Evolution of clutch size in insects. I. A review of static optimality models

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Abstract

This paper reviews the importance of constraint assumptions to the predictions of static optimality models of insect clutch size. This allows us to identify predictions that distinguish between models embodying different constraints on female oviposition behaviour and hence to determine which resources or other factors limit clutch size evolutionarily. We conclude that while some models may be distinguished using qualitative criteria, others require the testing of quantitative predictions. In a companion paper (Wilson 1994) these models are tested using the bruchid beetle *Callosobruchus maculatus*.

Introduction

Most animals lay their eggs in discrete batches, known as clutches, which may vary considerably in size both within and between species. Early theories of the evolution of clutch size centred on nidicolous birds (Lack, 1947), with later avian developments taking into account the cost of reproduction (Williams, 1966; Charnov and Krebs, 1974) and individual variation (Perrins and Moss, 1975; Högstedt, 1980). Theories concerned with the evolution of clutch size in insects grew independently out of optimal foraging models (Charnov, 1976; Parker and Stuart, 1976), and have often included the effects of more than one female

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ovipositing in a resource patch (Parker and Courtney, 1984; Skinner, 1985; Smith and Lessells, 1985; see also Iwasa et al., 1984). Such multiple oviposition requires a game theoretical approach predicting the evolutionarily stable strategy (ESS) (Maynard Smith, 1982).

Despite the independent origins of clutch size models for birds and insects, females of both taxa face the same problem of a diminishing rate of return in fitness when ovipositing. In birds this occurs because of the limitations imposed by parental care, and in insects because eggs are laid in patches of resource such as leaves, larvae or seeds that offer a finite food resource for the developing offspring. Thus, although the models presented below were sometimes formulated with particular insects in mind, and have been tested using granivorous beetles ovipositing on seeds (Wilson, 1994), they are appropriate to a wide range of ovipositing animals, including parasitoids laying on insect hosts, flies on dung pats or fallen fruit, lepidoptera on plants, amphibians in pools and fish, reptiles or birds in nests.

One of the main functions of optimality models is in gauging the completeness of our understanding of a character by testing assumptions about selection pressures. These assumptions may be divided into currency assumptions and constraint assumptions (Cheverton et al., 1985; Stephens and Krebs, 1986; Krebs and Kacelnik, 1991). Currencies are the criteria used for judging the merits of alternative values of a trait such as clutch size. Natural selection is expected to maximise the rate of increase of an allele, but optimality models generally use some other currency that can be more readily measured. Constraints determine how the currency is related to the trait, and may be either intrinsic or extrinsic to the individual. In models of the evolution of life history traits, such as clutch size, the most appropriate currency is often the intrinsic rate of increase (r) or reproductive value (RV), and the most important constraints are the cost of reproduction (the trade-off between current and future reproduction) and the trade-off between the number and fitness of offspring. However, in insects it is seldom possible, especially in the field, to measure the cost of reproduction completely in terms of future survival and fecundity and hence make quantitative predictions of the clutch size maximising RV. An alternative approach is to make predictions of the optimal clutch size under a number of constraint assumptions and determine which of these most closely resembles the behaviour of the ovipositing female. In essence, this amounts to asking what constraints females behave as though regarding important, and provides guidance as to what resources and other factors are limiting the evolution of clutch size.

There are two conditions that must be fulfilled for this approach to identify correctly the fitness-surrogate being maximised and hence offer insights into the main selection pressures acting: first, a comprehensive range of models encompassing all reasonable constraints must be considered and, second, the predictions that distinguish between these models must be identified. For example, many of the models of clutch size oviposition predict that females will never lay clutches that are larger than the most productive; that clutch size will increase with host quality or host size; and that clutch size will decrease as the time interval between clutches gets shorter. Clearly, qualitative agreement with any of these predictions is not sufficient

to distinguish between different constraint assumptions; quantitative tests are needed.

This paper therefore has two aims. First, to review previous insect clutch size models and construct novel models where necessary, and hence provide a comprehensive framework within which to examine oviposition decisions. Second, to ascertain what qualitative or quantitative predictions are sufficient to distinguish between the constraint assumptions embodied in the models. Our review differs from its predecessors (e.g. Godfray, 1987a) in attempting to consider all reasonable constraint assumptions in conjunction with multiple oviposition. It concentrates on static models which can be solved analytically, but the results of some dynamic models are also referred to (e.g. Iwasa et al., 1984; Mangel, 1987, 1989). The predictions of the models reviewed here are tested on a bruchid beetle, *Callosobruchus maculatus*, in a companion paper (Wilson, 1994).

Assumptions of the models

All of the models presented in this paper consider females ovipositing in patches of some sort, and ask what clutch size a female should lay if she is to maximise the total fitness of her offspring given certain constraints. These constraints include the kind of resource that limits her oviposition (e.g. eggs, oviposition sites, time, etc.) and the presence of other ovipositing females, but not the effects of parent-offspring conflict (Parker and Mock, 1987; Godfray 1987b), variation in sex allocation (Godfray, 1986) or egg size (Smith and Fretwell, 1974; Begon and Parker, 1986; Parker and Begon, 1986), or constraints associated with information or stochasticity (Godfray and Ives, 1987). In this section we describe the assumptions we have made about currencies and constraints. The symbols used to represent parameters of the models are given in Table 1.

1. Currencies

The currency of an optimality model is the unit used to judge the relative merits of alternative strategies (Cheverton et al., 1985; Stephens and Krebs, 1986; Krebs and Kacelnik, 1991). Given certain assumptions, maximising the intrinsic rate of increase (r) or reproductive value (RV) is equivalent to maximising the rate of increase of an allele (Charlesworth, 1980; Caswell, 1989). If the population is neither decreasing nor increasing then maximising r or RV will also be equivalent to maximising the net reproductive rate (R_0) (Williams, 1966; Taylor et al., 1974; Charlesworth, 1980; Yodzis, 1981; Goodman, 1982; Caswell, 1989). However, R_0 is not a complete measure of fitness if there are inter-generational effects (Andersson, 1978); in other words, if offspring vary in their quality in a way that affects their reproductive prospects. Such inter-generational effects are particularly likely in invertebrates where developmental conditions, including the level of larval competition, may have profound consequences for adult size (Salt, 1940; Klomp and

Table 1. Symbols used in the models

Symbol	Definition
N	Clutch size
N^*	Most productive clutch size (Lack's solution)
$\hat{N}$	Evolutionarily stable clutch size
E	Total number of eggs available (potential fecundity)
T	Total time available for laying (adult lifespan)
T_o	Time taken to lay each egg
T_t	time between successive encounters with hosts
$s(N, \hat{N}, x, i)$	Larval fitness function, relating *per capita* offspring fitness to N, $\hat{N}$, x and i
$s'(N, \hat{N}, x, i)$	First derivative, or partial derivative, of $s(N, \hat{N}, x, i)$ with respect to N
TOF	Total offspring fitness $= N \cdot s(N, \hat{N}, x, i)$
$\left.\begin{array}{l} a, b \\ \\ c \end{array}\right\}$	Parameters used in linear and exponential larval fitness functions
x	Current egg load of host
x_{max}	Predicted maximum egg load of host
i	Number of ovipositing females
β	Conversion rate between time and eggs: slope of regression line for realised fecundity against adult lifespan

Teerink 1967; Charnov and Skinner 1984), and hence for either the fecundity of females (Klomp and Teerink, 1967; Charnov and Skinner, 1984; Credland et al., 1986) or the mating success of males (Partridge and Farquhar, 1983; McLain, 1985; Juliano, 1985). These effects of emergence weight must be incorporated into any prospective currency (Charnov and Skinner, 1984, 1985; Takagi, 1985; Skinner, 1985; Smith and Lessells 1985).

2. Constraints

a) Larval competition: the trade-off between the number and fitness of individual offspring: One of the major constraints on the evolution of life history traits is the trade-off between the number and fitness of offspring (Lack, 1947). In insects this trade-off occurs because competition between larvae within a host reduces their survival and future reproductive success. Clutch-productivity incorporating these effects on survival and fecundity will be referred to as 'total offspring fitness' (TOF). The relationship between TOF and the number of larvae in a host has been referred to as the 'larval competition curve' (Smith and Lessells, 1985; Credland et al., 1986; Wilson, 1994) or the 'number fitness relationship' (Skinner, 1985).

The larval competition curve has been modelled using functions of a number of general forms, all of which share the property of a monotonic decrease in the *per*

capita fitness of eggs with increasing clutch size. Thus none of these functions considers the possibility of an 'Allee effect', in which per capita fitness of eggs increases with clutch size over the lower part of the range of clutch sizes. Except where explicitly stated, the consequences of an Allee effect have not been considered below. The general forms of the larval competition curves that are considered in this paper are:

Linear larval fitness function: $s(N) = a - b \cdot N$, (where $s(N)$ is the fitness of each egg, and N is the clutch size). This function originates from experimental studies of birds (Perrins and Moss, 1975), in which it often provides an adequate and simple fit to empirical data, despite the unrealistic feature that it becomes negative above clutch sizes of a/b (at which fitness of individual eggs is zero).

Exponential larval fitness function: $s(N) = e^{-c \cdot N}$. This function originates from theoretical studies, where its main attraction is analytical tractability (Parker and Courtney, 1984; Smith and Lessells, 1985; Waage and Godfray, 1985). Using this function, the *per capita* fitness of eggs declines at a decreasing rate with increasing clutch size, and approaches zero asymptotically.

Although our analyses have been restricted to models incorporating linear or exponential larval fitness functions, it should be noted that the predictions of these clutch size models are often sensitive to the precise fitness function used (Smith and Lessells, 1985; Waage and Godfray, 1985; Ives, 1989). This presents a problem that experimentalists should be aware of: the goodness-of-fit of these different functions to empirical data may be statistically indistinguishable, but the different functions yield quantitatively or qualitatively different predictions for female oviposition behaviour. In these circumstances, it is probably best to fit a range of functions and make predictions based on each of them. Of the functions generally considered, the exponential function tends to give predictions that differ qualitatively the most from other functions (Smith and Lessells, 1985; Waage and Godfray, 1985).

Both functions considered in this paper are continuous and therefore assume that the fitness gain increases smoothly during oviposition, whereas it must accrue in discrete increments as eggs are laid. The problems that this raises are discussed by Kacelnik (1984) and Houston (1987), but are relatively minor and have generally been ignored below (but see model 3).

b) Limiting resources: the cost of reproduction: The second major constraint on the evolution of life history traits is the trade-off between current and future reproduction, a trade-off known as the 'cost of reproduction' (Williams, 1966). This trade-off may occur because of some limiting resource which can be used only once, and if used for current reproduction is not available during future reproductive episodes. The major limiting resources that have been considered in clutch size models are oviposition sites (hosts), time and eggs. These may act singly or in combination and, if in combination, may or may not act independently of each other (Smith and Lessells, 1985). For instance, eggs and time might both potentially limit reproduction; individual females might run out of eggs or time. Moreover, these limiting resources might be independent of each other, so that a short fall in one resource could not be made good by excess of another, or they

might be dependent on each other, as would be the case if reserves of water, energy or other nutrients could be directed into either egg production or maintenance. The limiting resources that have been considered in the models below are as follows:

Model 1: Oviposition sites (hosts).

Model 2: Time. We have included under time constraints those models incorporating mortality risks (e.g. Parker and Courtney, 1984; Charnov and Skinner, 1985). This is because, regardless of whether time or mortality risk is the main constraint, the ovipositing female should convert time into fitness as efficiently as possible.

Model 3: Eggs.

Model 4: Reserves (i.e. eggs and time, dependently)

Model 5: Eggs and time, independently.

Model 6: Eggs and hosts, independently.

c) Multiple oviposition: presence of other ovipositing females: Many of the early models of insect clutch size considered a single female laying in a patch that was not subsequently visited by other females. (Here, such 'single oviposition' models are referred to by the suffix a.) However, the optimal clutch size will be modified if more than one female lays in a patch (see below). In this paper, two approaches have been used to model the effects of 'multiple oviposition'. The first approach (referred to by the suffix b) is to ask what clutch size a female would lay on a host that already contains some eggs, but on which she will be the last to lay (Charnov and Skinner, 1985; Skinner, 1985; Smith and Lessells, 1985). The second approach (referred to by the suffix c) is to ask what clutch size a female should lay if she is one of a group of females simultaneously laying on a host, each of whom knows how many other females are laying on that host (Smith and Lessells, 1985; Ives, 1989). (A third approach, employed by Parker and Courtney (1984) but not used here, is to ask what clutch size is optimal for a female to lay given a certain probability of a second female laying on that host. These authors concluded that the difference in clutch size between the first and second female is only weakly dependent on the frequency of double oviposition and can probably be ignored when there are several females, as it is in models of type c.)

d) Behaviour and physiology of ovipositing females: The following constraints imposed by the behaviour and physiology of the ovipositing females are also included in the models (after Stephens and Krebs, 1986):

i) Exclusivity of search and exploitation: females cannot search for new hosts while ovipositing.

ii) Sequential Poisson encounters: hosts are encountered one at a time and the host encounter rate is constant.

iii) Complete information: females recognise host-types and their gain curves immediately, and know their own expected lifespan and potential fecundity.

Table 2. General solutions for Optimal Clutch Size Models

Limiting resource	Optimal clutch size	Authority
1. Hosts	$\hat{N} = \hat{N}_H = \dfrac{-s(N, \hat{N}, x, i)}{s'(N, \hat{N}, x, i)}\bigg|_{N-\hat{N}}$	1–4, 8, 9, App. 2
2. Time	$\hat{N} = \hat{N}_T = \left[\dfrac{-s(N, \hat{N}, x, i)}{s'(N, \hat{N}, x, i)}\right] \cdot \left[\dfrac{T_t}{T_t + N \cdot T_o}\right]\bigg|_{N-\hat{N}}$	1 9, App. 3
3. Eggs	$\hat{N} = \hat{N}_E = 1$	6, 7
4. Reserves	$\hat{N} = \left[\dfrac{-s(N, \hat{N}, x, i)}{s'(N, \hat{N}, x, i)}\right] \cdot \left[\dfrac{\beta \cdot T_t}{\beta \cdot T_t + N}\right]\bigg|_{N-\hat{N}}$	3, 5, App. 4
5. Eggs and time	when: $T/E > (T_o + T_t)$ $\hat{N} = \hat{N}_E$ {see model 3}	
	when: $(T_o + T_t) \geq T/E \geq (T_o + T_t/\hat{N}_T)$ $\hat{N} = \dfrac{T_t}{(T/E) - T_o}$ 2, 6, 9, App. 5	
	when: $T/E < (T_o + T_t/\hat{N}_T)$ $\hat{N} = \hat{N}_T$ {see model 2}	
6. Eggs and Hosts	when: $E/H < 1$ $\hat{N} = \hat{N}_T$ {see model 3}	
	when: $1 \leq E/H \leq \hat{N}_H$ $\hat{N} = E/H$ 4, App. 6	
	when: $E/H > \hat{N}_H$ $\hat{N} = \hat{N}_H$ {see model 1}	

For key to symbols see Table 1. Authorities are: (1) Charnov and Skinner, 1984, (2) Parker and Courtney, 1984, (3) Charnov and Skinner, 1985, (4) Skinner, 1985, (5) Smith and Lessells, 1985, (6) Waage and Godfray, 1985, (7) Godfray, 1986, (8) Godfray 1987a, (9) Ives, 1989.

Predictions of the models

General solutions for the optimal clutch sizes for each of the models are given in Table 2, and specific solutions for models 1–4, assuming linear or exponential larval fitness functions, are given in Table 3 (specific solutions for models 5 and 6 may be deduced from these). In addition, predictions were made for each of the models on each of the following (Tab. 4):

1. The range of optimal clutch sizes $(\hat{N})$.

2. The maximum expected egg-load of a host (x_{max}) when several females are ovipositing.

3. The effect of host value on $\hat{N}$. Survival from some hosts may be higher than from others for several reasons, the most obvious being that they are larger and hence offer more food to the developing larvae. Hosts that are associated with high larval survival compared with other hosts containing the same number of larvae are said to be of high value (Skinner, 1985).

4. The effect of travel time between hosts (T_t) on $\hat{N}$.

5. The effect of oviposition time (T_o) on $\hat{N}$. T_o includes not only the time taken to lay an egg, but also any other time commitment resulting from the laying of an egg. For example, if females are unable to search while maturing an egg, this time

Table 3. Specific solutions for optimal clutch sizes for models 1–4 when the larval fitness functions are linear or exponential

Larval† Fitness Function	Optimal clutch size			
	1. Hosts	2. Time	3. Eggs	4. Reserves
Model a				
LIN	N^*	$\dfrac{-T_i + \sqrt{[T_i^2 + 2N^* \cdot T_i \cdot T_o]}}{T_o}$	1	$-\beta \cdot T_i + \sqrt{[\beta^2 \cdot T_i^2 + 2N^* \cdot \beta \cdot T_i]}$
EXP	N^*	$\dfrac{-T_i + \sqrt{[T_i^2 + 4N^* \cdot T_i \cdot T_o]}}{2T_o}$	1	$\dfrac{-\beta \cdot T_i + \sqrt{[\beta^2 \cdot T_i^2 + 4N^* \cdot \beta \cdot T_i]}}{2}$
Model b				
LIN	$N^* - \dfrac{x}{2}$	$\dfrac{-T_i + \sqrt{[T_i^2 + (2N^* - x) \cdot T_i \cdot T_o]}}{T_o}$	1	$-\beta \cdot T_i + \sqrt{[\beta^2 T_i^2 + (2N^* - x) \cdot \beta \cdot T_i]}$
EXP	N^*	$\dfrac{-T_i + \sqrt{[T_i^2 + 4N^* \cdot T_i \cdot T_o]}}{2T_o}$	1	$\dfrac{-\beta \cdot T_i + \sqrt{[\beta^2 \cdot T_i^2 + 4N^* \cdot \beta \cdot T_i]}}{2}$
Model c				
LIN	$\dfrac{2N^*}{(i+1)}$	$\dfrac{-T_i(i+1) + \sqrt{[T_i^2(i+1)^2 + 8N^* \cdot T_i \cdot T_o]}}{2T_o}$	1	$\dfrac{-\beta \cdot T_i(i+1) + \sqrt{[\beta^2 \cdot T_i^2(i+1)^2 + 8N^* \cdot \beta \cdot T_i]}}{2}$
EXP	N^*	$\dfrac{-T_i + \sqrt{[T_i^2 + 4N^* \cdot T_i \cdot T_o]}}{2T_o}$	1	$\dfrac{-\beta \cdot T_i + \sqrt{[\beta^2 \cdot T_i^2 + 4N^* \cdot \beta \cdot T_i]}}{2}$

For key to symbols see Table 1. For general solutions, and solutions for models 5 and 6, see Table 2.
† LIN refers to the linear larval fitness function, EXP to exponential function. Models of type a give the optimal solution for a single female ovipositing alone. Models of type b and c assume that several females lay on each host; in type b models, the female is the last to lay on a given host that already bears x eggs, and in type c models she is one of i females that will simultaneously lay on each host.

(which may be longer than the time needed to oviposit an egg) should also be included in T_o.

6. The effect of the female's total potential egg supply (E) on $\hat{N}$.

7. The effect of the female's expected lifespan (T) on $\hat{N}$.

8. The effect of the current egg load of the host (x) on $\hat{N}$.

9. The effect of increasing the number of ovipositing females (i) on $\hat{N}$.

In all cases where predictions are made on the effects of varying travel or oviposition time, host value, current egg-load and the number of ovipositing females, these are made for between rather than within habitat variation (Stephens and Krebs, 1986; see also Smith and Lessells (1985) for a comparison of these predictions for a reserves constraint model).

Single Oviposition Models

Model 1a: Hosts limiting: If opportunities to lay clutches are restricted, but the amount of time and number of eggs available are not limiting, natural selection will favour females that maximise fitness gain per clutch (or oviposition site) (Charnov and Skinner, 1984, 1985; Parker and Courtney, 1984; Skinner, 1985; Fig. 1a, Appendix 2). This situation probably rarely occurs, but will be approached in circumstances in which suitable oviposition sites are rarely encountered, or when the number of opportunities to breed is limiting, as when brood-guarding limits host-seeking. For instance, the bethylid wasp *Goniozus nephantidis*, a gregarious larval ectoparasitoid of the lepidopteran *Opisina arenosella*, guards its brood of developing larvae (from superparasitism, multiparasitism and hyperparasitism) until pupation. Thus, the amount of time and energy the female invests in each brood is large and apparently independent of brood size (Hardy and Blackburn 1991). This means that there are strong *a priori* reasons for expecting the female to maximise fitness gain per host or brood (Hardy et al., 1992). The maximisation of brood fitness was first considered by Lack (1947) for birds, and the optimal solution has been referred to as the *most productive brood size* (Charnov and Krebs, 1974) and *Lack's solution* (Charnov and Skinner, 1984; Godfray, 1987a). Lack's solution (N^*) is important as a reference against which other predictions may be compared.

The only parameter affecting N^* is host value. Travel time (T_t), oviposition time (T_o), the egg supply of a female (E) and the total time available for oviposition (T) have no effect on N^* (Tab. 4).

Model 2a: Time limiting: Laying eggs takes time. For instance, many Lepidoptera, including the noctuid moth *Spodoptera exempta*, lay clutches comprising several hundred eggs, each of which is placed individually in an ordered sequence such that the female may oviposit for 2 h or more before her clutch is complete (K. Wilson pers. obs.). If the amount of time taken to lay a clutch is dependent on its size, as it is in *S. exempta*, then there will be a trade-off between time spent ovipositing on a host $(N \cdot T_o)$ and

Table 4. Qualitative predictions of clutch size models

Prediction	Model (limiting resource)					
	1. (Hosts)	2. (Time)	3. (Eggs)	4. (Reserves)	5. (Eggs and Time)	6. (Eggs and Hosts)
$\hat{N} =$	N^*	$\leq N^*$	1	$\leq N^*$	$\leq N^*$	$\leq N^*$
x_{max}†(LIN) −	$2N^*$	$2N^*$	$2N^*$	$2N^*$	$2N^*$	$2N^*$
(EXP) =	∞	∞	∞	∞	∞	∞
Effect on $\hat{N}$ of increasing:						
Host value	+	+	+‡	+	+	+
T_l	0	+	0	+	+	0
T_o	0	−	0	0	−	0
E	0	0	0	0	+	+
T	0	0	0	0	−	0
x†(LIN)	−	−	−‡	−	−	−
(EXP)	0	0	0	0	0	0
i†(LIN)	−	−	−‡	−	−	−
(EXP)	0	0	0	0	0	0

For key to symbols see Table 1. 0 = no effect; + = $\hat{N}$ increases; − = $\hat{N}$ decreases.

† LIN refers to models that include a linear larval fitness function, and EXP to an exponential function.

‡ Here, the probability of host acceptance is affected, rather than clutch size *per se*. For authorities see text and Table 2. All predictions assume monotonically decreasing offspring *per capita* fitness function.
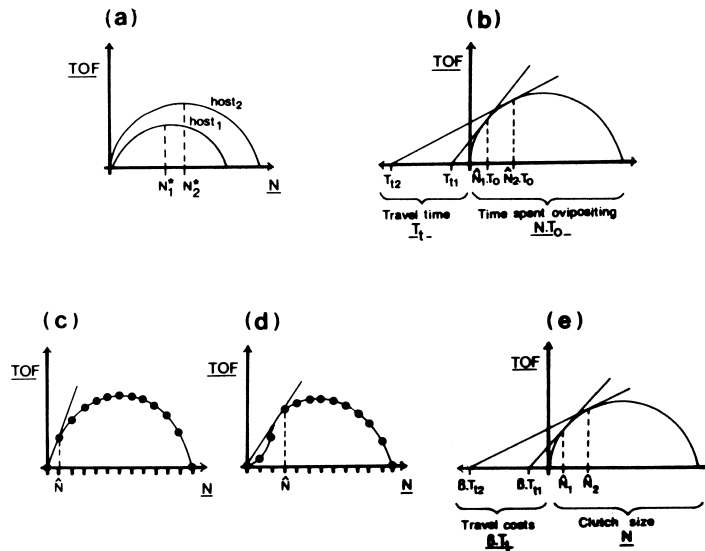
Fig. 1. Graphical solutions to models 1a–4a: predicted clutch sizes when hosts, time, eggs or reserves are limiting. Each curve represents a fitness gain function relating total offspring fitness (TOF) to oviposition effort. (a) Hosts limiting (model 1a): $\hat{N} = N^*$, the most preductive clutch size. Host 2 is of higher 'value' than Host 1 and therefore $\hat{N}_2 > \hat{N}_1$. (b) Time limiting (model 2a): optimal time spent ovipositing $(N \cdot T_o)$ is found by constructing a tangent from the travel time, T_t, to the fitness gain curve. As T_t increases between environments (from T_{t1} to T_{t2}) so $\hat{N} \cdot T_o$, and hence the optimal clutch size, increases (from $\hat{N}_1 \cdot T_o$ to $\hat{N}_2 \cdot T_o$). (c) and (d) Eggs limiting (model 3a): $\hat{N}$ is found by drawing a tangent from the origin to the larval competition curve, as represented by a step function. In (c), the larval fitness function decreases monotonically, and hence egg fitness peaks at 1 egg/host and $\hat{N} = 1$. In (d), $s'(N, \hat{N}, x, i)$ is initially positive (i.e. there is an Allee effect) and egg fitness peaks at a clutch size greater than 1 so that $\hat{N} > 1$. (e) Reserves limiting (model 4a): as for (b) except that clutch size replaces time spent ovipositing and an 'egg equivalent' travel cost $(\beta \cdot T_t)$ replaces travel time.

time spent searching for additional hosts (travel time, T_t). This trade-off has been modelled both analytically and graphically using the marginal value theorem (MVT, Charnov 1976; Fig. 1b and Appendix 3). These models seek the clutch size that maximises TOF per unit of time and predict that the optimum clutch size $(\hat{N})$ will be lower than N^* when T_t is short (relative to T_o) and will approach N^* as T_t approaches infinity (e.g. Parker and Courtney, 1984; Charnov and Skinner, 1984, 1985; Skinner, 1985, see also Iwasa et al., 1984). In other words, the optimal clutch size will converge on Lack's solution as the host encounter rate declines. Optimal clutch size also increases with increasing host value, but is unaffected by the egg supply of the female and the total time available to her (Tab. 4).

Model 3a: Eggs limiting: In some situations the total number of eggs that a female can oviposit during her lifetime may be limiting. This will be the case if reserves limit egg production and cannot be diverted from other uses such as maintenance, and is particularly likely to occur in proovigenic species which emerge with their full

complement of eggs. These include many Lepidoptera such as bombycids, lymantri-
ids and noctuids (see Englemann, 1970; Wigglesworth, 1972 and references therein).
When eggs are limiting but time and oviposition sites are plentiful, the optimal
solution is to maximise egg fitness (or TOF per egg). When *per capita* offspring
fitness decreases monotonically with increasing clutch size, $\hat{N} = 1$ for accepted hosts
(these on which eggs are laid) (Fig. 1c). When there is an Allee effect and *per capita*
fitness peaks at a clutch size greater than one (as it does in the bruchid beetle
Zabrotes subfasciatus; Utida, 1967), $\hat{N}$ is greater than one (Fig. 1d) and may
coincide with N^* (Godfray, 1987a). As in all the other models considered, host
value has an effect on optimal oviposition behaviour; however, in the absence of an
Allee effect this is manifested as an increased probability of laying a single egg on
a host rather than an increase in clutch size. None of the other parameters (T_t, T_o,
E and T) have an effect on optimal oviposition behaviour (Tab. 4).

Model 4a: Reserves limiting (eggs and time, dependently): Life history theory often
assumes that there will be a trade-off between the amount of resources directed into
reproduction and the amount directed into maintenance, such that the more eggs a
female lays, the shorter is her lifespan (Williams, 1966; see review by Bell and
Koufopanou, 1986). This sort of trade-off is likely to be particularly important to
animals that do not feed as adults and whose resources are hence limited to those
accumulated during larval development. For instance, in the seed-store environ-
ment, the granivorous beetle *Callosobruchus maculatus* has limited opportunities to
feed as an adult and so its lifespan and fecundity are constrained by the amount of
seed material that it can consume as a larva (Smith and Lessells, 1985; Credland et
al., 1986; Wilson, 1994). Moreover an increase in either fecundity or longevity
results in a concomitant decline in the other, suggesting that reserves can be
directed into reproduction or maintenance, as required (Wilson, 1994).

The cost of reproduction can be modelled using the marginal value theorem
(MVT) by specifying a conversion rate between eggs and time (Smith and Lessells,
1985) and is analogous to the time limiting model (above), except that the limiting
resource has changed from time to egg-equivalents. The predictions of the two
models are qualitatively the same (Tab. 4, Fig. 1c, Appendix 4); optimal clutch size
is higher when travelling is expensive relative to oviposition and when host value is
higher, but is unaffected by the egg reserves of the female or the total amount of
time available to her (provided that the conversion rate between eggs and time does
not vary with these two variables). However, because the cost of oviposition relative
to travelling is likely to be greater when measured in eggs rather than time, a given
change in travel time will produce smaller changes in $\hat{N}$ under a reserves constraint
(this model) than under a time constraint (model 2).

Model 5a: Eggs and time limiting, independently: This model considers the situation
in which both eggs and time may be limiting, but a reduction in the number of eggs
laid does not result in increased longevity, nor vice-versa. This is the situation in
insects for whom egg production and maintenance are constrained by different
resources such as protein and lipid, respectively, as is true of most leaf-feeding and

haematophagous insects (see Crawley, 1983; Strong et al., 1984; Wigglesworth, 1972, and references therein). Under independent egg and time constraints, the optimal clutch size depends critically on the amount of time available for laying each egg (T/E) (Appendix 5). Two threshold values of T/E can be recognised: a lower threshold, below which the only limiting resource is time (because the amount of time required to lay all the eggs is more than that available); and an upper threshold, above which the only limiting resource is eggs (because the amount of
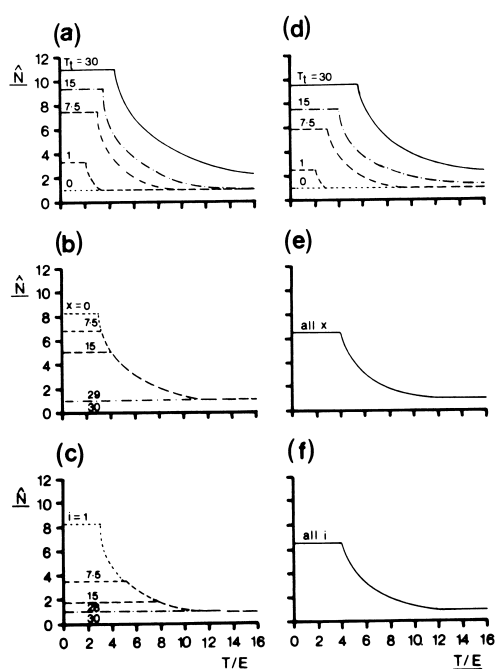
Fig. 2. Graphical solutions to models 5a–c: effect of travel time, current egg-load, and number of ovipositing females on optimal clutch sizes when eggs and time are simultaneously and independently limiting. Figures (a)–(c) illustrate the effect of travel time (T_t), current egg-load of the host (x) and number of ovipositing females (i), respectively, on the predicted optimal clutch sizes when the larval fitness function is linear. Figures (d)–(f) illustrate their similar effects when the function is exponential (see text). When eggs and time are independently and simultaneously limiting, the optimal clutch size ($\hat{N}$) is critically dependent on the value of T/E. Above the upper threshold for T/E (when $T/E > T_o + T_t$), eggs are the sole limiting resources and the optimal clutch size, $\hat{N} = 1$ (see model 3). Below the lower threshold (when $T/E < T_o + T_t/\hat{N}_T$), time is the sole limiting resource and $\hat{N} = \hat{N}_T$, where $\hat{N}_T$ is the marginal value clutch size (model 2). Between these two thresholds, eggs and time are both limiting and $\hat{N} = T_t/(T/E - T_o)$. For both larval fitness functions, travel time, T_t, affects both the position of the upper and lower thresholds, and the value of $\hat{N}$ at values of $T/E < T_o + T_t$ (Figs. (a) and (d)). Between the threshold values, $\hat{N}$ is independent of the egg load of the host (x) and the number of ovipositing females (i), but the lower threshold value of T/E may be sensitive to changes in both i and x depending on the shape of the larval fitness function (cf. Fig^c. (b) and (c) with (e) and (f)). In the illustrated example, $N^* = 15$, $T_o = 2$, $T_t = 10$ (except in (a) and (d)), $x = 0$ (except in (b) and (e)), and $i = 1$ (except in (c) and (f)). (See Tables 2 and 3 and Appendix 5).

time needed to lay all the eggs is less than that available). Between these two thresholds the optimal clutch size is a non-linear function of T/E (Figs. 2a and 2d; Tab. 2; Appendix 5). In all cases, optimal clutch size (or probability of host acceptance) increases with host value. Above the upper threshold of T/E the optimal clutch size is independent of T_i, T_o, E or T. Between the thresholds, optimal clutch size is affected by all four of these parameters, while below the lower threshold it is unrelated to E and T, but increases with increasing T_i/T_o (Tab. 4).

In some instances, for example if there is variation in the time-interval between host encounters, the ratio of remaining time to remaining eggs will vary in such a way that the optimal clutch size may change after oviposition. In this case, females should reassess their optimal clutch size after each clutch that they lay. As Mangel (1987) demonstrated using dynamic programming techniques, the temporal pattern of $\hat{N}$ depends on the interaction between E and T. If clutches are laid in quick succession, the optimal clutch size will decrease over time (Parker and Courtney, 1984; Begon and Parker, 1986; see also Iwasa et al., 1984; Mangel, 1987, 1989). However, if a female is deprived of hosts for some time, $\hat{N}$ may increase because the amount of time available for egg-laying decreases whilst the number of eggs available remains constant, resulting in time becoming more limiting (i.e. in T/E decreasing; see Fig. 2, Appendix 5).

Model 6a: Eggs and hosts limiting, independently: This model considers the case in which both eggs and hosts are potentially limiting, but a reduction in the number of eggs laid does not result in an increase in the number of hosts that can be found. For example, many drosophilids lay their eggs in ephemeral substrates, such as flower heads or fruiting bodies (e.g. Kambysellis and Heed, 1971). When suitable oviposition sites are present for only a short period, host availability may limit a female's reproductive success, whereas when the flowering or fruiting period is extended, it may be a female's egg supply that is the main limiting factor. As in the previous model, the optimal clutch size depends on the ratio of the two independent constraints (E/H in this case). When E/H is less than one, the model is equivalent to egg limitation (model 3) and the optimal clutch size is one egg, while if E/H is above an upper threshold, the model is equivalent to host limitation (model 1) and the optimal clutch size is equal to Lack's solution, N^*. Between these two thresholds, the optimal clutch size involves using up all available hosts and eggs (Mitchell, 1975; Skinner, 1985), and increases linearly from one to N^* as the ratio of eggs to hosts (E/H) increases (Fig. 3, Appendix 6). In all cases, optimal clutch size (or probability of host acceptance) increases with host value, and is independent of T_i, T_o and T. Between the two thresholds, but not below the lower or above the higher threshold, the optimal clutch size varies with E (Tab. 4).

Multiple Oviposition Models

Model 1: Hosts limiting: 1b) The optimal clutch size ($\hat{N}$) for a female that is the last to lay on a host already bearing x eggs depends on the shape of the larval fitness

(a)

(c)

(b)

(d)

E/H   E/H
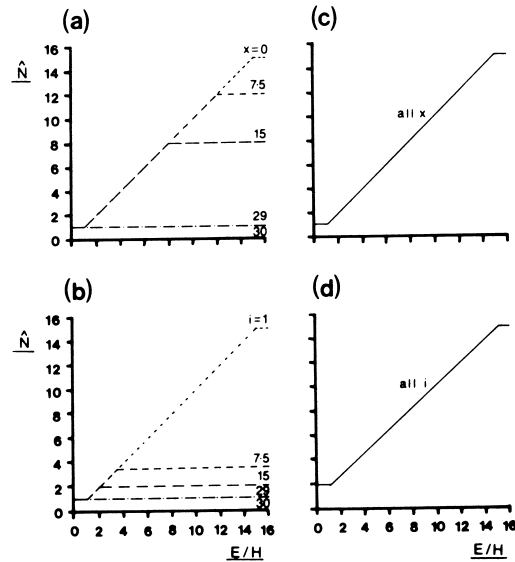
Fig. 3. Graphical solution to models 6a–c: effect of current egg-load and number of ovipositing females on optimal clutch sizes when eggs and hosts are simultaneously and independently limiting. Figures (a) and (b) illustrate the effect of the egg-load of the host (x) and the number of ovipositing females (i), respectively, on the optimal clutch size when the larval fitness function is linear. Figures (c) and (d) illustrate similar effects when the function is exponential (see text). When eggs and hosts are both potentially independently limiting, the optimal clutch size, $\hat{N}$, is determined by the value of E/H, the number of eggs available per host. Below the lower threshold, when $E/H < 1$, eggs are the sole constraint and $\hat{N} = 1$ (see model 3). Above the upper threshold, when $E/H > N_H$, hosts are the sole limiting resource and $\hat{N} = N_H$, the optimal clutch size when hosts are limiting (see model 1). Between these two thresholds, eggs and hosts both constrain clutch size and $\hat{N} = E/H$. $\hat{N}$ is not dependent on the value of E/H between the thresholds, but the position of the upper threshold is sensitive to the egg load of the host (x) and the number of ovipositing females (i) when the larval fitness function is linear (Figs. (a) and (b)), but not when it is exponential (Figs. (c) and (d)). In the illustrated example, $N^* = 15$. (See Tables 2 and 3 and Appendix 6).

function for individual larvae. When this function is the linear function described earlier, $\hat{N}$ is Lack's solution minus half the current egg-load of the host (Tab. 3), and because clutch fitness equals zero at some finite clutch size $(2N^*)$, there is an upper limit to the total number of eggs expected on a host (Tab. 4; Appendix 2).

However, when the larval fitness function is exponential, $\hat{N}$ is independent of the current egg-load, and is affected only by the severity of larval competition (Tab. 3). Consequently, with this fitness function, there is no upper limit to the number of eggs expected when all hosts have the same egg-load (Tab. 4). However, clutch size will be egg-load dependent when egg-loads vary within the environment (see Smith and Lessells' (1985) model 1b). This result does not hold for all non-linear fitness functions (unpublished analysis), and serves to underline the warning made by Smith and Lessells (1985) about making generalisations from specific functions (see also Ives, 1989). In summary, if the female behaves as if she is the last to lay on a

particular host and hosts are the major constraint on clutch size, then the female should be sensitive to both the shape of the larval fitness function and to the current egg-load of the host.

Skinner (1985) made the additional prediction that if progeny fitness declines as a function of the age of competing larvae in the host (as is true for some bruchid beetles, Bellows, 1982) then clutch size will decline with time between successive female visits.

1c) This model considers the number of eggs a female should lay given that $(i - 1)$ other females also oviposit on the same host. For the linear larval fitness function, $\hat{N}$ is equal to $2N^*/(i + 1)$ (Tab. 3, Appendix 2). In other words, $\hat{N}$ decreases as the number of laying females (i) increases and the predicted maximum number of eggs per host is equal to twice Lack's solution $(2N^*)$. However, this conclusion is not general; $\hat{N}$ may increase with i under some circumstances (Ives, 1989), or may remain unaltered, as when the larval fitness function is exponential (Tab. 3, Appendix 2).

For all of the remaining models, when the larval fitness function is exponential the optimal clutch size is unaffected by the number of ovipositing females or the egg-load of the host (and hence x_{max} always equals infinity). Therefore, discussion will be limited to models that encompass a linear larval fitness function.

Model 2: Time limiting: 2b) When time is the major constraint, the optimal clutch size declines as the initial egg-load of the host increases (Tab. 3 and 4, Appendix 3). This is because the MVT predicts that $\hat{N}$ will decrease as host value decreases, and the value of the host is reduced by the current egg-load of the host (see above). The optimal clutch size of the second female is smaller than that of the first, provided that the first and second females take the same length of time to find hosts (Skinner, 1985). When the larval fitness function is linear, the maximum number of eggs expected on a host (x_{max}) is the same as that when hosts are limiting (i.e. $2N^*$, model 1b).

2c) When a female is one of i females to lay on a host, her optimal clutch size is dependent on the shape of the fitness function, on the cost of travelling between hosts, and on the number of females ovipositing (Parker and Courtney, 1984) (Tab. 1). Again, when the larval fitness function is linear, x_{max} approaches $2N^*$ as the number of ovipositing females approaches infinity.

Model 3: Eggs limiting: 3b) If time and hosts are not limiting, then, in an environment in which all hosts have the same value and egg-load, a female that assumes that she is the last to lay should always lay one egg on each host, irrespective of its egg-load. However, in an environment with variable egg-loads, the problem is analogous to diet choice (Iwasa et al., 1984) and the optimal probability of laying on a host will be negatively correlated with the number of eggs on its surface.

3c) When i females are laying on the same host, the optimal clutch size is one. This result is more or less independent of the value of i (although if the fitness function becomes zero at some value of i, $\hat{N}$ will equal zero for equal or greater values of i).

Model 4: Reserves limiting (eggs and time, dependently): 4b) The predictions under a reserve constraint are qualitatively simlar to those under a time constraint. The

optimal clutch size decreases monotonically with increasing egg-load and, for larval fitness functions that intercept the abscissa at some point, there is a maximum expected egg-load (Smith and Lessells, 1985).

4c) If the female behaves as if other females will also lay on the same host, then the *ES* clutch size will be a decreasing function of the number of females ovipositing (i) and of the search costs (T_r) (Appendix 4). As i and T_r increase, so the maximum number of eggs expected on a host approaches $2N^*$. (Note that this solution differs from that derived by Smith and Lessells (1985), which is incorrect; M. Sjerps personal communication.)

Model 5: Eggs and time limiting, independently: 5b) The optimal clutch size when eggs and time are independently limiting is dependent on the ratio T/E. As in model 5a, there are two threshold values of T/E: below the lower threshold ($T/E < T_o + T_t \hat{N}_T$), time is the major constraint and the optimal clutch size is $\hat{N}_T$, the egg-load dependent marginal value clutch size (which decreases as egg-load increases; see model 2b). Above the upper threshold ($T/E > T_o + T_t$), eggs are the major constraint, and the optimal clutch size is unaffected by egg-load and is equal to one (see model 3b). At intermediate values of T/E, intermediate values of $\hat{N}$ are predicted (see model 5a) which are independent of egg-load (Fig. 2b). As the egg-load of the host increases, the slope of the transition curve from $\hat{N} = 1$ to $\hat{N} = \hat{N}_T$ remains constant, but the critical value of T/E at which $\hat{N}$ diverges from $\hat{N}_T$ increases (see Appendix 5). The situation becomes more complicated if egg-loads vary within environments: $\hat{N}$ is then dependent on the frequency of low egg-load hosts in the environment (analogous to an optimal diet choice model).

5c) The predictions of this model are qualitatively the same as for the model above when all hosts have the same egg-load (see Fig. 2c and Appendix 5).

Model 6: Eggs and hosts limiting, independently: 6b) and c) The optimal clutch size when eggs and host are limiting depends on the ratio E/H (the number of eggs available per potential host; see model 6a and Appendix 6). Increasing the egg-load of the current host (x) or the number of females laying (i) effectively reduces the value of N^* (see model 1b) and hence lowers the upper threshold value of E/H (Fig. 3a). When x or i are sufficiently large, $\hat{N}$ will equal one and be independent of E/H.

As for model 5b and c, quantitative predictions become more difficult if egg-loads vary within an environment, but one would expect $\hat{N}$ to decrease as the current egg-load increases, and that for some hosts the optimal clutch size will be zero, i.e. hosts will be rejected.

Discussion

Our main aim in reviewing models of insect clutch size was to determine whether such models could be distinguished by qualitative criteria alone or whether quantitative predictions must be tested. This cannot be considered without first discussing the role of phenotypic plasticity. Traits are said to be phenotypically plastic when a single genotype produces a range of phenotypes depending on the environment.

If the optimal phenotype (in this case clutch size) varies with the environment (e.g. host value, travel time, or the number of other ovipositing females), a match between phenotype and environment may be achieved either by genetic differentiation or by phenotypic plasticity.

Phenotypic plasticity is particularly advantageous when the environment changes on a small scale geographically, or at the same or shorter interval than a generation time (Bradshaw, 1965). An obvious example is foraging behaviour, where it is often tacitly assumed that individuals will show adaptive phenotypic plasticity in response to variation in environmental parameters such as patch quality or travel time. Conversely, genetic differentiation is more likely when associations between populations and environments persist over many generations (e.g. Karban, 1989). However, the evolution of adaptive phenotypic plasticity depends on the existence of environmental cues that accurately predict future conditions. The upshot is that individuals may not show phenotypic plasticity even when it would be adaptive for them to do so. They may instead produce a more or less fixed phenotype which is adapted to their average environmental conditions (for instance the average level of multiple oviposition). Thus, if an organism shows phenotypic plasticity, we can reject hypotheses that predict a constant phenotype, but if the reverse occurs – the organism shows no phenotypic plasticity – we cannot reject those hypotheses which predict phenotypic plasticity. This is an important consideration in the testing of most optimality models, but is seldom discussed.

Returning to the task of discriminating between the models of oviposition behaviour, two of the single oviposition models make extreme predictions: under an oviposition site constraint (model 1a) optimal clutch size equals Lack's solution (N^*), the value of which can be determined experimentally by measuring the larval competition curve or larval fitness function (Tab. 4). In contrast, under an egg constraint (model 3a) the optimal clutch size is one egg, while under the 4 other models (2a, 4a, 5a, 6a) optimal clutch size ranges from 1 to N^*. Moreover, in both the extreme cases, as well as for model 6a, the optimal clutch size is independent of travel time between oviposition sites, whereas in the other cases the optimal clutch size increases with travel time. Thus if clutch size shows phenotypic plasticity with respect to the encounter rate with hosts, models 1a, 3a and 6a can be rejected, though the converse is not true if there is no phenotypic plasticity (see above). Models 2a and 5a predict that clutch size should be sensitive to oviposition time; this, however, is likely to be of limited utility in testing the models because it is not easily manipulated. Models 5a and 6a predict that clutch size will vary with the egg supply of the female; again, the existence of phenotypic plasticity may be used only to reject the remaining models, but a lack of phenotypic plasticity cannot be used to reject models 5a and 6a. Only model 5a predicts that clutch size will be sensitive to variation in the female's lifespan, or her residual lifespan. Lastly, all of the models predict variation in clutch size (or the probability of laying a single egg) with host value; this prediction is therefore useless in qualitative tests of the models. In conclusion, the existence of phenotypic plasticity with respect to some parameters (T_t, T_o, E, T) allows some of the models to be rejected, but in many cases quantitative tests will be needed to distinguish between the models.

The multiple oviposition models offer no additional qualitative criteria for distinguishing between oviposition sites, eggs or time, or combinations of these as constraints. When the female is the last to lay on a host (type b models), optimal clutch size may generally decrease with increasing current egg-load of the host (but not when the larval fitness function is exponential; Tab. 4). Similarly, when the female is one of i females to oviposit on the host, optimal clutch size decreases with increasing i. So if clutch size is phenotypically plastic with respect to current egg-load of the host or number of ovipositing females, the single oviposition models may be rejected. Care should be taken, however, in interpreting a response to an increased number of co-ovipositing females; interference competition may have energetic costs (e.g. Wightman, 1978) resulting in a change in the conversion rate, in energetic terms, between travelling and ovipositing. Yet again, a lack of phenotypic plasticity does not exclude the multiple oviposition models.

In conclusion, the clutch size models presented here cannot be adequately tested using qualitative information alone; if the main selection pressures acting on clutch size are to be elucidated then precise quantitative predictions must be examined. This is attempted in a companion paper (Wilson, 1994) using bruchid beetles ovipositing on cowpeas.

Acknowledgements

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Appendices

Appendix 1. Finding the Optimal Clutch Size

(i) The rate of fitness gain relative to the limiting resource, W, is expressed as a function of the clutch size laid per host, N.

(ii) The evolutionarily stable clutch size, N, is then given by the solution of the equation (Oster and Wilson, 1978; Parker and Begon, 1986; Ives, 1989)

$$\partial W/\partial N = 0|_{N = \hat{N}} \tag{1}$$

provided that

$$\partial^2 W/\partial N^2 < 0|_{N = \hat{N}} \tag{2}$$

In general, $\hat{N}$ is a function of the fitness of each offspring, itself a function $(s(N, \hat{N}, x, i))$ of N, $\hat{N}$, the number of females laying on a single host (i) and the egg-load of the host (x) before any of these i females begin to oviposit. Primes denote the first partial derivative with respect to N. $\hat{N}$ can be found for specific larval fitness functions by substituting those functions and their first derivatives into the general solutions.

(iii) *Linear function:*

$$s(N, \hat{N}, x, i) = a - b[N + (i - 1) \cdot \hat{N} + x] \tag{3}$$

$$s'(N, \hat{N}, x, i) = -b \tag{4}$$

(iv) *Exponential function:*

$$s(N, \hat{N}, x, i) = e^{-c[N + (i - 1) \cdot \hat{N} + x]} \tag{5}$$

$$s'(N, \hat{N}, x, i) = -c \cdot e^{-c[N + (i - 1) \cdot \hat{N} + x]} \tag{6}$$

(v) $\hat{N}$ for models a, b and c respectively (Table 2) can be found by substituting (a) $i = 1$, $x = 0$; (b) $i = 1$; (c) $x = 0$; into the general solutions.

(vi) The maximum egg-load expected per host $(x_{max};$ Table 4) can be found for b models by setting $\hat{N} = 0$ and solving for x, and for c models by finding $i \cdot \hat{N}$ as i tends to infinity. If $\hat{N}$ is independent of x or i respectively (i.e. optimal clutch size is independent of the current egg-load of a host or of the number of other females ovipositing), then x_{max} is infinite.

These steps are followed in Appendices 2–4, and used to derive the solutions given in Tables 2 and 3.

Appendix 2. Hosts Limiting

(i) The rate of fitness gain per clutch

$$F(N, \hat{N}, x, i) = N \cdot s(N, \hat{N}, x, i) \tag{7}$$

(ii)

$$\hat{N} = -s(N, \hat{N}, x, i)/s'(N, \hat{N}, x, i)|_{N = \hat{N}} \tag{8}$$

When a single female oviposits per host (model 1a), $\hat{N}$ is equal to the most productive clutch size, N^* (also referred to as Lack's solution). Values of $\hat{N}$ for other models can frequently be expressed, by substitution, as functions of N^*. For the linear function for the fitness of each offspring:

$$N^* = a/2b \tag{8}$$

and, for the exponential function:

$$N^* = 1/c \tag{9}$$

(iii) For the linear larval fitness function:

$$\hat{N} = (a - bx)/[b(i + 1)]$$
$$= (2N^* - x)/(i + 1) \tag{10}$$

(iv) For the exponential larval fitness function:

$$\hat{N} = 1/c = N^* \tag{11}$$

Appendix 3. Time Limiting

(i) The rate of fitness gain with respect to time

$$G(N) = N \cdot s(N, \hat{N}, x, i)/(T_t + N \cdot T_o) \tag{12}$$

(ii)

$$\hat{N} = \frac{-s(N, \hat{N}, x, i)}{s'(N, \hat{N}, x, i)} \cdot \frac{T_t}{(T_t + N \cdot T_o)}\Bigg|_{N = \hat{N}} \tag{13}$$

(iii)

$$\hat{N} = \frac{-T_t(i + 1) + \sqrt{[T_t^2(i + 1)^2 + 4(a/b - x)T_t \cdot T_o]}}{2T_o}$$
$$= \frac{-T_t(i + 1) + \sqrt{[T_t^2(i + 1)^2 + 4(2N^* - x)T_t \cdot T_o]}}{2T_o} \tag{14}$$

(iv)

$$\hat{N} = \frac{-T_t + \sqrt{[T_t^2 + 4T_t \cdot T_o/c]}}{2T_o}$$
$$= \frac{-T_t + \sqrt{[T_t^2 + 4N^* \cdot T_t \cdot T_o]}}{2T_o} \tag{15}$$

Appendix 4. Reserves Limiting

(i) The rate of fitness gain with respect to reserves measured as 'egg equivalents'

$$H(N) = N \cdot s(N, \hat{N}, x, i)/(\beta \cdot T_t + N) \tag{16}$$

(ii)

$$\hat{N} = \frac{-s(N, \hat{N}, x, i)}{s'(N, \hat{N}, x, i)} \cdot \frac{\beta \cdot T_t}{(\beta \cdot T_t + N)}\bigg|_{N = \hat{N}} \tag{17}$$

(iii)

$$\hat{N} = \frac{-\beta \cdot T_t(i + 1) + \sqrt{[\beta^2 \cdot T_t^2(i + 1)^2 + 4(2N^* - x) \cdot \beta \cdot T_t]}}{2} \tag{18}$$

(iv)

$$\hat{N} = \frac{-\beta \cdot T_t + \sqrt{[\beta^2 \cdot T_t^2 + 4N \cdot \beta \cdot T_t]}}{2} \tag{19}$$

Appendix 5. Eggs and Time Limiting

If the female uses all the eggs, E, and time, T, available to her, she will lay a clutch of size

$$N(E, T) = (E \cdot T_t)/(T - E \cdot T_o) \tag{20}$$

and her total fitness

$$W = E \cdot s(N(E, T), \hat{N}, x, i) \tag{21}$$

Females should use all of the time available at all values of T for which $\partial W / \partial T \geq 0$.

$$\partial W / \partial T = -s'(N(E, T), \hat{N}, x, i) \cdot T_t / (T/E - T_o)^2 \tag{22}$$

In the absence of an Allee effect (i.e. when $s'(N, \hat{N}, x, i)$ is negative for all N), this expression is positive for all values of T, implying that as T increases females should use all of T and hence lay smaller clutches. However, clutches are constrained to integer values, hence the smallest clutch size is one egg. When females lay clutches of one, they use a total of $T/(T_t + T_o)$ eggs. Hence, females cease to use all of the available time (and eggs are the only constraint; model 3) when

$$T/E \geq T_t + T_0 \tag{23}$$

Females should use all of the eggs available at all values of E for which $\partial W / \partial E \geq 0$.

$$\partial W / \partial E = s'(N(E, T), \hat{N}, x, i) \cdot (N(E, T)^2 / T_t) \cdot (T/E) + s(N(E, T), \hat{N}, x, i) \tag{24}$$

Substituting $s(N, \hat{N}, x, i)/s'(N, \hat{N}, x, i)$ from (13), equating $N(E, T)$ with $\hat{N}_T$ (the optimal clutch size when time is limiting), and solving for $\partial W / \partial E$, females cease to use all of the available eggs (and time is the only constraint; model 2) when

$$T/E < (T_t/\hat{N}_T) + T_o \tag{25}$$

Below this threshold, $\hat{N} = \hat{N}_T$. Between the thresholds given by (23) and (25), females should use all available time and eggs and the optimal clutch size is thus given by (20). This optimum is not a function of x or i and hence, between the

thresholds, $\hat{N}$ is independent of the egg-load of the host and the number of ovipositing females. However, both the position of the lower threshold (25) optimal clutch sizes below it (17) are functions of x and i, and hence may depend on the current egg-load of the host or the number of ovipositing females, depending on the specific larval fitness function used (see Figures 2b and 2c).

Appendix 6. Eggs and Hosts Limiting

If a female uses all of the eggs, E, and hosts, H, available to her, she will lay a clutch size

$$N(E, H) = E/H \tag{26}$$

and her total fitness

$$W = E \cdot s(N(E, H), \hat{N}, x, i) \tag{27}$$

Females should use all of the hosts available at all values of H for which $\partial W/\partial H \geq 0$

$$\partial W/\partial H = -s'(N(E, H), \hat{N}, x, i) \cdot E^2/H^2 \tag{28}$$

This expression is positive for all H, but because clutch sizes are constrained to integer values, eggs will become the only constraint (model 3) and optimal clutch size one egg when

$$E/H < 1 \tag{29}$$

Similarly, females should use all of their eggs at values of E for which $\partial W/\partial E \geq 0$.

$$\partial W/\partial E = s'(N(E, H), \hat{N}, x, i) \cdot E/H + s(N(E, H), \hat{N}, x, i) \tag{30}$$

Substituting $s(N, \hat{N}, x, i)/s'(N, \hat{N}, x, i)$ from (8), and solving for $\partial W/\partial E \leq 0$, females cease to use all of their eggs (and hosts are the only constraint; model 1) when

$$E/H > N^* \tag{31}$$

Above this threshold, $\hat{N} = N^*$. Between the thresholds given by (29) and (31), females should use all available time and eggs and $\hat{N}$ is given by (26). As in model 5, this optimum is independent of the number of females laying (i) and the current egg-load of the hosts (x). However, the position of the upper threshold (31), and optimal clutch sizes above it, are sometimes dependent on i or x, depending on the specific larval fitness function (see Appendix 2 and Fig. 3).