HOST EFFECTS ON FUNCTIONAL AND OVIPOSITIONAL RESPONSES OF *Bracon hebetor*

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**SUMMARY**

(1) This study describes the effects of host species (*Anagasta kühniella* (Zeller) and *Plodia interpunctella* (Hübner)) and size on the 'functional' and 'ovipositional' responses of the gregarious parasitoid *Bracon hebetor* Say, and its preferences between these host types.

(2) Attack rates followed a Type II functional response (Holling 1959), with strong interference among parasitoids (Hassell & Varley 1969; Free, Beddington & Lawton 1977). In contrast, both the number of hosts oviposited on per wasp and the number of eggs laid per wasp were essentially independent of host and wasp densities.

(3) There were no significant differences in the responses to different sizes of a given host species. There also were not any significant preferences between host sizes, though there was a trend towards preference for the larger, more suitable hosts.

(4) The 'handling time' for *A. kühniella* was greater than for *P. interpunctella*, and there was an active preference for attacking the latter; both results may be due to the defensive writhing of the former species. More eggs were laid on each parasitized *A. kühniella*, which are larger and so can support more larvae (Taylor 1988), but there were no differences in the numbers of each species oviposited on.

**INTRODUCTION**

In the preceding paper (Taylor 1988) it was shown that the host’s size and species affect growth and development of larvae of the gregarious parasitoid *Bracon hebetor* (Say) (Hymenoptera: Braconidae). Specifically, survival was lower and competition more intense on smaller hosts. It was suggested that *B. hebetor* females as a result might prefer to parasitize, or might put more eggs on, larger hosts, and indeed that the dynamical consequences of these host effects on larvae would largely depend on the nature of maternal behavioural responses to the hosts.

Many parasitoids do adjust clutch sizes in response to host size (see reviews in Salt 1961; Waage 1986), and some prefer ‘better’ hosts (Hafez 1961; Wylie 1967; Cornell & Pimentel 1978; Mueller 1983; Hopper & King 1984; Nechols & Kikuchi 1985; Bellows 1985b). For no parasitoid, however, do we have complete information on both behavioural responses (functional responses and clutch sizes, in both choice and no-choice experiments) to different hosts, and on the effects of these hosts on parasitoid larvae.

The study reported here was therefore undertaken to describe the responses of adult female *Bracon hebetor* to the hosts (*Anagasta kühniella* (Zeller) and *Plodia interpunctella* (Hübner), both Lepidoptera: Pyralidae), whose effects on larvae were described in the preceding paper. The aims were: (i) to test the evolutionary predictions of a preference for,
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and higher egg densities on, larger hosts; and (ii) to determine how foraging and
ovipositional behaviour might interact with larval competition in determining reproduc-
tive dynamics of *B. hebetor* on the different hosts.

MATERIALS AND METHODS

The experimental system

The stocks of the parasitoid, *B. hebetor*, and its hosts, *A. kühniella* and *P. interpunctella*,
were the same as those in the preceding paper. Features of the biology of *B. hebetor*
relevant to the present study are that: (i) females sting and paralyse hosts before laying
eggs on them; (ii) essentially all paralysed hosts die even if no eggs are laid on them (Beard
1952); (iii) under some conditions females must relocate the hosts to oviposit on them, and
so do not always parasitize all the hosts they attack (Ulyett 1945; Hagstrum 1983;
Hagstrum & Smittle 1977; cf. Benson 1973); (iv) it is moderately gregarious, laying
typically four to ten eggs per host; and (v) eggs are laid and larvae develop on the exterior
of the host.

Design

Responses to single host types

Two experiments were performed, each using two sizes of one of the two host species
(the small and medium host sizes of the preceding paper: 10–15 and 15–20 mg for *P.
interpunctella*, and 20–25 and 27.5–32.5 mg for *A. kühniella*). Three parasitoid densities
(one, two and four per arena) were used, in a balanced incomplete design giving (for each
experiment) six replicates in nine blocks (plus a partial tenth block in the *A. kühniella*
experiment necessitated by a mistake in randomization). For each wasp density, host:
wasp ratios of two, four, eight, and sixteen were generally used, with an additional
density of thirty-two hosts with single wasps. Both host sizes were used in each block.

Preferences

One experiment described preferences between the two sizes of *A. kühniella*, and a
second described those between the two species of hosts (using the medium sizes: 15–20
mg for *P. interpunctella* and 27.5–32.5 mg for *A. kühniella*). Each experiment consisted of
one treatment: eight hosts of each type exposed to one wasp. The species comparisons
contained twenty-seven replicates in six blocks (three to six replicates per block); the size
comparison had five blocks of five replicates each.

Procedure

Female parasitoids used in the experiments were all 48–72 h old (post-emergence), and
had been kept with males since emergence and with small numbers of hosts during the
preceding 48 h. Fifth instar, predominantly late 'wandering stage' host larvae, were
collected and sorted into weight classes. Parasitoids and hosts were then placed in large
(150 mm diameter) plastic Petri dishes according to the designs above (with each block on
a different day), with treatments in random order.

The wasps were temporarily removed by gentle aspiration 6 h later, the number of
paralysed hosts counted, and the wasps returned to the dishes. After another 18 h the
wasps were removed from the dishes, and the numbers of unparalysed, paralysed and
### Table 1. Statistical summary of host-type effects in single-host-type experiments

<table>
<thead>
<tr>
<th>Response</th>
<th>Anagasta (1, 9)</th>
<th>Plodia (1, 8)</th>
<th>Species (1, 17)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hosts attacked</td>
<td></td>
<td></td>
<td>111.46***</td>
</tr>
<tr>
<td>$a$</td>
<td>0.01</td>
<td>0.21</td>
<td>0.05</td>
</tr>
<tr>
<td>$T_h$</td>
<td>0.07</td>
<td>0.67</td>
<td>43.79***</td>
</tr>
<tr>
<td>$m$</td>
<td>0.17</td>
<td>0.45</td>
<td>3.10*</td>
</tr>
<tr>
<td>Hosts oviposited on</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Regression on hosts</td>
<td>N.A.</td>
<td>0.22</td>
<td>2.12*</td>
</tr>
<tr>
<td>Eggs laid</td>
<td>0.49*</td>
<td>4.15*</td>
<td>6.91*</td>
</tr>
</tbody>
</table>

Entry for the species effect on the overall functional response is a multivariate $T_1$ with 21 and 17 degrees of freedom. Others are $F$ statistics, with degrees of freedom as at heads of columns, except: $^a$ 1, 135; $^b$ 1, 8; $^c$ 1, 86; $^d$ 1, 91. Significance levels are: *** $P < 0.001$; * $P < 0.05$. Hosts oviposited on, and eggs laid, are per wasp. N.A. indicates regressions were not significant on either host size and so were not compared.

‘usable’ (i.e. not shrivelled, blackened, or eaten by other caterpillars), and ‘unusable’ hosts, and of *B. hebetor* eggs on each paralysed host, were counted.

**Statistical analyses**

Block effects were treated as random throughout (Sokal & Rohlf 1981). The between-species comparisons of the single-host-type responses were treated as split-block designs, with blocks nested within species: the species-effect mean square was tested over that for blocks within species (Federer 1975).

Attack rates were analysed as log-transformed proportions of hosts not paralysed in 6 h, after zeroes were eliminated by the transformation: $Y = (S + 1)/(N + 2)$, were $S$ is the number of survivors, $N$ the initial number, and $Y$ the transformed proportionate survival (Brunk 1975). These data were described by a non-linear functional response model (see Results). The significance of each parameter of this model, and of the effects of host size (within species) on these parameters, was tested by a non-linear analysis of covariance described in the Appendix. The effect of host species on the functional response was examined by a multivariate analysis of variance on parameter (pseudo-) estimates also described in the Appendix.

To analyse preferences, Manly’s index (Manly, Miller & Cook 1972; Manly 1974; Chesson 1978, 1983) was calculated for: (i) the number of each host type paralysed at 6 h; (ii) the proportion of these paralysed at 24 h which had eggs laid on them; and (iii) the number of eggs per paralysed host. Preferences in (iv) the total number of eggs laid on each host type, and (v) the mean number of eggs per parasitized host of each type, were also calculated, as differences between the numbers on the two host types. Analyses of variance were performed to remove block effects on these preference indices. The mean square errors from these analyses were then used as variance estimates in $t$-tests comparing the mean observed preferences to neutrality and to the ‘innate’ preferences (Hassell 1978) predicted from the results of the single-host-type experiments. ‘Preferences’ in the number of eggs laid, and in the mean number of eggs per parasitized host, were predicted as one-half the difference in the means, in the single-host-type experiments, for single wasps provided with sixteen hosts.)
Parasitoid responses to host type

Fig. 1. The number of hosts paralysed in 6 h, as a function of host and wasp densities, by host type. Ticked bars indicate least squares means ± 1 S.E. (calculated on log-transformed proportions of hosts not paralysed, adjusted for block effects; shown detransformed). Fitted model is $Y = X\cdot[(1 - \exp[-a \cdot P^{-m}]/(1 + a \cdot P^{-m} \cdot T_h \cdot X)],$ where $X =$ host density, $Y =$ number of hosts paralysed, $P =$ number of parasitoids. (——) 1 wasp; (•—•—•) 2 wasps; (×⋯×) 4 wasps. (a) Medium A. kühniella ($a = 1.06$, $T_h = 0.077$, $m = 0.66$). (b) Small A. kühniella ($a = 0.93$, $T_h = 0.088$, $m = 0.59$). (c) Medium P. interpunctella ($a = 1.01$, $T_h = 0.021$, $m = 0.49$). (d) Small P. interpunctella ($a = 1.03$, $T_h = 0.025$, $m = 0.41$).

RESULTS

Single-host-type responses

Number of hosts attacked

The ‘functional’ responses (Fig. 1) showed a typical type II functional response (Holling 1959) to host density, and the search rate decreased at higher wasp densities (Hassell & Varley 1969; Hassell 1971). These data were described by the model:

$$Y = H \cdot (1 - \exp[-a \cdot P^{-m}]/(1 + a \cdot P^{-m} \cdot T_h \cdot H)],$$

where $Y$ is the number of hosts killed, $P$ is the density of parasitoids, and $H$ is the density of hosts.

The functional response did not differ significantly between the sizes of each species of host, but were very significantly different between the two species (Table 1, Fig. 1). This species effect was principally on the parameter $T_h$, which was greater on A. kühniella; $m$ also was greater on A. kühniella, but not significantly so, and $a$ did not differ between the species.

Number of hosts parasitized

Up to a level of about four hosts per wasp, virtually all available (paralysed and healthy) hosts were parasitized; above this level the number of hosts parasitized per wasp
increased only slightly as more hosts were available and was independent of the number of wasps (Fig. 2).

There were no significant effects of host size or species on the number of hosts parasitized per wasp (Table 1, Fig. 2), though it was slightly higher, and increased more rapidly with increasing numbers of available hosts, on *P. interpunctella*.

**Number of eggs laid**

The number of eggs laid per wasp (Fig. 3) was independent of the densities both of parasitoids and of available hosts (all *F*’s non-significant), even at low densities of hosts at which the number of hosts available was less than the number which would ordinarily be used.

Wasps laid slightly but significantly fewer eggs when provided with small rather than with medium *P. interpunctella*; this size effect was not significant on *A. kühniella*. More eggs were laid per wasp when provided with *A. kühniella* caterpillars than with *P. interpunctella* hosts (Fig. 3, Table 1). (The effect of the number of wasps on the number of eggs laid per wasp also differed significantly between the species of hosts, but was considerably smaller than the effect of the species of the host, and did not shown any interpretable pattern).
Parasitoid responses to host type

Fig. 3. The number of eggs laid per wasp in 24 h, as a function of host and wasp densities, by host type. Lines connect least square means (adjusted for block effects); ticked bars to left indicate overall means ± 1 S.E. (pooled) for each wasp density. Symbols as in Fig. 1. (a) Medium A. kühniella. (b) Small A. kühniella. (c) Medium P. interpunctella. (d) Small P. interpunctella.

Table 2. Preferences for medium-sized over small A. kühniella hosts

<table>
<thead>
<tr>
<th>Response</th>
<th>Mean</th>
<th>d.f.</th>
<th>S.E.</th>
<th>Neutral</th>
<th>t</th>
<th>P</th>
<th>Predicted</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number paralysed&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.55</td>
<td>20</td>
<td>0.04</td>
<td>0.5</td>
<td>1.29</td>
<td>N.S.</td>
<td>0.53</td>
<td>0.39</td>
<td>N.S.</td>
</tr>
<tr>
<td>Proportion parasitized&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.53</td>
<td>20</td>
<td>0.05</td>
<td>0.5</td>
<td>0.71</td>
<td>N.S.</td>
<td>—</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Share of total eggs&lt;sup&gt;c&lt;/sup&gt;</td>
<td>0.54</td>
<td>20</td>
<td>0.05</td>
<td>0.5</td>
<td>0.76</td>
<td>N.S.</td>
<td>0.54</td>
<td>0.01</td>
<td>N.S.</td>
</tr>
<tr>
<td>Total number of eggs&lt;sup&gt;d&lt;/sup&gt;</td>
<td>2.32</td>
<td>20</td>
<td>2.23</td>
<td>0.0</td>
<td>1.04</td>
<td>N.S.</td>
<td>1.46</td>
<td>0.38</td>
<td>N.S.</td>
</tr>
<tr>
<td>Eggs per parasitized host&lt;sup&gt;e&lt;/sup&gt;</td>
<td>0.59</td>
<td>17</td>
<td>1.03</td>
<td>0.0</td>
<td>0.09</td>
<td>N.S.</td>
<td>0.21</td>
<td>0.37</td>
<td>N.S.</td>
</tr>
</tbody>
</table>

<sup>a</sup>At 6 h: paralysed medium/total paralysed.
<sup>b</sup>At 24 h, as proportion of 'available' (paralysed, usable) hosts: proportion of medium/(proportion of medium + proportion of small).
<sup>c</sup>At 24 h, eggs per 'available' host: eggs per medium host/(eggs per medium host + eggs per small host).
<sup>d</sup>At 24 h: eggs on medium/total eggs.
<sup>e</sup>At 24 h: eggs per medium host—eggs per small host.
TABLE 3. Preferences for *A. kühniella* over *P. interpunctella* hosts

<table>
<thead>
<tr>
<th>Response</th>
<th>Mean</th>
<th>d.f.</th>
<th>S.E.</th>
<th>Neutral</th>
<th>t</th>
<th>P</th>
<th>Predicted</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number paralysed</td>
<td>0.33</td>
<td>20</td>
<td>0.05</td>
<td>0.5</td>
<td>-3.31</td>
<td>&lt;0.01</td>
<td>0.51</td>
<td>-3.52</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Proportion parasitized</td>
<td>0.50</td>
<td>18</td>
<td>0.06</td>
<td>0.5</td>
<td>-0.07</td>
<td>N.S.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Share of total eggs</td>
<td>0.59</td>
<td>18</td>
<td>0.06</td>
<td>0.5</td>
<td>1.45</td>
<td>N.S.</td>
<td>0.60</td>
<td>-0.15</td>
<td>N.S.</td>
</tr>
<tr>
<td>Total number of eggs</td>
<td>3.54</td>
<td>18</td>
<td>1.84</td>
<td>0.0</td>
<td>1.92</td>
<td>&lt;0.10</td>
<td>3.25</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eggs per parasitized host</td>
<td>3.41</td>
<td>11</td>
<td>0.81</td>
<td>0.0</td>
<td>4.21</td>
<td>&lt;0.01</td>
<td>1.70</td>
<td>2.10</td>
<td>&lt;0.10</td>
</tr>
</tbody>
</table>

a Responses as in Table 3, but substituting *A. kühniella* for ‘medium’ and *P. interpunctella* for ‘small’.

Preferences

*Host size*

All the responses showed a slight preference for medium-sized over small *A. kühniella*, but none of these apparent preferences were significantly different either from neutrality or from the predicted weak preferences for the larger hosts (Table 2).

*Host species*

The wasps preferred to paralyse *P. interpunctella* rather than *A. kühniella*, a response which differed both from neutrality and the predicted slight preference for *A. kühniella* (Table 3). As in the single-host-type experiments, there was no difference in the proportion of hosts on which eggs were laid, relative to the number of hosts paralysed (Table 3). Substantially more eggs were laid on *A. kühniella* than on *P. interpunctella*, a difference similar to that in the single-host-type experiments but not statistically significant, due to its large variability among blocks (Table 3). This larger number of eggs on fewer hosts (because fewer were paralysed) resulted in significantly more eggs per parasitized host on *A. kühniella* (Table 3); this difference was greater than that observed in the single-host-type experiments but not significantly so.

DISCUSSION

Some of these results do indeed support the expectation that the larger hosts, being more suitable for larval development, would be ‘preferred’. Others, however, do not, and some even contradict it. Imperfect correlations between ovipositional behaviour and host suitability are in fact common: some parasitoids prefer less suitable (Hafez 1961) or even unsuitable hosts (Temerek 1983, 1984), while other do not distinguish between hosts of differing suitability (Mueller 1983; Takagi 1986) or respond different to host types between which there are no apparent suitability differences (Nechols & Kikuchi 1985; Bellows 1985a,b). Two points are clear: factors other than host ‘suitability’ are sometimes important, or even paramount, and for *Bracon hebetor* the different stages of parasitization, from attack through oviposition, were affected in different ways by host characteristics.

In the present study the clearest example of the importance of factors other than larval suitability was the higher mortality rate of the smaller host species, *Plodia*. In the single-
host-type trials this difference was due to the greater ‘handling time’ ($T_h$) for *A. kühniella*. ‘Handling time’, however, only affects the time available for searching, not relative encounter rates, so the preference for *P. interpunctella* in the choice trials was active, due to a change in behaviour (perhaps avoidance of *A. kühniella* when encountered). A possible cause of both the difference in handling times and this active preference is the much more vigorous defensive action of *A. kühniella* caterpillars. This might actively discourage wasps from attacking *A. kühniella* caterpillars when an alternative is present, or might have led to the evolution of a preference for *P. interpunctella* as an adaptation to the greater time required, or risk incurred (Iwasa, Suzuki & Matsuda 1984), in attacking *A. kühniella*, a cost not entirely offset by the slightly greater benefit of parasitizing the larger host.

Some of the other responses differed little among hosts; in particular, the preferences between sizes were weaker than those between species despite the greater effect of host size than species on survival and net reproductive success (Taylor 1988). The simplest explanation for weak host-type effects of course would be that the parasitoids cannot distinguish between (and have similar rates of encounter with) these fairly similar hosts. This explanation, however, is not entirely adequate: *B. hebetor* females can distinguish size differences, at least if gross (they do not attack early-instar hosts), as well as species differences (as evidenced by the differences in egg loads). An alternative explanation for some of the weak host effects may well be that responses to the experimental factors of size and species were obscured by responses to uncorrelated qualitative differences among hosts, such as the unpredictable unsuitability of *P. interpunctella* hosts reported in the preceding paper.

The one clear correlation between wasp behaviour and host suitability was in numbers of eggs per host: mean egg densities (in the choice trials) were more than half again as large on *A. kühniella* as on *P. interpunctella*, and were larger (though not significantly so) on medium than small *A. kühniella* (this latter effect perhaps being smaller because of the smaller difference in host sizes). In retrospect, this is quite sensible: the profitability of attacking a host may depend on many factors (e.g. the cost of subdued it), but once hosts are paralysed and a wasp has begun laying eggs there probably are few relevant differences between hosts other than their suitability for larvae.

It is worth noting, though, that the difference in egg densities between host species was less than might have been expected: the eggs laid on *A. kühniella* hosts would suffer less competition than those on *P. interpunctella* hosts (Taylor 1988), despite their higher densities. This presumably was because ovipositional behaviour was a balance between maximization of gain per host (favouring host-size-dependent clutch sizes exactly offsetting differences in competition) and of gain per egg (predicting clutch sizes less variable with host type); the combination of these would lead to both larger clutches and greater net yield from the larger hosts (Isawa, Suzuki & Matsuda 1984; Parker & Courtney 1984; Ikawa & Okabe 1985; Skinner 1985; Smith & Lessells 1985; Waage & Godfray 1985), as was observed. Evidently even the ovipositional response to paralysed hosts was affected not only be a given host’s suitability but by additional factors, in this case the ‘perception’ of the trade-off between reproduction on that and on other hosts.

**Population dynamics**

One aim of this study was to determine how the ovipositional behaviours of *Bracon hebetor* females might translate the effects of host characteristics on *Bracon* larvae into effects on population dynamics. It seems clear, in fact, that the dynamics of the interaction
will be shaped much more by these behaviours—and by the dynamics of attack and oviposition in general—than by host effects on larval development.

In part, this primacy of maternal behaviour is because the differences in egg density partially negate the host differences in larval competition, as the previous paper suggested they might. Thus, while parasitoid reproduction would be lower, and slightly more density-dependent on *P. interpunctella*, these differences would be less than predicted from larval studies alone. Any effects of differences in larval competition on abundances or stability (Taylor 1987) therefore would also be minor. The difference in ‘handling time’ on the two species probably would be more important; like the difference in larval competition, this would tend to make an interaction with *Plodia* more stable, but in contrast it would produce lower host densities.

When all three species co-occur, maternal behaviours—in this case, the parasitoid’s active preferences—would again be of primary importance: the wasps would inflict greater mortality on *Plodia* than *Anagasta* caterpillars, while maintaining a high reproductive rate by ovipositing more on the more suitable *Anagasta*. This combination presumably would be to the disadvantage of *Plodia*, though the competitive interaction between the hosts, which has not been studied, would of course also be important.

The most important dynamical phenomenon seen in the present paper, however, is the decoupling of host mortality and parasitoid reproduction, independent of host type. Because of the short-term limit to the wasps’ egg supply, their reproductive response to increases in host density, and thus their ability to regulate the hosts, would be reduced. For the same reason, the interference shown in the attack rates would not result in density-dependent regulation of parasitoid reproduction, and so would have little stabilizing effect. Contrary to what would be predicted from the functional response alone (with strong interference, somewhat offset by large ‘handling times’), then, this ovipositional limitation of *Bracon hebetor* presumably would result in very unstable dynamics, regardless of the host.

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REFERENCES


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APPENDIX

Comparison of non-linear regressions: added sum-of squares technique

The non-linear functional responses to the different sizes of hosts (within species), and in the preceding paper the density–size responses on the different hosts, were compared by the 'extra sum of squares' technique used by Mead (1970) and recommended by Ratkowsky (1983). The 'mean square' attributable to a factor is estimated by fitting a model with and without the factor, then dividing the difference in residual sum-of-squares by the difference in residual degrees of freedom. Appropriate ratios of such 'mean squares' are then compared to $F$ distributions.

For example, to compare the effect of host size on the parameter $a$ of the functional response model (with other parameters the same on both sizes) required fitting the following models:

$$Y = -aP^{1-m}/(1+aP^{-m}T_h'H),$$  \hspace{5cm} (A1)

$$Y_i = -a_iP^{1-m}/(1+a_iP^{-m}T_h'H),$$  \hspace{5cm} (A2)

$$Y_{ij} = -a_{ij}P^{1-m}/(1+a_{ij}P^{-m}T_h'H),$$  \hspace{5cm} (A3)

where $Y = \ln$(proportion of hosts not attacked), $P =$ number of parasitoids, and the subscripts $i$ and $j$ refer to host size and block, respectively, so that $a$ is a common value for all host sizes and blocks, $a_i$ has a separate value for each host size, and $a_{ij}$ has a separate value for each block and host size (in practice, a dummy-variable scheme and separate parameters are used). The $F$ statistic was then

$$\frac{[RSS(A1) - RSS(A2)]/[RDF(A1) - RDF(A2)]}{[RSS(A2) - RSS(A3)]/[RDF(A2) - RDF(A3)]},$$

with $[RSS(A1) - RSS(A2)]$ and $[RDF(A1) - RDF(A2)]$ degrees of freedom, where $RSS(X) =$ residual sum of squares for model $X$, and $RDF(X) =$ residual degrees of freedom for model $X$.

MANOVA of parameter estimates

The preceding procedure could not be used to compare functional responses to the two species of hosts: the appropriate analysis of this was as a split-plot design, and the large number of parameters required for this (with separate block parameters for each species), relative to the number of data points, in some cases prevented the non-linear fitting procedure from converging.

An analogue of an alternative approach to linear ANCOVA with random blocks was therefore adopted. The essential idea was to fit the model separately to the data for each block and host type, and then analyse the resulting parameter estimates by standard MANOVA; in practice, the model could not be fitted to the few data points (usually 4) for
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each block–host type combination, so ‘pseudoestimates’ were obtained by a jack-knife procedure (Sokal & Rohlf 1981) and entered into the MANOVA. An ANOVA on parameter estimates for blocks is strictly equivalent to a random-block linear ANCOVA only with a balanced design, and the functional response experiment was not completely balanced. The imbalance was reasonably modest, however, and in addition the jack-knife procedure presumably would somewhat lessen the effects of the imbalance, so I assume the imbalance to be unimportant.

Justification

Both procedures are justified by their analogy to standard linear ANCOVA procedures. Their performance therefore depends on how close to linearly the model–data combination behaves (Ratkowsky 1983). The virtue of the ‘extra sum of squares’ technique is that it is affected only by the ‘intrinsic’ non-linearity of the ‘solution locus’, which is typically small for models such as those analysed in this and the preceding paper (Bates & Watts 1980; Ratkowsky 1983).

Parameter estimates, on the other hand, are affected also by ‘parameter-effects’ non-linearity, which can often be substantial (Bates & Watts 1980; Ratkowsky 1983); the ‘ANOVA’ of parameter estimates method may therefore be less robust. However, if the experimental design is balanced, as it approximately was in this study (ignoring the split-plot aspect of the blocking), and if the null hypothesis is true—i.e. the parameters are the same for the different treatments—the portions of the solution locus representing each of the host types will have identical shapes. If, in addition, the error variances are the same, the parameter–effects curvatures will be the same; in other words, if the parameters really are the same, their estimates will be biased, but similarly. Thus, a test of whether they consistently differ would be unaffected by this bias. In the functional response experiment, unfortunately, the error variance is not the same on the two host species ($F_{135,146} = 1.73$, $P < 0.001$), so the biases of the estimates may differ; how serious a problem this poses I cannot evaluate, but visual inspection of the data suggests that it is highly unlikely that the statistical difference between the functional responses on the two species is entirely an artefact of biases due to non-linearity.

REFERENCES


