

## Evolution of clutch size in insects. II. A test of static optimality models using the beetle *Callosobruchus maculatus* (Coleoptera: Bruchidae)

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### Abstract

Wilson and Lessells (1993) analysed the effect of constraint assumptions on the predictions of static optimality models for insect clutch size. They concluded that the models could be reliably distinguished between (and hence the main constraints identified) only after precise quantitative predictions had been examined. The present paper describes a series of laboratory experiments, using the bruchid beetle *Callosobruchus maculatus*, that allow these quantitative predictions to be made and tested. Experiments in which female encounter rate with hosts was altered gave qualitative support for 3 out of 6 basic (single oviposition) models, but the quantitative fit of them all was poor. However, when the (*a priori*) condition was included in these models that several other females would oviposit on the same hosts (the multiple oviposition models), the time limiting multiple oviposition model alone produced quantitative predictions that were supported by observations. In other words, the results suggest that the main constraints on bruchid oviposition behaviour are the amount of time available for laying eggs and the number of other females ovipositing. However, additional qualitative predictions indicate that the number of eggs available to the female may also constrain clutch size evolutionarily. The usefulness of static optimality models for examining clutch size decisions in insects is discussed in the context of these results.

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## Introduction

Proponents of optimality theory often cite the success of insect clutch size models in support of their cause (e.g. Endler, 1986) despite the fact that, almost without exception, the evidence does not hold up to quantitative inspection (Godfray, 1987; Lessells, 1991). Moreover, as two recent reviews have emphasised, models based on very different assumptions concerning the evolutionary constraints on clutch size may make similar qualitative predictions (Godfray, 1987; Wilson and Lessells, 1994). For example, most of these models predict that clutch size will never exceed that which is most productive and, given that the ovipositing insect exhibits appropriate adaptive phenotypic plasticity (Wilson and Lessells, 1994) that clutch size will increase with host value and decrease with host encounter rate and number of ovipositing females. Qualitative support for most of these predictions has been obtained from within the Lepidoptera, Diptera, Hymenoptera and Coleoptera (see Godfray, 1987 and references therein). However, I know of only one study providing quantitative data implicating any of the models that predict an optimal clutch size of greater than one egg per host: Godfray (1986) demonstrated that the most common clutch size for the leaf-mining fly *Pegomya nigratarsis* ovipositing in the field (3 eggs/host) was also the most productive. However, the importance of this result is tempered by the fact that the most productive clutch size coincides with that giving the highest *per capita* fitness to offspring, and therefore all of the models make the same prediction.

Both Godfray (1987) and Wilson and Lessells (1994) conclude their reviews of invertebrate clutch size models by emphasising the importance of testing quantitative, as well as qualitative, predictions. The present paper describes a series of laboratory experiments, using the bruchid beetle *Callosobruchus maculatus*, that not only provide the fundamental data required to make such predictions but also enable quantitative comparisons to be made between observed behaviour patterns and those predicted by the different models. It is stressed that the purpose of this and similar studies is not to test the so-called 'adaptationist paradigm', as has sometimes been suggested (Lewontin, 1983; Pierce and Ollason, 1987), but to determine the major evolutionary constraints on behaviour and so gain insights into the main selection pressures acting on the organism (see e.g. Cheverton et al., 1985).

### *The Study Animal*

*C. maculatus* is a small and economically important pest of pulses in seed stores throughout the tropics and sub-tropics. Female beetles lay their eggs singly on to the testae of host seeds and, after three or four days, the first instar larva burrows through the egg chorion directly into the cotyledon on which it will feed. The larva continues feeding within the seed chosen by its mother until pupating at about 26 days of age (Bellows, 1982a). Two days later, the mature adult ecloses and the cycle is completed. Reproductively mature adults emerge weighing 2–10 mg wet weight and usually live for 7–10 days (but virgins may live for up to three times as long;

present study). Both sexes will mate within an hour of emergence from the seed, and females start laying the first of their (80 or more) eggs soon after this (El-Sawaf, 1956). Clutch sizes usually range between 1 and 10 eggs per seed-visit, but females may lay their entire egg-complement on a single seed, over several visits, if no others are provided (personal observation).

As the number of larvae per seed increases so too does the amount of competition between larvae for food. Larval competition is reflected not only in reduced *per capita* survival but also in reduced emergence weights, and hence realised fecundities (Smith and Lessells, 1985; Credland et al., 1986, present study). The number of female offspring emerging from a seed multiplied by their potential fecundities is sometimes referred to as 'total offspring fitness' (Smith and Lessells 1985, Wilson and Lessells, 1994). The definition of total offspring fitness used in the present study does not include the effects of larval competition on male offspring and it is assumed that competition affects the sexes to an equal extent. A consequence of larval competition is that the rate at which an ovipositing female accrues fitness declines as clutch size increases. This trajectory of fitness gain is often referred to as the 'larval competition curve' (Smith and Lessells, 1985; Credland et al., 1986; Wilson and Lessells, 1994).

### *The Approach*

The models described by Wilson and Lessells (1994) vary in the evolutionary constraints they incorporate. These constraints can be divided into 4 main types: those associated with larval competition (the trade-off between the number and fitness of offspring); those associated with limiting resources (such as oviposition sites, time, eggs, reserves or any combination of these); those associated with multiple oviposition (the presence of other ovipositing females) and those associated with the behaviour and physiology of the insects (such as information constraints).

The major differences between these models concern the primary limiting resource(s) and Wilson and Lessells (1994) discuss the importance of these limiting resources to the qualitative predictions of the models. However, as these authors emphasise, quantitative differences in the models' predictions can be established only after careful experimentation. For example, it is first necessary to describe the relationship between the fitness pay-off to the female (total offspring fitness) and the limiting resource (hosts, eggs, time, etc.; see Wilson and Lessells, 1994). This involves determining the shape of the larval competition curve; defining the relationship between clutch size and time spent ovipositing; and specifying an energetic conversion rate between time and eggs. Once this has been done, quantitative predictions can be made for each of the models with respect to travel time between oviposition sites ( $T_i$ ), number of ovipositing females ( $i$ ) and residual egg-complement ( $E(t)$ ) and lifespan ( $T(t)$ ). The response to egg-load and host value has been published elsewhere (Messina and Renwick, 1985; Wilson, 1988, 1989, in preparation; see also Avidov et al., 1965) and will not be addressed here. The criterion of success for this study is that a single optimality model is implicated by both the quantitative and qualitative predictions.

## Materials and methods

### *General methods*

The beetles used in the present study are of Brazilian origin and have been cultured, using the same techniques, for at least 150 generations (see Bellows 1982a, b). The strain is the same as that used by Bellows (1982a, b) and Wilson (1988, 1989; Wilson and Hill, 1989). All stocks were maintained on cowpeas (black-eyed beans), *Vigna unguiculata*, in a constant environment room at  $30 \pm 1^\circ \text{C}$  with a 16 h light: 8 h dark photoperiod. Unless otherwise stated, all experiments were performed at 70% r.h.

Virgin females of known maximum age were obtained by isolating individual seeds containing pre-emergence adults in (8 cm<sup>3</sup>) cells of square repli dishes (Gallenkamp Ltd., Loughborough, U.K.) the requisite time before the start of the experiment. All females that were found alone in a cell were then of known maximum age and oviposition experience, and were virgins. Females were generally mated to virgin males of similar age.

Emergence weight or elytral length was used as a measure of body size, as convenient. Body weights were measured within 12 h of emergence, to the nearest 0.001 mg, using a Cahn 29 automatic electrobalance, after first anaesthetising the insects with carbon dioxide for several minutes. Elytral lengths were measured less than 12 h after death, to the nearest 0.025 mm, using a stage microscope and micrometer eye-piece. Emergence weight and elytral length are strongly correlated ( $r^2 = 0.87$ ,  $n = 28$ ,  $P < 0.001$ ).

### *Predicting Optimal Clutch Sizes*

For all of the models described by Wilson and Lessells (1994), optimal clutch sizes can be determined once the relationship between total offspring fitness and either the number of eggs laid per seed-visit or the amount of time spent ovipositing per seed-visit has been determined. If the rate of egg-laying is known, then only one of the relationships need be measured.

Although all components of the larval competition curve can be measured in a single experiment, it is usually more practical to do it in two or more. In the present study, Experiment 1 measured the number and weight of females emerging as a function of the number of larvae per seed, and Experiment 2 measured female fecundity as a function of emergence weight.

Three more pieces of information are required before predictions can be made for all of the models: the cost of reproduction in terms of the reduction of longevity for each egg laid (Expt. 3); mean oviposition time; and the effect of travel time and clutch size on this mean (both Expt. 4).

*Experiment 1. Effects of larval competition:* In order to measure the effects of larval competition on survival, sex ratio and emergence weight, a range of egg-loads was generated by placing varying numbers of recently emerged adults (about 16, 80

130 and 200) into 400 ml plastic containers with approximately 100 cowpeas. The adults were removed after one day and all the seeds kept for a week before being categorised according to the number of hatched eggs on their surface. Each seed was kept separately at 30° C and 35% r.h. until all adults had emerged. The date that each beetle emerged from the seed, its sex and emergence weight were noted. Egg-loads up to twenty were produced in this experiment and although they were all naturally generated, manipulated egg-loads produce similar trends (Wilson, 1989, in preparation).

*Experiment 2. Effect of female emergence weight on realised fecundity:* Fourteen females were weighed at emergence and retained in a 50 ml container with a male until the female died. The pair was provided with 4 fresh seeds daily and the number of eggs laid during the previous day counted, so that lifetime egg-production could be determined.

*Experiment 3. Cost of reproduction:* The cost of reproduction was determined by experimentally manipulating the number of eggs laid by females through the availability of mates and oviposition sites. Four experimental treatments were set up: group 1 females were given a single mate for the duration of the experiment and four pristine seeds each day; group 2 females were given a mate but no seeds; group 3 females were allowed to mate once, then the male removed and the female given 4 new seeds each day; and group 4 females were mated once and given no seeds on which to oviposit. The experiment was conducted at 30° C and 35% r.h. Each female was checked twice daily (at 0830 and 2030 h) so that longevity was determined to the nearest half-day, and the number of eggs laid by each female, on both seeds and the container, was determined.

*Experiment 4. Effect of travel time and clutch size on oviposition time:* Eighteen hour old virgin females were mated and two hours later given a seed on which to lay. When the female left the seed and walked at least one seed-length away, the clutch was deemed complete and the cowpea removed and its egg-load determined. Subsequent seeds were presented to females at intervals of 1, 10, 120 (2 h) or 1440 (1 d) min, after leaving the previous seed. Oviposition time was estimated as the total amount of time spent on a seed divided by the number of eggs laid, for the first five clutches laid.

#### *Measuring Observed Clutch Sizes*

The clutch size models reviewed by Wilson and Lessells (1994) predict quantitatively (and sometimes qualitatively) different responses to several factors. The response of ovipositing females to the following factors was examined: host encounter rate (Expt. 5), number of conspecific females encountered during an oviposition bout (Expt. 6), lifespan (Expt. 7) and residual lifespan and residual egg-complement (Expt. 8).

*Experiment 5. Effect of travel time on clutch size:* Data were collected during Experiment 4 and therefore the experimental protocol was the same as that described above. Clutch size was determined for the first five clutches laid by females experiencing travel times of 1 min, 10 min, 2 h or 1 d.

*Experiment 6. Effect of conspecific females on clutch size:* The influence of conspecific females on observed clutch sizes was examined by allowing females to lay clutches in the presence of one or more other females. Recently emerged virgin females were allowed to mate for 2 h and placed in 35 ml containers with 0, 1 or 4 similar females for 24 h. Each female was then presented with a pristine seed on which to oviposit and, when the clutch was complete, the seed removed and its egg-load determined. Subsequently, females were presented with new seeds at 2 h intervals and the size of their first 3 clutches determined. Although females from the same group were physically prevented from interfering with one another during egg-laying, they were in visual contact with each other at all times.

*Experiment 7. Effect of emergence weight on lifespan of virgin females:* Thirty-five newly-emerged virgin females were retained separately without mates or seeds in 50 ml containers and checked twice daily to determine the time of death. Elytral lengths were subsequently measured.

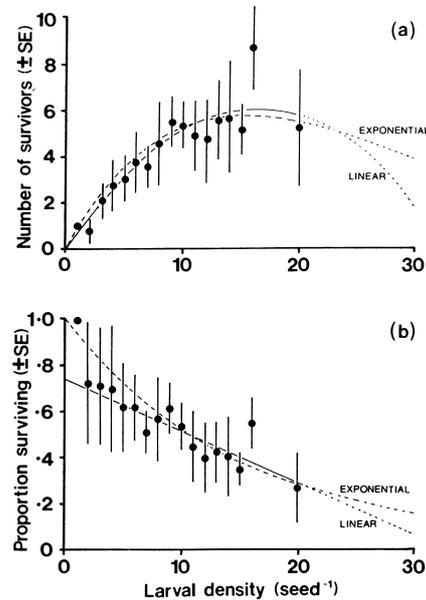
*Experiment 8. Effect of female age and previous oviposition experience on clutch size:* The relative importance of residual lifespan ( $T(t)$ ) and egg-complement ( $E(t)$ ) on clutch size was determined by varying the length of time that individual females were retained without oviposition sites and then presenting all females with seeds at a similar rate.

Mated females were retained singly for 1–8 days before being presented with a single seed on which to oviposit. When the clutch was complete, the seed was removed, its egg-load determined and the female again retained in isolation. Subsequent seeds were generally given to females at daily intervals, but individuals given their first seed when they were 5, 6, or 7 days old were given a second seed immediately after their first and then dissected to determine their residual egg-complements.

## Results

### *Predicting Optimal Clutch Sizes*

*Experiment 1. Effects of larval competition:* The number of adults emerging from each seed was a non-linear function of the number of larvae present (Fig. 1(a)). Models based on linear and exponential larval fitness functions explained similar amounts of variance in the number of survivors (about 90%), and both peaked at around 16 eggs/seed (see legend to Fig. 1). The lack of data of egg-loads above



**Fig. 1.** Effect of larval density on the number and proportion of adult *C. maculatus* surviving. (a) Number of survivors  $\pm$  SE; (b) proportion surviving  $\pm$  SE (mean and SE are based on arcsine transformed data that has been back-transformed). Each mean is based on emergences from between 3 and 25 seeds. Model parameters for linear ( $s(N) = a - b \cdot N$ ) and exponential ( $s(N) = e^{-c \cdot N}$ ) larval fitness functions (see Wilson and Lessells, 1994, and text, for details) were determined by non-linear least squares regression (means  $\pm$  approximate SEs:  $a = 0.7361 \pm 0.0318$ ,  $b = 0.0220 \pm 0.0025$ ,  $c = 0.0651 \pm 0.0022$ ).

twenty makes it impossible to distinguish between these two functions. However, Credland et al. (1986) performed a similar experiment with another Brazilian strain of *C. maculatus* (Campinas strain) using initial larval densities ranging between 1 and 35 larvae per seed, and found that the most productive larval density was 15 per seed and that the larval fitness function was approximately linear (see Fig. 1, Credland et al., 1986).

The adult sex ratio was independent of egg-load ( $F_{1,221} = 0.01$ ,  $P > 0.9$ ) and 54% of adults emerging were female.

Adult emergence weight declined linearly with the number of larvae per seed (Fig. 2) and at a similar rate for both sexes (comparison of slopes:  $t = 1.08$ ,  $df = 222$ ,  $p > 0.2$ ). The relationship between the number of larvae per seed ( $N$ ) and female emergence weight ( $W$ ) was described by the function:

$$W(N) = 4.86 - 0.04 N \quad [1]$$

*Experiment 2. Effect of female emergence weight on lifetime egg production:* Lifetime egg production ( $E$ ) of mated females given 4 seeds per day increased linearly with

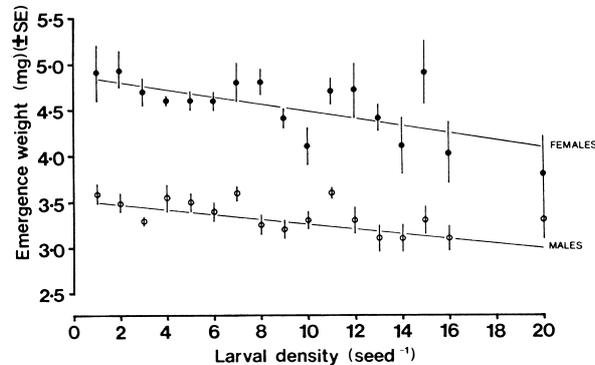


Fig. 2. Effect of larval density on emergence weights of male and female *C. maculatus*. Regression equations: Females (solid circles):  $W = 4.86 - 0.04 N$ ;  $F_{1,188} = 12.04$ ,  $P < 0.001$ . Males (open circles):  $W = 3.53 - 0.02 N$ ;  $F_{1,176} = 13.21$ ,  $P < 0.001$ . Vertical bars are standard errors. Each mean is based on emergences from between 3 and 25 seeds.

female emergence weight. The relationship was described by the function:

$$E(W) = -31.18 + 17.49 W \quad [2]$$

In other words, lifetime egg production increased by approximately 17 eggs for every increase of 1 mg in emergence weight (Fig. 3). This regression coefficient is similar to that reported by other authors (e.g. Credland et al., 1986). The effect of larval competition on *per capita* fecundity was estimated by substituting Equation 1 into Equation 2. Fecundity as a function of the number of larvae per seed was described by the function:

$$E(N) = 53.82 - 0.70 N \quad [3]$$

Total offspring fitness of larvae from single seeds was estimated by multiplying the observed number of adult females emerging by their predicted fecundities (using Eqn. 3). Larval competition curves and offspring *per capita* fitness curves based on linear and exponential fitness functions were then fitted to this manufactured data (Fig. 4).

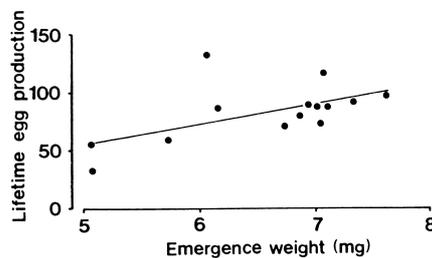
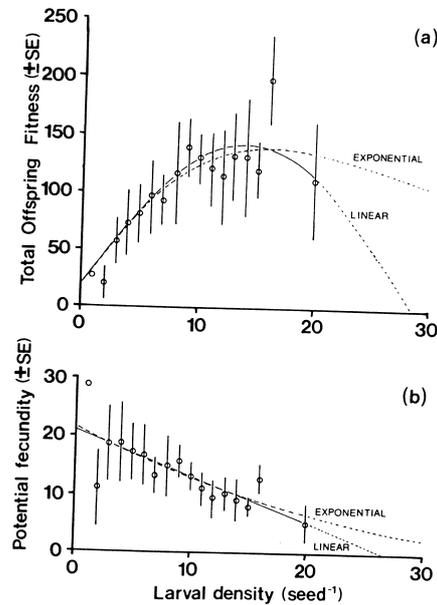


Fig. 3. Relationship between lifetime egg production and female emergence weight for *C. maculatus*. Regression equation:  $E = -31.18 + 17.49 W$ ;  $F_{1,13} = 5.04$ ,  $P < 0.05$ .



**Fig. 4.** Effect of larval density on the Total Offspring Fitness (TOF) and potential fecundity of female *C. maculatus*. (a) TOF (number of females emerging  $\times$  their potential fecundity)  $\pm$  SE; (b) female potential fecundity (as estimated using equation 3, text)  $\pm$  SE. Each mean is based on emergences from 3–25 seeds. Model parameters for linear and exponential functions were fitted by non-linear least squares regression (see Fig. 1 for details) (means  $\pm$  approximate SEs:  $a = 0.8784 \pm 0.0342$ ,  $b = 0.0310 \pm 0.0027$ ,  $c = 0.0613 \pm 0.0053$ ). Figure (a) is also referred to as the larval competition curve and figure (b) as the larval fitness function.

The shape of the larval competition curve was similar to that describing the number of survivors at different larval densities and a similar amount of variance in total offspring fitness was explained (around 90%). Larval competition curves based on linear and exponential larval fitness functions peaked at clutch sizes of 14 and 16, respectively (see legend to Fig. 4). As stated earlier, the lack of data for egg-loads greater than 20 eggs/seed means that it is not possible to distinguish between the different fitness functions. However, the larval competition curve produced by Credland et al. (1986) for the Brazilian Campinas strain peaked at a similar clutch size and the larval fitness function appears linear.

*Experiment 3. Cost of reproduction:* Figure 5 illustrates the cost of reproduction for *C. maculatus*. A linear regression on the mean lifespans and fecundities for the four groups produced a regression coefficient of  $-0.163 \pm 0.025$  (SE), and this was significantly different from zero ( $t = 6.595$ ,  $df = 3$ ,  $P < 0.01$ ). In other words, each egg 'cost' 3.9 h of life.

El-Sawaf (1956, pp 71–79) manipulated the number and size of cowpeas he gave to female *C. maculatus* and measured their subsequent lifespans and fecundities.

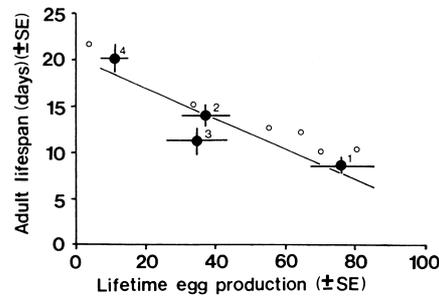


Fig. 5. The cost of reproduction in *C. maculatus*: relationship between adult lifespan and lifetime egg production. Solid circles are means ( $\pm$ SEs) obtained during Experiment 3, present study. Regression on means:  $T = 20.18 - 0.16 E$ . Figures next to means refer to group numbers, see text for details of manipulations. Means are based on 14 or 15 females. Open circles are from El-Sawaf (1956), see text.

Re-analysis of these data suggests a similar cost of reproduction: the regression coefficient was  $-0.149 \pm 0.007$  (SE), which was not significantly different from that calculated in the present study ( $t = 0.291$ ,  $df = 8$ , NS; Fig. 5).

*Experiment 4. Effect of travel time on oviposition time:* Oviposition time ( $T_o$ ) was calculated by dividing the amount of time a female spent on each seed by the size of the clutch she laid. Median oviposition times generally increased as the time between successive seed encounters,  $T_i$ , increased (Fig. 6). Within each treatment group,  $T_o$  was relatively constant over successive clutches, though there was a tendency for females given seeds at daily intervals to take longer over later ovipositions ( $r_s = 0.343$ ,  $n = 25$ ,  $0.05 < P < 0.1$ ).

Oviposition time was independent of the number of eggs laid in a clutch. This was true for all females laying their first clutch ( $r_s = -0.189$ ,  $n = 50$ , NS) and for females that were laying their second clutch up to 10 minutes after their first ( $r_s = 0.048$ ,  $n = 31$ , NS). Total oviposition time divided by the number of eggs laid therefore appears to be an accurate approximation of  $T_o$ .

The importance, in evolutionary terms, of the positive correlation between  $T_o$  and  $T_i$  is not immediately obvious: it may reflect an adaptive response by the female to differences in the perceived value of seeds encountered at different rates, or it may be simply a consequence of ageing. In other words,  $T_o$  may be treated as a decision variable or a constraint (see Stephens and Krebs 1987; Krebs and Kacelnik, 1991). As a conservative test of the models, the variation in oviposition time associated with  $T_i$  was included in the analyses that follow.

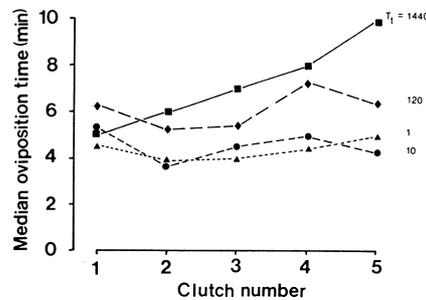
#### Model parameters

The parameter values used in the clutch size models are listed in Table 1, and are derived from the experiments described above. Where parameters exhibited significant variation, the extreme values of their range were entered into each model and

**Table 1.** Parameter values used in clutch size models.

Parameter		Range used in models
$T_o$	(time taken to lay each egg)	3.6 – 10.0 min
$T$	(total time available for laying)	8.5– 20.0 days (12240 – 28800 min)
$E$	(total number of eggs available)	40–80 eggs
$T/E$	(time available for laying each egg)	153–720 min/egg
$N^*$	(the most productive clutch size)	15 eggs/seed
$s(N)$	(Larval fitness function)	$a - bN$ (linear) and $e^{-cN}$ (exponential)
$\beta$	(energetic conversion rate)	0.0026–0.0122 eggs/min

See text for methods of derivation.



**Fig. 6.** Relationship between median oviposition time and clutch number at various travel times for *C. maculatus* ovipositing on cowpeas. Travel times: 1440 min (squares),  $n = 5$  females; 120 min (diamonds),  $n = 14$ ; 10 min (circles),  $n = 15$ ; 1 min (triangles),  $n = 16$ . Except at clutch 1, oviposition time differed between treatments for all of the first 5 clutches (Kruskal-Wallis tests,  $H \geq 13.1$ ,  $df = 3$ ,  $P \leq 0.01$ ). Median oviposition time was independent of clutch number at all travel times.

the associated predictions compared. For example, median oviposition time varied between 3.6 and 10.0 min over the first five clutches, depending on the value of  $T_t$  (Fig. 6). Therefore, these two values of  $T_o$  were entered into the models and the effect on the optimal clutch size ( $\hat{N}$ ) observed.

The range of values for  $T$  (female lifespan), was determined from the mean values for females given a mate and oviposition sites and those denied access to both of these (Fig. 5). The range of values for  $E$  (lifetime egg production) was determined from the mean number of eggs laid by females given continuous access to mates and seeds and that by mated females denied access to seeds (Fig. 5). Note that this will tend to underestimate the smallest value of  $E$ . The range of values for  $T/E$  (the amount of time available to lay each egg) was determined by the ranges of  $E$  and  $T$ . The predicted clutch size when eggs and hosts are limiting is dependent on the ratio  $E/H$  (Wilson and Lessells, 1994). There are at least 2 methods that the ovipositing female may use to estimate the value of  $H$  (the number of hosts available). The first is to use the rate of host encounter as a cue (i.e.  $H = T/T_t$ ) (in which case, the predicted clutch size will increase with decreasing host encounter

rate and will approximate the predicted clutch size under an eggs and time constraint; see Wilson and Lessells, 1994). The second is to use the number of hosts observed at each host encounter as a cue to the total number of seeds available. In the present study, this latter method was used and  $H$  was set to 1 in all the models (because seeds were presented to females singly). The most productive clutch size was set equal to 15. The range used for the conversion rate between time and eggs ( $\beta$ ) was taken from the 95% confidence limits of the regression coefficient for the regression of longevity on fecundity.

### Predictions

The values of  $T_i$  (travel time) included in the models were 1, 10, 120 and 1440 min and the values of  $i$  (number of ovipositing females) were 1, 2, 5, and 10. Current egg-load,  $x$ , was set to zero for all models. The predictions of the single oviposition models are presented in Table 2, and those for the multiple oviposition in Table 3 (see Wilson and Lessells, 1994 for the formulae used to calculate these predictions).

Of the single oviposition models that predict an increase in clutch size with travel time (models 2, 4 and 5), only the time limiting model predicts clutch sizes in excess of 1 or 2 eggs/seed at travel times of less than 10 min (Tab. 2). This model predicts

**Table 2.** Quantitative predictions of clutch size models: single oviposition.

Model	Parameter values	Travel time, $T_i$ (min)			
		1	10	120	1440
1a. Hosts		15	15	15	15
2a. Time	Linear: $T_o = 3.6$ $= 10.0$	3	7	13	15
		2	5	10	14
	Exponential: $T_o = 3.6$ $= 10.0$	2	5	11	15
		1	3	8	14
3a. Eggs		1	1	1	1
4a. Reserves	Linear: $\beta = 0.0026$ $= 0.0122$	1	1	3	8
		1	2	5	11
	Exponential: $\beta = 0.0026$ $= 0.0122$	1	1	2	6
		1	1	4	10
5a. Eggs and Time	Linear: $T/E = 153$ $= 720$	1	1	1	10
		1	1	1	2
	Exponential: $T/E = 153$ $= 720$	1	1	1	10
		1	1	1	2
6a. Eggs and Hosts		15	15	15	15
Observed Clutch Sizes		2.3	3.0	4.0	5.5

Predicted values are given as the integer with the highest associated fitness return.

Parameter values not included in column 2 do not substantially alter the predictions of the model. See Table 1 for list of parameters included in the models.

**Table 3.** Quantitative predictions of clutch size models: multiple oviposition

Model	Number of ovipositing females ( <i>i</i> )																
	<i>i</i> = 2				<i>i</i> = 5				<i>i</i> = 10								
	Travel time ( $T_t$ , min)																
	1	10	120	1440	1	10	120	1440	1	10	120	1440					
1c. Hosts	-----10-----				-----5-----				-----3-----								
2c. Time	2-3	4-6	8-9	10	2	3-4	5	5	1-2	2-3	3	3					
3c. Eggs	-----1-----				-----1-----				-----1-----								
4c. Reserves	1	1	2	3	5	6	9	1	1	2	4	4	5	1	1	2	3
5c. Eggs and Time	1	1	1	2-10	1	1	1	2-5	1	1	1	2	3				
6c. Eggs and Hosts	-----10-----				-----5-----				-----3-----								

Predicted clutch sizes when the number of ovipositing females (*i*) varies between 2 and 10. See legend to Table 2. Predictions assume a linear fitness function (when the larval fitness function is exponential, the value of *i* has no effect and the predicted clutch sizes are the same as those predicted by the single oviposition models: see Wilson and Lessells submitted).

that at travel times of 1 d clutch sizes will approximate the most productive (i.e. 15 eggs/seed). The reserves limiting model predicts a gradual increase in clutch size with travel time, with clutch sizes estimated at 2-5 when seeds are encountered at 2 h intervals, and 6-11 when they are encountered at daily intervals. The eggs and time limiting model predicts an optimal clutch size of 1 egg/seed for travel times less than 1 d, when they increase to between 2 and 10 eggs/seed.

Assuming a linear larval fitness function, increasing the number of ovipositing females decreases the predicted clutch sizes of all the models (there is no effect if the function is exponential). When the number of ovipositing females is equal to 10, all of the models predict clutch sizes between 1 and 3 at all travel times.

*Comparing Observed and Predicted Clutch Sizes*

*Experiment 5. Effect of travel time on clutch size:* The size of the first clutch was independent of treatment group (as expected, because all females were of similar age and oviposition experience) and was equal to  $3.54 \pm 0.33$  eggs/seed ( $n = 50$ ; Fig. 7). The mean size of the next 4 clutches increased with travel time (Fig. 7; see also Fig. 9). However, this relationship disappeared after clutch 5, due primarily to a decline in the size of clutches laid by females given seeds at daily intervals. A functional explanation for this decline is not obvious (but see Wilson, 1989, in preparation).

There was a negative correlation between body size and size of the first clutch ( $r_s = -0.448$ ,  $n = 45$ ,  $P < 0.002$ ; Fig. 8), but only females given seeds at 1 minute intervals showed a significant negative correlation over the first five clutches as a whole ( $r_s = -0.729$ ,  $n = 16$ ,  $P < 0.002$ ).

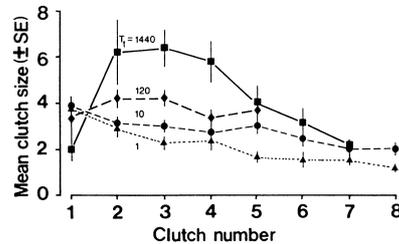


Fig. 7. Relationship between mean clutch size and clutch number at various travel times for *C. maculatus* ovipositing on cowpeas. Travel times, sample sizes and symbols are as for Fig. 6. Except at clutch 1 mean clutch size differed between treatments for each of the first 5 clutches (Kruskal-Wallis tests,  $H \geq 11.8$ ,  $df = 3$ ,  $P \leq 0.01$ ).

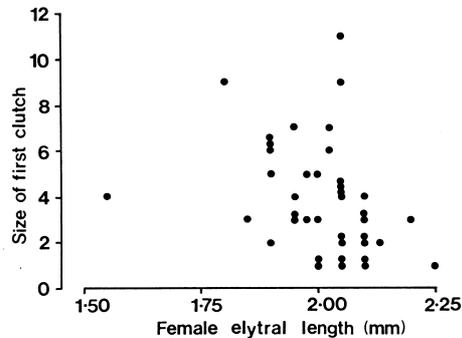


Fig. 8. Relationship between size of first clutch and female elytral length for female *C. maculatus*. The size of the first clutch laid by females was negatively correlated with elytral length ( $r_s = -0.448$ ,  $n = 40$ ,  $P < 0.002$ ). Note that sample sizes are slightly smaller than in Figs. 6 and 7 because the elytral lengths of 5 females were not measured.

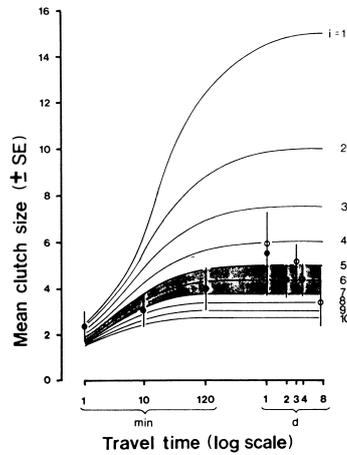
The positive correlation between clutch size and  $T_t$  is in qualitative agreement with models 2, 4 and 5 (Tab. 4), but not with models 1, 3 and 6, which predict that clutch size will be independent of  $T_t$ . These models can therefore be rejected and will not be discussed further. Quantitatively, none of the remaining single oviposition models fit the data well: the reserves limiting and eggs and time limiting models fit reasonably well at large values of  $T_t$ , but fail at shorter travel times, whilst the time limiting model fails at longer travel times (Tab. 2).

When the larval fitness function is exponential, the optimal clutch size is unaffected by the number of ovipositing females (see Wilson and Lessells, 1994), therefore the following comparisons are limited to the case where the larval fitness function is linear. Inspection of Table 3 indicates that models 4 and 5 again fail to fit the data when travel times are short (predicted clutch sizes never exceed 1 or 2 eggs/seed at  $T_t \leq 10$  min). However, when the number of females laying on each host ( $i$ ) is equal to between 5 and 10, the time limiting multiple oviposition (TLMO) model fits the data well. Figure 9 suggests a value for  $i$  of around 5 to 7 females.

**Table 4.** Qualitative Predictions of Clutch Size Models

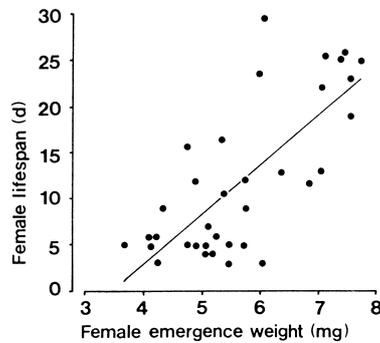
Prediction	Model						Observed	Authority
	1	2	3	4	5	6		
1. $\hat{N} =$	$N^*$	$\leq N^*$	1	$\leq N^*$	$\leq N^*$	$\leq N^*$	$\leq N^*$	Expt. 5
2. $x_{\max} =$	----- $2N^*$ -----						N/A	
<i>Effect on <math>\hat{N}</math> of increasing:</i>								
3. Host value	----- + -----						+	(1), 2, 5, 6
4. $T_l$	0	+	0	+	+	0	+	Expt. 5
5. $T_o$	0	-	0	-	-	0	N/A	
6. $T/E$	0	0	0	0	-	0	-	Expt. 8
7. $x$	----- - -----						-	2-6
8. $i$	----- - -----						0	Expt. 6

This table is adapted after Table 4 in Wilson and Lessells (1994). It differs in that  $E$  (the number of eggs available) and  $T$  (the amount of time available) are subsumed within a single constraint,  $T/E$ . 0 = no effect; + =  $\hat{N}$  increases; - =  $\hat{N}$  decreases; N/A = not applicable (no experiments have yet tested this prediction). Authorities: 1 = Avidov et al. (1965), 2 = Mitchell (1975), 3 = Messina and Renwick (1985), 4 – Wilson (1988), 5 = Wilson (1989), 6 = Wilson (in preparation). All predictions assume a linear larval fitness function (see Wilson and Lessells, 1994 for details).



**Fig. 9.** Comparison between clutch sizes laid by *C. maculatus* and those predicted by the time limiting multiple oviposition model at different travel times. A linear larval fitness function is assumed. For details of the formula used to calculate the predicted clutch sizes, see Appendix 3, Wilson and Lessells, 1994. The solid symbols refer to data from Experiment 5, open symbols to Experiment 8.

*Experiment 6. Effect of conspecific females on clutch size:* Females given seeds at 2 h intervals laid clutches of more or less constant size over time, irrespective of whether or not conspecifics were present. There was no significant difference in clutch size between the 3 treatments (Kruskal-Wallis test:  $H = 1.67$ ,  $df = 2$ ,



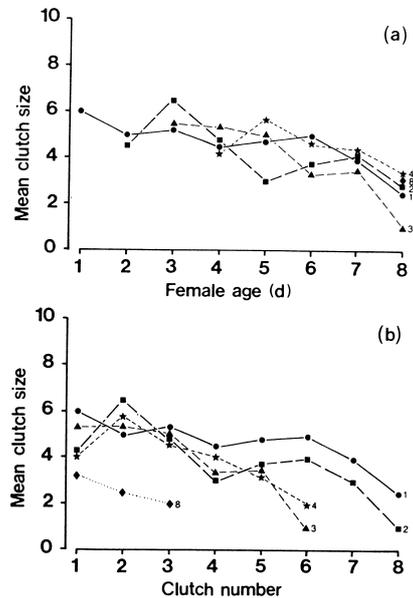
**Fig. 10.** Relationship between adult lifespan and emergence weight for virgin female *C. maculatus*. Regression equation:  $T = -9.47 + 2.70 W$ ;  $F_{1,33} = 43.45$ ,  $P < 0.001$ ,  $r^2 = 0.57$ .

$P > 0.4$ ): median clutch sizes for females maintained singly, with 1 other female, and with 4 other females were 2.7 ( $n = 19$ ), 3.2 ( $n = 30$ ), and 3.0 ( $n = 25$ ), respectively.

*Experiment 7. Effect of emergence weight on lifespan of virgin females:* Lifespan of virgin females was positively correlated with emergence weight and increased by about 5 days for each increase of 1 mg in emergence weight (Fig. 10). Predictions of the TLMO model are unaffected by variation in lifespan because long-term rate of fitness gain, rather than lifetime fitness gain, is maximised in this model.

*Experiment 8. Effect of female age and previous oviposition experience on clutch size:* The decline in clutch size at low host encounter rates appears to be a function of female age rather than of clutch number (or number of eggs laid; Fig. 11). This point is illustrated by comparing Figs. 11(a) and (b): lines joining clutches laid by females that had completed the same number of clutches were indistinguishable when clutch size was plotted against female age (Fig. 11(a)), but were separated when plotted against clutch number. In other words, the decline in clutch size appears to be due to a behavioural response to the reduction in the amount of time available for laying ( $T(t)$ ) or to physiological constraints associated with ageing; it does not appear to be directly influenced by previous egg-laying experience (at least when clutches are laid at such a low rate). It should be noted, however, that because of the small sample sizes none of these differences were statistically significant and the results must therefore be viewed with some caution. The mean clutch sizes of these females are plotted against travel time in Fig. 9. At all 5 of these travel times, the estimated value of  $i$  did not differ significantly from that estimated for shorter travel times ( $T_i \leq 1 d$ ).

For females denied seeds for between 5 and 7 days, the duration of seed deprivation did not influence clutch size or the number of mature eggs in the oviducts, and so data for the three days have been combined in the following



**Fig. 11.** Relationship between clutch size and female age and between clutch size and clutch number for *C. maculatus* laying clutches at daily intervals, starting on days 1–8. Females were given seeds at daily intervals starting on day 1 (circles;  $n = 4$ ), day 2 (squares;  $n = 4$ ), day 3 (triangles;  $n = 3$ ), day 4 (stars;  $n = 4$ ), or day 8 (diamonds;  $n = 4$ ). Figure (a) plots mean clutch size against female age; figure (b) plots the same data against clutch number. Hence for females given their first seed on day 1, the graphs are identical. In (a), the lines representing different treatment groups overlap each other, whereas in (b) the lines separate out such that clutch size is generally larger for females given their seeds earlier rather than later. This suggests that at low host encounter rates, clutch size is more a function of female age than clutch number. Due to small sample sizes no statistical tests are possible.

analyses. Twenty-one females, out of 24, started to lay a second clutch within a minute of finishing their first; and of these females, 19 had mature eggs in their oviducts when dissected immediately after completing the second clutch (mean number of eggs  $\pm$  SD =  $5.25 \pm 4.35$ ). These results strongly suggest that the decline in clutch size after day 5, which is not predicted by the TLMO model, is due to a behavioural response to the reduction in residual lifespan (or residual egg-complement) rather than to egg limitation or physical exhaustion.

## Discussion

### *Qualitative Evidence*

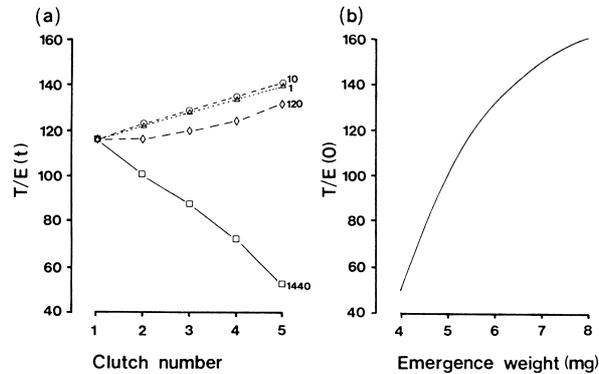
Table 4 compares the observed trends in clutch size with those predicted by the six models (adapted after Tab. 4, Wilson and Lessells, 1994). Predictions 2,

3, 7 and 8 are the same for all of the models: the maximum number of eggs per seed will be 30 ( $=2N^*$ ), and oviposition propensity will increase with host value and decrease with egg-load and number of ovipositing females. These predictions are therefore useless in distinguishing between the models. Prediction 4 also has limited utility, because oviposition time is not easily manipulated and was not manipulated during the present study. All of the remaining predictions (numbers 1, 4 and 6), may be used to reject models 1, 3 and 6 (the hosts limiting, eggs limited, and eggs and hosts limiting models). In order to distinguish between the remaining 3 models (2, 4 and 5), the response to  $T/E$  must be examined. (Note that  $T$  and  $E$  have been subsumed within the single constraint ( $T/E$ ) because it is not possible to distinguish between the two using qualitative criteria alone if the value of  $E$  varies as a function of time in the absence of oviposition, as it does when oogenic and resorption processes are occurring; Wilson and Hill, 1989).

The time limiting and reserves limiting models (2 and 4) predict no change in clutch size with  $T/E$  (Wilson and Lessells, 1994). This is because they assume that eggs are never limiting and therefore that it always pays the female to maximise her long-term average rate of offspring production (per unit time or reserves). The eggs and time limiting model (5), on the other hand, predicts that clutch size will decline with increasing  $T/E$  (see Fig. 2, Wilson and Lessells, 1994) and there are two lines of evidence to support this prediction. Firstly, clutch size declined over successive clutches (except when the interval between clutches was large) and, secondly, the size of first clutches was negatively correlated with female emergence weight.

A decline in clutch size with age is predicted if residual egg-complement,  $E(t)$ , declines at a faster rate than residual lifespan,  $T(t)$ , such that there is a decline over time in the residual  $T/E$  (i.e. in the amount of time left to lay the remainder of the eggs) and that the opposite trend is predicted (i.e. a temporal increase in clutch size) if  $T$  decreases at a faster rate than  $E$ , as when oviposition sites are withheld (Wilson and Lessells, 1994; see Mangel, 1987, 1989 for a similar prediction). The influence of travel time on temporal variation in residual  $T/E$  is illustrated in Fig. 12(a), using data from Experiment 5. This shows that for  $T_i \leq 120$  min,  $T/E(t)$  increases with clutch number and the rate of increase (and hence the predicted rate of decrease in clutch size) is greater at relatively short travel times ( $T_i \leq 10$  min) than relatively long ( $T_i = 120$  min). Moreover, a decrease in  $T/E(t)$ , and hence a predicted increase in clutch size, occurs at very long travel times ( $T_i = 1440$  min). Because, in *C. maculatus*, the rate of oviposition influences egg maturation and resorption rates, and hence lifetime egg production (Wilson and Hill, 1989), more complicated temporal patterns would undoubtedly be predicted if these additional factors were included in the models.

Model 5 predicts that small females may lay bigger first clutches than large females if the value of  $T/E$  at emergence is greater for large than small females (see Fig. 2, Wilson and Lessells, 1994). Calculation of  $T/E$  at emergence ( $T/E(0)$ ) using the regression equations for female lifespan on emergence weight and fecundity on emergence weight (Figs. 3 and 10, present study) suggests that this is indeed the case:  $T/E(0)$  increases with body weight (Fig. 12(b)) such that, for



**Fig. 12.** Effect of travel time and emergence weight on the estimated values of  $T/E$  for *C. maculatus* females. (a) Travel time,  $T_i = 1$  min: triangles;  $T_i = 10$  min: circles;  $T_i = 2$  h: diamonds;  $T_i = 1$  d: squares. At short travel times ( $T_i \leq 120$  min), the estimated value of  $T/E$  at time  $t$ ,  $T/E(t)$  ( $\text{min egg}^{-1}$ ), increases over successive clutches, whereas at long travel times ( $T_i = 1440$  min) it decreases. If eggs and time are limiting, this will result in clutch size tending to decrease at high host encounter rates, and increase at low host encounter rates (Wilson and Lessells, 1994). The calculations for  $T/E(t)$  assume that all females emerge with their full complement of eggs (for a female weighing 6 mg this averages 74 eggs; Fig. 3) and live for a mean of 6.73 days (the average for a 6 mg female, Fig. 10).  $T(t)$  decreases with time spent travelling between seeds and ovipositing, and  $E(t)$  decreases only when eggs are laid (it is assumed that the clutch laying frequency does not influence the value of  $E$ ). Mean clutch sizes were extracted from Fig. 7. (b) The effect of emergence weight (mg) on the value of  $T/E$  at emergence,  $T/E(0)$ , was established by calculating expected lifespans and fecundities as a function of emergence weight (see Figs. 3 and 10).

example, a female weighing 8 mg has a value of  $T/E$  at emergence which is more than 3 times that of one weighing half that weight (4 mg). Subsequent values of  $T/E(t)$  depend not only on when the next clutch is laid, but also on the size of the previous clutch. Therefore, although the direction of initial clutch size differences may be predicted, subsequent trends with respect to clutch size and body size, cannot be easily predicted. Note that for any given value of  $T/E$ , the optimal clutch size is independent of body size. Similar conclusions were reached by Begon and Parker (1986) for the case when egg reserves are limiting and females suffer mortality between host-visits.

### Quantitative Evidence

Quantitative analysis of the response of ovipositing females to changes in the host encounter rate implicates the time limiting multiple oviposition model, suggesting that time is the major limiting resource and that clutch size is also constrained, evolutionarily, by the threat of multiple oviposition. Regardless of whether or not conspecifics were present during egg-laying, ovipositing females behaved as though 5–7 other females would subsequently lay eggs on the same seeds. Thus, the

female's response to *future* levels of multiple oviposition appears genetically fixed, rather than phenotypically labile, suggesting that the number of females encountered during an oviposition bout is probably a poor cue to the number of eggs that will subsequently be added to clutches (Wilson, 1989; Wilson and Lessells, 1994, see also Lively, 1986). Conversely, the response to *present* levels of multiple oviposition is clearly phenotypically plastic: clutch size is negatively correlated with the egg-load of the current seed and females may distinguish between seeds differing in egg-load by as few as 1 or 2 eggs (Mitchell, 1975; Messina and Renwick, 1985; Wilson, 1988, 1989, in preparation). The benefits a female accrues by responding to present levels of multiple oviposition are obvious. However, the selective advantage of anticipating future levels of multiple oviposition with a fixed response is not so clear, particularly when these levels vary greatly within and between generations.

Future multiple oviposition must be invoked to explain the observed quantitative trends in clutch size because the observed maximum mean clutch size (6 eggs/seed) was considerably smaller than that which is most productive (15 eggs/seed), even at travel times in excess of a day. Interestingly, if it is assumed that the most productive clutch size was actually equal to 6 eggs/seed (due to factors not accounted for thus far, such as maternal effects on offspring fitness or because larval competition affects males to a greater degree than females), then time is still implicated as the major constraint, though now there is no need to invoke multiple oviposition.

Another possible explanation for why none of the single oviposition models provide a good quantitative fit is that the major constraint on clutch size changes with travel time. For example, at high host encounter rates, time may be the major limiting resource and travelling between seeds would then be costly relative to laying; whereas at low host encounter rates, reserves may be limiting and egg laying costly. This would be the case if the cost of travelling between seeds, in fitness units, was a decelerating function of travel time. Such a function is feasible, and would result if, for example, females spent increasing proportions of their time engaged in energetically inexpensive activities, such as 'lounging' (Wilson, 1988), as the interval between seeds increased. However, even if this was the case, an additional factor would probably still need to be invoked to explain why clutch size never exceeded 6 eggs/seeds even when travel times were greater than a day. Wilson (1989, in preparation) has suggested that this factor may be the insect's 'rule of thumb' mechanism for determining clutch size, which acts as a constraint at very low host encounter rates.

The qualitative predictions clearly implicated the eggs and time limiting model (see above). However, quantitatively this model performed poorly. At travel times ranging between 1 and 120 min, it predicted a clutch size of just 1 egg/seed, whereas observed mean clutch sizes ranged between 2 and 4 eggs/seed. In order for the eggs and time limiting model to predict clutch sizes as large as these,  $T/E$  would need to be less than 10 min/egg (see Fig. 2, Wilson and Lessells, 1994). In other words, if  $E$  is assumed to range between 30 and 80 (the oviduct capacity and fecundity, respectively, of the average female; Wilson and Hill, 1989), then  $T$  would have to range between 5 and 13 h. Thus, a good quantitative fit would be obtained only if

females behaved as if making decisions over a short time scale (less than a day). If this is true, then it may be that the models tested in this paper, and described by Wilson and Lessells (1994), are inappropriate for studying the life-histories of these insects. Whilst they may be useful in excluding some possible constraints on clutch size and implicating others, they are, nonetheless, essentially static and deterministic in nature and we may be asking too much of them in trying to explain dynamic decisions in a stochastic world.

The limitations of static models in making precise, quantitative predictions about fine-scale decisions has recently been highlighted by Houston et al. (1988). An obvious next step for the present study would be to examine the oviposition behaviour of *C. maculatus* in the context of Stochastic Dynamic Programming models (Mangel and Clark, 1986; McNamara and Houston, 1986; Houston et al., 1988). Clutch size decisions are particularly amenable to the dynamic programming approach because after each oviposition the internal state of the female (e.g. the number of mature and immature eggs in the oviducts) has changed, and hence, if eggs or reserves are limiting, the optimal size of the next clutch may also have changed (see Mangel, 1987, 1989, 1992; McNamara and Houston, 1992 for details of this approach). Wilson (1989, in preparation) has recently examined some internal state variables that may influence the clutch size decisions of *C. maculatus* and concludes that the oviduct-capacity of the female and her rates of egg maturation and resorption may be key factors constraining clutch size. Dynamic programming models that include these state variables are currently being developed.

In conclusion, although the time limiting multiple oviposition model provides the best quantitative fit with respect to host encounter rate, this model fails to predict the observed temporal patterns in clutch size, or variation with respect to female phenotype, that the eggs and time limiting model predicts. Therefore, although both models implicate time as an important constraint on clutch size, the criterion of success for the present study (namely that a single model should explain both qualitative and quantitative trends) has not been satisfied. The functional basis for the observed trends in clutch size must therefore remain in some doubt until more appropriate models have been developed.

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