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FORAGING AND OVIPOSITION DECISIONS IN THE PARASITOID *APHYTIS LINGNANENSIS*: DISTINGUISHING THE INFLUENCES OF EGG LOAD AND EXPERIENCE

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SUMMARY

(1) We used an experimental protocol that allowed us to distinguish the relative influences of egg load and experience with host contact on foraging behaviour and clutch size decisions in the gregarious parasitoid *Aphytis lingnanensis* Compere. Egg load was manipulated without concurrent changes in experience by exploiting size-related variation in fecundity and by holding parasitoids at different temperatures to vary the rate of egg production.

(2) Egg load influenced the intensity of searching behaviour. Parasitoids with smaller egg loads required more time within a foraging arena to discover hosts.

(3) Parasitoids with smaller egg loads and parasitoids with a prior experience with host contact deposited smaller clutches.

(4) Total host handling time was inversely related to parasitoid egg load. Increased egg load had a similar accelerating influence on each of the component activities that comprise host handling, including preparation for oviposition, oviposition, and post-oviposition grooming and resting.

(5) The probability of successful parasitoid egg to adult development was independent of clutch size. Progeny size, however, decreased with increasing number of competing sibs.

(6) *A. lingnanensis* clutch size decisions do not conform to the static expectations of a forager maximizing the fitness gained per egg, per host, or per unit time. Rather, clutch size decisions appeared to be fundamentally dynamic, responding to changes in parasitoid physiology (egg load) and the parasitoid's perception of host availability (experience).

INTRODUCTION

Much effort has recently been devoted to developing optimality models of insect oviposition decisions. Many models developed for phytophagous and entomophagous insect parasites have focused on questions of which hosts to utilize and what clutch size to deposit. Although a variety of modelling approaches have been used, existing models may be broadly grouped by their choice of the parameter to be optimized (the 'currency'): (i) fitness gained per clutch (the single host maximum or 'Lack solution'; Charnov & Skinner 1984, 1985; Parker & Courtney 1984; Waage & Ng

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1984; Godfray 1986; Godfray & Ives 1988; Ives 1989), (ii) the rate of fitness gain (Charnov & Skinner 1984, 1985; Parker & Courtney 1984; Skinner 1985; Charnov & Stephens 1988; Strand & Godfray 1989; Ives 1989), or (iii) lifetime reproductive success (Weis, Price & Lynch 1983; Parker & Courtney 1984; Iwasa, Suzuki & Matsuda 1984; Begon & Parker 1986; Godfray 1986; Mangel 1987a, b, 1989a, b; Godfray & Ives 1988). Existing models therefore represent a hierarchical assemblage of techniques of increasing complexity, and models of different levels of complexity may be best suited for investigating theoretical issues or explaining the details of empirically observed patterns of oviposition.

While the predictions of many models are in agreement, there are some noteworthy exceptions. Dynamic optimization models, which maximize lifetime reproductive success and employ dynamic state variables to describe the changing physiological condition of the foraging insect, predict that optimal decisions may vary over time in response to changing egg load, history of host encounters (henceforth 'experience'), and other variables (Iwasa, Suzuki & Matsuda 1984; Mangel 1987a, b, 1989a, b), whereas the remaining models generally predict fixed, optimal decisions for a host of given quality (e.g. Skinner 1985; Godfray & Ives 1988). Although modifications of models maximizing the rate of fitness gain to include constraints on egg production (e.g. Charnov & Stephens 1988) have yielded predictions approaching those of the dynamic optimization models, differences remain. These differences include not only the details of predicted behaviour but also the expected fitnesses obtained through foraging (Houston & McNamara 1986; Mangel 1989b), and are therefore evolutionarily significant.

These differences are furthermore instructive in that they focus experimental research efforts. Two questions are highlighted. First, do oviposition decisions vary over time? And second, if variation is observed, what are the relative roles of egg load versus experience in shaping behavioural shifts?

A rapidly growing body of observational and experimental evidence suggests that an individual's oviposition behaviour may indeed vary substantially over time. Much of this evidence is derived from host deprivation experiments, in which oviposition behaviour of individuals deprived of host contact is contrasted with that of individuals maintained with hosts (i.e. a qualitative difference in host encounter; Fitt 1986, 1990 and pers. comm.; Pilson & Rausher 1988; Harris & Rose 1989; Odendaal & Rausher 1990; Völkl & Mackauer 1990). Similar experiments have documented behavioural plasticity over a sequence of host encounters following a period of deprivation or in response to variation in the rate of host encounter (i.e. quantitative differences in host encounter; Podoler, Rosen & Sharoni 1978; van Lenteren & DeBach 1981; Ikawa & Suzuki 1982; Singer 1982; Roitberg & Prokopy 1983; Ikawa & Okabe 1985; Simbolotti, Putters & van den Assem 1987; Reeve 1987; Strand & Godfray 1989). These manipulative experiments have been supplemented with observations of oviposition in natural populations, where variation in behaviour has been linked either to weather-induced changes in host access (Root & Kareiva 1984) or variation in egg load (Odendaal & Rausher 1990; Tatar, in press). These host-deprivation and closely allied studies have generally revealed increased host range breadth and/or increased clutch size in response to host deprivation and/or increased egg load. Thus, the question of temporal variability in oviposition behaviour has been answered in the affirmative.

These studies have only partially clarified, however, the relative influence of egg load and experience. Host deprivation protocols generally have simultaneous influences on both egg load and experience. An exception occurs for some proovigenic insects (i.e. insects that complete egg maturation before adult eclosion), where host deprivation enforced after egg maturation has been completed can influence only the forager's experience; differences in behaviour between deprived and non-deprived individuals may therefore be attributed to experience (e.g. Harris & Rose 1989). In addition, some experiments have demonstrated behavioural changes after very brief periods of host deprivation, during which substantial changes in egg load are unlikely to have occurred (e.g. Roitberg & Prokopy 1983); again, these effects may therefore be attributed to experience. In the remaining cases, however, the relative roles of egg load and experience cannot be resolved; in general, host deprivation experiments cannot manipulate egg load without also changing experience. This difficulty is emphasized by the varying interpretations applied to the results of host deprivation experiments, with some authors supporting an exclusive role for egg load (e.g. Fitt 1986, 1990; Simbolotti, Putters & van den Assem 1987; Pilson & Rausher 1988; Odendaal & Rausher 1990), others an exclusive role for experience (e.g. Ikawa & Suzuki 1982; Ikawa & Okabe 1985), and still others a role for both factors (e.g. Harris & Rose 1989; Völkl & Mackauer 1990). Field observations, because they have not controlled for potentially varying histories of host encounter, likewise are unable to isolate the influence of egg load. Thus, host deprivation studies and field observations have not satisfactorily resolved the relative influences of egg load and experience on oviposition decisions, and none of the aforementioned studies has isolated the effect of egg load.

Recent studies have employed quantitative genetic techniques to investigate the influence of egg load on host range. Courtney, Chen & Gardner (1989) and Courtney & Hard (1990) demonstrated significant positive genetic correlations between egg load and acceptance of low-ranking hosts for two *Drosophila* species. Jaenike (1989), however, found the reverse trend in a third *Drosophila* species; fecundity was negatively correlated with acceptance of a less-preferred host. Interpretations of genetic correlations like these must be made cautiously, as significant results could indicate either that linkage disequilibrium exists between loci affecting fecundity and preference or that one of these traits has a significant pleiotropic effect on the other.

Here we attempt to use direct behavioural assays to evaluate the relative influences of egg load and experience on clutch size decisions in the parasitoid *Aphytis lingnanensis s. l.* Compere (Hymenoptera: Aphelinidae). We employ an experimental protocol that manipulates egg load without concurrent changes in history of host contact. The influence of egg load on the intensity of parasitoid searching behaviour and components of host handling time is also investigated. Knowledge of egg load effects on oviposition decisions should contribute to the development and validation of a general model of host range and clutch size determination in insect parasites.

MATERIALS AND METHODS

Life histories and laboratory cultures

The biosystematics, behaviour, and ecology of the genus *Aphytis* have been reviewed by Rosen & DeBach (1979, 1990). *Aphytis* are facultatively gregarious ectoparasitoids of armoured scale insects (Homoptera: Diaspididae), a group of sessile sucking insects that includes many important pests of horticultural or agricultural crop plants (Rosen 1990). Armoured scale insects secrete wax filaments to form a protective covering, the scale cover. *Aphytis* drill through the scale cover with their ovipositors, probe the host's body to arrest host development, and may then deposit one to several eggs on the host's body. *Aphytis* may also feed on host haemolymph after ovipositor probing. Egg to adult parasitoid development occurs under the scale cover.

Tests were performed with a uniparental population of *Aphytis*, morphologically indistinguishable from *A. lingnanensis*. The parasitoid culture was initiated in October 1987 when parasitized hosts, *Aonidiella* sp. growing on mandarin, *Citrus* sp., were collected in the Philippines. Use of a uniparental strain simplified the interpretation of the behaviour assays because parasitoids made clutch size decisions without having to simultaneously allocate sex; optimal sex allocation and optimal clutch size may frequently be interdependent (Godfray 1986). Laboratory *Aphytis* cultures were maintained at 24 ± 1 °C and a photoperiod of 16 L:8 D, parasitizing a biparental strain of the oleander scale, *Aspidiotus nerii* Bouché, grown on butternut squash, *Cucurbita moschata* (Duchesne). The host scale insects used in all behaviour assays were large virgin female third instar California red scale, *Aonidiella aurantii* (Maskell), also grown on butternut squash. Six squash were used sequentially during the assays. Host scale insects were maintained as virgins by caging them individually under one end of a gelatin capsule (size 02) affixed to the squash surface with a ring of adhesive gum ('Blu-Tack', Bostik, Leicester) to prevent male access. Mated female California red scales undergo morphological changes, including sclerotization of the integument, which render them unsuitable as hosts (Baker 1976; J.A.R. unpublished).

Behaviour assay

We first summarize our experimental protocol and the rationale of our experimental design. Our objectives were to provide scale insect hosts of known quality to parasitoids that (i) had a uniform history of host encounter, but different egg loads, and (ii) had different histories of host encounter, and known egg loads. Egg load was manipulated by exploiting size-related variation in fecundity (e.g. Opp & Luck 1986) and by holding parasitoids at different temperatures to vary the rate of egg production. Parasitoids were first confined with a single host, and foraging and oviposition were observed. To avoid the possibility of clutch size decisions being constrained by the lack of additional mature eggs to deposit, parasitoids were then confined with a second host; only parasitoids ovipositing on both hosts were used in the analyses. After parasitizing the second host, *Aphytis* were dissected to quantify egg load. Oviposition on the second host was used as a measure of egg availability in addition to the final dissections to preclude the possibility, suggested for other parasitoids (Donaldson & Walter 1988), that the attainment of the final, mature egg morphology might occur before eggs could be deposited. Finally, to test the influence of the change in the parasitoid's perception of host density that accompanied host contact, clutch sizes allocated to the first and second hosts were contrasted.

We obtained parasitoids with uniform experience but varying egg loads as follows. Parasitoid pupae were collected from under scale covers and held singly in 1·5 ml glass vials provisioned with honey droplets for the emerging adults. By choosing pupae from host scale insects that varied in size and supported different numbers of developing *Aphytis*, we obtained a large range of body sizes. Pupae were checked twice daily. Newly emerged adults collected in the morning (0–12 h after emergence) were sorted by approximate size, and each size-class then divided into two groups to be held for an additional day at 18 ± 1 °C and 26·5 ± 1 °C, respectively, 70 ± 5% r.h., and a photoperiod of 14·5 L:9·5 D. Preliminary experiments had demonstrated that the low-temperature treatment slows egg production.

Parasitoids were tested on the day after the temperature treatments, 08.00–17.00 h. Individuals from the 18 °C treatment were brought to the testing temperature, 26·5 ± 1 °C, at least 30 min prior to testing. Within each day we alternated tests of parasitoids from the two temperature treatments and, to the extent possible, tested individuals of a range of sizes. A small number of emerging parasitoids had obvious mechanical defects (e.g. difficulty in walking), and were excluded from the assays. Parasitoids were transferred into the small end of a gelatin capsule (size 02; diameter 6·5 mm, height 9 mm), which was affixed with adhesive gum to the squash, confining the parasitoid with a single host scale insect. The squash was held under a stereoscope, illuminated with fibre-optic lighting, and parasitoid behaviour observed continuously at 10× magnification.

We measured the time required for the parasitoid to 'discover' the host scale insect as an index of search intensity. We considered hosts discovered when searching parasitoids became arrested on the scale cover and initiated drumming of the scale cover with the antennae. In our experiments host discovery was nearly equivalent to host contact; 96·1% (219 of 228) of all initial contacts with host scale covers resulted in arrestment. This and all other time measurements were made to the nearest second. Trials were terminated after 30 min if parasitoids failed to discover the host.

Parasitoids exhibited stereotyped behaviour upon recognizing the host scale insect. The behaviour we observed was identical to that described for two *Aphytis* species by Luck, Podoler & Kfir (1982). We direct the reader to their study for the details of oviposition behaviour. Our measurements included the following. (i) The duration of 'drumming and turning,' during which the parasitoid drummed the scale with its antennae while walking repeatedly across the scale cover. (ii) The time between the first adoption of the 'drilling' posture (which marked the end of drumming and turning) and the initiation of the oviposition sequence, marked by a series of rhythmic pumping movements. This phase, which we will simply call 'preparation,' included from one to several sequences of drilling and ovipositor probing within the scale insect body. (iii) The duration of oviposition, measured from the initiation of pumping until ovipositor withdrawal, which marked the deposition of a single egg. (iv) The duration of the 'post-oviposition pause,' during which the parasitoid that had just withdrawn her ovipositor groomed or rested before recommencing drumming and turning.

These data were recorded for each oviposition sequence, except that drumming and turning was separated from the other activities comprising preparation only for the initial oviposition. We define total handling time as the time between host discovery and abandonment of the host to resume searching.

Parasitoids completing oviposition on the first host were immediately transferred to a second host. To execute the transfer, parasitoids were lightly touched with a fine brush inserted under the edge of the gelatin capsule, causing them to jump off the squash surface and onto the capsule walls. The gelatin capsule was then repositioned over a second host, and we repeated the same set of observations. The second assay was terminated after 60 min if the host was not discovered. Parasitoids that host fed without ovipositing on the second host were provided with a third host.

Immediately following the assay the dimensions of the round or ellipsoid scale covers were measured with an ocular micrometer to the nearest 0·02 mm; two perpendicular diameters, including the longest diameter if one was apparent, were measured. The scale cover was flipped on the first host to measure body dimensions (length and width), and then replaced. Scale cover and scale insect body areas were calculated as $(\pi/4) \times (\text{length}) \times (\text{width})$, the area of an ellipse. During preliminary experiments and the initial replicates of the main experiment, the body of the first scale insect was also inspected to count *Aphytis* eggs. These inspections revealed that the behavioural observations were a reliable indicator of oviposition (125 observed pumping sequences resulted in the deposition of exactly 125 eggs), and the inspections were therefore discontinued. Parasitoids were frozen immediately following the assay and held for dissection later in the day. The ovaries were dissected from the abdomen in a drop of saline by grasping the ovipositor and terminal abdominal segments and slowly pulling them distally while holding the parasitoid's thorax with a fine needle. Full-sized, mature-form eggs (i.e. elongate-oval eggs with dark cytoplasm, without associated trophocytes, and located at the bases of the ovarioles) were then teased from the ovarioles and counted. To produce an index of parasitoid size, parasitoids were slide mounted, and the lengths of the hind tibiae were measured with an ocular micrometer to the nearest 0·0015 mm and averaged. Parasitoid egg load at the beginning of the assay was calculated as the sum of eggs deposited and eggs counted during dissection. Altogether, 124 replicates were performed.

Influence of clutch size on parasitoid development

To estimate the general form of the relationship between observed clutch sizes and clutch sizes yielding the maximum fitness gain per egg and per host, we monitored developmental mortality rates at different clutch sizes and the size of the resulting offspring. Parasitized scale insects were enclosed under gelatin capsules and held for at least 30 days at 26·5 ± 1 °C, 60 ± 10% r.h. and a 14·5 L:9·5 D photoperiod for development and emergence of parasitoid progeny to be completed. Hind tibiae of emerging adults were measured as before. Developmental mortality was categorized as having occurred during the egg or larval stages (dead larvae were without exception the very small first and second instars) versus the post-feeding stages (prepupa, pupa, and adults that died before exiting from under the scale cover).

Influence of experimental treatments on risk of forager mortality

Theory suggests that clutch size decisions may reflect the forager's risk of mortality (Weis, Price & Lynch 1983; Parker & Courtney 1984; Iwasa, Suzuki & Matsuda 1984; Godfray 1986; Houston & McNamara 1986; Mangel 1987a, b, 1989a, b). We therefore tested the influence of our experimental treatments (parasitoid size and holding temperature) on age-specific mortality rates under laboratory conditions. Parasitoids were prepared exactly as described above for behavioural assays, but were then held individually in 1·5 ml glass vials provisioned with honey-saturated pieces of filter paper at 26·5 ± 1 °C, 60 ± 10% r.h., and a 14·5 L:9·5 D photoperiod.

Vials were checked daily, and dead parasitoids removed to measure hind tibia lengths. Logistical difficulties precluded testing the impact of experimental treatments on parasitoid longevity under field conditions, which would have been preferrable.

Statistical analyses

Polychotomous stepwise logistic regression was used to assess influences on clutch size decisions, with clutch size treated as an ordered variable with four discrete states (for clutch sizes 1–4) (Dixon 1990). This analysis enabled us to assess simultaneously the influences of independent variables that were continuous or approximately continuous (parasitoid size, scale cover area, scale insect body area, egg load) or categorical (temperature treatment, prior history of host contact, squash number). Factors influencing (i) parasitoid discovery of hosts and (ii) successful parasitoid egg to adult development (binary dependent variables) were analysed with stepwise logistic regression. Factors influencing the durations of the various parasitoid behaviour sequences (continuous dependent variables) were analysed with stepwise multiple linear regression. Temperature treatment effects on continuous dependent variables were assessed by grouping data by temperature treatment and then testing the regression equations identified by the stepwise regressions for equality of slopes and intercepts across the temperature groups. The value of the egg load variable was adjusted for each analysis to reflect current egg loads. Unless noted otherwise, means are presented throughout ± 1 S.E.

RESULTS

Treatment effects on egg load

The size and temperature treatments yielded *Aphytis* with a wide range of egg loads (Fig. 1). Strong positive relationships were observed between parasitoid size and egg load. These relationships differed significantly across temperature treatments ($F_{2,\,120} = 58{\cdot}0$, $P < 0{\cdot}001$); parasitoids from the low-temperature treatment had on average 3·0–4·4 fewer eggs than comparably sized parasitoids from the high-temperature treatment.

Treatment effects on risk of mortality

Neither the size nor the temperature treatment had a substantial influence on *A. lingnanensis* mortality rates. Longevity was not significantly related to parasitoid size, although larger parasitoids in both temperature groups lived slightly longer (low temperature: $r = 0{\cdot}25$, $n = 29$, $P = 0{\cdot}19$; high temperature: $r = 0{\cdot}23$, $n = 32$, $P = 0{\cdot}20$). In the only other test of size-specific longevity for an *Aphytis* species, Reeve (1987) also found a non-significant relationship for *Aphytis melinus* DeBach. Parasitoids in the low-temperature group lived slightly longer than those in the high-temperature group (mean longevity = 15·55 days, S.D. = 3·44, and 13·69 days, S.D. = 2·75, respectively), but the best fit size–longevity regressions for the two temperature groups were only marginally significantly different ($F_{2,\,57} = 3{\cdot}15$, $P = 0{\cdot}051$). There was no mortality in either group until day 7, 5 days after the day on which behaviour assays were performed.

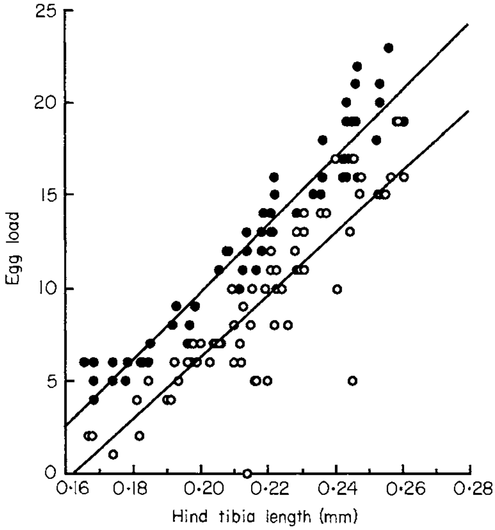

FIG. 1. Influences of the size and temperature treatments on egg load in *A. lingnanensis*. Linear regression for the high temperature group (●, $n = 60$): egg load = 181·8(hind tibia length) − 26·7; $r^2 = 0{\cdot}92$, $P < 0{\cdot}0001$; for the low temperature group (○, $n = 64$): egg load = 166·9(hind tibia length) − 27·2; $r^2 = 0{\cdot}75$, $P < 0{\cdot}0001$.

Searching activity

Parasitoids with small egg loads had a significantly reduced probability of discovering the first host during the 30-min assay (stepwise logistic regression: improvement $\chi^2 = 5{\cdot}8$, $P = 0{\cdot}016$; mean egg load of successful searchers and parasitoids failing to discover the host were 11·4 ± 0·47, $n = 109$, and 8·07 ± 1·67, $n = 15$, respectively). Parasitoid size, temperature treatment, and squash number had non-significant effects ($P > 0{\cdot}5$ for all variables). Although not quantified, unsuccessful searchers were observed to spend most or all of the 30-min assay period grooming or resting. Among parasitoids that searched successfully, however, none of the variables (egg load, parasitoid size, temperature treatment, and scale cover area) had a significant influence on the time required to encounter the first host (stepwise multiple linear regression, $P > 0{\cdot}5$ for all variables).

Only three of 108 parasitoids failed to discover the second host during the 60-min assay. Although the small number of unsuccessful foragers precluded a detailed analysis, the three parasitoids had some of the smallest egg loads (2, 3 and 6 eggs). Furthermore, parasitoids with smaller egg loads required substantially longer to locate the second host (Fig. 2, Table 1); these parasitoids were again observed to spend more time grooming and resting. Larger scale insects were also discovered more rapidly, while parasitoid size and temperature treatment had non-significant effects (Table 1; influence of temperature: $F_{3,\,97} = 0{\cdot}3$, $P > 0{\cdot}5$).

Clutch size decisions

All *Aphytis* ($N = 102$) discovering the first host oviposited, depositing clutches of

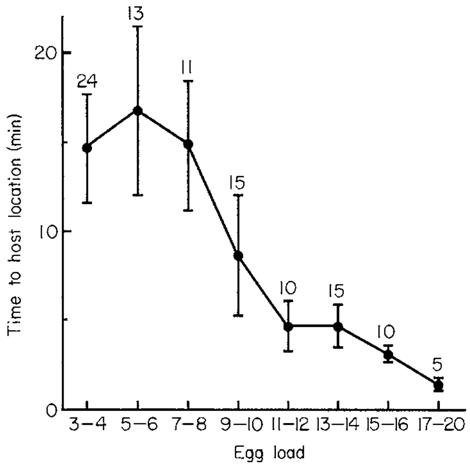

FIG. 2. Influence of egg load on the time required to discover the second scale insect host. Shown are the mean search times ± 1 S.E.; numbers above the S.E. bars are sample sizes.

TABLE 1. Stepwise multiple regression of factors influencing the time required for searching *A. lingnanensis* to locate the second scale insect host. Significant independent variables are listed in order of incorporation into the regression model

Independent variable	*B*	Partial correlation	*F* to enter	*P*
Egg load	−1·11	−0·42	18·5	<0·001
Scale cover area	−7·69	−0·20	4·0	0·05
Hind tibia length	77·6	0·08	0·7	N.S.

y-intercept = 40·6; total $r = 0·43$.
N.S., not significant.

one ($n = 3$), two ($n = 44$), three ($n = 53$), or four ($n = 2$) eggs. The stepwise polychotomous logistic regression identified egg load as the primary determinant of clutch size (Table 2a, Fig. 3a); *Aphytis* with larger egg loads deposited larger clutches. The proportion of parasitoids depositing clutches of 1 or 2 eggs decreased from 27/34 (79%) among females with the smallest egg loads (4–8 eggs) to 1/11 (9%) among females with the largest egg loads (19–23 eggs).

Scale cover area was also an important determinant of clutch size (Table 2a, Fig. 4); larger scale insects received larger clutches. The choice of extreme clutch sizes (clutch = 1 or 4) in particular appeared to be linked to encounters with the smallest or largest hosts. Within the relatively narrow range of host sizes used in our assays, scale cover area and scale insect body area were only modestly correlated ($r^2 = 0·32$, $N = 108$); Hare, Yu & Luck (1990) reported even lower correlations for mature female California red scale grown on *Citrus* spp. hosts. The observation that clutch size was strongly influenced by scale cover area but independent of scale

TABLE 2. Stepwise polychotomous logistic regression of factors influencing clutch size choice by *A. lingnanensis*

(a) First host

Step number	Variable entered	Coefficient (± S.E.)*	d.f.	Improvement χ^2	P
1	Egg load	0·197 ± 0·053	1	23·6	< 0·001
2	Scale cover area	3·30 ± 0·85	1	15·4	< 0·001
3	Temperature	1·14 ± 0·49	1	5·7	0·017

Variables not entered	d.f.	Approximate χ^2 to enter	P
Hind tibia length	1	0·5	0·50
Scale body area	1	1·1	0·29
Squash number	5	5·0	0·42

(b) Second host

Step number	Variable entered	Coefficient (± S.E.)*	d.f.	Improvement χ^2	P
1	Egg load	0·232 ± 0·067	1	14·3	< 0·001

Variables not entered	d.f.	Approximate χ^2 to enter	P
Temperature	1	0·2	0·68
Hind tibia length	1	0·3	0·58
Scale cover area	1	2·5	0·12
Squash number	5	3·0	0·70

* Coefficients (b_i) of the logistic equation; proportion of clutches greater than size j, $P(\text{clutch} > j) = e^u/(1 + e^u)$, where $u = b_0 + b_1x_1 + b_2x_2 + \ldots + b_nx_n$, and x_i is the independent variable. Scale cover area coded in mm^2 and temperature as a categorical variable (low temperature = 0, high temperature = 1).

insect body area (Table 2a) suggests that external (scale cover), rather than internal (scale body), cues may be of primary importance in the assessment of host size by *A. lingnanensis*.

The remaining independent variables had either no effect (hind tibia length, squash number) or a small effect (temperature treatment) on clutch size. However, when the analysis was repeated withholding egg load as an independent variable, the two 'treatment' variables became highly significant (temperature treatment: improvement $\chi^2 = 12{\cdot}5$, $P < 0{\cdot}001$; hind tibia length: improvement $\chi^2 = 12{\cdot}1$, $P < 0{\cdot}001$). Thus, the treatments did exert significant influences on clutch size decisions, but were doing so indirectly through their influence on egg load. Finally, when the analysis was repeated with parasitoid hind tibia length forced into the model at the first step, the final model retained the key effects of egg load (improvement $\chi^2 = 18{\cdot}2$, $P < 0{\cdot}001$) and scale cover area (improvement $\chi^2 = 15{\cdot}6$, $P < 0{\cdot}001$), but the small effect for the temperature treatment was replaced by a small effect for hind tibia length (improvement $\chi^2 = 4{\cdot}5$, $P = 0{\cdot}033$).

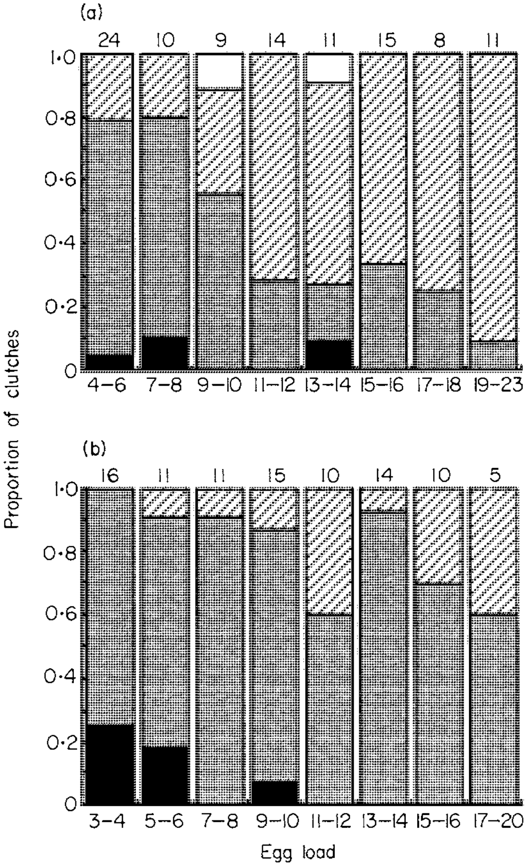

Fig. 3. Influence of egg load on clutch size decisions in *A. lingnanensis*. Clutch size = four (□), three (▨), two (□) or one (■). Numbers above columns are sample sizes. (a) First host, (b) second host.

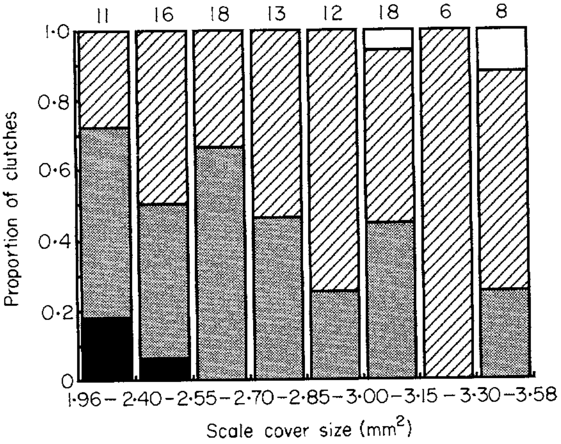

Fig. 4. Influence of scale cover area on clutch size decisions in *A. lingnanensis*; first host. Clutch size = four (□), three (▨), two (□) or one (■). Numbers above columns are sample sizes.

Aphytis discovering the second host showed four classes of responses: oviposit only ($n = 95$); oviposit and host feed ($n = 3$); host feed only ($n = 3$); and host rejection ($n = 1$). Analysis of clutch size allocation to the second host was performed with only those parasitoids that oviposited without host feeding and that were still carrying at least three mature-form eggs (three eggs was the largest clutch deposited on the second host). Parasitoids with fewer than three eggs were excluded to reduce the likelihood that clutch size decisions observed had been constrained by egg availability. Although we cannot completely exclude the possibility that some mature-appearing eggs were not ready to be deposited, our observations of females who deposited their entire complement of 4–5 eggs during the assays ($n = 2$) or who deposited 3–5 eggs and retained only a single additional mature-form egg ($n = 8$) suggest that egg counts were good estimates of true egg availability.

Aphytis deposited clutches of one ($n = 7$), two ($n = 71$), or three ($n = 14$) eggs on the second host. Egg load was identified as the sole significant influence on clutch size (Table 2b, Fig. 3b); females with larger egg loads deposited larger clutches. Withholding the egg load variable and repeating the analysis resulted in hind tibia length becoming significant (improvement $\chi^2 = 8{\cdot}0$, $P = 0{\cdot}004$) and the temperature treatment marginally significant (improvement $\chi^2 = 3{\cdot}2$, $P = 0{\cdot}08$). When the analysis was repeated with hind tibia length forced into the model at the first step, the final model still identified egg load as the sole significant influence on clutch size; once the egg load variable was incorporated into the model the contribution of hind tibia length became non-significant ($P = 0{\cdot}6$). Scale cover area and squash number were non-significant in all analyses. Oviposition on the second host therefore confirmed the key conclusion derived from oviposition on the first host, namely that egg load, as influenced by parasitoid size and temperature treatment, was the main determinant of clutch size.

The influence of experience on clutch size was tested by comparing clutch sizes allocated to the first and second hosts. We treated each parasitoid encounter with a host as a replicate, and included in the analysis an additional binary independent variable: prior experience with a host. Parasitoids with egg loads < 4 were excluded. In addition to reiterating the previously identified influences of egg load and scale cover area, a stepwise polychotomous logistic regression identified experience as a significant factor shaping clutch size decisions (Table 3). Because the analysis explicitly incorporates the effect of egg load, we conclude that the experience of contacting the first host, independent of the decrease in egg load resulting from oviposition, contributes to the trend of decreasing clutch sizes that occurred across the two host encounters (Fig. 3a, b).

Handling time

Total host handling time was inversely related to egg load and positively related to clutch size deposited for both the first and second hosts (Table 4a, b). Parasitoid size influenced handling time for the first host, but not the second. As expected, more time was required to deposit more eggs. Less predictably, as egg load increased mean handling time decreased by 49·0% and 57·8% for clutches of two and three eggs on the first host, respectively (Fig. 5a), and by 60·0% for clutches of two eggs on the second host (Fig. 5b).

To determine if egg load was influencing total handling time through an effect on

TABLE 3. Stepwise polychotomous logistic regression of factors influencing clutch size choice by *A. lingnanensis*; oviposition on the first and second hosts considered together

Step number	Variable entered	Coefficient (± S.E.)*	d.f.	Improvement χ^2	*P*
1	Egg load	0·385 ± 0·082	1	41·1	< 0·001
2	Experience	−1·14 ± 0·39	1	23·8	< 0·001
3	Scale cover area	2·39 ± 0·59	1	16·5	0·001
4	Hind tibia length	−33·2 ± 14·3	1	5·4	0·02

Variables not entered	d.f.	Approximate χ^2 to enter	*P*
Temperature	1	0·6	0·45
Squash number	5	2·8	0·73

* Experience coded as a categorical variable (no previous host contact = 0, one previous host contact = 1); hind tibia length coded in mm. See footnote to Table 2 for additional information.

TABLE 4. Stepwise multiple regression of factors influencing total host handling time in *A. lingnanensis* ($N = 108$). Significant independent variables are listed in order of incorporation into the regression model

(a) First host

Independent variable	*B*	Partial correlation	*F* to enter	*P*
Egg load	−0·86	−0·46	28·5	< 0·001
Clutch size	2·15	0·29	7·2	< 0·01
Hind tibia length	69·6	0·22	5·2	0·02
Scale cover area	−0·21	−0·02	0·0	N.S.
Scale body area	1·07	0·04	0·1	N.S.

y-intercept = 1·35; total $r = 0·55$.
N.S., not significant.

(b) Second host

Independent variable	*B*	Partial correlation	*F* to enter	*P*
Egg load	−0·71	−0·52	24·2	< 0·001
Clutch size	3·20	0·28	8·1	< 0·01
Hind tibia length	3·80	0·01	0·0	N.S.
Scale cover area	0·43	0·02	0·1	N.S.

y-intercept = 9·90; total $r = 0·52$.
N.S., not significant.

a specific element of the behaviour sequence comprising host inspection, preparation, and egg deposition, handling time was divided into more narrowly defined activities, which were then used as dependent variables in a series of regression analyses (Table 5). Egg load was the most important influence on all of the component activities; parasitoids with larger egg loads showed accelerated drumming and turning,

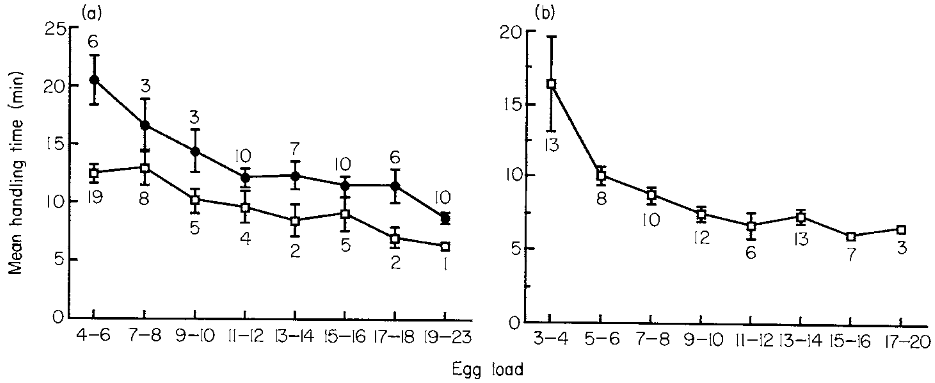

FIG. 5. Influence of egg load on host handling time. Shown are the mean handling times ± 1 S.E.; numbers above or below the S.E. bars are sample sizes. Clutch size = two (□) or three (●). (a) First host, (b) Second host.

TABLE 5. Stepwise multiple regression of factors influencing the time required for *A. lingnanensis* to complete component tasks of total host handling. Tasks are listed in order of execution; numbers appended to task names refer to the deposition of successive eggs. Independent variables: EL, egg load; HTL, hind tibia length; SCA, scale cover area; SBA, scale insect body area; T, temperature. Regressions performed only when sample sizes >40. Criterion for statistical signficance, $P < 0{\cdot}05$

Task	Mean duration (min, ± S.D.)	*N*	Significant variables	Partial correlation	Non-significant variables
(a) First host					
Drumming and turning	0·46 ± 0·22	108	–	–	EL, HTL, SCA, SBA
Preparation-1	5·23 ± 4·07	108	EL	−0·46	SCA, SBA, T
			HTL	0·27	
Oviposition-1	0·80 ± 0·21	97	EL	−0·27	HTL, SCA, SBA, T
Post-oviposition pause-1	0·48 ± 1·13	94	EL	−0·28	HTL, SBA, T
			SCA	−0·24	
Preparation-2	2·45 ± 1·08	91	EL	−0·39	HTL, SCA, SBA, T
Oviposition-2	0·67 ± 0·16	90	HTL	−0·27	EL, SCA, SBA, T
Post-oviposition pause-2	0·17 ± 0·33	49	EL	−0·56	HTL, SCA, SBA, T
Preparation-3	2·47 ± 1·16	48	EL	−0·48	HTL, SCA, SBA, T
Oviposition-3	0·81 ± 0·41	50	EL	−0·33	HTL, SCA, SBA, T
(b) Second host					
Drumming and turning	0·47 ± 0·62	99	EL	−0·23	HTL, SCA, T
Preparation-1	4·59 ± 3·10	96	EL	−0·60	HTL, SCA, T
Oviposition-1	0·86 ± 0·22	89	HTL	−0·48	EL, SCA, T
Post-oviposition pause-1	0·70 ± 3·32	80	EL	−0·26	HTL, SCA, T
Preparation-2	2·30 ± 1·39	78	HTL	−0·38	EL, SCA, T
Oviposition-2	0·81 ± 0·48	79	SCA	0·33	EL, HTL
			T	–	
Post-oviposition pause-2	0·16 ± 0·16	14	–	–	–
Preparation-3	2·19 ± 1·06	13	–	–	–
Oviposition-3	1·38 ± 2·02	13	–	–	–

preparation, oviposition, and post-oviposition pauses. Oviposition times showed the least variability and also the weakest evidence of being influenced by egg load; larger parasitoids may also have oviposited more rapidly. Egg load appears to influence total handling time through a pervasive effect on the level of parasitoid activity rather than a specific influence on a narrowly defined behaviour sequence.

Clutch size and parasitoid development

Of 286 deposited eggs whose development was monitored, 114 died in the egg or early larval stages, 11 died in post-feeding stages, and 161 successfully emerged as adults. Treating these three outcomes as ordered values of a discretely distributed developmental success variable, a stepwise logistic regression identified only squash number as a significant predictor variable (Fig. 6; improvement $\chi^2 = 30{\cdot}7$, $P < 0{\cdot}0001$). Clutch size, scale cover area, and whether the scale cover had been flipped and replaced did not produce significant effects ($P < 0{\cdot}3$ for all variables). We were unable to discern what determined a squash's suitability for parasitoid development; scale insects developed and reproduced normally on all squash, and mean scale cover area per squash was not correlated with overall per cent successful parasitoid development per squash (Kendall's rank correlation coefficient $= -0{\cdot}40$, $n = 5$, $P > 0{\cdot}10$).

Because of the high incidence of parasitoid mortality in the egg and early larval stages, primary clutch size was a poor index of the amount of competition for food experienced by developing larvae (correlation between primary clutch size and number of larvae completing the larval feeding stages, $r = 0{\cdot}48$). To assess the influence of competition on resulting adult parasitoid size, we therefore used the number of sibs successfully developing through the feeding stages (larval instars 1–3) as an index of competition. Total per cent developmental success observed per squash was used as a measure of squash quality. Stepwise linear regression identified the competition variable as the sole significant influence on parasitoid

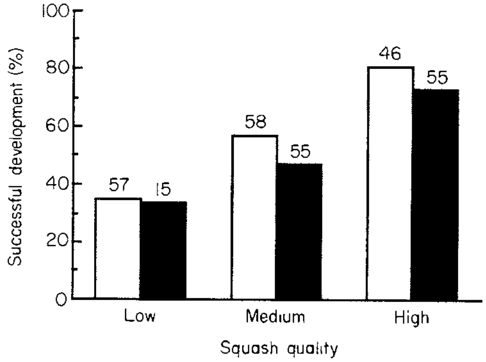

FIG. 6. Influence of squash number and clutch size on percentage of *A. lingnanensis* eggs successfully developing to emerged adults. Clutch size = 1–2 (□) or 3–4 (■). Squash were grouped into quality classes by overall per cent successful development: low quality (squash 1; 33·3% development; squash 2, 36·7% development), medium quality (squash 3, 57·1% development; squash 5, 49·3% development), and high quality (squash 4, 76·2% development).

size (Fig. 7; $F = 93{\cdot}6$, $r = 0{\cdot}62$, $P < 0{\cdot}0001$; regression equation: parasitoid size $= (-0{\cdot}0223)(\text{sib number}) + 0{\cdot}245$). Of the remaining variables, clutch size, scale cover area, and whether the scale cover had been flipped and replaced were non-significant ($P > 0{\cdot}05$); squash quality was marginally significant (partial correlation coefficient, $r = -0{\cdot}14$; $0{\cdot}10 < P < 0{\cdot}05$).

DISCUSSION

Our experimental design has enabled us to distinguish the effects that egg load and experience have on clutch size decisions in *A. lingnanensis*. Our main result is that both factors operate: parasitoids with fewer eggs and parasitoids with a recent experience of host contact deposited smaller clutches. The experimental treatments used to manipulate egg load (parasitoid size and holding temperature) had little or no direct effect on clutch size decisions, but rather operated indirectly through their influence on egg load. Egg load was additionally found to modulate parasitoid searching activity and a suite of activities comprising host handling; in all cases parasitoids with larger egg loads showed an accelerated completion of tasks.

Clutch size and lifetime reproduction

Our results suggest that *A. lingnanensis* clutch size decisions do not conform to the static expectations of a forager maximizing the fitness gained per clutch or per unit time. Rather, clutch size decisions appear to be fundamentally dynamic, responding to changes in physiology (egg load) and the parasitoid's perception of local host availability (experience).

The observed pattern of decreasing clutch sizes with decreasing egg load is as predicted by dynamic optimization models for parasitoids maximizing lifetime reproductive success (Iwasa, Suzuki & Matsuda 1984; Mangel 1987a, b, 1989a, b), given the key assumption of fitness increments that decrease as the number of eggs deposited on a host increases. Our data on parasitoid development support this assumption for *A. lingnanensis*; although survivorship was approximately constant

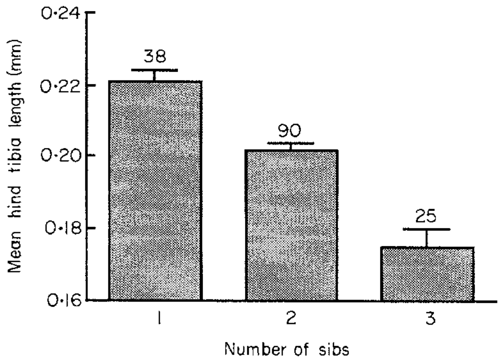

FIG. 7. Influence of the number of parasitoid sibs developing on a host through the larval feeding stages on the size of the resulting adults. Shown are mean hind tibia lengths ± 1 S.E; numbers above the S.E. bars are sample sizes.

over clutches of 1–4, the size of resulting adults showed a monotonic decrease (Fig. 7). Given the observed relationship between size and parasitoid fecundity (Fig. 1), total fitness obtained per host appears likely to exhibit a maximum at some intermediate clutch size.

However, neither the data collected here nor those obtained for any other insect parasite permit the precise calculation of the clutch size producing the single host maximum fitness, or Lack solution. To do this requires not only a knowledge of developmental mortality rates at different clutch sizes and the size of resulting offspring (relationships that may be estimated in the laboratory), but also a knowledge of the relationship between size and lifetime reproductive success, which can only be measured meaningfully in the field. For female parasitoids, the final form of the size–fitness relationship will reflect the relationships between size and fecundity, longevity, and foraging ability. Estimating the size–fitness relationship for males may also be quite difficult (e.g. van den Assem, van Iersel & Losden Hartogh 1989).

Although the relationship between a female parasitoid's size and fecundity provides some insight into the maximum fitness that a female of a given size may realize, it does not describe the relationship between female size and expected fitness, which will depend on the likelihood that the reproductive success of females in some part of the size distribution becomes limited by egg supply (Begon & Parker 1986). The substitution of the size–fecundity relationship for the size–fitness relationship in calculations of Lack solution clutch sizes rests upon the implicit assumption that all females live to deposit their total complement of eggs. This assumption will be violated in species for which time constraints may limit lifetime reproduction; in these species, individuals with relatively smaller egg loads may expect to deposit a greater proportion of their total egg production than individuals with larger egg loads, assuming equality of expected longevity. Time limitation may be important in some phytophagous insects; for example, Dempster (1983) reviewed data for several species of Lepidoptera where long-term ecological studies identified failure of females to deposit their full complement of eggs as a 'key factor' generating changes in population density. Although no studies have assessed the question of time versus egg limitation for entomophagous parasitoids, the increased difficulty of finding insect hosts as compared to plant hosts suggests that egg limitation may be a less general phenomenon, perhaps occurring only in areas or times of great host abundance. Finally, calculation of the Lack solution is further complicated by the observation that the size–fecundity relationship may itself respond to variation in field conditions, e.g. the availability of food for adult parasitoids (Takagi 1985). Quantifying the incidence of egg versus time limitation and measuring the relationship between size and lifetime reproductive success are, we feel, important areas for additional research in parasitoid evolutionary biology.

Despite these difficulties, we propose a simple interpretation of the observed clutch size variation in *A. lingnanensis*. Parasitoids maximizing lifetime reproductive success should choose clutch sizes from a range of values whose minimum corresponds to the clutch yielding the maximum fitness per egg (here apparently realized when eggs are deposited singly) and whose maximum corresponds to the maximum fitness per host (the Lack solution, here apparently realized for clutches of three or perhaps greater), assuming that the time required to deposit eggs is trivial compared to the time required to locate a host. The actual choice should depend on what the parasitoid perceives as its risk of being egg-limited versus its risk of being time-limited. Factors tending to increase the likelihood of being time-limited (e.g. low host density, high predation rates, or large egg loads) will favour the choice of larger clutch sizes. Factors tending to increase the likelihood of being egg-limited (the opposite of those just listed; i.e. high host density, low predation rates, or low egg loads) will favour the choice of smaller clutch sizes. The models of Iwasa, Suzuki & Matsuda (1984) and Mangel (1987a, b, 1989a, b) suggest how optimal clutch size decisions may be made within this framework. Here we have shown that *A. lingnanensis* does decrease clutch size in response to two factors that will increase the risk of becoming egg limited: (i) low initial egg load, and (ii) the increase in perceived host density that accompanies host contact.

Search intensity and host handling time

Foraging theory has been developed for animals facing a variety of trade-offs between competing activities (Mangel & Clark 1986; Stephens & Krebs 1986); for example, Mangel (1987b) has modelled parasitoids choosing between foraging for oviposition sites and foraging for feeding sites. However, existing models do not appear to predict the decreased search intensity (Fig. 2) or the increased handling times (Fig. 5, Table 5) associated with decreased egg loads in *A. lingnanensis*. Similar changes in search intensity have been observed for a number of phytophagous and entomophagous insect parasites in response to some (unresolved) combination of egg load and oviposition experience (Jones 1977; Pak *et al.* 1985; Collins & Dixon 1986; Donaldson & Walter 1988; Odendaal 1989; Trudeau & Gordon 1989; Odendaal & Rausher 1990).

Changes in search intensity or handling time may have important effects on the population dynamics of host–parasitoid interactions. Decreased search intensity and increased handling times associated with falling egg load alter the parasitoid's functional response, decreasing the parasitoid's ability to respond to increased host density with increases in the number of hosts parasitized. For gregarious parasitoids, this process may be counterbalanced in part by the tendency to decrease clutch size as egg load decreases or host encounter rate increases, enabling parasitoids to spread a fixed number of eggs over a larger number of hosts. Because of the central importance of the functional response curve in (i) determining the equilibrium levels and stability of host and parasitoid population densities (Hassell 1978), and (ii) translating patterns of density-dependent parasitoid foraging into patterns of density-dependent parasitism (Hassell 1982; Rosenheim 1990), additional research efforts, both empirical and theoretical, investigating the role of egg load on functional response parameters seem justified.

Implications for studies of insect learning

Our observation that egg load and experience influence foraging and oviposition in *A. lingnanensis* has ramifications for the design and interpretation of experimental studies of insect learning. The role of learning in shaping insect parasite behaviour has recently become the focus of intense research efforts (reviewed by Papaj & Prokopy 1989). Many, perhaps most, learning experiments use a protocol in which insects are given an opportunity to learn characteristics of the host or host microhabitat while parasitizing the host. Such protocols potentially confound learning effects with two other processes: first, changes in the insect's perception of local host density ('experience') and second, changes in the insect's egg load. This problem can be minimized in some cases by experimental designs using reciprocal exposures to different host types (e.g. Papaj *et al.* 1989), but in many cases it may be difficult to fully disentangle the influences of learning, experience, and egg load. All three represent mechanistic explanations for shifts in insect behaviour. This inherent ambiguity is exemplified by our evolving understanding of the observation that individual insect parasitoids may alter their tendency to superparasitize hosts. Temporal changes in superparasitism were initially regarded as examples of learning, but more recently have been reinterpreted as examples of conditional strategies based on host availability (Ikawa & Suzuki 1982; van Alphen & Visser 1990). Still unclear is the relative importance of experience and egg load in altering the threshold (*sensu* Singer 1982; Courtney, Chen & Gardner 1989), for accepting previously parasitized hosts. An awareness of the potentially important influence of egg load on insect behaviour should permit the design of readily interpreted experiments in insect learning.

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