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Effect of host density on egg dispersion and the sex ratio of progeny of *Bracon hebetor* (Hymenoptera: Braconidae)

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Abstract

Egg dispersion and the sex ratio of progeny were studied in relation to the host density of the parasitoid, *Bracon hebetor* Say, infesting larvae of *Plodia interpunctella* (Hübner). Females appeared to allocate eggs in relation to host density to avoid laying more eggs than could complete development on a host. The dispersion pattern of the parasitoid ovipositions among hosts was influenced by host density. Multiple visitations and ovipositions by females on hosts caused a highly aggregated pattern at low-host densities. Hatch rate of eggs decreased as the number of eggs on a host increased. Females seemed to regulate progeny sex ratio (male/total) based on the number of eggs on the hosts and the clutch size of the hosts they encountered. However, the overall progeny sex ratio remained at approximately 0.5 regardless of host density, probably because the allocation of eggs was related to host density. © 2003 Elsevier Science Ltd. All rights reserved.

Keywords: *Bracon hebetor*; Egg dispersion; Host density; *Plodia interpunctella*; Sex ratio

1. Introduction

Some gregarious parasitoids can optimise their reproductive potential by regulating the number of eggs on a host (clutch size) and progeny sex ratio (see van Alpen and Jervis, 1996; Godfray, 1994; Waage, 1986).

Many reports suggest that parasitoids regulate clutch size based on the host size or host quality. Le Masurier (1987), for instance, showed a positive relationship between host size and clutch size in 52 species of *Apanteles*. *Trichogramma embryophagum* (Hartig) laid more eggs on larger hosts

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than on smaller ones (Klomp and Teerink, 1967). *Bracon hebetor* Say attacking larvae of *Plodia interpunctella* (Hübner) also showed similar oviposition behaviour related to host size (Taylor, 1988b) depositing more eggs on larger hosts than smaller ones. Presumably, the parasitoid is adjusting clutch size to the nutritional value of the host, thereby avoiding larval competition among progeny (Taylor, 1988a).

Parasitoids may also adjust clutch size based on the host density. *Cephalonomia gallicola* (Ashmead), a parasitoid of *Lasioderma serricorne* (F.), laid more eggs on a host when the hosts were rarely encountered (Kearns, 1934). Ulyett (1945) reported that *B. hebetor* regulates allocation of eggs among hosts by decreasing the number of eggs laid on a host as host density increases (see also Doult, 1959; Hagstrum and Smittle, 1977). Waage (1986) and Charnov and Skinner (1988) discussed the relationship between the clutch size and frequency of host being encountered based on optimization theory, suggesting that clutch size of a parasitoid should decrease as host density increases.

Theoretical models proposed to explain observed changes in the progeny sex ratio (male/total) of gregarious parasitoids focus on female bias. The “local mate competition model” (LMC) predicts that the optimum progeny sex ratio of inbreeding parasitoids can be described as a function of the number of females colonizing the patch (Hamilton, 1967); thus, optimum sex ratio is $(n - 1)/(1 + g)n$, where n is the number of females colonizing the patch and g is the differential genetic relatedness ($g = 1$ and 2 under complete outbreeding and inbreeding, respectively) (Werren, 1987). Under this model, sex ratio will be highly female biased when only a few females colonize a patch. However, *B. hebetor* is an outbreeding species, and previous studies have suggested that the female biased sex ratio of the parasitoid cannot be explained by LMC, but rather by (1) constrained oviposition of females, (2) ovicide, or (3) differential dispersal of males and females (Antolin et al., 1995; Ode et al., 1996, 1997, 1998).

The biology of *B. hebetor* has been intensively studied because of its suitability as a model organism since it is easy to rear in the laboratory and also because it has potential as a biological control agent of stored product moths (e.g., Benson, 1973; Brower and Press, 1990; Hagstrum and Smittle, 1977; Nikam and Pawar, 1993; Reinert and King, 1971; Ohh, 1993; Rotary and Gerling, 1973; Taylor, 1988a, b; Yu et al., 1999).

When parasitoids adjust clutch size to the host density, they could also regulate progeny sex ratio and clutch size to maximize overall fitness for a given host density. However, the question of whether individual female parasitoids could regulate the sex ratio of their own progeny in relation to the number of eggs she lays on a host has rarely been considered. This study was conducted to elucidate the relationship between clutch size, sex ratio and host density, using the gregarious larval parasitoid, *B. hebetor* attacking *P. interpunctella*. We ask the question: does host density influence both clutch size and overall sex ratio?

2. Materials and methods

2.1. Experimental conditions

The test insects were cultured and the experiments were carried out at $28 \pm 0.5^\circ\text{C}$ and 70–75% r.h. with a photoperiod of 16:8 (L:D).

The stock culture of *P. interpunctella* originated from infested dried vegetables stored in a warehouse located in Taegu, Korea in 1994 and has been maintained on dried green bok choy, *Brassica campestris* L. ssp. *chinensis* Jusl. in the Laboratory of Population Ecology at Korea University. For the present experiments, moths 1–2 d old were collected from the stock culture and held in 500 ml beakers filled with dried green bok choy for 24 h for oviposition. The resulting fifth instar larvae were used as hosts for *B. hebetor*. The mean head capsule width (\pm s.d.) and weight (\pm s.d.) of the fifth instar used were 1.14 ± 0.027 mm and 0.017 ± 0.003 mg, respectively.

B. hebetor was collected from a stock culture of *P. interpunctella* in 1996 and has also been maintained on *P. interpunctella* infesting dried green bok choy. Fifteen *P. interpunctella* fifth instar larvae were introduced into a Petri dish (diameter 90 mm) containing 10 g of dried green bok choy and allowed to settle for 2 h. One pair (female and male) of *B. hebetor* <24 h old was introduced into the Petri dish and allowed to attack the hosts for 48 h and the resulting adult parasitoids were used in the experiments.

2.2. Experimental procedure

One, 2, 4, 8, 16 or 32 fifth instar *P. interpunctella* were introduced into a Petri dish (diameter 90 mm) containing 10 g of dried green bok choy and allowed to settle for 2 h. One pair of the parasitoids (female and male <24 h) was introduced and allowed to attack the hosts for 24 h. The number of eggs laid on each host was recorded, then parasitised hosts were incubated individually. The number of parasitoids hatching and emerging per host, and the progeny sex ratio per host, were recorded daily. Each treatment was replicated more than 40 times.

The dispersion pattern of parasitoid eggs among the hosts was estimated by the Green index defined as: $C_x = [(s^2/m) - 1]/(\Sigma x - 1)$, where s^2 , m and Σx are variance, mean and total number of eggs laid, respectively (Green, 1966). This index was reported to be least correlated with the mean (Myers, 1978). Values of C_x may vary from $-1/(\Sigma x - 1)$ through 0 to +1 as the dispersion pattern ranges from perfectly uniform through random to perfect clumping.

2.3. Data analysis

The relationship between progeny sex ratio and the number of *B. hebetor* eggs per host and related factors was examined by analysis of variance (ANOVA) and correlation analysis. The data were transformed into $\arcsin\sqrt{x}$ before statistical analysis as necessary. The means were separated by using the Fisher least significant difference (LSD) ($\alpha = 0.05$) (SAS Institute, 1990).

3. Results

The number of hosts attacked (paralysed and oviposited hosts) increased with host density in the manner of a type 2 functional response (Holling, 1959), from 1.0 ± 0.0 at the density of 1 to 26.75 ± 3.20 at the density of 32 (Fig. 1a). The total number of eggs per female *B. hebetor* per day (mean \pm s.e.) increased from 12.64 ± 0.31 to 29.35 ± 0.80 with the host density increasing from 1 to 16 and then decreased to 25.03 ± 0.65 when the density increased further to 32 ($F = 24.58$; $df = 5, 240$; $P < 0.0001$; $LSD = 3.33$) (Fig. 1b), suggesting a dome-shaped response. Although the

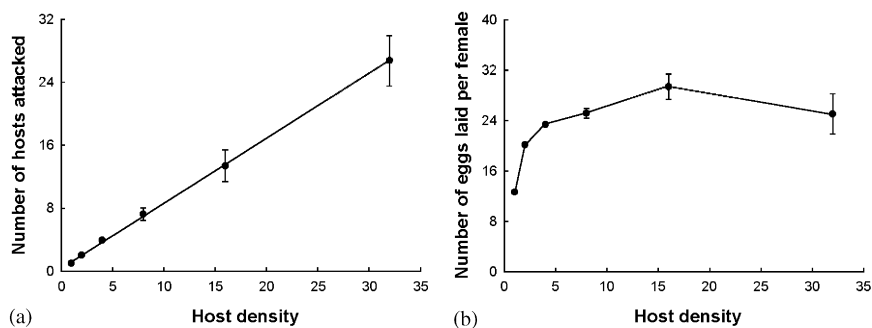


Fig. 1. The number of hosts parasitised (N_a) (a) and number of eggs laid per female (b) in relation to the host density (N_i). The vertical lines indicate standard error of the mean. The functional response in a was fitted to Holling's disk equation as: $N_a = (0.894N_i)/(1 + 0.894 \times 0.003N_i)$ ($r^2 = 0.990$).

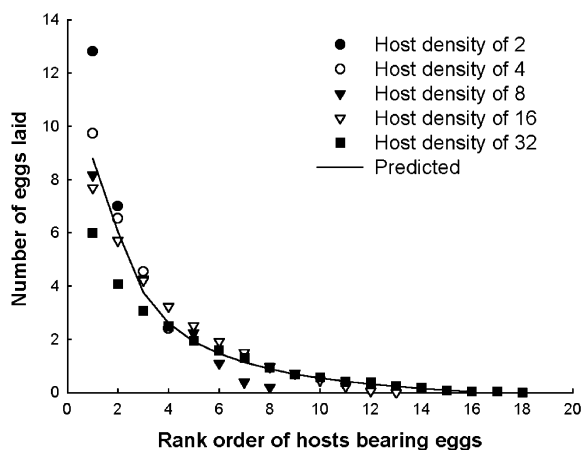


Fig. 2. Relationship between rank order of hosts bearing eggs of *Bracon hebetor* and number of eggs laid on the host at five different host densities.

female parasitoids paralysed most available hosts, they laid eggs on a maximum of 16 paralysed hosts per day, leaving some hosts without eggs (Fig. 2). Fig. 2 shows the relationship between the number of eggs on a host and the rank order of hosts bearing eggs of the parasitoid. The number of eggs on a host could be described as a function of the host rank order: $y = -0.83 + 13.75/x$ ($F = 81.91$; $df = 1, 16$; $P < 0.00001$; $r^2 = 0.84$), where y is the number of eggs on the host of the rank order (x). The hosts which bear highest numbers of parasitoid eggs among the hosts exposed in a treatment (density), constitute the host of rank 1 and so on.

The dispersion pattern of the parasitoid eggs among the hosts was clumped, regardless of host density: Green Index (C_x) values were statistically significant from zero (based on 95% confidence intervals). Except for the value at the density of 2, all the values were estimated to be similar and ranged from 0.08 ± 0.002 to 0.10 ± 0.010 , suggesting that the dispersion of eggs is approximately constant. At a host density of 2, the value was estimated to be higher than other values (0.18 ± 0.05), but not statistically different (Fig. 3a). The number of observed eggs on the host of

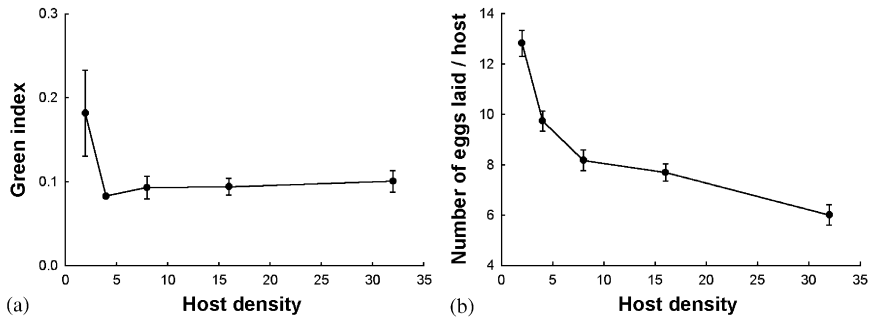


Fig. 3. Dispersion of the parasitoid eggs on hosts. Dispersion index of egg density of *Bracon hebetor* (a), and changes in the number of eggs on the host of rank 1 in relation to host density (b). The vertical lines indicate standard errors of the mean.

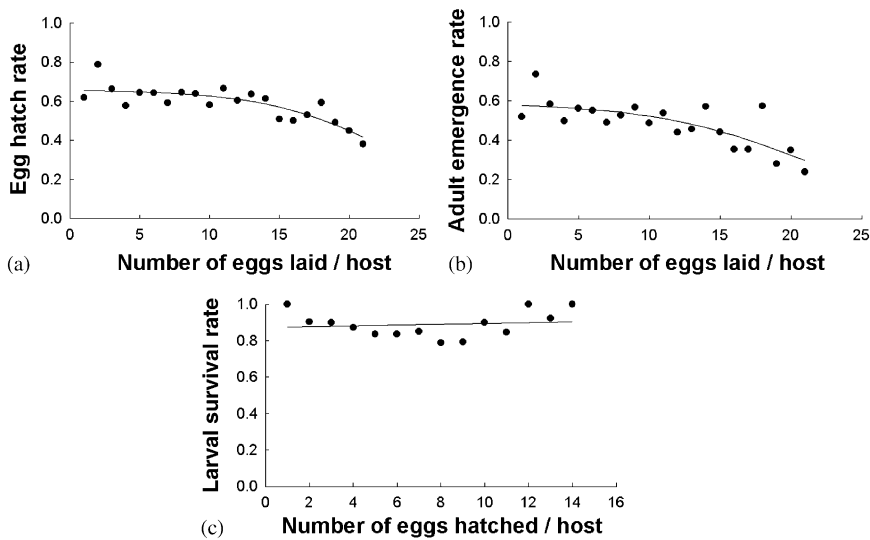


Fig. 4. Egg hatch rate (a), adult emergence rate (b), and survival rate in larval stage (c) of *Bracon hebetor* in relation to the number of eggs on a host. The circles and lines indicate the observed and estimated values, respectively (see text).

rank 1 decreased from 12.82 ± 0.51 to 6.00 ± 0.41 ($F = 35.27$; $df = 5, 222$; $P < 0.0001$) as the host density increased from 2 to 32, indicating that at low host densities, the parasitoids made multiple attacks on individual hosts (Fig. 3b). The high variance of the C_x value at the density of 2 reflected this phenomenon.

Both the hatch rate and the emergence rate of the parasitoids (mean \pm s.e.) decreased as the number of eggs laid per host increased from 1 to 21 (Fig. 4a and b). The relationships were calculated as $0.66 / (1 + \exp(0.22(NE - 23.39)))$ ($r^2 = 0.6514$) and $0.59 / (1 + \exp(0.18(NE - 21.07)))$ ($r^2 = 0.5416$) for egg hatch rate and adult emergence rate, respectively, where NE is the number of eggs laid. The correlation between the two rates was significant ($r = 0.92$; $df = 19$; $P < 0.01$), but the number of eggs hatched did not have any influence on larval survival rate (Fig. 4c).

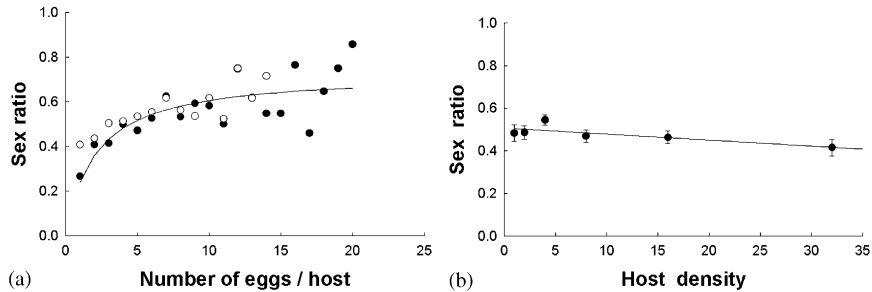


Fig. 5. Effects of the number of *Bracon hebetor* eggs per host (a) and host density (b) on the progeny sex ratio (male/total) of the parasitoid. The closed and open circles in a indicate the sex ratio based on the number of eggs laid (sex ratio/the number of eggs laid) and the number of eggs hatched (sex ratio/the number of eggs hatched), respectively. The vertical lines indicate standard error of the means.

The progeny sex ratio (male/total) increased as the number of eggs laid on a host increased (Fig. 5a) and was positively correlated with hatch rate ($r = 0.6233$; $df = 19$; $P < 0.01$) and emergence rate ($r = 0.6112$, $df = 19$; $P < 0.01$), but not with larval survival rate ($r = 0.1457$, $df = 19$; $P > 0.05$). It seemed that larval competition, which could result in density-dependent larval mortality, was not the major factor increasing the sex ratio with the number of eggs on a host (Fig. 5a). What is interesting is that the sex ratio based on the number of hatched larvae on an individual host was higher than that based on the number of eggs laid on an individual host (Fig. 5a).

4. Discussion

Although a female *B. hebetor* could lay more than 25 eggs per day (Fig. 1b), she laid an average of 12.6 eggs when only one host was exposed, suggesting that the parasitoid has a tendency to avoid laying more eggs than the host can support. Yu (1999) reported that immature mortality of *B. hebetor* increased abruptly when the number of eggs on a host (fifth larvae of *P. interpunctella*) was higher than about ten, similar to the mean number of eggs laid per female provided with one host. Benson (1973) also reported that larval mortality of *B. hebetor* parasitising *Cadra cautella* (Walker) increased abruptly when the number of eggs on a host exceeded approximately eight, suggesting a scramble-like competition between the larval parasitoids. Hagstrum and Smittle (1977) observed that *B. hebetor* preferred an unparasitised host for oviposition when given a choice between parasitised and unparasitised *C. cautella*.

The dome-shaped ovipositional response of the parasitoid (Fig. 1b) could be attributed to the parasitoid's characteristic ovipositional behaviour. Because *B. hebetor* paralyses the hosts encountered and then relocates the paralysed hosts for oviposition (Ullyett, 1945; Hagstrum and Smittle, 1977), the parasitoid would spend more time travelling among hosts as the host density increased. Consequently, the total time for oviposition could be decreased (Ullyett, 1945), which, in turn, would result in a decrease in the total number of eggs laid per female. We did not record the total transit time of the parasitoids in relation to the host density and thus could not present any clear evidence for the hypothesis. Nevertheless, the dome-shaped response did not result in a

dome-shaped relationship between the host density and the number of females emerged, which showed a typical type 2 response curve.

Taylor (1988b) reported that the total number of eggs laid by *B. hebetor* was independent of the host density, which was opposite to our findings. This was probably due to differences in strains or experimental procedure between the two studies. Other authors (Doutt, 1959; Benson, 1973) have observed differences in the parasitisation behaviour between strains of *B. hebetor*.

The fact that egg dispersion was influenced by host density (Fig. 3) suggested that the probability of a host being oviposited repeatedly became lower with an increase in the host density. The apparent egg dispersion pattern became near random at high host densities. Typically, a female parasitoid that encounters a paralysed host will lay 1–7 eggs and then locate randomly another paralysed host (Na et al., personal observations; see also Benson, 1973). Therefore, the number of eggs on the host of rank 1 decreased with the host density. When the host density is low, repeated oviposition on a host resulted in eggs accumulating on the individual host and a highly aggregated dispersion pattern of eggs.

What is interesting is that the number of eggs on a host could be described as a function of the host rank order of the host bearing parasitoid eggs (Fig. 2), which suggested that the number and dispersion of eggs among the hosts could be reasonably estimated in relation to host density. Being synovigenic (Jervis et al., 1994), the parasitoid will have a limited number of mature eggs to be laid at the time of host attack. Therefore, *B. hebetor* oviposition behaviour could be caused by three factors: (1) laying 1–7 eggs per host according to the egg load of the parasitoid (see also Ulyyett, 1945), (2) the limited number of matured eggs and (3) the limited time for the eggs to mature which results in egg depletion. The fact that the numbers of eggs on the hosts of rank 1 were rather similar, except at extremely low host densities, supports this consideration (Fig. 3).

Rotary and Gerling (1973) suggested that differential mortality of females and males could result in male-biased sex ratio in *B. hebetor*, and that the progeny sex ratio (male/total) increased as the host/parasitoid ratio decreased (see also Benson, 1973). In the present study, we could not examine the initial sex ratio of the progeny on a host, and thus, not be certain whether the progeny sex ratio was regulated by ovipositing females (primary sex ratio) or differential larval mortality (secondary sex ratio). But the fact that emergence rate was not related to the number of hatched larvae (Fig. 4c) suggested that the effect of differential larval mortality might not be as likely as female regulation of sex ratio (see also Taylor, 1988a; Galloway and Grant, 1989). In such regulation, the female would not discriminate her own eggs from those of others. Moreover, the sex ratio shown in the case of one egg on a host being lower than that of one hatched larva on a host also suggested the regulation of progeny sex ratio by the ovipositing females (Fig. 5a). The resulting sex ratio showed clutch size-related features similar to that predicted by the LMC model, even though *B. hebetor* is an outbreeding species. The relationship is described by: $sr = (x - 1)/1.5x$, where sr is the sex ratio and x the number of eggs on a host, suggesting that sex ratio of *B. hebetor* changed from female bias to male bias as the number of eggs on a host increased.

Although the parasitoid regulates the progeny sex ratio on a host based on the total number of eggs, the overall progeny sex ratio (male/total) was not affected by host density (Fig. 5b). The parasitoid allocates eggs in relation to the host density so as to avoid laying more eggs that would trigger intense competition between the progeny. Because parasitoids regulate progeny sex ratio based also on the clutch size, the overall sex ratio should be stable.

Progeny sex ratio in other studies has been variable, ranging from 0.3 to 0.5 (Antolin and Strand, 1992; Nikam and Pawar, 1993; Ohh, 1993; Reinert and King, 1971; Rotary and Gerling, 1973). These studies suggest variation in the sex ratio can be due to differences in the strains of *B. hebetor*, the host species tested, host and parasitoid density tested or test arena (see Benson, 1973; Heimpel et al., 1997; Schöller, 2000), suggesting adaptability of the parasitoid to variable environments. But, further studies of the sex ratio are necessary with *B. hebetor* in different environments to elucidate the overall sex ratio of the parasitoid populations.

The parasitisation behaviour of *B. hebetor* suggested that it could optimise host exploitation by varying clutch size and the resulting progeny sex ratio with reference to the number of available hosts, so that the overall sex ratio might stabilise at about 0.5. If this is true, the host–parasitoid system could be regulated largely by the host-density-dependent allocation of the progeny of the parasitoid, which would result in a suppression of oviposition and low hatchability at low host density. Further, at high densities the paralysed hosts without parasitoid eggs could have important consequences for system dynamics (Jervis et al., 1994). Nickle and Hagstrum (1981) found also that providing *B. hebetor* with the paralysed hosts could increase the parasitoid's efficiency for controlling *E. cautella* on stored inshell peanuts. A long-term experiment in this context would elucidate the relationship more precisely.

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