

# Effect of Host Size on Adult Size and Sex Ratio of *Bracon mellitor* (Hymenoptera: Braconidae)

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**ABSTRACT** The purpose of this research was to determine the effect of the size of the host, *Anthonomus grandis grandis* Boheman, on adult size, sex ratio, longevity, and fecundity of the ectoparasitoid *Bracon mellitor* Say. Adult size of *B. mellitor* was directly related to host size; larger parasitoids developed on larger host larvae. Host size also affected sex ratio so that predominately male wasps were produced on small hosts. The male bias on smaller hosts was caused by differential oviposition of male and female eggs by adult females. Female longevity and fecundity were directly related to adult size; larger females lived longer and subsequently produced greater numbers of progeny than smaller females.

**KEY WORDS** *Bracon mellitor*, *Anthonomus grandis grandis*, host size

SALT (1940) WAS ONE of the first scientists to determine that a direct relationship exists between the size of a parasitoid and the size of its host. He reared the trichogrammatid *Trichogramma evanescens* Westwood on eggs of the Angoumois grain moth, *Sitotroga cerealella* (Oliver), the Mediterranean flour moth, *Anagasta kuehniella* (Zeller), and the cutworm *Agrotis c-nigrans* (L.). The largest adults emerged from the largest host, *A. c-nigrans*. This is a frequent phenomenon in parasitoids (Holdaway & Smith 1933, Arthur & Wylie 1959, Klomp & Teerink 1962, Jackson 1968, Kishi 1970, Assem 1971, Sandlan 1979, Charnov et al. 1981, Opp & Luck 1986). For many parasitoid species, host size also influences sex ratio such that females tend to emerge from large hosts and males from small hosts (Chewyreu 1913, Holdaway & Smith 1933, Brunson 1937, Clausen 1939, Assem 1971, Sandlan 1979, Charnov et al. 1981, Jones 1982, Opp & Luck 1986).

The braconid *Bracon mellitor* Say, an arrhenotokous species, is a solitary ectoparasitoid of the boll weevil, *Anthonomus grandis grandis* Boheman. Females of this parasitoid usually lay eggs on third-instar boll weevils. Normally, the female oviposits only one egg on or near the host (Adams et al. 1969, McGovern & Cross 1974). The female stings and paralyzes the host before oviposition, after which the host dies (Folsom 1936, Adams et al. 1969, McGovern & Cross 1974). Host feeding by *B. mellitor* adult females was observed by O'Neil (1980). He also deter-

mined that females can discriminate to a certain degree between hosts previously parasitized by other females. Many Coleoptera and Lepidoptera are reported to be hosts of this parasitoid in native vegetation. Tillman & Cate (1989) published a list of all recorded hosts of this parasitoid. From 1981 to 1983, a study of native hosts of *B. mellitor* in central Texas was conducted; a wide variety of host species of differing sizes were collected (Tillman & Cate 1989). Larger parasitoids and more females emerged from the larger field-collected hosts than from smaller hosts, suggesting a possible influence of host size on adult progeny size and sex ratio (Tillman 1985). Based on these preliminary findings, we conducted laboratory studies to define better the effect of host size on adult parasitoid size and sex ratio.

## Materials and Methods

**Source of Hosts and Wasps.** A colony of *B. mellitor* was maintained in the laboratory in a 38.7-cm<sup>3</sup> Plexiglas sleeve cage at 26-29°C, 70-80% RH, and a photoperiod of 12:12 (L:D) h. Adult parasitoids were fed a solution of honey and water (1:1). This colony originated from individuals collected in cotton squares at Weslaco, TX, in 1981. Adult parasitoids were exposed to boll weevil larvae obtained from the GAST Rearing Facility at Starkville, MS. Boll weevil larvae were held individually in enclosed parafilm cells (Cate 1987). Parasitized hosts were held for adult emergence in a 946-ml cardboard carton.

**Host Size and Parasitoid Adult Size.** Experiment 1 was conducted to study the effect of host size on *B. mellitor* adult size. In this experiment, 200 boll weevil larvae, ranging from 1.1 to 50.0

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mg in weight, were simultaneously exposed to females of the *B. mellitor* colony for 4 h. Boll weevil larvae were weighed, then randomly distributed in parafilm cells. Larval weight was used as the measure of host size. Each *B. mellitor* egg, together with its host, was then placed into a well (8 by 15 mm) of a plastic-tissue pressure plate with 96 wells. Resulting adult parasitoids were killed by freezing 1 d after emergence. Sex of the individuals was then determined. Dead *B. mellitor* adults were weighed after being vacuumed and dried for 7 d in a Bel-Art plastic vacuum desiccator (Bel-Art Products, Pequannock, NJ) containing silica gel. Adult weight was used as the measure of adult parasitoid size. Host remains also were weighed after being vacuumed and dried.

**Host Size and Sex Ratio.** Experiment 2 was conducted to investigate the ability of a *B. mellitor* female to adjust sex ratio according to host size. A parafilm sheet containing 50 each of small (>1.0 mg and ≤12.0 mg), medium (>12.0 mg and ≤24.0 mg), and large (>24.0 mg and ≤48.0 mg) third-instar boll weevils was placed in the *B. mellitor* colony for 4 h. Eggs oviposited on small boll weevil larvae were transferred to recently paralyzed large third instars (without eggs) to avoid mortality from insufficient host food (there were no transfer effects because none of the immatures died). Each egg and its host was then placed in a developmental well as above. Sex of the eggs was ascertained upon emergence of the adults.

*Bracon mellitor* females normally do not oviposit on small third-instar boll weevils in cotton squares. To determine the ability of this parasitoid to produce female offspring on a small host species, 13 larvae of the weevil *Anthonomus signatus* Say were exposed to five mated *B. mellitor* females. The weevil larvae were collected from the host plant *Rubus trivialis* Michaux. Fully grown last instars of *A. signatus* are much smaller (2.0–2.7 mm long) than fully grown third-instar boll weevils (5.6–8.1 mm long) (Ahmad & Burke 1972). These *A. signatus* weevils were exposed to female parasitoids for 24 h. Parasitized hosts were held for adult emergence in individual petri dishes. The sex of the progeny was determined upon emergence.

**Parasitoid Adult Size and Longevity and Fecundity.** Experiment 3 was conducted to determine the effect of adult *B. mellitor* female size on longevity and fecundity. In this experiment, 18 females of varying sizes (ranging from 0.2 to 1.1 mg in weight) were allowed to oviposit on boll weevil larvae throughout their lifetimes. Upon emergence, adult females were placed individually in plastic petri dishes with four females for 4 d to ensure mating. A sufficient supply of honey and distilled water was maintained in each petri dish. Females were exposed to hosts 2 d after emergence every other day until

they died. Ten large boll weevil larvae were used as hosts. All exposures of females to hosts were for 24 h. The numbers of progeny emerging from these hosts and the longevity of parent females were recorded. Dead females were weighed individually after drying in a Bel-Art plastic vacuum desiccator containing silica gel.

**Data Analysis.** Regression (SAS Institute 1984) assessed the relationship of host weight and *B. mellitor* weight, amount of host consumed and *B. mellitor* weight, and host weight and amount of host consumed. Student's *t* test was used to compare mean male and female adult weight and mean host consumption for males and females.

An estimate of the amount of host consumed by an immature parasitoid was calculated by subtracting the weight of the host remains from the initial weight of the boll weevil larva. This equation does not account for the water lost during development of the immature parasitoid or for water removed by vacuuming the host remains (although the host remains were hard and "dry" before vacuuming and drying). Therefore, the value calculated for host consumption is only an estimate of amount of host consumed. It was not possible to determine the dry weight of a larva, then expect a parasitoid to develop on it, nor could amount of water loss be determined during development. Thus the value we calculated is the best estimate available for determining if any relationship occurred between amount of host consumed and *B. mellitor* adult weight.

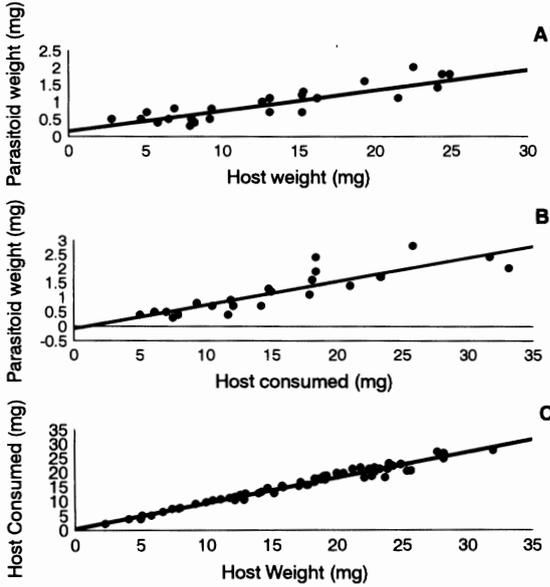
For experiment 2, the null hypothesis was that the sex ratio was not different from 1:1 (male/female) for each host size category.  $\chi^2$  analyses (SAS Institute 1984) were used to test this hypothesis.

Regression (SAS Institute 1984) assessed the relationship of *B. mellitor* adult female weight and female longevity (days), *B. mellitor* adult female weight and total number of progeny per female (fecundity), and adult female longevity and *B. mellitor* fecundity.

## Results and Discussion

Using the data from experiment 1, a linear relationship was detected between host weight and adult parasitoid weight (Fig. 1A) ( $F = 81.4$ ;  $df = 1$  [model], 22 [residual];  $Y = 0.06X + 0.11$ ;  $r^2 = 0.79$ ;  $P = 0.0001$ ). It can be concluded from this analysis that larger adult parasitoids were able to develop on larger hosts. This relationship between host size and adult parasitoid size occurs with other parasitoid species (Holdaway & Smith 1933; Arthur & Wylie 1959, Klomp & Teerink 1962, Jackson 1968, Kishi 1970, Assem 1971, Sandlan 1979, Charnov et al. 1981, Opp & Luck 1986).

Linear relationships were detected between the amount of host consumed and adult parasitoid weight (Fig. 1B) ( $F = 64.2$ ;  $df = 1$  [model],



**Fig. 1.** (A) Regression of host weight (x axis) and parasitoid weight (y axis), where  $Y = 0.06X + 0.11$ ,  $r^2 = 0.79$ ,  $P = 0.0001$ . (B) Regression of host consumed (x axis) and parasitoid weight (y axis) where  $Y = 0.08X - 0.08$ ,  $r^2 = 0.75$ ,  $P = 0.0001$ . (C) Regression of host weight (x axis) and host consumed (y axis) where  $Y = 0.88X + 0.49$ ,  $r^2 = 0.97$ ,  $P = 0.0001$ .

21 [residual];  $y = 0.08x - 0.08$ ;  $r^2 = 0.75$ ;  $P = 0.0001$  and between host weight and the amount of host consumed (Fig. 1C) ( $F = 2123.6$ ;  $df = 1$  [model], 67 [residual];  $y = 0.88x + 0.49$ ;  $r^2 = 0.97$ ;  $P = 0.0001$ ). It can be concluded from these analyses that immature parasitoids consumed greater amounts of host food on larger hosts and that the resulting adults were larger.

Female adults generally weighed more than male adults (Table 1). These females also consumed more of the host than the males (Table 1). Thus, females were more expensive to produce than males.

The number of male and female eggs oviposited on larvae in each of the three size categories of experiment 2 are shown in Table 2. If females do not preferentially oviposit more male than female eggs, the sex ratio of progeny should be 1:1 (male/female). The sex ratio of progeny from medium and large larvae was no different from a

**Table 2.** Number of male and female *B. mellitor* progeny from small, medium, and large boll weevil larvae

Host size category	No. hosts exposed	No. hosts parasitized	No. female progeny	No. male progeny	$\chi^2$
Small	50	50	41	9	20.48 <sup>a</sup>
Medium	50	30	16	14	0.14
Large	50	48	25	23	0.08

<sup>a</sup> Sex ratio significantly different from 1:1 (male/female) at  $P = 0.05$  ( $\chi^2$  analysis [SAS Institute 1984]).

1:1 (male/female) ratio. However, the sex ratio of progeny from small larvae was different from an expected ratio of 1:1 (male/female). Thus, parent females preferentially oviposited more male eggs on small larvae.

Exposure of *A. signatus* to *B. mellitor* females resulted in the development of two female and six male parasitoids. It was concluded that mated females of this parasitoid will oviposit on small hosts when given no alternative and that both sexes can be produced thereon. This can be important for survival of this species in native vegetation, especially when no other hosts are available. This does occur in central Texas during the late summer-early fall when only the very small host *Anthonomus heterothecae* Pierce exists in the heads of the composite *Heterotheca latifolia* Buckley (Tillman 1985). This plant species is important to the population survival of *B. mellitor* because the parasitoid overwinters in this plant (Tillman 1985). Because both males and females can develop and overwinter on weevil larvae in this plant, there is a high probability that the population can mate and begin growing again upon adult emergence in the spring.

Using the data from experiment 3, linear relationships were detected between *B. mellitor* adult female weight and longevity (days) ( $F = 16.39$ ;  $df = 1$  [model],  $df = 16$  [residual];  $Y = 47.76X + 14.21$ ;  $r^2 = 0.51$ ;  $P = 0.0009$ ), between female weight and fecundity (total number of progeny per female) ( $F = 20.1$ ;  $df = 1$  [model],  $df = 16$  [residual];  $Y = 119.12X + 2.28$ ;  $r^2 = 0.56$ ;  $P = 0.0004$ ) and between longevity and fecundity ( $F = 97.32$ ;  $df = 1$  [model],  $df = 16$  [residual];  $Y = 2.2X - 21.17$ ;  $r^2 = 0.86$ ;  $P = 0.0001$ ) (Fig. 2A, B, and C, respectively). It was concluded from these results that larger females could live longer, and by living longer, they were able to produce more offspring over their lifetimes than smaller females. Thus size of the host on which an immature *B. mellitor* developed could indirectly affect fecundity of a resulting adult female. This relationship between female size and fecundity exists for *Aphytis lingnanensis* Compere and *A. melinus* DeBach (Opp & Luck 1986).

The tendency of *B. mellitor* to oviposit more female eggs on large hosts than on small ones indicates they were able to regulate the sex of

**Table 1.** Male and female adult weights and amount of host consumed by males and females of *B. mellitor*

	Sex	n	Mean $\pm$ SE	Min	Max	t
Adult wt, mg	♂	20	1.43 $\pm$ 0.43	0.9	2.1	7.34 <sup>a</sup>
	♀	20	3.6 $\pm$ 0.95	1.8	4.9	—
Amount of host consumed, mg	♂	20	16.37 $\pm$ 7.59	2.2	35.0	4.89 <sup>a</sup>
	♀	20	22.02 $\pm$ 8.55	6.3	42.8	—

<sup>a</sup> Means significantly different at  $P = 0.05$  (Student's *t* test).

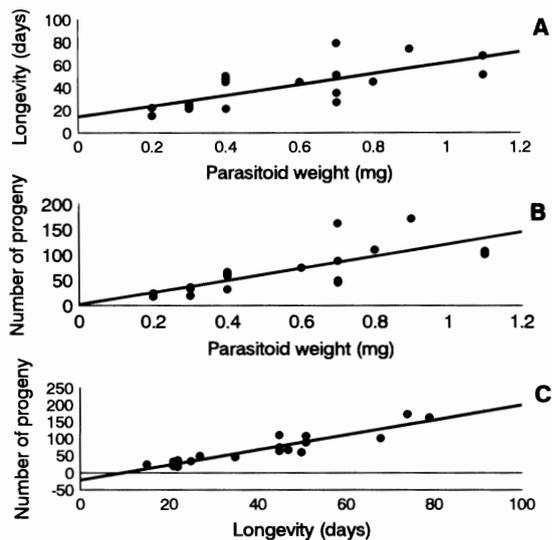


Fig. 2. (A) Regression of parasitoid weight (x axis) and longevity (y axis) where  $Y = 47.76X + 14.21$ ,  $r^2 = 0.51$ ,  $P = 0.0009$ . (B) Regression of parasitoid weight (x axis) and total number of progeny per female (y axis) where  $Y = 119.12X + 2.28$ ,  $r^2 = 0.56$ ,  $P = 0.0004$ . (C) Regression of longevity (x axis) and total number of progeny per female (y axis) where  $Y = 2.2X - 21.17$ ,  $r^2 = 0.86$ ,  $P = 0.0001$ .

their eggs in response to the size of the boll weevil larvae. Chewyreu (1913) proposed that females of *Pimpla* spp. selectively oviposited more fertilized eggs on large hosts than on small ones. This theory was supported by Brunson (1937), who demonstrated experimentally that more female eggs of *Tiphia popilliavora* Rohwer were oviposited on third instars of its host than on the smaller second instars. More recently, Jones (1982) has shown that with *Heterospilus prosopidus* Viereck, another braconid species, females often oviposited male eggs on small larvae and female eggs on the larger larvae of its host. The sex ratio differences in this case were caused by preferential oviposition. As with *H. prosopidus*, a *B. mellitor* female can assess the size of a host larva and control the sex of its egg accordingly. Female eggs are oviposited on larger hosts. The female immatures developing on these larger hosts develop into larger females, which in turn produce greater numbers of progeny. Hosts, therefore, are used more efficiently than if male and female eggs were oviposited randomly on hosts of varying sizes.

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