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Efficiency of host utilisation by coleopteran parasitoid

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ABSTRACT

In insect larvae, optimising food utilisation with respect to available meals and time is essential for achieving maximum adult body size, which is a relevant proxy of fitness. We studied the efficiency of food conversion, body size, mortality, and development time in a solitary idiobiont ectoparasitoid, *Brachinus explodens* (Coleoptera: Carabidae), reared in the laboratory on the pupae of another carabid genus, *Amara*. The efficiency of conversion index (ECI – ratio of ingested to assimilated food) was, on average, $54.1 \pm 1.1\%$ (n = 76), with a minimum of 26.9% and a maximum of 81.6%. The rate of increase in biomass gained (W_{gained}) with biomass of the host was constant in females, but it decreased in males over the range of host body mass. Females, therefore, grew heavier from hosts of the same mass compared to males. Body length increased with the host mass and was correlated with W_{gained} identically for both sexes. Mortality was unaffected by the host mass, but it significantly increased below $20 \,^{\circ}$ C. In contrast, the development time of the feeding phase of the larva increased with the host mass at 20.3 and $23.7 \,^{\circ}$ C. Jo our knowledge, our data are the first on food utilisation in solitary idiobiont coleopteran ectoparasitoids, and they present the highest values of ECI in insects.

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1. Introduction

Balancing food consumption and the efficiency of its utilisation is an important problem in larval development (Slansky and Scriber, 1985). Larval nutrition not only has a direct impact on development time and mortality during the larval stage, but it also affects adult body size (Slansky and Scriber, 1985), which is an important determinant of fecundity (Honek, 1993) and fitness (Roitberg et al., 2001). In general, insect larvae possess a range of options to deal with limited or low quality food, including increasing food intake or maximising the conversion of ingested food (Slansky and Scriber, 1985). The selection of strategies that might be adopted is, however, constrained by affiliation to a particular trophic guild (Scriber and Slansky, 1981).

Idiobiont parasitoids develop on hosts of determined size, such as eggs, pupae or paralysed larvae or adults. Such hosts represent a "nutritional package" of a limited amount of food (Vinson and Barbosa, 1987). Gregarious idiobionts respond to variation in host size by optimising clutch size (Vinson and Iwantsch, 1980) to ensure the necessary food supply and lifetime fitness for each larva. Solitary idiobionts can only choose whether to accept a host of particular size or not, and this choice has a pivotal consequence because the body size and fitness of the offspring will be correlated with that of the host (Vinson and Iwantsch, 1980; Cohen et al., 2005). If large hosts are not available, any adaptations that improve the utilisation of the small host and enable it to increase body size contribute to its fitness. The effect of host size on the final size of an adult parasitoid may be modified by variation in host quality (Greenblatt and Barbosa, 1981) and possibly by abiotic conditions during development, particularly temperature and humidity (Atkinson, 1994).

Mortality during development and the duration of development are fitness proxies with consequences that are less studied than those of size variation (Harvey, 2005). Due to rapid deterioration of the parasitised host, it is expected that idiobiont parasitoids should develop quickly to ensure low mortality (Otto and Mackauer, 1998). Because development time increases with increasing size of the host (Harvey, 2005), enforced fast development may decrease adult size with negative consequences for fitness. Whether a species favours large body size or short development time may depend on the host's exposure to environmental risks. Harvey and Strand (2002) found that parasitoids developing on concealed hosts favour size due to low risk of predation. Temperature obviously affects development time (Atkinson, 1994; Pair, 1995; Saska and Honek, 2005), but how it influences pre-imaginal mortality remains poorly understood in parasitoids (Pair, 1995).

In this paper, we study host utilisation and successful development in *Brachinus explodens* Duftschmid (Coleoptera: Carabidae), a solitary idiobiont ectoparasitoid developing on the pupae of another carabid genus, *Amara* (Saska and Honek, 2005). The first





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instar larvae search for the concealed hosts through the soil. When a larva finds a host, it attaches to its surface. The living host dies because of parasitoid feeding. Therefore, the development of *B. explodens* is very fast – the host (200–600 times larger than the parasitoid) is consumed within ca. 5–6 days (at 25 °C) after attachment (Saska and Honek, 2004) – and it requires rapid consumption and, presumably, the effective conversion of host tissues into the parasitoid body. Body size in field-collected *B. explodens* varies enormously (Hurka, 1996), suggesting that this variation may be related to variation in host size, as with other parasitoids (Salt, 1941), including the North American species *Brachinus lateralis* Dejean, a polyphagous parasitoid of the pupae of water beetles (Juliano, 1985). *B. explodens* may therefore favour the attainment maximum size over minimum development time, in line with the hypothesis of Harvey and Strand (2002).

In our study of *Brachinus* nutrition, we focused on the effects of host size on the efficiency of food utilisation and the developmental success of this coleopteran parasitoid. The research questions were the following: (i) How efficient is the development of *B. explodens*? (ii) Is the final body size (both in terms of biomass and length) of adult *B. explodens* related to host mass, and if so, is this relationship affected by temperature and sex? (iii) Are the development time and mortality of the parasitoid larvae affected by the host mass and temperature?

2. Material and methods

2.1. Rearing

Adult carabid host and parasitoid species were collected using pitfall traps at Praha – Ruzyně (50°06'N, 14°15'E) in May and June 2002, 2003 and 2010. Pupae of the host species, *Amara aenea* (DeGeer), *A. familiaris* (Duftschmid) and *A. similata* (Gyllenhal), were reared using the protocol of Saska and Honek (2003). The adults were kept in pairs in plastic Petri dishes filled with a sieved garden soil at 18 ± 0.5 °C and under a long day (17L:7D) photoperiod. Twice a week, the beetles were fed with pieces of *Tenebrio molitor* (Linnaeus) larvae and seeds of *Capsella bursa-pastoris* (L.) Med. (*A. aenea* and *A. similata*) or *Stellaria media* (L.) Vill. (*A. familiaris*). The eggs were sieved out and hatched, and the larvae were kept individually using the same equipment and conditions as for adults. The pupae provided to the *Brachinus* larvae were less than 48 h old to assure that the host age would not affect the host quality (Vinson and Iwantsch, 1980; Harvey, 2005) and parasitoid performance.

Adult B. explodens were kept in groups of 10 per Petri dish under the same conditions as Amara and were fed with pieces of T. molitor larvae. Twice a week, the adults were moved to another Petri dish and the soil with previously deposited eggs was then inspected daily. The neonate 0-24-h-old Brachinus larvae were selected and used for parasitism. The Brachinus larvae were individually placed in glass Petri dishes (5 cm diameter, 1 cm high) filled to a depth of 0.4 cm with plaster of paris mixed with charcoal and moistened with several drops of tap water twice a week (Saska and Honek, 2004). Each larva was provided with one Amara pupa of either species of known body mass (see below) and placed in temperature-controlled cabinets. In each cabinet, the temperature oscillated only slightly around the mean, which ranged from 15 to 27.4 °C, respectively. The mean temperatures were calculated from hourly records logged by Tinytalk[®] dataloggers. The development of Brachinus was recorded twice daily (at 8:00 and 18:00) until death or the completion of development.

2.2. Conversion efficiency

Nutritional indices are frequently used to quantify the efficiency of food consumption and its utilisation (Scriber and Slansky, 1981).

The index of the efficiency of the conversion of ingested food (ECI) indicates the proportion of ingested food, *I*, converted to the body mass of the consumer, W_{gained} , by an individual during a given period (Waldbauer, 1968). The ECI is calculated as

$$\text{ECI} = (W_{gained}/I) * 100[\%] \tag{1}$$

Because *Brachinus* larvae consume their hosts almost entirely (Saska and Honek, 2004) and the minute remnants of the host bodies (often liquid-like and attached to the parasitoid larvae) could not be measured, the dry body mass of the *Amara* pupae was used as a proxy of the ingested food, *I*. Due to the destructive manner of dry body mass determination, it had to be approximated from the fresh body mass. The fresh body mass was determined for individual host pupae using a Sartorius[®] balance with 10^{-5} g accuracy (*A. familiaris* – mean fresh mass ± SE = 11.6 ± 0.89 mg; *A. aenea* – 18.4 ± 1.07 mg; *A. similata* – 23.1 ± 1.14 mg). Eighteen host pupae were dried at 70 °C for 24 h, after which their dry body mass was determined. The resulting values (dry body mass = 0.173 ± 0.007 of the fresh body mass [*N* = 18]) were used to recalculate the host fresh mass.

The weight gained by the parasitoid during development was calculated as

$$W_{gained} = W_{final} - W_{initial} \tag{2}$$

where W_{final} and $W_{initial}$ are the "final" and "initial mass" of the parasitoid, respectively. $W_{initial}$, i.e., the dry body mass of the first instar larva, was impossible to measure individually due to its minute size. A batch of forty dried (70 °C/24 h) larvae were weighed instead, and the individual dry body mass was estimated as $W_{initial} = 10.25 \ \mu$ g. W_{final} was estimated by weighing each adult parasitoid 0–24 h after pupation and three days after adult moulting (without access to food or water) to ensure complete melanisation and sclerotisation, and it was recalculated to dry mass (dry body mass of parasitoid pupae: 0.193 ± 0.038 of the fresh weight [N = 3]; dry body mass of adult parasitoids: 0.172 ± 0.007 of the fresh weight [N = 8]). The dry body mass of the pupae was solely used to estimate the costs of pupal-adult metamorphosis, and thus, the W_{gained} was calculated for the entire pre-imaginal development of the parasitoid.

The adults were killed with ethyl acetate, dry mounted and identified for sex using tarsal characters and the body length was measured from the apices of the mandibles to the tip of the abdomen under a LEICA MS5 stereomicroscope with calibrated eyepieces. The body length was determined also for 26 field-collected adults. All voucher specimens are preserved in the senior author's personal collection.

2.3. Data processing

The differences in host utilisation by the *Brachinus* larvae were analysed using the analysis of covariance (Raubenheimer and Simpson, 1992) rather than ANOVA using ECI as the response variable because interpretation of the results of ANOVA on ratios (as ECI is) may lead to erroneous conclusions when the assumptions of the analysis of ratios are violated (see, e.g., Packard and Boardman, 1988; Raubenheimer and Simpson, 1992; Horton and Redak, 1993 for detailed discussion). All calculations were made in R 2.12.1 (Crawley, 2005).

 W_{gained} was used as response variable in the ANCOVAs, and temperature and parasitoid sex were categorical factors. The dry body mass of the host pupa was used as a covariate in all analyses. The goodness-of-fit of the models was visually checked by plotting standardised residuals against fitted values and against explanatory variables and by plotting the ordered residuals against expected ordered statistics (Crawley, 2005). If needed, the appropriate transformation of response variable was used. The analyses

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