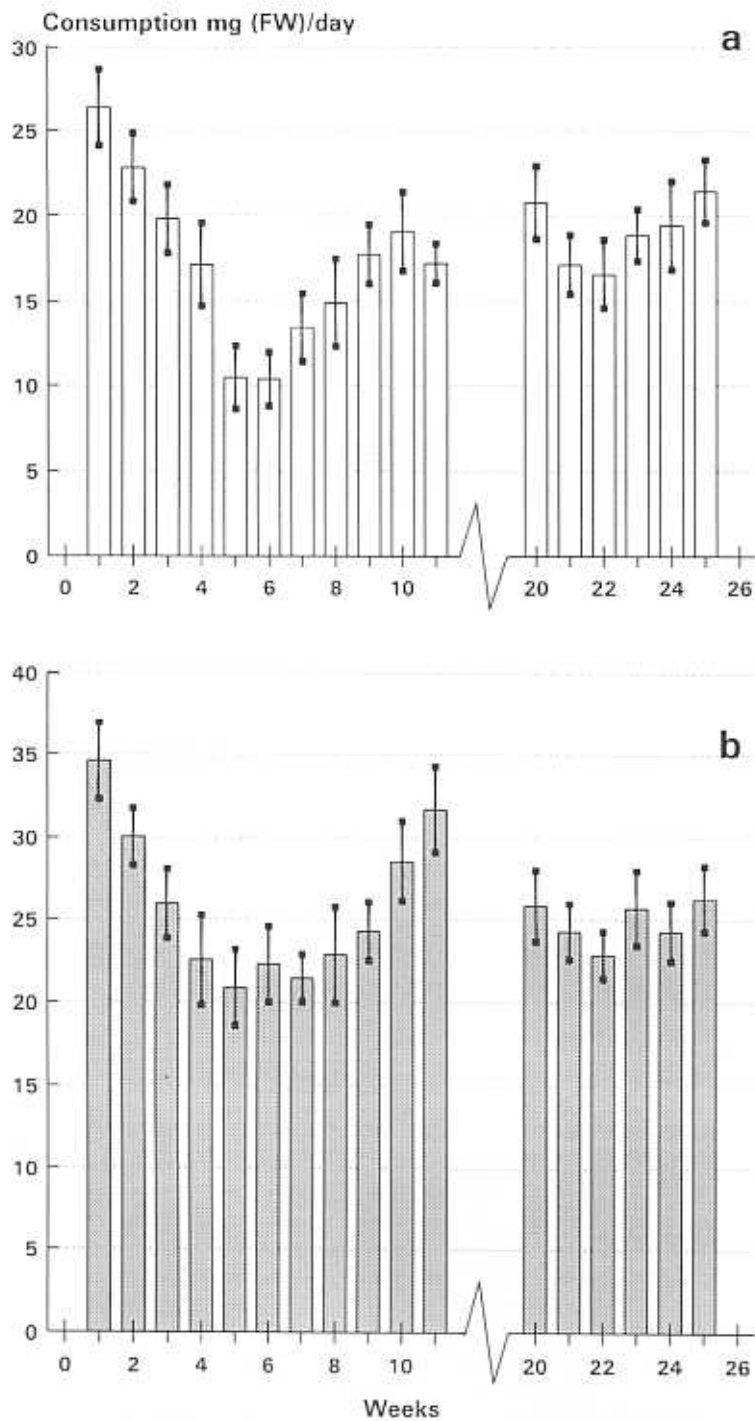


Fig. 4. Daily consumption (mean \pm standard deviation) of ground beef meat (mg of fresh weight) by hibernated *A. ater* adults a) in males and b) in females. Measurements were interrupted from week 12 to week 19

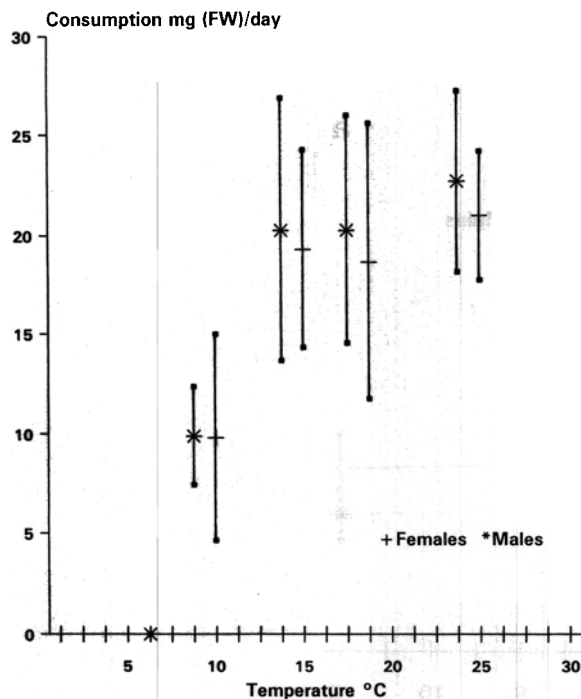


Fig. 5. Dependence of beef meat consumption by adult male and female *A. ater* on temperature (mean \pm standard deviation)

meat/day (Fig. 3), increased week by week until it reached a maximum of about 45 mg, 6 weeks after imaginal emergence. Although we did not keep on measuring consumption during the weeks 8 to 14, the beetles were fed continuously twice a week with almost constant amounts of meat. The remains were larger week by week, and two months after their peak consumption, their feeding rate had become more or less constant at about 25 mg per day.

Hibernated imagoes: After a 10-week hibernation, the consumption started at about 25 mg of fresh meat/day for males (Fig. 4a) and 35 mg for females (Fig. 4b). Then it decreased, reached a minimum value after 5–6 weeks and increased again, stabilising around 18 mg in males and 24 mg in females. In females, the increase in consumption coincided with egg production. Egg laying started on the 9th week and lasted for about 4 weeks.

Influence of temperature

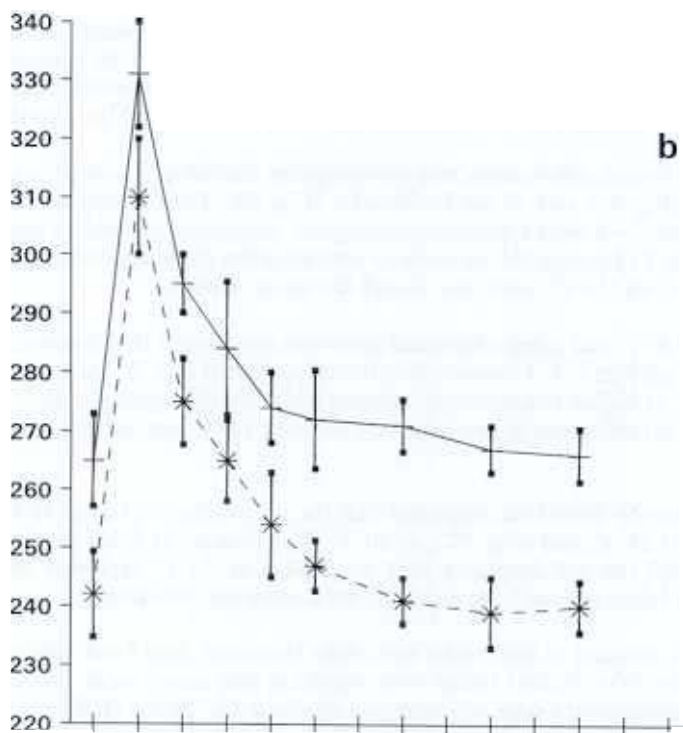
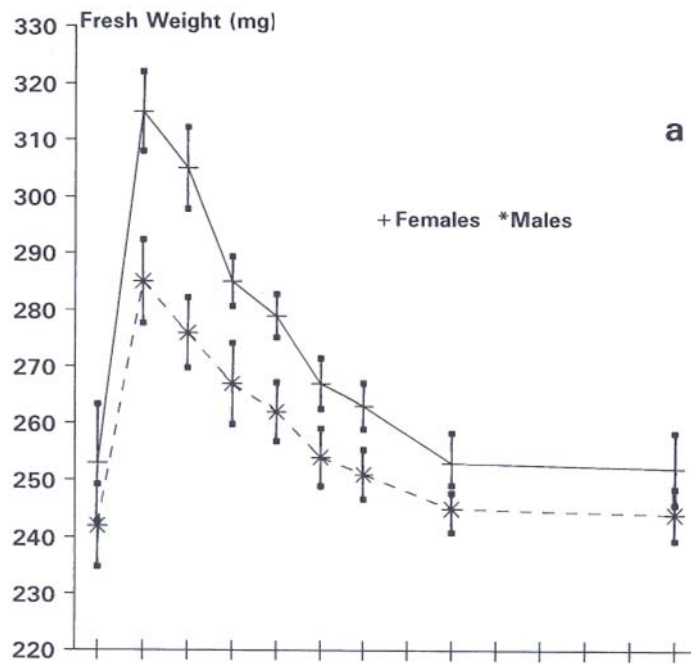
There was no consumption at 4 °C, and some additional observations showed that it stayed at zero until temperature reached 6 or 7 °C. Consumption therefore started at 7 °C, increased until 15 °C and stayed steady at higher temperatures: although the graph suggests a slight increase, there was no significant difference in consumption between 15 °C and either 25 °C or the fluctuating 18°/15 °C.

Speed of gut transit

Independent observations made by dissection suggested that the gut is almost cleared 48 h after a meal for beetles kept at 25 °C, and after 72 h at 10 °C. The changes in fresh weight after a meal (Fig. 6) confirmed the gut emptying in 1 or 2 days at 25 °C. However at 18 °C/15 °C, and at 10 °C, 4 to 8 days seemed to be necessary for a complete clearance.

Influence of food nature

When first fed on earthworms (instead of beef meat) the adults increased their food intake immediately, swallowing up to 70% of their initial own weight in one single meal. Some earthworm meals later, they maintained a high consumption of about 40–50 mg (FW)/day, about twice than on beef meat and representing daily 17–19% of their own weight. The speed of gut transit was found to be the same as with beef meat.



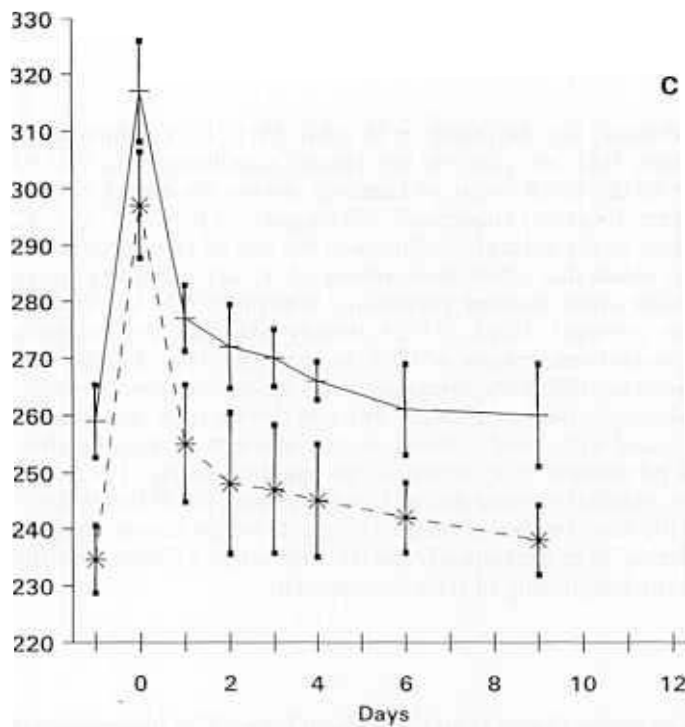


Fig. 6. Weight decrease after a meal of ground beef meat in female (solid lines) and male (broken lines) *A. ater* adults at a) 10 °C, b) 18/15 °C and c) 25 °C (mean \pm standard deviation)

Total food uptake by adults

In order to compare larval and adult food consumption, we estimated how much beef meat or earthworm tissue an imago in its first year (after emergence) or in its second year (after hibernation) would consume under the same summer conditions and during the same time laps of 7 months as the duration of larval development (Table 2).

Table 1. Cumulative consumption of earthworms by *A. ater* larvae grown under summer conditions

Instar	L1	L2	L3	Total
Duration of stage (days)	25	35	143	203
Cumulative consumption of earthworms (mg FW)	121	315	1905	2341
Mean daily consumption (mg FW)	4.8	9.0	13.3	11.5

Table 2. Estimated cumulative consumption (during 7 months) by adult *A. ater* reared under summer conditions

	females 1 st year	females 2 nd year	males 2 nd year
Cumulative consumption of beef meat (mg FW)	5740	5350	
Mean daily consumption of beef meat (mg FW)	27.3	25.5	18.3
Same items for earthworms:		multiply by ≈ 2	

Discussion

Rearing conditions

The "summer laboratory conditions" (i.e. day/night = 16 h/8 h, 18 °C/15 °C, humidity at saturation) were chosen because they are close to the natural conditions that can be experienced in the litter layer of the beech forest of Lembeek during the month of July (Loreau 1984a). And the "winter laboratory conditions" (day/night = 8 h/16 h, 3 °C/1 °C, humidity at saturation) are close to the natural conditions in the soil of this beech forest in January. It is interesting to notice that a full development of *A. ater*, from egg laying till imaginal moulting, is possible under summer conditions. It required 221 to 265 days in our rearing (241 days on average). Löser (1972) already obtained the complete development of *A. ater* at a constant temperature of 18 °C in 165–255 days (213 days on average), which shows that there is no obligatory dormancy in any stage of *A. ater*. However, the three emerging female individuals did not produce any egg during their first year of imaginal life (although they mated with "wild" males); their consumption was therefore related only to imaginal tissue production. They started to lay eggs in February 1992, after a 10-week hibernation. It is worthwhile to notice that in Löser's rearings the 3^d larval instar development never exceeded 105 days but lasted on an average 143 days in our rearings. Let us remember that these larvae were dramatically cooled; this might explain both the decrease of consumption and the lengthening of their development.

Larval consumption

The cumulative consumption by larvae (Table 1) may have been lowered by the accidental cooling that they suffered during the 18th week of their development. However the consumption by the larvae caught in the field was even lower during the last 9 weeks of their development (684 mg) than for the laboratory-born larvae (742 mg). In fact, when caught in the field in October, the 3^d-instar larvae weighed already 180 mg and did not significantly increase their weight during the following 9 weeks. On the other hand, the laboratory-grown larvae weighed about 160 mg when they were accidentally cooled and increased subsequently their weight to about 180 mg before their pupal moulting.

To our knowledge, these data are the second quantitative figures ever provided for consumption during carabid larval development. The first ones were provided by Hondo (1984): about 308 mg of fresh caterpillars were required for producing a 28 mg 3^d-instar of *Parona perforata*. In our rearings, 2350 mg of fresh earthworms were consumed to reach a weight of 180 mg and produce a pupa. In fact, a higher amount of earthworms is required since only part of the pre-digested food is ingested: in most of our measurements, the remains accounted for 10 to 50% of the provided food. Also recall that most of the gut content was expelled from the earthworm pieces prior to providing them to the carabid larvae, which can explain that on an average 70 to 80% of the provided food was consumed.

Imaginal consumption

Earthworm maintenance or production in great quantities is not easy in the laboratory. That is the reason why only the larvae were fed on earthworms while the adults were fed on ground beef meat, a food item that the larvae do not appreciate that much (they appear to be more specialised predators than the adults). Some cutting of paraffin-included worms showed that their gut content (essentially made of decayed vegetal particles) accounted for about 31% of their total volume. Moreover, the water content account for 80% of fresh weight in earthworms and only 71% in beef meat. A control experiment (see influence of food nature) showed that the adults ate about twice more when fed on earthworms than

on ground beef meat. Since the adult *A. ater* swallow their prey entirely, one can estimate that 2 g of worm accounts for about 276 mg of dry weight tissues and 1 g of beef meat for about 290 mg of dry weight tissues. Therefore, behind the difference between worm- and beef consumptions, the amounts of dry weight digestible tissues are almost the same. This should be converted into energy units for an ultimate comparison.

Comparison with other adult carabid beetle

Very few data have been gathered on carabid consumption. Scherney's (1960) data seem unlikely. Such high figures as a daily consumption of 2 to 3 times its own weight is even a higher food uptake than that of the homeothermic shrews. Van Dinther (1966) already criticised these data and obtained much lower figures: daily fed on eggs and larvae of the housefly, small *Bembidion* species ingested up to 80% of their own weight and larger *Harpalus* species less than 30%; however such a large species as *Pterostichus lepidus* also ingested 74% of its own weight daily. According to Ernsting (1987), the adults of *Notiophilus biguttatus*, a small collembolan feeder weighing about 6 mg, consume a springtail of about 3 mg daily at 20°/10 °C. Our results suggest that *Abax ater* would only consume daily 17 to 19% of its own weight when fed on earthworm or about 7 to 10% when fed on ground beef meat. However in our experiments, food was not provided every day but only twice a week, which can at least partially explain the difference with Van Dinther's data. Our measurements of gut transit showed that 4–8 days were required for a complete gut clearance at 18°/15 °C but 50% of emptying were already attained 1–2 days after food uptake. This is significantly longer than Jaspar-Versali's (1986) results, obtained by a radiographic technique and worked out at laboratory temperature: the total duration of gut transit for *A. ater* was estimated at 60 hours. Our results are more consistent with those obtained by Loreau (1983, 1990): he found residues of prey in the gut of *A. ater* until 72 hours after a meal at ambient temperature. It seems very likely that our beetles would have eaten more if they had been fed more often. But all the consumption data, including ours, have been obtained under laboratory conditions: they should be considered as potential consumptions. We believe that they are higher than those reached in the field since a) Loreau (1983) showed that 38 to 53% of the *A. ater* caught in the field had empty guts, suggesting that they do not feed more than one or two times a week, and b) our results were obtained under constant summer conditions and we showed that lower temperatures decreased the beetles' consumption.

Conclusions

Compared with other carabid species whose consumption has been measured in the laboratory, *A. ater* appears to be an especially frugal species. Also, total consumption in the larval stages is relatively low compared with that of adults. These features conform well with the developmental and demographic characteristics of this species, i.e. a great adult longevity, a continuous reproduction, a low fecundity, and a remarkably stable population density (Loreau 1985, 1990), which mark it out as a K-selected species among carabids. Its moderate food requirements added to its opportunistic feeding behaviour (at least in adults) and its long period of activity are likely to explain its marked dominance in the beech forest studied, in which food resources are relatively poor and variable (Loreau 1984b).

Acknowledgements

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