Influence of adult nutrition on the relationship between body size and reproductive parameters in a parasitoid wasp

T. MARTIJN BEZEMER[1,2,3], JEFFREY A. HARVEY[3] and
NICK J. MILLS[4]   [1]Laboratory of Nematology, Wageningen University and Research Centre, the Netherlands,
[2]Laboratory of Entomology Wageningen University and Research Centre, the Netherlands, [3]Netherlands Institute of
Ecology (NIOO-KNAW), the Netherlands and [4]Insect Biology, Wellman Hall, University of California, U.S.A.

Abstract. 1. An important constraint upon life-history evolution in parasitoids is the limit imposed by body size on allocation of limited metabolic resources to different fitness-related physiological functions such as reproduction and survival.

2. The influence of adult nutrition on reproductive and maintenance variables was studied in the synovigenic ectoparasitoid *Mastrus ridibundus*, and it was determined whether resource allocation to these different functions depends on body size.

3. Over the course of adult life there was a positive relationship between body size and the number of mature eggs in adult females both in the presence and absence of food. However, only in the presence of food did egg maturation rates increase significantly with body size. Starved wasps produced significantly smaller eggs than fed ones, which has not been documented before. Moreover, starved wasps produced fewer offspring than fed wasps, and attacked fewer hosts.

4. The availability of food had a major effect on longevity, with fed females living about 10 times longer than starved ones. There was also a positive relationship between body size and longevity. In starved wasps, this relationship was the same both in the presence and absence of hosts, but in fed wasps there was a positive relationship between body size and longevity in the absence of hosts only. Allocation to initial eggs relative to lifetime progeny production did not decline with body size.

5. The data reveal that in *M. ridibundus* the trade-off between maintenance and reproduction varies with life expectancy.

Key words. Egg maturation, egg production, egg size, reproductive strategies, resource allocation, size–fitness relationship, synovigeny.

Introduction

One of the most challenging areas in evolutionary biology and ecology has been to determine the relationship between adult body size and fitness. Across a range of vertebrate and invertebrate taxa, numerous empirical studies have

reported that body size is correlated with life-history and demographic traits such as mating efficiency, dispersal capability, and, most importantly, lifetime reproductive success (Berrigan, 1991; Blackburn, 1991; Visser, 1994; Luiselli *et al.*, 1996; Barbraud *et al.*, 2000; Rasa *et al.*, 2000; Sokolovska *et al.*, 2000; Bezemer & Mills, 2003; Bochdanovits & De Jong, 2003; Jervis *et al.*, 2003; Skow & Jakob, 2003; Wissinger *et al.*, 2004).

Parasitoid wasps have traditionally been the focus of research for examining the size–fitness hypothesis in arthropods (Godfray, 1994). Parasitoids are insects that develop

Correspondence: Dr T. M. Bezemer, Laboratory of Nematology, Wageningen University and Research Centre, PO Box 8123, 6700 ES Wageningen, the Netherlands. E-mail: martijn.bezemer@wur.nl

on, or in, the bodies of other organisms, usually other insects, and only the larval stages are parasitic, whereas adults are free-living. Parasitoids rely on a single host to obtain all of the resources necessary for the completion of growth and reproduction. Furthermore, many parasitoid species attack hosts that are of approximately equivalent size to themselves, or that have the potential to grow only marginally larger (Harvey *et al.*, 2004). Consequently, parasitoids are under intense selection to optimise efficient uptake and allocation of limited host resources to competing fitness-related functions such as reproduction and survival. For some parasitoid species, whose adults do not obtain proteins via 'host-feeding' behaviour, all of the resources (e.g. fat body) necessary for egg production are obtained during larval feeding and are carried over to the adult stage (Jervis & Kidd, 1986; Rivero & West, 2002). At the same time, in the absence of a carbohydrate source such as nectar, fat body reserves may be metabolised for maintenance and repair (Ellers *et al.*, 1998, 2000). An extrinsic source of sugar, such as nectar, can slow the rate of uptake of fat body for maintenance functions (Rivero & West, 2002). Because parasitoid wasps appear to be unable to synthesise the lipids needed for yolk production from sugars (e.g. Ellers, 1996; Rivero *et al.*, 2001; Rivero & West, 2002; Giron & Casas, 2003b), sugars cannot be used directly for reproduction. Consequently, the optimal phenotype is likely to be determined by a trade-off between life-history characters when extrinsic sources of nutrition are in short supply (Rivero & West, 2002).

Furthermore, nutrient limitation or stress might also indirectly affect other fitness traits such as host-finding and dispersal efficiency, the ability to overcome behavioural host defences, and even the production of paralysing venom, the latter an important prerequisite for idiobiont parasitoids attacking non-sessile hosts (Taylor, 1988; Nakamatsu & Tanaka, 2003). Non-host feeding parasitoids must therefore allocate exogenous or endogenous resources to optimise a suite of fitness-related traits. However, little attention has thus far been paid to these areas at the empirical level (but see Fletcher *et al.*, 1994; Pexton & Mayhew, 2002; Rivero & West, 2002).

Large body size is often correlated with an increase in the amount of resources carried over from the larval to the adult stage (Spradberry & Sands, 1981; Honek, 1993; Ellers *et al.*, 1998). Large size enables individual parasitoids both to store more energy reserves (which influences longevity) and to produce more eggs (which influences reproductive success) than smaller conspecifics. Numerous laboratory studies have reported that longevity and fecundity in parasitoids are positively correlated with body size (Waage & Ng, 1984; Bellows, 1985; Heinz & Parrella, 1990; Hardy *et al.*, 1992; Harvey *et al.*, 1994, 2001; Nakamura, 1995; Zaviezo & Mills, 2000), although in field studies the results are more idiosyncratic, with some fitness variables responding to size but not others (Visser, 1994; Kazmer & Luck, 1995; West *et al.*, 1996; Bezemer & Mills, 2003).

The timing of egg production [allocation to initial egg load relative to lifetime potential fecundity, expressed as the ovigeny index (Jervis *et al.*, 2001)] is yet another important trait in parasitoids (Ellers & Jervis, 2003; Jervis & Ferns, 2004). Many parasitoid species emerge with a only small fraction of their potential egg complement but continue to mature eggs for variable periods throughout the course of adult life (so-called 'synovigenic species', *sensu* Flanders, 1950; Jervis & Kidd, 1986). The ovigeny index is known to vary in relation to body size both within and between species. Whereas interspecifically, initial egg load accounts for most of the body size-related variance in ovigeny index, intraspecifically both initial egg load and potential fecundity contribute significantly (Jervis & Ferns, 2004). Both intraspecifically and interspecifically, ovigeny index declines with increasing body size, in accordance with the prediction of general life-history theory that the proportion of the adult's biomass that is invested in offspring (eggs) should be inversely related to body size (see Jervis & Ferns, 2004 for a review of the evidence).

In addition to fecundity, differential resource investment may also affect associated life-history traits such as egg size (Pexton & Mayhew, 2002; Giron & Casas, 2003a). In many insects, egg size is considered to be a reliable predictor of offspring fitness (Wiklund *et al.*, 1987; Giron & Casas, 2003a). This raises the question as to why parasitoids exhibit different egg maturation strategies. Endoparasitoids usually produce copious numbers of small, ostensibly yolkless 'hydropic' eggs containing very low concentrations of lipids and proteins (Chapman, 1998). By contrast, parasitoids that lay their eggs externally typically produce large, yolky (anhydropic) eggs containing sufficient lipids and proteins to complete embryogenesis. Therefore, the amount of resource invested per egg is much greater in ecto- than in endoparasitoids. Consequently, under conditions of resource limitation, ectoparasitoids that reallocate reserves from reproduction to maintenance may still be able to maintain egg production if fewer reserves are invested per egg, e.g. by producing smaller eggs. Recent work suggests that parasitoids hatching from small eggs suffer higher mortality than neonates emerging from larger eggs (Giron & Casas, 2003a).

This study examines the effects of adult nutrition on reproductive parameters in the gregarious idiobiont ectoparasitoid, *Mastrus ridibundus* (Hymenoptera: Ichneumonidae) developing on cocooned larvae (prepupae) of its host the codling moth, *Cydia pomonella* (Lepidoptera: Tortricidae). For wasps of different size (i) egg maturation rates, (ii) egg size, (iii) longevity, and (iv) patterns of reproduction (measured as daily fecundity), when supplied *ad libitum* with honey or when starved, were compared. Given that exogenous (sugar) and endogenous (fat body) resources may be limiting, the following questions were asked: (i) How does a parasitoid allocate scarce resources to different functions (reproduction or maintenance), given that both influence the reproductive success of the parasitoid? (ii) Is the pattern of resource allocation allometric or isometric? The results of this investigation are discussed

with respect to trade-offs in the metabolic allocation of resources in parasitoids to competing fitness functions.

Materials and methods

Biology and insect culturing

The codling moth is a key pest of apple, pear, and walnut production in California and worldwide (Bezemer & Mills, 2001a). As part of an ongoing biological control programme, *M. ridibundus* has been imported from the region of origin of the codling moth in Central Asia for culture and release in California and the Pacific Northwest. In Central Asia, *M. ridibundus* naturally occurs in apple orchards under environmental conditions similar to those found in California. *Mastrus ridibundus* appears to be a more specialised parasitoid of the codling moth, and is a non host-feeding idiobiont that attacks mature host larvae once they have spun a cocoon beneath the bark of the host tree. *Mastrus ridibundus* was cultured on diapausing codling moth cocoons under constant conditions of 25 °C and LD 16:8 h photoperiod (Bezemer & Mills, 2001b). Female parasitoids were maintained in sleeved oviposition cages (45 × 45 × 45 cm) with glass lids and provided with both undiluted honey and water. All experiments were carried out under controlled conditions in the laboratory (25 °C; 70% RH).

Egg load, maturation rate, and size

To determine whether female size or life expectancy influenced egg load or maturation rates, unmated females were kept individually from the time of emergence in plastic vials (7 × 4 × 4 cm) in the presence or absence of honey (hereafter described as 'fed' or 'starved' cohorts). Twenty females varying in size were dissected immediately after emergence to determine the number of mature eggs present in the ovarioles at emergence (= initial egg load), and subsequent sets of 20–22 females from each treatment were dissected 8 h, 1 day, 2 days, 3 days, 4 days, 7 days, 10 days, and 14 days after emergence and the number of mature eggs determined. For each female hind tibia length (a widely used comparative measure of body size) was also recorded. The majority of starved females did not survive for more than 3 days, resulting in only 10 females being dissected after 3 days. For each day the relationship between female size and number of mature eggs was determined using linear regression. The influence of food availability on the number of mature eggs per female was determined by comparing slopes (*t*-test) followed by ANCOVA (when slopes were not significantly different) with female size as a continuous factor. Data were analysed for each time period separately (8 h, 1 day, 2 days, and 3 days). To determine egg maturation rates over the first 3 days in the presence and absence of honey, for female size classes (hind tibia lengths 0.9 ± 0.05, 1.0 ± 0.05,

1.1 ± 0.05, 1.2 ± 0.05, 1.3 ± 0.05, 1.4 ± 0.05, and 1.5 ± 0.05 mm) the relationship between number of mature eggs and time (in days) since emergence was determined using linear regression and the estimated slope of each function was plotted against the mid-point of the corresponding female size class. In the absence of honey there were only three females with size 0.9 ± 0.05 mm so maturation rate could not be determined. The remaining regressions were based on $n = 7$–25.

For a range of different female sizes the influence of size and food deprivation on the size of mature eggs was studied. Single female wasps, together with a male to ensure mating, were kept in plastic vials (7 × 4 × 4 cm) from emergence in the presence (*n* = 27) or absence (*n* = 23) of honey. After 48 h females were dissected and the length of all mature eggs was recorded. For each female, mean egg size was calculated and hind tibia length recorded. The influence of food availability on egg size was determined by comparing slopes (*t*-test) followed by ANCOVA (when slopes were not significantly different) with female size as a continuous factor.

Longevity and patterns of reproduction

To estimate life expectancy in the absence of hosts, the longevity of two sets of newly emerged unmated females (1–3 h old) was monitored every 4–6 h, one set in the absence (*n* = 66) and the other in the presence (*n* = 68) of undiluted honey, replenished daily. At death the hind tibia length of each female was recorded and the relationship between female size and longevity was determined using linear regression.

In the presence of excess of hosts, the effect of body size and food availability on longevity and oviposition decisions was also studied. Newly emerged females (1–3 h old) were kept individually in plastic vials (7 × 4 × 4 cm), in the presence (*n* = 34) or absence (*n* = 74) of honey, with eight diapausing codling moth cocoons replaced daily. *Mastrus ridibundus* usually parasitises one to two hosts a day, and has never been observed to parasitise more than four hosts a day (Bezemer & Mills, 2003). Each day, survival of the female parasitoids was recorded, and after death hind tibia length of each female was determined. Host cocoons were incubated and for each day the number of successfully parasitised hosts and the number of progeny surviving to pupation was determined. Data were adjusted for first day of reproduction, and for both data sets (starved and fed), days to first reproduction, daily number of offspring, and number of hosts successfully parasitised were calculated. For each day, for surviving females that did not produce offspring during that day 'zero' was entered for number of offspring and hosts parasitised. The influence of honey on daily number of offspring and hosts parasitised over the first 3 days was analysed using repeated measures ANOVA (Gurevitch & Chester, 1986). To avoid missing values, for this analysis, a 'zero' was entered for day 2 or 3 for females that had reproduced but did not

survive for 3 days after first reproduction. The proportion of females that did not produce any offspring during their lifetime was also determined for starved and fed females using the size classes described above. For reproducing females the relationship between female size and lifetime offspring was determined using linear regression. The mean number of hosts parasitised during days 1–3 was also calculated and the relationship with female size determined using linear regression. An *F*-test was used to compare the slopes of the relationships between female size and longevity in presence and absence of hosts.

The relationship between ovigeny index and body size was also examined using the size classes described above. For empirical purposes, lifetime potential fecundity (the denominator in the ovigeny index) can be measured as the average maximum realised fecundity. In this study lifetime progeny production was used as a close approximation. The mean maximum lifetime potential fecundity was also measured as this was used, along with mean lifetime potential fecundity in the dynamic programming model of Ellers and Jervis (2003), although the relationships between life-history variables (body size, initial egg load, lifetime egg production, allocation to reserves) made no qualitative difference to the model's output (Ellers & Jervis, 2003).

Results

Egg load, maturation rate, and size

There was a strong positive linear relationship between body size and the number of mature eggs for both fed and starved wasps for each age group (Fig. 1). Although *M. ridibundus* is a synovigenic wasp 25% of females emerged without mature eggs, while even up to 2 days after emergence a small proportion of dissected females lacked mature eggs (Fig. 1). Significantly fewer mature eggs in relation to size were found in females deprived of food but only for females aged 24 and 72 h (test for different slopes: 24 h $t_{2,27} = 0.669$, $P = 0.51$; 72 h $t_{2,16} = 1.252$, $P = 0.22$; ANCOVA 24 h $F_{1,38} = 12.01$, $P < 0.01$; 72 h $F_{1,27} = 27.27$, $P < 0.001$). In the presence of honey, there was a positive relationship between female size and egg maturation rate (test for slope greater than zero $t = 6.06$, $P = 0.001$), while no such relationship was found in absence of honey ($t = 0.58$, $P = 0.59$; Fig. 2). The size of mature eggs also linearly increased with female size, but was significantly smaller in starved females (test for different slopes: $t_{2,47} = 1.58$, $P = 0.126$; ANCOVA $F_{1,47} = 11.82$, $P = 0.001$; Fig. 3).

Longevity and patterns of reproduction

In the absence of hosts, longevity decreased markedly when females were deprived of food. Without honey, females survived up to 4 days, while in the presence of honey, females lived up to 40 days. In the absence of hosts, longevity significantly increased with body size both in the absence

($F_{1,65} = 44.51$, $P < 0.001$; Fig. 4a) and in the presence of honey ($F_{1,66} = 15.89$, $P < 0.001$; Fig. 4c) but the relationship between body size and longevity was much stronger in the absence of honey (no honey: $r^2 = 0.41$; honey: $r^2 = 0.19$). In the presence of hosts and absence of honey, the positive relationship between body size and longevity was also significant ($F_{1,73} = 29.43$, $P < 0.001$; Fig. 4b) and the slope did not differ from that based on longevity in the absence of hosts and honey ($F_{2,136} = 2.40$, $P = 0.34$). With both hosts and honey, however, the relationship between female size and longevity was no longer significant ($F_{1,33} = 3.85$, $P = 0.06$; Fig. 4d).

Over the first 3 days of reproduction, females produced significantly more offspring with access to honey ($F_{1,72} = 15.21$, $P < 0.001$; Fig. 5a), and parasitised more hosts ($F_{1,72} = 15.11$, $P < 0.001$; Fig. 5b). This difference became more apparent over time, resulting in a significant honey × age interaction (offspring produced: $F_{2,144} = 3.26$, $P = 0.04$; hosts parasitised: $F_{2,144} = 6.98$, $P = 0.001$). In the absence of honey, the time to first reproduction appeared to be reduced but this was not significant (mean number of days ± SE for honey present: 1.14 ± 0.27; honey absent: 0.69 ± 0.08, $t_{72} = 1.90$, $P = 0.06$). There was no significant relationship between body size and time to first reproduction in either the absence ($F_{1,43} = 0.02$, $P = 0.88$) or presence of honey ($F_{1,27} = 1.79$, $P = 0.19$). In the absence of honey, 39% of females did not produce any offspring and the proportion of non-reproducing females declined with female size. In presence of honey, 15% of females did not reproduce and there was no clear relationship with female size (Fig. 6a). There was a positive relationship between female size and lifetime number of offspring both in the absence ($F_{1,43} = 14.11$, $P < 0.001$) and presence of food ($F_{1,27} = 15.59$, $P < 0.001$) but, independent of size, there was a large amount of variation between individual females (Fig. 6b,c). In the presence of honey, there was a significant positive relationship between female size and mean number of hosts attacked during the first 3 days of reproduction ($F_{1,27} = 18.57$, $P < 0.001$; Fig. 7b) but for starved females there was no relationship between size and host attack rate ($F_{1,43} = 0.13$, $P = 0.72$; Fig. 7a). In the presence of honey, a number of females also survived for up to 10 days after they last produced offspring (mean ± SE, 3.10 ± 0.50). This was not related to female size ($F_{1,27} = 3.32$, $P = 0.08$) or to the total number of offspring produced ($F_{1,27} = 2.79$, $P = 0.11$) but there was a strong positive relationship with longevity ($F_{1,27} = 27.70$, $P < 0.001$; Fig. 8).

Although initial egg load increased with body size (Fig. 1), the estimate of ovigeny index did not decline with body size when either mean (ovigeny index: mean ± SE, 0.10 ± 0.01) or maximum (ovigeny index: mean ± SE, 0.08 ± 0.01) lifetime progeny production was used as the index's denominator.

Discussion

The results of this study reveal that *M. ridibundus*, like other parasitoids (Rivero & West, 2002), exhibits
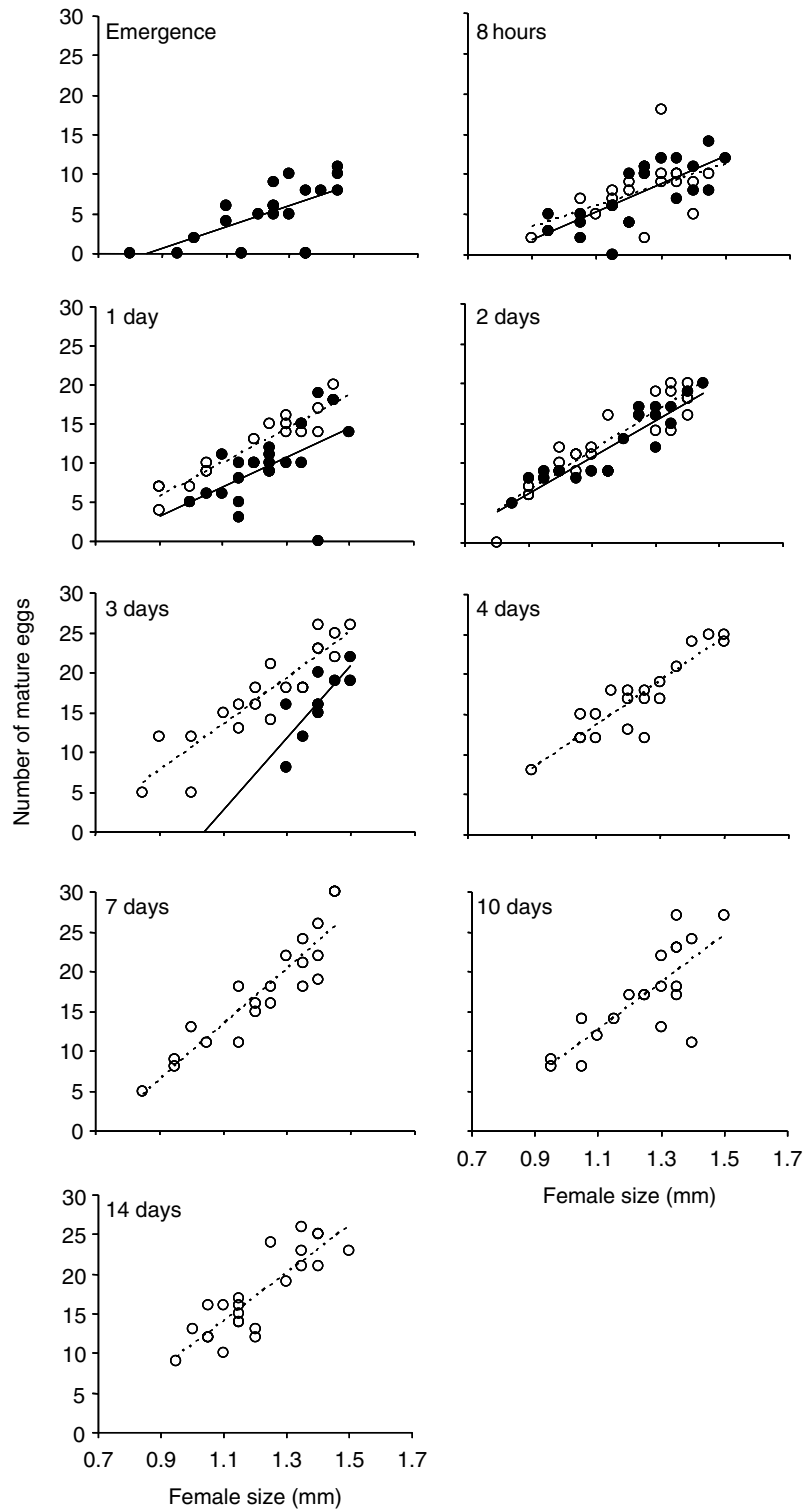
Fig. 1. Relationship between body size and number of mature eggs for females in the absence (——●——) or presence of honey (---○---). Regressions: Emergence: number = 13.4(size) − 11.4, $F_{1,19} = 11.72$, $P < 0.01$, $r^2 = 0.39$; 8 h no food, number = 17.2(size) − 13.5, $F_{1,19} = 25.39$, $P < 0.001$, $r^2 = 0.57$; 8 h food: number = 12.9(size) − 8.10, $F_{1,19} = 5.64$, $P < 0.05$, $r^2 = 0.24$; 1 day no food: number = 18.94(size) − 13.9, $F_{1,20} = 9.48$, $P < 0.01$, $r^2 = 0.33$; 1 day food: number = 21.4(size) − 13.5, $F_{1,19} = 103.35$, $P < 0.001$, $r^2 = 0.85$; 2 days no food: number = 22.9(size) − 14.5, $F_{1,20} = 87.81$, $P < 0.001$, $r^2 = 0.82$; 2 days food: number = 24.82(size) − 15.9, $F_{1,20} = 110.03$, $P < 0.001$, $r^2 = 0.85$; 3 days no food: number = 45.6(size) − 47.5, $F_{1,9} = 13.17$, $P < 0.01$, $r^2 = 0.62$; 3 days food: number = 29.3(size) − 18.8, $F_{1,19} = 83.63$, $P < 0.001$, $r^2 = 0.82$; 4 days food: number = 27.3(size) − 16.45, $F_{1,19} = 81.37$, $P < 0.001$, $r^2 = 0.82$; 7 days food: number = 35.0(size) − 25.2, $F_{1,19} = 97.92$, $P < 0.001$, $r^2 = 0.84$; 10 days food: number = 29.6(size) − 19.9, $F_{1,19} = 27.14$, $P < 0.001$, $r^2 = 0.60$; 14 days food: number = 30.3(size) − 19.3, $F_{1,22} = 58.95$, $P < 0.001$, $r^2 = 0.74$.
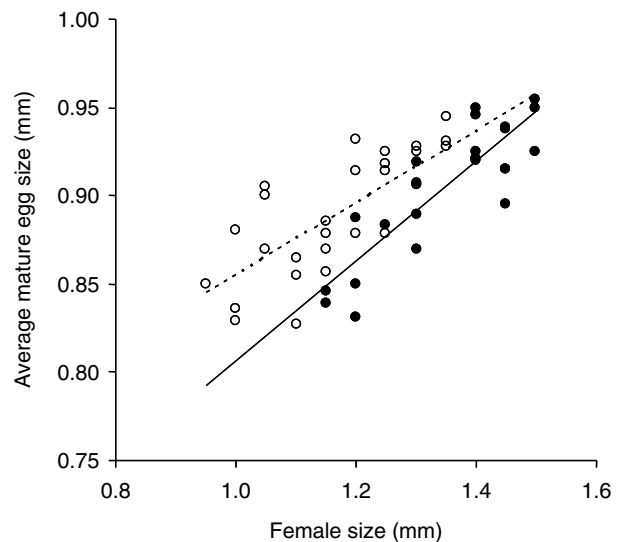
phenotypic plasticity in several important reproductive variables and that egg-load dynamics and oviposition decisions vary with life expectancy (in this study generated by the presence or absence of honey). Moreover, the extent to which these traits were affected varied significantly with body size at eclosion. With increasing body size, initial egg load and the number of eggs matured on each subsequent day increased when wasps were supplied with honey,
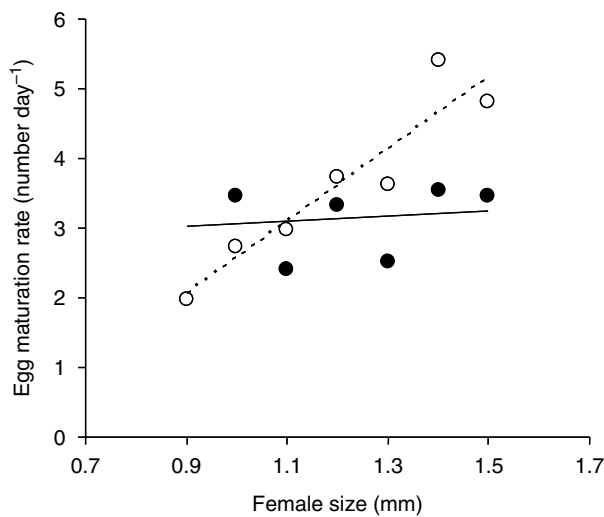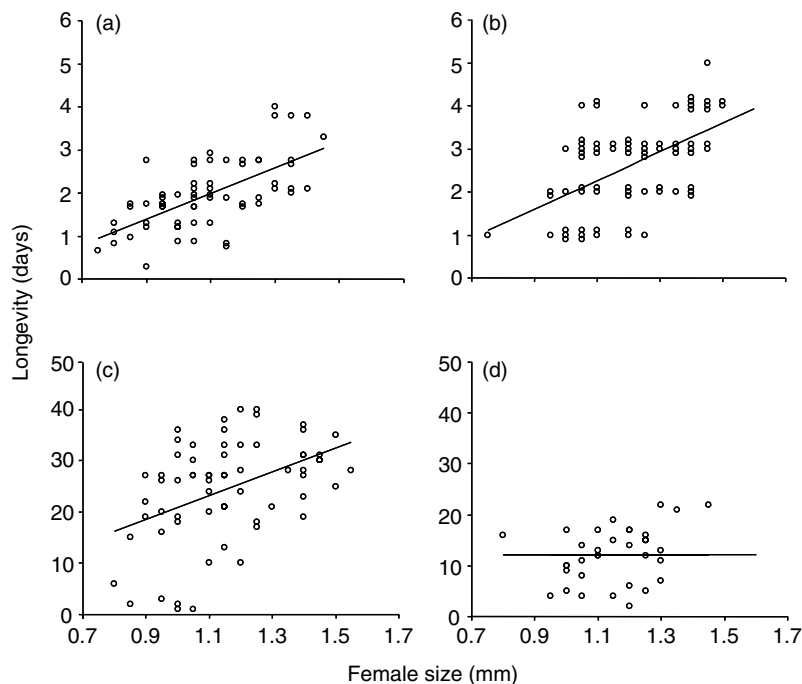
Fig. 2. Relationship between female size and egg maturation rate, estimated over the first 3 days after emergence for females in the absence (—●—) or presence of honey (---○---). Regressions: no food: $F_{1,5} = 0.34$, $P = 0.59$; food: maturation rate = 5.2(size) − 2.6; $F_{1,6} = 36.70$, $P < 0.001$, $r^2 = 0.88$.


Fig. 3. Relationship between female size and mature egg size for females in the absence (—●—) or presence of honey (---○---). Regressions: no food: egg size = 0.28(size) + 0.53, $F_{1,22} = 62.70$, $P < 0.001$, $r^2 = 0.75$; food: egg size = 0.20(size) + 0.65, $F_{1,26} = 33.33$, $P < 0.001$, $r^2 = 0.57$.

but remained static when females were deprived of honey. Egg size also increased with adult female size, but fed wasps consistently produced larger eggs than their starved counterparts. Other studies have also shown that fed parasitoids mature more eggs (Rivero & West, 2002), but hitherto no study has shown that the availability of food can influence egg size in parasitoids. However, egg size is known to decline with female age (Giron & Casas, 2003a), indicating

that egg size can change depending on life expectancy and resource availability. Smaller eggs might result in offspring that suffer a reduction in fitness, in terms of reduced survival, smaller adult size, and/or longer development time (Nakasuji, 1987; McIntyre & Gooding, 2000; Giron & Casas, 2003a).
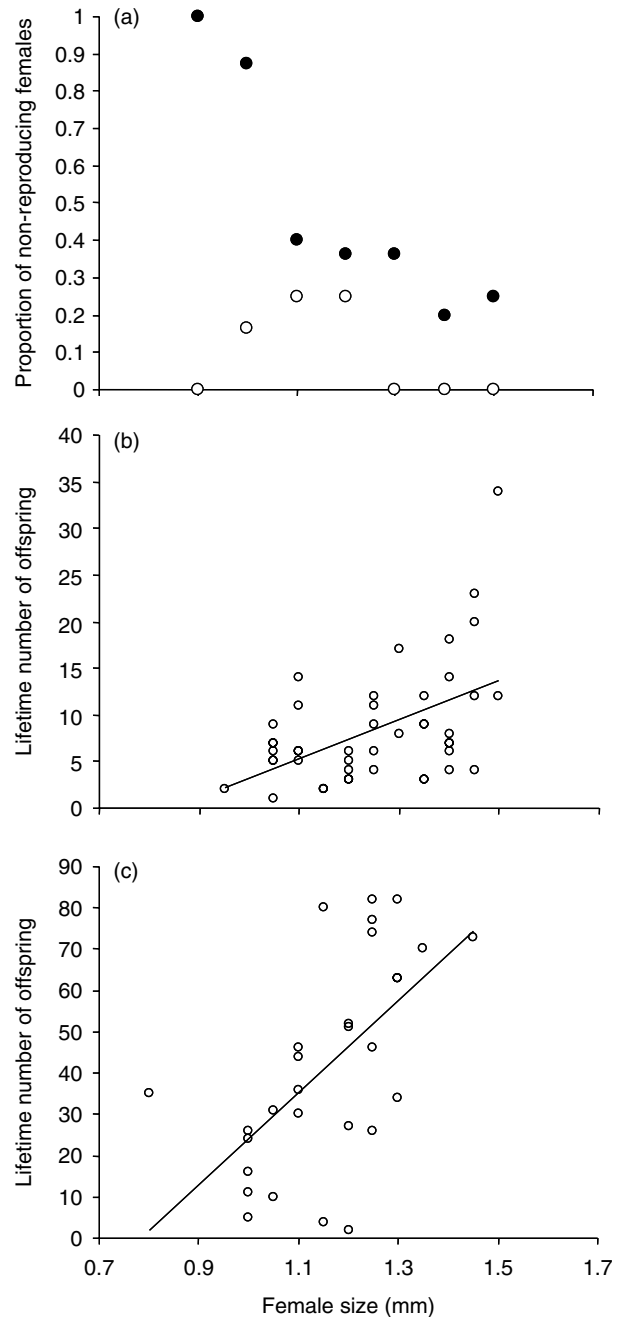

Fig. 4. Relationship between female size and longevity for females in the absence (a, b) or presence of honey (c, d), and in the absence (a, c) or presence (b, d) of hosts. Regressions: (a) longevity = 3.0(size) − 1.3, $F_{1,65} = 44.51$, $P < 0.001$, $r^2 = 0.41$; (b) longevity = 3.3(size) − 1.4, $F_{1,73} = 29.43$, $P < 0.001$, $r^2 = 0.29$; (c) longevity = 23.0(size) − 2.2, $F_{1,67} = 15.89$, $P < 0.001$, $r^2 = 0.19$; (d) $F_{1,33} = 3.85$, $P = 0.06$.
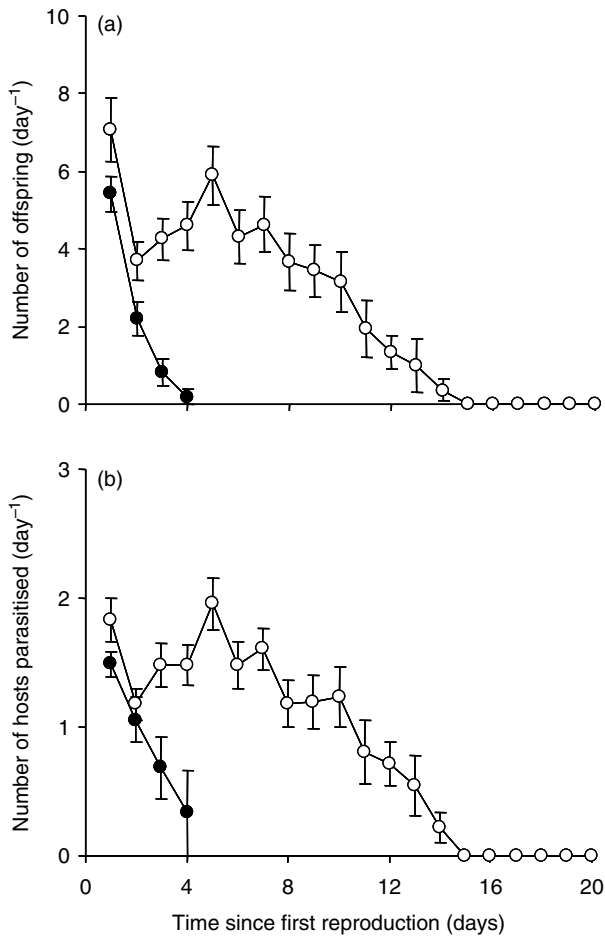
Fig. 5. Mean ($\pm$ SE) number of offspring produced per day (a) and number of hosts parasitised per day (b) in relation to reproductive age in the absence ($\bullet$) or presence ($\circ$) of honey.

In holometabolous insects, including parasitoid wasps, the fat body is accumulated during larval feeding and is carried over through pupation to the adult stage, where it may be metabolised for egg production or somatic maintenance. Large size benefits parasitoids directly by making more fat body available to competing fitness functions, such as reproduction and survival (Ellers *et al.*, 1998; Rivero & West, 2002). However, in the absence of a carbohydrate source, such as nectar (or honey in these experiments), the female parasitoid must utilise fat reserves for maintenance functions that might otherwise be used for egg production. In order to economise on the use of metabolic resources during periods of food deprivation, parasitoids may also invest fewer resources per egg, thus maintaining a fairly constant level of egg production whilst producing smaller eggs. This may explain why starved *M. ridibundus* produced smaller eggs than conspecifics that were constantly supplied with honey. Most importantly, the observed trade-offs in reproductive characteristics in *M. ridibundus* probably represent an adaptive use of limited metabolic
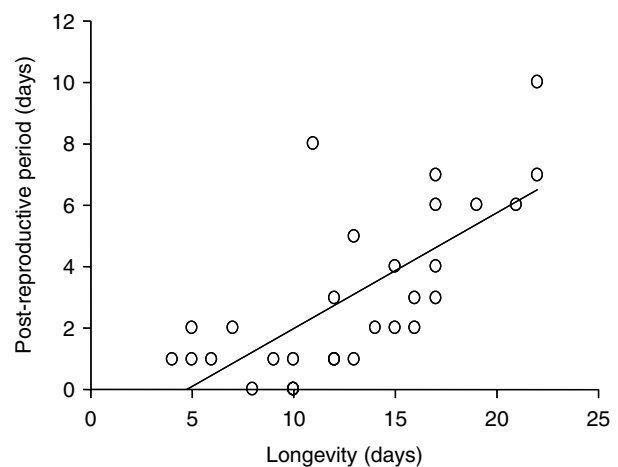

Fig. 6. Relationship between female size and (a) proportion of non-reproducing females in absence ($\bullet$) or presence ($\circ$) of honey, and lifetime number of offspring for females in the absence (b), or presence (c) of honey. Regressions: (b) number = 20.7(size) – 17.5, $F_{1,43} = 14.10$, $P < 0.001$, $r^2 = 0.24$; (c) number = 111.1(size) – 86.9, $F_{1,27} = 15.59$, $P < 0.001$, $r^2 = 0.37$.

resources under sub-optimal conditions. In the field, where conditions may be highly stochastic, and thus environmental quality is unpredictable, a single parasitoid female may have to respond to similar constraints even over the course of her lifetime.
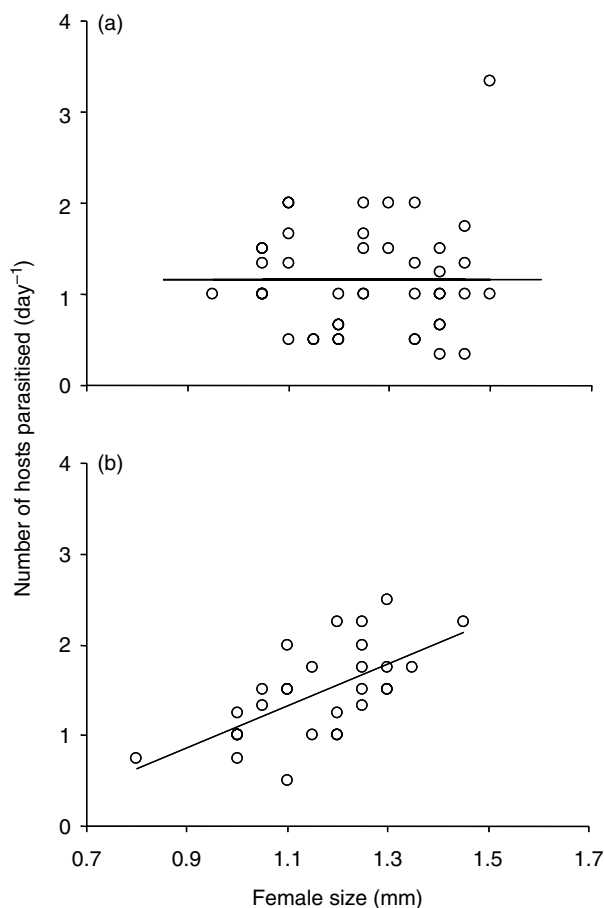
Fig. 7. Relationship between female size and mean number of hosts successfully parasitised per day (based on days 1–3) for females in the absence (a), or presence (b) of honey. Regression: (a) $F_{1,43} = 0.13$, $P = 0.72$; (b) attack rate = 2.3(size) – 1.2, $F_{1,27} = 18.57$, $P = 0.001$, $r^2 = 0.41$.

Fig. 8. Relationship between longevity and post-reproductive period for females in the presence of honey. Regression: post-reproductive period = 0.38(longevity) – 1.77, $F_{1,27} = 27.70$, $P < 0.001$, $r^2 = 0.51$.

Many idiobiont ectoparasitoids inject venom during the oviposition sequence that permanently paralyses the host (Quicke, 1997). Large, yolky eggs are then laid on the moribund host; these eggs must contain all of the resources (fat, proteins, lipids, etc.) necessary to complete embryogenesis (Flanders, 1942, 1950; Jervis & Kidd, 1986). In non-host feeding species, such as *M. ridibundus*, proteins for oogenesis can be mobilised only from fat body reserves, even in high quality environments with ample sources of adult nutrition available (Papaj, 2000; Lauziere *et al.*, 2001; Harvey *et al.*, 2001). Consequently, larger wasps, with greater fat reserves at eclosion, are presumably better able to allocate metabolic resources for maintenance than can small wasps, which have accumulated fewer resources during larval development. This may explain why, in both fed and starved *M. ridibundus*, body size was positively correlated with lifetime reproductive success. Another adaptation of many parasitoids producing anhydropic (yolk-rich) eggs is the capacity of females to resorb egg proteins in situations where hosts are scarce and/or sources of

nutrition are limited (Jervis & Kidd, 1986). Resorption prevents the accumulation of comparatively large eggs in the ovaries, where they may be costly to store (Jervis & Kidd, 1986). However, *M. ridibundus* does not apparently resorb ovulated, stored eggs (Bezemer & Mills, 2003). This is another factor that may select for economisation of metabolic resources in nutrient-poor environments.

A large number of studies have shown for parasitoids that there is a positive intraspecific relationship between body size and longevity (reviewed by Godfray, 1994). Similarly, in this study larger females were shown to live longer. However, for honey-fed females that were allowed to reproduce no such relationship occurred. Larger females produced more offspring, and had a higher host attack rate. It appears that for *M. ridibundus*, under optimal conditions (excess food and hosts) resources are mainly allocated to reproduction rather than maintenance. Interestingly, under optimal conditions females had a post-reproductive period of up to 10 days. Moreover, females that lived longer had a longer post-reproductive period, independent of body size. Dissection of some females, at death, with post-oviposition periods of at least 5–6 days revealed that although females did not produce any offspring, mature eggs were still present in the ovarioles (M. Bezemer, pers. obs.). In view of this, other factors such as venom production may have been more important in limiting reproduction than egg availability.

Although it is known that metabolic resources are utilised for maintenance and/or reproduction, little is known about their role in maintaining other important functions, such as venom production. Jervis *et al.* (1994) revealed that the gregarious idiobiont parasitoid, *Bracon hebetor*, continues to paralyse hosts for variable periods in post-reproductive life, i.e. after the egg supply has been exhausted. However, *H. hebetor* is a host-feeding species, and therefore resources obtained from this behaviour may be mobilised for venom

production even when the ovaries cannot produce further eggs. Since, in this study, there was a positive relationship between female size and host attack rate only in the presence of food, this indicates that limiting resources are directed towards maintenance under bad conditions (low life expectancy), or towards reproduction when conditions are good. The results also clearly show that, although most studies focus on egg production, other factors such as host attack ability (venom) may also be a limiting factor for reproduction.

No evidence was found that ovigeny index declined with increasing body size, a prediction of the Ellers and Jervis (2003) model. According to Ellers and Jervis (2003) small females being shorter-lived, experience the habitat as being more stochastic in terms of encounters with hosts (spatial heterogeneity, measured in terms of variance relative to mean), so compared with larger females their optimal initial egg load needs to exceed anticipated host availability by a proportionally higher amount (Ellers & Jervis, 2003). The mismatch between the present data and the predicted relationship could, however, have been due to progeny production poorly approximating potential fecundity.

In conclusion, this study has shown that there are trade-offs between maintenance and reproduction and that the way *M. ridibundus* deals with this depends on its life expectancy. Because larger females are able to store more metabolic resources than small females, they are thus able to more effectively allocate their resources for reproduction or maintenance depending on environmental conditions.

Acknowledgements

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