HOST EFFECTS ON LARVAL COMPETITION IN THE GREGARIOUS PARASITOID *BRACON HEBETOR*

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SUMMARY

(1) This study describes the effects of host species and size on larval competition, survival and development in the gregarious parasitoid, *Braccon hebetor* Say (Hymenoptera: Braconidae). Wasp eggs were placed at a range of densities on three sizes of two host species—*Anagasta kikniella* (Zeller) and *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae)—and the number, sex, size, and date of emergence of emerging adults were recorded.

(2) The mean size of emerging adults was strongly density-dependent, and 'carrying capacity' was linearly related to host mass, both within and across host species. Survival also was density-dependent on the smaller host species, and on the larger species when very high densities were used. Competition among these parasitoids thus appears to be largely determined by the amount of food which the host constitutes.

(3) Survival was lower on small hosts of both species, independent of density. In addition, *Plodia* hosts from some cultures were unsuitable (produced no parasitoids), independent of size and density. Development time was unaffected by egg density or host size, and only very slightly by host species. The sex ratio of survivors was not affected by any of the experimental factors; the absence of a sexual differential in competitive mortality suggests that previous findings of density-dependent sex ratios in *B. hebetor* may have been due to maternal manipulation.

INTRODUCTION

For insect parasitoids an individual host is the entire larval food source. 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 parasitoid larvae (see e.g. reviews in Vinson & Iwantsch 1980; Charnov et al. 1981). Furthermore, the intensity of larval competition may often depend on the quantity and quality of the host as food resource; studies on larval competition in parasitoids have indeed often assumed this, scaling larval density relative to the mass of the host (Shiga & Nakanishi 1968; Rabinovich 1971; Boulètreaux 1977; Takagi 1985).

This relationship between host characteristics and larval competition has both ecological and evolutionary consequences. Ecologically, effects of hosts on larval competition could produce differences in parasitoid density dependence, and thus qualitatively different dynamics (Taylor 1987), in populations of a parasitoid on different hosts. Evolutionarily, larval competition is a major determinant of optimal clutch size (see, e.g. Waage 1986) and sex ratio (Suzuki & Iwasa 1980; Charnov 1982; Godfray 1986),

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so an interaction between host type and larval competition could cause clutch sizes and sex ratios to also depend on the host (Skinner 1985; Waage & Godfray 1985). Klomp & Teerink (1967) and S. W. Skinner (unpublished, see Charnov & Skinner 1984, 1985) found correlations between larval competition and host size, using interspecific and intraspecific host comparisons, respectively, but these relationships were not quantified. More generally, the maximum number of progeny per host is sometimes correlated with the size of the host (Flanders 1935; Nozato 1969; Luck & Podoler 1985), but this addresses only one aspect of competition. There is not, then, any evidence specifically supporting the assumption that competition intensity is proportional to host size, or concerning whether the effects of different host species can be explained by the effects of size differences within a host species.

The experiment reported below was therefore carried out to examine, quantitatively, the interaction between host size, host species, and larval competition in a gregarious parasitoid. Specifically, I wanted to answer the following questions: (i) Is this competition affected by host size and species? (ii) Are these effects, for a given host species, proportional to host size? (iii) To what extent can the differences between host species be explained by this same size effect? (iv) What density-independent host-type effects occur, and how strong are they relative to the density-dependent effects?

**METHODS**

*Experimental species*

The wasp *Bracon hebetor* Say (Braconidae) was used in this study. It is a gregarious ectoparasitoid: eggs are laid, and larvae develop, in small groups on the outside of hosts which have been paralysed by the mother wasp. Both its basic ecology (reviewed in Benson 1972, 1973b, 1974; Taylor 1984) and its possible use in biological pest control (e.g. Keever, Arbogast & Mullen 1985) have been studied extensively.

The host species used were *Anagasta (= Ephestia) kühniella* (Zeller) (Lepidoptera: Pyralidae), the Mediterranean flour-moth, and *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae), the Indian meal-moth. The general biology and ecology of both hosts are reviewed by Richards & Thomson (1932) and Benson (1973a).

The stocks of *B. hebetor* and *A. kühniella* were descended from field collections from single populations approximately 10 months (about twenty generations for *B. hebetor* and ten for *A. kühniella*) prior to the experiment. *P. interpunctella* hosts were from a stock obtained twenty-five to thirty generations previously from the Stored Product Insects Laboratory, U.S.D.A. Agricultural Research Service (Savannah, Georgia). Details of collections and rearing are in Taylor (1984).

*Design*

The main experiment consisted of a factorial design in which density, host species and host size were crossed. Densities were 4, 8, 12, 16 and 20 eggs per host, a range similar to that observed in laboratory studies of oviposition (Ulltrett 1945; Benson 1973b; Taylor 1984, 1988); unfortunately, field data do not exist. Host size classes were: 20–25, 27.5–32.5, and 35–40 mg for *A. kühniella*, and 10–15, 15–20, and 20–25 mg for *P. interpunctella*.

The experiment was divided into ten blocks, each including one replicate of the above design and conducted on a separate day. Unfortunately, about half the *P. interpunctella* hosts in the last five blocks produced no parasitoid adults, despite live parasitoid larvae
having been seen on them (these being distinct from another twenty-two units, randomly
distributed throughout the experiment, in which no wasps of any stage were observed).
These 'late' failures were not associated with larval density (Somers' $D = -0.035$,
asymptotic $\text{S.E.} = 0.099$, N.S. (Goodman & Kruskal 1979)) and host size ($D = -0.092$,
A.S.E. = 0.109, N.S.), and may have been due to a pathogen which caused the hosts to
decay before the larvae had eaten enough to survive. These hosts clearly were different
from those in the remainder of the experiment (only three of which produced 'late'
failures), and provided no useable data. To maintain an approximately balanced design,
therefore, all data from the last five blocks were omitted from comparisons of host effects.

In addition, a further ten blocks were conducted using only medium-sized $A. \text{kühniella}$
hosts and a range of higher densities: 12, 20, 28, 36 and 44 eggs per host.

**Procedure**

Eggs had been oviposited during the 24 h preceding each block, by 48–72 h old females
which had been kept with males since emergence and with hosts during the preceding 48 h.
Fifth-instar hosts, mostly in the prepupal 'wandering' phase, were collected, sorted into
weight classes, and placed for 24 h with several $B. \text{hebetor}$ females, to paralyse the hosts;
all wasp eggs laid during this period were removed at the start of the experiment.
Treatments were then created by placing parasitoid eggs on hosts, both being selected
randomly with regard to the treatments to which they were assigned. Since the natural
clustering of eggs has been shown to affect larval competition (Benson 1973b) I retained
this as much as possible by transferring entire clusters of eggs.

I then reared the wasps to adulthood, each experimental unit (larvae on a single host) in
a separate Petri dish, at 30 ± 2 °C, 60–70% r.h., and a 16:8 h light:dark cycle. Daily
counts were made of the number and sexes of all emerged adults in each dish. Once
emergence was complete the wasps were killed and their head widths measured with an
ocular micrometer.

**Statistical analysis**

A non-linear model was used to analyse the size of surviving wasps. To test the
significance of the parameters in this model, and to compare the density responses on the
different hosts, I used an 'extra sum of squares' method exactly analogous to standard
procedures in linear regression and ANCOVA; this procedure is summarized in the
Appendix of the following paper (Taylor 1988).

Tests of significance were as appropriate for the randomized-blocks design of the
experiment (Sokal & Rohlf 1981), except that the residual mean square of the fullest
model was used as the denominator of the $F$ ratio whenever this yielded a less significant
result.

Statistics will only be summarized here; full ANCOVA tables are in Taylor (1984).

**RESULTS**

**Survival**

Most dishes which produced no survivors clearly were outliers, and so were excluded.
At 4 eggs per host, however, this distinction was not clear, so all data from this density
were omitted from analyses of survival.
At the low densities used in the main experiment, the overall effect of density on survival (log proportional survival) was not significant ($F_{1,4} = 2.99$, $P > 0.10$) (Fig. 1). The density regression on *P. interpunctella* hosts alone was significant ($F_{1,4} = 10.06$, $P < 0.05$, $R^2 = 0.16$), but that on *A. kühniella* hosts alone was not ($F_{1,4} = 0.00$), nor was the difference between these regressions on the two species ($F_{1,4} = 1.09$). When higher densities were used (on medium-sized *A. kühniella*), survival did decrease substantially with density, from 67% at the lowest densities to 33% at 44 eggs per host. There was considerable block-to-block variation in the effects of density or host type on survival: interactions involving block terms accounted for 39% of the variance and several were significant.

The strongest effect on survival (apart from the ‘failures’) was a density and host-species-independent effect on host size: survival was lower on the small size-class than on the medium-sized or large hosts ($F_{1,4} = 12.64$, $P < 0.025$, $R^2 = 0.15$) (Fig. 1). Survival did not differ between medium and large hosts ($F_{1,4} = 0.36$, N.S.)

**Adult size**

On all sizes of *A. kühniella*, mean parasitoid sizes (head widths) at 4 eggs per host were slightly smaller than at 8 eggs per host (Fig. 2a). Because of difficulties this caused in fitting the density–response model, the data for 4 eggs per host were excluded from the following analyses.

Mean head widths were smaller on the smaller hosts, and decreased with density on all host types (Fig. 2a). The non-linear response model $H = d + c/[1 + (aN)^b]$ (from Farazdagh & Harris 1968; $H$ = mean head width of adults, $N$ = initial density) was chosen to analyse these data because it provided the best fit, of a number of models tested, to the data for the extended range of densities on medium *A. kühniella*, and because its parameters have clear interpretations (see Discussion).

I first examined host effects on $a$ with all other parameters identical for all hosts and blocks. The inverse of the host’s mass had the most significant effect ($F_{1,4} = 98.17,$
Fig. 2. (a) Effect of density on adult size, by host type. Notation as in Fig. 1. (b) Fitted model for interaction of density and host mass: $Y = 0.49 + 0.08/[1 + (1.73 \times H/M)^{0.1}]$, where $Y =$ mean head width, $X =$ initial density, and $H/M =$ host mass in mg. (——□) large $A. \text{kühniella}$ (mass midpoint = 37.5 mg); (———○) medium $A. \text{kühniella}$ (mass = 30 mg); (———■) small $A. \text{kühniella}$ and large $P. \text{interpunctella}$ (mass = 22.5 mg); (———●) medium $P. \text{interpunctella}$ (mass = 17.5 mg); (———♦) small $P. \text{interpunctella}$ (mass = 12.5 mg).

$P < 0.001$, $R^2 = 0.27$). Once host size was included in the model no other factors had significant effects on $a$.

With $a$ modelled as a constant multiple of (host mass)^{-1}, no significant effects of host type were found on either of the parameters $c$ and $d$ (though for both there were correlations with the inverse of host mass which approached significance: $c: F_{1,4} = 5.56$, $P < 0.10$; $d: F_{1,4} = 5.66$, $P < 0.10$). The shape parameter $b$ could not be analysed in this way because when it was allowed to differ among blocks or host types the non-linear regression procedure produced non-sensical results.

The final model resulting from this analysis, then, had $a$ inversely proportional to host mass and all other parameters independent of host type (Fig. 2b).

**Time to emergence and sex ratio**

The host species had a significant but small effect on the mean time to emergence of the wasps: wasps reared on $A. \text{kühniella}$ caterpillars emerged, on average, in 9.25 days,
compared with 9.03 days on *P. interpunctella* (Fig. 3; $F_{1,4} = 37.25$, $P < 0.005$). Neither host size within species ($F_{3,8} = 1.19$) or density ($F_{1,4} = 5.88$) had significant effects. In contrast, differences among the five blocks were substantial: block means ranged from 8.6 to 10.3 days ($F_{4,45} = 148.92$, $P < 0.0001$, $R^2 = 0.79$).

There were no significant treatment effects on the sex ratio of surviving wasps (Fig. 4); there was, if anything, a suggestion of an increase in the female bias at high densities.

**DISCUSSION**

*Host effects on competition*

The main (host-effects) experiment used fairly low densities and a limited range of host types (all being last-instar of two similar, entirely suitable species). It therefore described
the rather modest effects of competition and host variation under normal rather than extreme circumstances. Nevertheless, a clear and simple relationship between host type and competition was seen.

Since the main effect of density was on wasp size, its interaction with host type was also clearest with regard to wasp size. Similarly, both Klomp & Teerink (1967) and S.W. Skinner (unpublished, cited in Charnov & Skinner 1984, 1985) emphasize the effect of host size on density-dependent wasp size rather than survival. In the model used to describe this response, $1/a$, which was closely correlated with host mass, can be taken as a measure of 'carrying capacity': it is the density at which competition has half its maximum impact. The intensity of competition among larvae of *B. hebetor*, as it affects adult size, thus is directly proportional to the quantity of resource. That survival was density-dependent on the smaller host species (*P. interpunctella*) but not on the larger (*A. kühniella*) is also consistent with competition being more intense on smaller hosts, though this pattern is less clear because of the weakness of density effects on survival.

The first two questions in the Introduction, then, can be answered positively: host differences affect larval competition, in proportion to host mass. Furthermore, this relationship held across host species so the answer to the third question is also yes, indicating that *A. kühniella* and *P. interpunctella* caterpillars are of similar nutritional quality.

These findings confirm that the relevant measure of density—for this parasitoid and these hosts—is indeed the number of parasitoids per unit mass of host, and that host size can be taken as an indicator of the strength of density dependence (e.g. in studies of clutch size evolution). These results furthermore suggest that the mechanism of competition among *Braccon* larvae is simply consumption of the resource.

**Density-independent host effects**

The most striking of the density-independent effects of host type was the high frequency of complete mortality ('failure') on *P. interpunctella* hosts in the last five blocks. This
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clearly was due to differences in resource quality rather than quantity. The lower survival
on small hosts, independent of both density and host species and in the absence of a
difference between medium-sized and large hosts, may also have been a suitability effect:
the small hosts may have been slightly younger, less developed, or less healthy, than the
medium and large hosts. Whatever its cause, the magnitude of this effect is surprising,
since even the small size-classes were last-instar and essentially suitable hosts.

The importance of the lower survival on small hosts and of the density and host-size-
dependent decrease in size can be compared by examining density–response curves of
predicted potential fecundity on the different hosts (Fig. 5). It is evident, even though
these curves neglect size effects on longevity, that the effect on survival is more substantial
than the effect on wasp size: the latter only just equals the strength of the former (a
decrease of 33%) at the highest densities tested, on the smallest hosts. The unpredictable
effect of ‘failures’, omitted from these calculations, is also obviously massive. The answer
to the fourth question posed in the Introduction, therefore, is that qualitative host effects
unrelated to larval competition are very substantial in this system.

Implications

This combination of density-dependent and density-independent effects might result in
different dynamics in populations of Bracon hebetor exploiting different hosts. The
density-independent effects, strong as they are, probably would only affect equilibrium
abundances. The differences in the intensity of larval competition, however, could affect
the density dependence in the parasitoid population, and thus the stability of the
interaction (Taylor 1987).

The effects of host type on the larvae, however, might also select for behavioural
responses which would tend to offset the direct effects of hosts on parasitoid dynamics. In
particular, the density-dependent host differences should select for larger clutch sizes on
the larger hosts (Parker & Courtney 1984; Charnov & Skinner 1984, 1985; Iwasa, Suzuki
& Matsuda 1984; Smith & Lessells 1985); this would reduce the differences in the intensity
of competition and thus perhaps in stability. The density-independent effects might also
select for a preference for the more ‘profitable’ hosts (e.g. Jaenike 1978): the larger sized
hosts within a species, and (less strongly) the larger species. Any such preferences between
the two host species (as well as any differences in clutch size or larval competition) would
obviously affect the interaction when the hosts co-occur.

Behavioural responses of B. hebetor to these different species and sizes of hosts
therefore not only are a primary expected result of the observed interaction between host
size and competition, but will be a major determinant of the actual ecological
consequences of this interaction. These responses are described in the following paper
(Taylor 1988).

Finally, this study indicates that B. hebetor females may alter their clutch sex ratios in
response to egg densities: the absence of a sex difference in mortality (cf. Grosch 1948;
Benson 1973b) suggests that previous findings of decreasing proportions of females at
high densities (Kanungu 1955; Benson 1973b; Rotary & Gerling 1973) may have been due
to maternal manipulation of the primary sex ratio, which the previous studies did not
exclude as did mine. The larval competition shown in this study would itself be a possible
reason for the evolution of such behaviour, if the fitness of female progeny was more
sensitive than that of males to, e.g. decreases in adult size (Charnov 1979, 1982; Charnov
et al. 1981; Taylor 1984). Furthermore, since this competition has been seen to depend on
host size, comparison of the density dependence of the primary sex ratio on different hosts
would be a powerful means of distinguishing this evolutionary cause from the principal alternative, 'local mate competition' (Hamilton 1967). These questions obviously warrant further study, but are beyond the scope of the following paper (Taylor 1988).

ACKNOWLEDGMENTS

I thank Drs H. Wilbur, J. Antonovics, D. Burdick, M. Rausher, and M. Uyenoyama for their advice on this work and its presentation, and in particular H. Wilbur for his patient support and D. Burdick for his statistical help. M. Strand and two anonymous reviewers made helpful comments on the manuscript. This work was supported by a Grant-in-Aid of Research from Sigma Xi and by the Duke University Department of Zoology.

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(Received 23 March 1987)