Pakistan J. Zool., vol. 49(0), pp 000-000, 2017. DOI: http://dx.doi.org/10.17582/journal.pjz/2017.49..........

Effect of Host Size on Larval Competition of the Gregarious Parasitoid *Bracon hebetor* (Say.) (Hymenoptera: Braconidae)

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Article Information
Received 15 March 2016
Revised 8 November 2016
Accepted 29 January 2017
Available online

Authors' Contribution
SR performed experimental work. KA statistically analyzed the data. SA helped in collection of samples. MA helped in experimental work. AM and HS reared host-parasitoid culture. MT helped in experimental work and manuscript preparation. ZA wrote the article and supervised the work.

Key words
Bracon hebetor*, Larval competition, Egg density, Adult emergence, Sex ratio, *Galleria mellonella, Spodotera litura, ectoparasitoid.

ABSTRACT

The effect of size of two host species *Galleria mellonella* (Pyralidae: Lepidoptera) and *Spodotera litura* (Noctuidae: Lepidoptera) was studied on larval competition, survival and development of a gregarious ectoparasitoid *Bracon hebetor* (Say.) (Hymenoptera: Braconidae). The number of adults, sex ratio and size of emerging adults were recorded. Smaller and larger host species were used to determine the survival potential of the wasp. It was observed that maximum number of adult wasps emerged from the hosts *G. mellonlla* (95±2.30 (se) and *S. litura* (81±1.15 (se)) by placing the lowest number of wasp eggs (4 eggs per larvae) on the hosts larvae and minimum number of adult wasps was recorded from the hosts *G. mellonella* 44±1.15 (se), and *S. litura* (39±0.57 (se) by placing the highest number of wasp eggs (20 eggs per larvae) on the hosts larvae. Likewise mean width of the head of adult wasp emerged from *G. mellonella was* 0.60 mm and *S.litura* 0.50 mm when 4 eggs were placed on each host larvae, whereas mean head width of developing wasp adults were reduced when 20 eggs had been placed. It may be speculated that due to less availability of nutrient resources, head size of the developing wasp was reduced. It may be concluded that intensity of competition among larvae of *B. hebetor* affects adult size and development that is directly proportional to the quantity of resources available.

INTRODUCTION

Insect parasitoid progeny vigor depends on different factors such as host size, species and age. Host size is the main quality parameter studied for fitness of parasitoid progeny. Many studies have been conducted on larval competition among developing larvae of parasitoid that influences their fitness as well as survival potential when single host larva is the only food source for parasitoid development from egg to adulthood. As a result, both the number of other larvae with which a host is shared and host characteristics such as size, stage or species, can affect the survival or growth of the parasitoid larvae (Vinson and Iwantsch, 1980; Charnov *et al*., 1981). In general, large hosts contain more resources and in terms of parasitoid fitness are considered to be qualitatively superior. Furthermore, the intensity of larval competition may often depend on the quantity and quality of the host as food resource (Shiga and Nakanishi, 1968; Rabinovich, 1971; Bouletreau, 1977; Takagi, 1985). Host quality influences main components of parasitoid fitness such as survival until they reached adulthood, parasitoid development time and parasitoid size and fecundity of adults (Godfray, 1994).

The body size of adult parasitoids is positively correlated with many other fitness components, such as adult longevity and fecundity for females and mating ability for males (Visser, 1994; Kazmer and Luck, 1995; West *et al*., 1996; Ellers *et al*., 1998; Otto and Mackauer, 1998; Ueno, 1998; Eijs and Van Alphen, 1999; Sagarra *et al*., 2001; Ellers and Jervis, 2003; Jervis *et al*., 2003). Larger female parasitoids often have higher mature egg load, and live longer due to larger energy reserves than smaller females (Eijs and van Alphen, 1999; Sagarra *et al*., 2001). Therefore, many studies take body size as the easiest proxy for real fitness in parasitoids (Roitberg *et al*., 2001).

Bracon hebetor is a gregarious larval ecto-parasitoid and due to its rapid rate of growth and development is regarded an important biological control agent for numerous lepidopterous pests (Keever *et al*., 1985; Prozell and Scholler, 1998; Hentz *et al*., 1998). *Galleria mellonella* and *spodoptera litura* are ubiquitous pests of honey bee colonies (Paddock, 1918; Williams, 1997; Gillard, 2009; Ellis *et al*., 2013) and many economically

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0030-9923/2017/0004-0001 $ 9.00/0

important crops *e.g,* tobacco, pulses, bendy, cotton, caster, chilli and groundnuts (Armes *et al*., 1997; Niranjankumar and Regupathy, 2001), respectively.

Generally parasitoid development from egg to adult emergence, sex ratio and longevity parameters are directly influenced by host size (Traynor and Mayhew, 2005; Liu and Sun, 2011). Milonas (2005) reported interaction between *B. hebetor* larval competition and host size in *Adoxophyes orana, Plodia interpunctella* and *Lobesia botrana*. Little is known about the relationship between host size and parasitoid fitness in *G. mellonella* and *S. litura*. For successful biological control of these two pests, it is important to study the adult emergence of parasitoid on these two voracious pests. This project was planned to study availability of nutritional resources of three different weight classes of these two species (*G. mellonella* and *S. litura*) for parasitoid offspring emergence.

MATERIALS AND METHODS

Rearing of hosts larvae

The larvae, pupae and adults of the host, greater wax moth, *G. mellonella* were collected from the infested bee hives located at the main campus of University of Agriculture, Faisalabad, Pakistan. Pairs of adult male and female *G. mellonella* were placed in the jars (having fresh wax) for mating. After 24 h mating period female starts egg lying as egg firing by extruding its ovipositor and flattering wings. Laid eggs were placed in incubator for hatching under controlled conditions. The whole culture having eggs, larvae, pupae and adults were maintained at 27±1°C temperature, 65±5% relative humidity (RH) and constantly dark environment.

The second host *Spodoptera litura* was collected from a horticultural area of Agriculture University Faisalabad. Specimens were collected from different crops like wheat, berseem, cauliflower, cabbage and tomato crop, for experimental purpose. They were not reared in the laboratory.

Rearing of B. hebetor

The ectoparasitic larval parasitic wasp *B. hebetor* (Say) (Hymenoptera: Braconidae) was reared in the laboratory on the 5th instar larvae of *G. mellonella* by following a slightly modified approach as described by Anam *et al*. (2015). The adults of the parasitoid, *B. hebetor* were collected directly from the berseem crop, *Trifolim alexandrium* L., located at the campus of the University of Agriculture, Faisalabad, Pakistan. The collected parasitoids were identified on the basis of morphological characters by making comparison with the available literature. The parasitoid culture was also maintained in glass jars, at 27±1°C, 65±5% relative humidity (RH) and 18 h light/6 h dark photoperiod.

Experiment procedure

On first day of the experiment three host classes based on weight, of both host larvae species were made as follows: for *G. mellonella* G1=85-95 mg, G2= 140-150 mg, G3= 230-240 mg and for *S. litura* S1=300-500 mg, S2=600-800 mg, S3=900-1000 mg. In each class five larvae were selected and placed in separate petri-dish. The eggs of the parasitoid were obtained by releasing freshly emerged 24 h pre-mated *B. hebetor* male and female pair on each larva of the *G. mellonella* and *S. litura* placed in petri-dish as stated above. The females of the parasitoid started to parasitize the larvae of the host by first injecting a small quantity of paralyzing venom in to mature (5th instar) larvae of the host before depositing up to twenty eggs on the outside of the host. Twenty four hours post-parasitism the egg density on each larva of both hosts was manipulated by removing and shifting eggs in range of 4, 8, 12, 16, 20 eggs per larva. Since the natural clustering of eggs had been shown to affect larval competition (Benson, 1973). I retained this as much as possible by transferring entire clusters of eggs. The eggs hatched within 2-3 days into transparent larvae, which were directly feed on the body of the host larvae. After completing their development period, larvae started to pupate outside the body of the host. Then data regarding competition effects on adult emergence and sex ratio was recorded on different host size and species on daily basis.

The percentage of sex ratio was calculated by following formula:

$$\%\ of\ female\ (or\ male)\ emergence = \frac{No.\ of\ female\ (or\ male)\ merged}{Total\ adult\ emergence} \times 100$$

Statistical analysis

The data was statistically analyzed by using Analytical Software, 2003 (Statistix 8.1) in factorial design and means were separated by using least significant difference test at significance level of P<0.05.

RESULTS

Adult emergence of B. hebetor *from the hosts*

Table I shows number of adult emerged at three different larval weights (85-95, 140-150 and 230-240 mg). Parasitoid emergence was significantly affected by egg density when reared on *G. mellonella* but this did not appear on *S. litura* larvae. Parasitoid adult emergence decreased as the egg density increased. The data shows that maximum number of adult emergence (95±2.30 (se), LSD test, p<0.05) was recorded at higher larval weight

(230-240 mg) where minimum eggs were placed (4 eggs). In contrast, when 20 eggs were placed at large host size (230-240 mg), the number of adults (69±1.15) emerged was lower. Effect of egg density on adult emergence decreased from 81 at the lowest density (4 eggs) to 64 at the highest density (20 eggs) on *S. litura* host weight (900-1000 mg) (Table II). Number of adult emergence on *G. mellonella* host weight (85-95 mg) was less (58±1.15) (se) and 44±1.15 (se) on 4 and 20 eggs placed, respectively as compared to large size host. Similarly, the effects of density on number of adult emergence was more intense on *S. litura* host weight (300-500 mg) and it decreased from 52 at the lowest density to 39 at the highest density used in this experiment (Table II). Parasitoid adult emergence was higher at the large size than at medium or small sized larvae for each host. Moreover, the interaction effects (egg density and host weight) was significant on the adult emergence (ANOVA, df=8, F=12.58, P<0.05) occurred for *G. mellonella* species. While the interaction of egg×weight is non-significant (ANOVA, df=8, F=0.49, P<0.05) occurred for *S. litura*. However, adult emergence was affected by host species and host size. On average more adult parasitoids were emerged when reared on *G. mellonella* than on *S. litura*.

Sex ratio of B. hebetor *emerging from the host*

The data regarding sex ratio was recorded by placing different number of eggs on different host size larvae. Female ratio was significantly affected by egg density when reared on both host species, female ratio decreased as the egg density increased. Table I showed that female percentage (61±0.57 (se), LSD test, p<0.05) was high at larger weight (230-240 mg) on *G. mellonella* larvae, where minimum eggs were placed (4 eggs). While, on same size host where 20 eggs were placed, minimum percentage of female ratio (43±0.57) was emerged. The effect of egg density on female percentage (31.2%) was more on *S. litura* higher weight (900-1000 mg) at the lowest density where as 16.7% at the highest density (Table II). Female emergence percentage on *G. mellonella* smaller weight host (85-95 mg) was 45±0.00 and 30±0.57 where 4 and 20 eggs placed respectively. Similarly, at lowest density (4 eggs) female percentage was more (20%) on *S. litura* on smaller host weight (300-500 mg) followed by 8% was recorded on highest density on the same weight respectively (Table II). Our results explained that as weight of larvae increased female ratio was also increased. On average more female parasitoids emerged when reared on *G. mellonella* than on *S. litura*.

Male emergence

The data regarding sex ratio was recorded by placing different number of eggs on different host size larvae. The data given in Table I show that male percentage (70±0.57, LSD test, p<0.05) was high at smaller weight (85-95 mg) larvae, where maximum eggs were placed (20 eggs).

Table I.- Effect of egg density of *B. hebetor* and host size of *Galleria mellonella* larvae on the adult emergence and sex ratio of *B. hebetor*.

Eggs / host	Weights of host larvae								
	85-95 mg			140-150 mg			230-240 mg		
	Adults	♂	♀	Adults	♂	♀	Adults	♂	♀
4	58±1.15fg	55±0.57ef	45±0ef	69±1.15 cd	48±0.57ij	52±0.88 c	95±2.30 a	39±0.57 l	61±0.57 a
8	54±1.73 g	56±0.57def	44±0.57efg	66±0.57cde	51±0.57 hi	49±0.57 d	91±0.57 a	42±0 k	58±0.57 b
12	46±1.15 h	59±0.57 c	41±0.57 h	63±1.73def	54±0.57fg	46±0.57 e	83±0.57 b	47±0.57 j	53±0.57 c
16	45±1.15 h	66±0 b	34±0.57i	62±1.73ef	58±0.57cd	42±0gh	70±0 c	52±0.57gh	48±0.57 d
20	44±1.15 h	70±0.57 a	30±0.57 j	58±0fg	64±0.57 b	36±0.57i	69±1.15cd	57±0.57cde	43±0.57fgh

Table II.- Effect of egg density of *B. hebetor* and host size of *Spodoptera litura* larvae on the adult emergence and sex ratio of *B. hebetor*.

Eggs / host	Weights of host larvae								
	300-500 mg			600-800 mg			900-1000 mg		
	Adults	♂	♀	Adults	♂	♀	Adults	♂	♀
4	52±0.57hi	80±1.15 de	20±2.30bc	63±1.73ef	69.5±0.28 g	30.5±1.44 a	81±1.15 a	68.8±1.21 g	31.2±1.15 a
8	49±1.15ij	86±0.57abcd	14±0.57def	58±1.15fg	79.2±0.11ef	20.8±0.46 b	77±0.57ab	72.2±1.27 g	27.8±1.21 a
12	46±1.15jk	89±1.73abc	11±0.57efg	55±0.57gh	83.3±1.90cde	16.7±0.57bcd	73±1.15bc	73.2±0.46fg	26.8±0.57 a
16	43±1.15kl	90±2.30 ab	10±0.57fg	51±0.57hij	84±0.57bcde	16±1.15bcde	69±1.73cd	79.2±0.11ef	20.8±1.27 b
20	39±0.57 l	92±1.15 a	8±1.15 g	47±0.57ijk	85±1.15bcde	15±1.15cdef	64±1.15de	83.3±1.17cde	16.7±0.46bcd

While, on same size host where 4 eggs were placed, minimum percentage of male ratio (55±0.57) was emerged. On *S. litura* smaller host weight (300-500 mg) and higher egg density (20 eggs) male emergence was maximum (92%) whereas 80% was recorded on lower density (4 eggs) (Table II). Male emergence percentage on *G. mellonella* host weight (230-240 mg) was increased (39±0.57 (se) and 57±0.57 (se) where 4 and 20 eggs placed, respectively. Similarly, the effect of density on male emergence was more (83.3%) at higher density and large host weight (900-1000 mg) and 68.8% at the lowest density (Table II). Male percentage was more on smaller weight where 20 eggs were placed and our results revealed that as the size of host increased, percentage of male emergence decreased.

Table III.- Effect of egg density and host weight of *Galleria mellonella* on the width size (mm) of emerging parasitoid, *B. hebetor* heads.

Eggs / host	Weight of host larvae		
	85-95 mg	140-150 mg	230-240 mg
4	0.54±0.005^{bcd}	0.57±0.01^{ab}	0.6±0.005^{a}
8	0.53±0.005^{cd}	0.55±0.011^{bcd}	0.57±0.005^{ab}
12	0.52±0.005^{de}	0.54±0.005^{bcd}	0.56±0.005^{bc}
16	0.49±0.005^{ef}	0.52±0.005^{de}	0.55±0.005^{bcd}
20	0.43±0.005^{g}	0.48±0.005^{f}	0.53±0.005^{cd}

Table IV.- Effect of egg density and host weight of *Spodoptera litura* on the width size (mm) of emerging parasitoid, *B. hebetor* heads.

Eggs / host	Weights (mg)		
	300-500 mg	600-800 mg	900-1000 mg
4	0.44±0.005^{bcd}	0.47±0.005^{ab}	0.5±0.005^{a}
8	0.43±0.005^{cd}	0.45±0.011^{bcd}	0.47±0.005^{ab}
12	0.42±0.005^{de}	0.44±0.005^{bcd}	0.46±0.005^{bc}
16	0.39±0.01^{ef}	0.42±0.005^{de}	0.45±0.005^{bcd}
20	0.33±0.005^{g}	0.38±0.005^{f}	0.43±0.005^{cd}

Width size of the wasp head

Tables III and IV show the size of emerging adults for each host. Mean head width of emerging parasitoids from each host species was 0.60 ± 0.0005 (se) mm for *G. mellonella* and 0.50±0.005 (se) for *S. litura*, respectively. Different egg density had a significant effect on the size of emerging adults from each host. Mean head widths decreased as egg density increased. Host weight of *G. mellonella* and *S. litura* also had a significant effect on the size of emerging adult parasitoids. The size of emerging parasitoids was smaller on smaller hosts especially at the higher egg densities was examined.

DISCUSSION

The results showed that difference in host weight and egg density affected certain aspects of the biology of *B. hebetor* within each host. In gregarious parasitoids, the number of developing parasitoids from the host also depends on their fitness. Different egg density had a strong effect on the size of emerging wasps. As the egg density increased from 4 to 20 eggs per host, adult size decreased. Our findings are in close agreement with Milonas (2005) who claimed that as the egg density increased from 4 eggs per host to 18 eggs per host the adult size decreased. It has been found that mean head width of adults of *B. hebetor* decreased with density on larvae of *P. interpunctella* and *A. kuehniella* (Taylor, 1988). Antolin *et al*. (1995) reported that larger clutches resulted in smaller males and females of *B. hebetor* when cultured on mid weight larvae of *P. interpunctella*. The same response was also reported for the gregarious ectoparasitoid *Colpoclypeus florus* on *A. orana* (Dijkstra, 1986).

Several studies have reported that the host size also influences sex ratio. The females tend to emerge from large hosts and males from small hosts (Chewyreuv, 1913; Jones, 1982; Opp and Luck, 1986). Females may adjust progeny sex ratios in response to cues obtained during oviposition. Idiobiont parasitoids paralyze the host before ovipositing, and their offspring develop in limited resources. These parasitoids typically allocate male progeny to smaller or lower quality hosts, while reserving female offspring for larger hosts, in accordance with the host size hypothesis proposed by Charnov *et al*. (1981).

Sex ratio of *B. hebetor* was greatly influenced by different sizes of host species, as the size of host increased female ratio was also increased. In higher weight larvae with minimum number of eggs (4 eggs), maximum mean percentage of females was recorded. This might be due to less competition and availability of more nutritional resources. The mean percentage of males was maximum in lower weight with maximum number of eggs (20 eggs) which showed that when competition among larvae increased with increased egg densities, male emergence was more as compared to the female. Similar results have been reported by Anam *et al*. (2015) who observed that progeny sex ratio (male/total) increased with the increase in host density. The above findings are in close agreement with that of Joyce *et al*. (2002) who reported that parasitized 2-week-old beetle larvae of *Phoracantha* spp. produced only male *S. lepidus* progeny, whereas older larval hosts produced increasing proportions of female parasitoids (up to 80% females from 5-week-old hosts). The sex ratio of emerged *S. lepidus* shifted from 100% male to strongly female biased as host size increased, for both *Phoracantha* spp. Although 2-week-old *P. semipunctata* produced larger galleries than similar aged *P. recurva* larvae, 2-week-old hosts of both species produced only male parasitoids. In contrast, 5-week-old *Phoracantha* larvae produced approximately 20% males, a significantly lower proportion than that emerging from younger and smaller hosts.

Tillman and Cate (1993) reported that host size also affected sex ratio and predominantly 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. Large sized females lived longer and consequently produced greater number of offspring than smaller ones.

Different host sizes had significant impact on the size of emerging adult parasitoids as well. Larger parasitoids emerged from large size larvae than from smaller ones. Many experiments have been conducted for many gregarious and solitary parasitoids which explain the host size effects on the final size of emerging wasps (Godfray, 1994; Hora *et al*., 1995; Jervis and Copland, 1996; Ueno, 1999; Karamaouna and Copland, 2000). Most probably different sizes of host eventually influence the fitness of parasitoid, especially size of female wasp which affect their egg lying ability as well as longevity (Antolin *et al*., 1995). The relationship of adult size and its fitness in terms of longevity, fecundity and parasitism, or increased coupling ability of males, is revealed for many parasitoid species (Dijkstra, 1986; Godfray, 1994; Antolin *et al*., 1995; Ueno, 1999). On the other hand, bigger hosts are not always correlated with better performance for the parasitoids (Godfray, 1994; Chau and Mackauer, 2001). Small clutches of gregarious species may suffer problems in growing on bigger hosts.

Our results show highly significant interaction between density and host weight for *G. mellonella* host species. This interaction explains density dependent competition among larvae of parasitoid, in term of wasp adult size, which is directly related to availability of food source. The host size is the main quality parameter for fitness of parasitoid progeny. In general, adult female wasps laid large number of eggs on larger hosts and greater number of wasps develops as size of the host increased (Le Masurier, 1987). The current study showed that parasitoid adult emergence was significantly affected by egg density on *G. mellonella* larvae. Emergence of adult parasitoid was greatly influenced by larval competition. As the competition among larvae increases with increase in egg density resulting in less number of adults emerged. Reduction in parasitoid emergence results from increased food source competition, in the gregarious parasitoid species competition is usually restricted to availability of host food sources. This finding is in disagreement with Taylor (1988) who demonstrated that different weights of larvae of *P. interpunctella* have no significant effect on survival of *B. hebetor* and mentioned that host weight effects the survival of larvae of *A. kuehniella*, only between small and medium size larvae, but not between medium and large size-classes. Benson (1973) also described that when egg density on a host increased, mortality of larvae of *B. hebetor* parasitizing *Cadra cautella* (Walker) increased, proposing a scramble-like competition among the larvae of parasitoids. Emergence of parasitoids was also influenced by different host species. Parasitoid number was reduced drastically when reared on larvae of *S. litura* as compared to *G. mellonella*. Since larvae of *S. litura* were large compared to the other host, due to their strong immune system and parasitoid larvae were not nourished properly resulting in less number of parasitoid emerged. It is likely that different host species differ in terms of quantity and quality, so that parasitoid emergence may vary with host species.

CONCLUSION

Our data reveals that that there is a strong influence of different host species on a survival and size of the wasp *B. hebetor* during its developmental process. On the basis of experimental evidence *Spodoptera litura* was not suitable host for the normal development and rearing of *B. hebetor*.

ACKNOWLEDGEMENT

We are grateful to HEC (Higher Education Commission) Government of Pakistan for providing financial support (No. 20-3247/NRPU/R&D/HEC/14/408, 25.11.2015).

Statement of conflict of interest

Authors have declared no conflict of interest.

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