Integrating theory of clutch size and body size evolution for parasitoids

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The way that parents allocate resources amongst offspring has been a subject of interest since the beginnings of modern life history theory (Roff 1992, Stearns 1992). Many animals, such as altricial birds and many insects, deposit eggs together in discrete groups, called clutches, where the offspring develop together for some time. Variation in clutch size is typically then studied as a route to understanding the selective pressures and constraints on the resource allocation strategy of the organism. Here we propose a neglected but complementary route to understanding resource allocation in insect parasitoids involving offspring body size as a focal parameter. Our message is that consideration of both body size and clutch size variation simultaneously can enhance understanding or resource allocation strategies in this group of organisms, illustrating the value of an integrated life history approach.

Parasitoids are insects (the vast majority wasps) which lay their eggs on or in the bodies of other arthropods. The young parasitoids feed on the still-living body of their host, eventually killing it. Parasitoids may lay from one to several hundred eggs on or in a host, variability which begs explanation. In the mid-1980s, theory of clutch size evolution, which developed under an ornithological tradition, began to be applied to parasitoids and other insects, and many models were developed based around the trade-off between clutch size and offspring fitness (reviewed in Godfray 1994). In testing those models, it was realized that one of the major fitness related variables which trades off with clutch size is the body size of resulting offspring: because host insects represent a resource of limited size, larger clutches or broods tend to result in smaller-bodied offspring, especially in idiobiont species whose hosts do not grow after parasitoid oviposition. The optimal clutch size then depends upon how adult body size is related to fitness, a relationship which itself has spawned a small industry of research.

Parasitoids can either develop solitarily or gregariously. In solitary parasitoids only one offspring develops successfully from each host, and the offspring frequently display contest competition for resources. In gregarious species several offspring may complete development from a single host and competition more closely approaches a scramble situation. A multitude of studies (reviewed in Godfray 1994), have demonstrated that body size in solitary parasitoids tends to be positively correlated with host size; if the host is fully consumed (see Harvey et al. 2000 for an exception) and only one offspring develops per host, then larger hosts providing more resources for growth should lead to larger offspring. Less intuitively though, a number of studies have shown that offspring body size increases with host size within and across gregarious species (Opp and Luck 1986, le Masurier 1987, Hardy et al. 1992, Ode et al. 1996, Mayhew 1998, Mayhew and Hardy 1998). This trend is surprising because it has been widely found that gregarious species will lay larger clutches of eggs on larger hosts (Godfray 1994), a fact which intuitively leads us to expect that they are compensating for the extra resources provided by larger hosts. Apparently though, gregarious species tend to undercompensate when adding eggs to larger hosts such that larger hosts still provide more per capita resources for offspring (Mayhew 1998).

We do not know of models which have explicitly tried to explain this trend. Parasitoid clutch size models rarely explicitly consider body size. Several more general life history models have tried to address the simultaneous optimization of clutch size and offspring size (normally egg or seed size), but are not easily applied to the present problem where both growth and mortality occur after eggs are laid (i.e. when provisioning of offspring is finalized) and contribute towards final offspring size. Predicting parasitoid body size requires a return to previously published models of parasitoid clutch size to make them explicitly consider body size as a fitness-related trait.

In the following paragraphs we review and modify some previously published clutch size models to make initial predictions about how and in what way parasitoid body size might evolve. Our explicit aim is to observe how optimization models can predict an increase in body size with host size within and between populations of gregarious species. Because these qualitative trends are seen in nature, models which do not predict them can be eliminated from scientific inquiry at an early stage; conversely models which do predict these trends point to assumptions sufficient to explain reproductive allocation in these species.

First consider the Lack model of clutch size evolution (Lack 1947). The Lack model defines clutch fitness, F, as the product of clutch size, c, and individual offspring fitness, f, which is itself a decreasing function of c.

$$F(c) = cf(c). \tag{1}$$

The optimal clutch size is found where the derivative of F with respect to c is zero, that is by solving

$$c = \frac{-f(c)}{\partial f(c)/\partial c}. \tag{2}$$

The clutch size determines the resources allocated per offspring. If the host is of size R, the per capita resources are given by $m = R/c$. The maximal clutch fitness can then be solved as an optimal per capita resources problem, and Eq. 1 can be written

$$F(m) = \frac{R}{m} f(m). \tag{3}$$

This is the model of optimal size versus numbers of offspring, as described by Smith and Fretwell (1974). The maximum of $F(m)$ is obtained by solving

$$m = \frac{f(m)}{\partial f(m)/\partial m}, \tag{4}$$

which is independent of host size R. Whatever the host size, a female should lay a clutch c^* so that each offspring gets a constant amount of food, m^*. If the size of an offspring, s, depends on food available ($s = s(m)$), the optimal offspring size is independent of host size.

Thus, the Lack model suggests that a female parasitoid should try to distribute its eggs amongst hosts such that each offspring achieves the same body size regardless of the size of host it developed on. One possible way for body size to vary within the confines of Lack's assumptions is when the relationship between size and fitness, $f(m)$ varies. This cannot easily occur within a population but should more realistically occur between different populations or species which experience different ecological pressures. Empirical studies of the relationship between size and fitness have shown a variety of different forms of relationship of the sort that would lead to variation in the optimal body size (see Bennett and Hoffmann 1998). In order for body size to increase with host size across populations/species, wasps attacking larger hosts must benefit more from size than wasps attacking small hosts. Whether this is so is unknown at present.

In order to predict an increase in body size with host size within a population one or more of Lack's assumptions must be relaxed. Skinner (1985) added a time trade-off between present and future reproduction, such that time spent in present reproduction may lead to lost opportunities elsewhere. In Skinner's model, although the optimal clutch size increases with host size, larger hosts receive a lower ratio of eggs to developmental resources than smaller hosts, and offspring size increases with host size (Fig. 1). This particular prediction is a consequence of the way that time spent ovipositing relates to net fitness gain for a female (Fig. 2). If the loading curve, describing how fitness gain to the female wasp is related to time spent at the host, is convex, the tangent to the loading curve which describes the optimal time to leave, hits it at a steeper angle on larger hosts, hence proportionally further away from its peak. As a result the optimal time to leave is only slightly longer in large than in small hosts (Fig. 2). Again, Skinner's model applies only to different populations experiencing different average host size distributions. If two populations of parasitoids were distributed so that one experienced larger hosts on average, it would tend to produce larger-bodied offspring, predictions consistent with empirical findings across species. The empirical evidence for lifetime trade-offs in parasitoids is slim at present (see Ellers 1996), although they are expected to be widespread.

Skinner's model, like the Lack model, provides important insights into how and why variation in body size can arise across populations or species, but again fails to suggest reasons for within-population variation. Here we extend Skinner's approach to consider optimal egg allocation to a population of hosts of different sizes. For simplicity we assume that hosts come in discrete sizes R_i. Let λ_i be the encounter rate with hosts R_i. Upon encountering a host of size R_i, a female lays c_i eggs. Offspring fitness can be viewed as consisting of survival and size. For simplicity we ignore development time in this model, although cases are known which would require its inclusion (see Harvey et al. 2000). The offspring fitness is defined as the product of its survival probability and the fitness of the survivor, f, which depends on size. We also assume that the host is fully consumed (or that an equal proportion is consumed irrespective of host size) and divided equally amongst the surviving offspring. Let $a(c)$ be the number of survivors. The per capita amount of food is determined by

$$m(c) = \frac{R}{a(c)}. \tag{5}$$

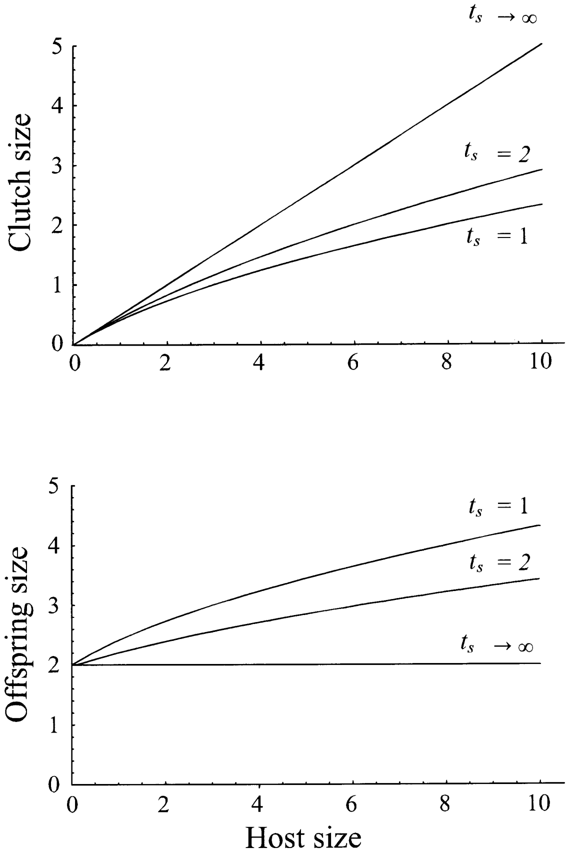

Fig. 1. Optimal clutch size and offspring size in different populations as a function of different average host sizes predicted from Skinner (1985). We used his Eq. 1 as our number-fitness function, with the following parameters: $b = 1$, $s = 1$, $r_0 = 1$. The three lines represent three travel times (t_s). An infinite travel time is equivalent to zero lifetime trade-off (the Lack solution), and so predicts constant offspring size.

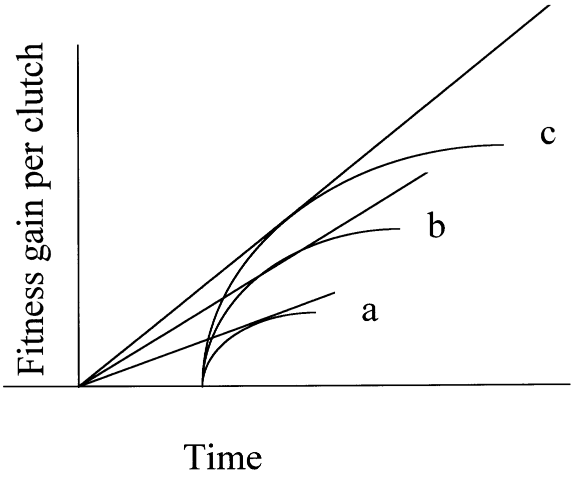

Fig. 2. Graphical illustration of clutch size optimization with variable host size from Skinner's model (Skinner 1985). Three convex "loading curves" are shown, representing the fitness gain from each clutch against time, for parasitoids encountering three host types of increasing size; a, b and c. The intersection of the loading curves with the x axis is the time when parasitoids first encounter them; time to the left of this is time spent searching, whilst time to the right is time spent handling and ovipositing. The optimum times spent at the three hosts is given by the intersection of the tangents to the loading curves. The optimum time is greater on larger hosts, but only slightly greater.

When there is no developmental mortality, $a(c) = c$, fitness depends only on size, and hence the available food per offspring, $m(c)$. In common with previous clutch size models (reviewed in Wilson and Lessells 1994), we take $f(c)$ to be a decreasing function of clutch size of the form

$$f(c) = 1 - e^{-m(c) + m_0} \tag{6}$$

where m_0 is the minimum resource needed to reach a sufficiently large size at pupation to survive. Oviposition time is initially considered to be proportional to clutch size. $T_0(c)$ is the time required to lay a clutch of c eggs. The long-term fitness gain rate of a female wasp is then given by

$$F(c) = \frac{\sum_{i=1}^{i_{\max}} \lambda_i a(c_i) f(c_i)}{1 + \sum_{i=1}^{i_{\max}} \lambda_i T_0(c)}. \tag{7}$$

The optimal clutch sizes, c_i^*, as a function of host sizes can be obtained by finding the zero of the derivative of Eq. 7 with respect to c_i. This can be done numerically and the optimal offspring size is obtained with Eq. 5. This model predicts that the optimal clutch size should increase linearly with host size, so per capita resource is constant, and offspring size is independent of host size.

The rate function in Eq. 7 is made up of three components: offspring survival, the fitness of surviving offspring, and the time cost of oviposition. The optimal offspring size is susceptible to variation in all three components, but since the fitness function is unlikely to vary within populations we consider only the other two. First, we introduce developmental mortality through contest competition. Now clutch size affects offspring survival, Ψ, such that

$$\Psi(c) = c^{-p} \tag{8}$$

where p is a parameter measuring the strength of offspring competition. The model predictions are given in Fig. 3. Body size is constant on all host sizes when competition is just scramble ($p = 0$ and $a(c) = c$), but increases with host size at a rate dependent on the level of contest competition. When $p = 1$, only one offspring can survive per host ($a(c) = 1$). Thus, solitary species in our model emerge as just an extreme form of gregarious species. The size of offspring in this case is predicted to be strongly correlated with the size of the host, as observed in numerous solitary species.

However, to explain within-population variation in some gregarious species (e.g. Hardy et al. 1992, Ode et al. 1996, Mayhew 1998), keeping the present model framework, we need to alter instead our assumptions about the time cost of oviposition. Species from the family Bethylidae are synovigenic (the eggs are matured during adult life), the eggs are large, and take considerable time to mature. In two species, eggs do not mature until after hosts are first encountered (Pérez-Lachaud and Hardy 1999, Stokkebo and Hardy 2000), whilst in two others, time from initial host encounter until the eggs are laid increases with clutch size, presumably as a result of extended egg maturation time (Luft 1993, Mayhew and Heitmans 2000). Eggs in both species are laid rather rapidly at the end of a long period of host encounter. If maturing more eggs after host encounter imposes costs per egg, such as longer time spent at the host, which are greater for each additional egg laid, females might be selected to leave large hosts to find new ones after laying only small clutches. In *Goniozus legneri* clutch size is asymptotically related to host size (Gordh et al. 1983), a trend interpreted by the authors as due to time constraints on egg production after host encounter. Egg maturation patterns such as these are potentially widespread, though certainly not universal, in parasitoids and other insects (Papaj 2000). The simplest way to explore the implications theoretically is to describe total oviposition time, $T_0(c)$, as a function of clutch size:

$$T_0(c) = t_0 c^i \tag{9}$$

where i determines the strength of the increase in handling time with clutch size. Eq. 9 can be substituted into Eq. 7 to find the optimum as before. The additional time cost for larger clutches now induces an increase in per capita resources on larger hosts, giving

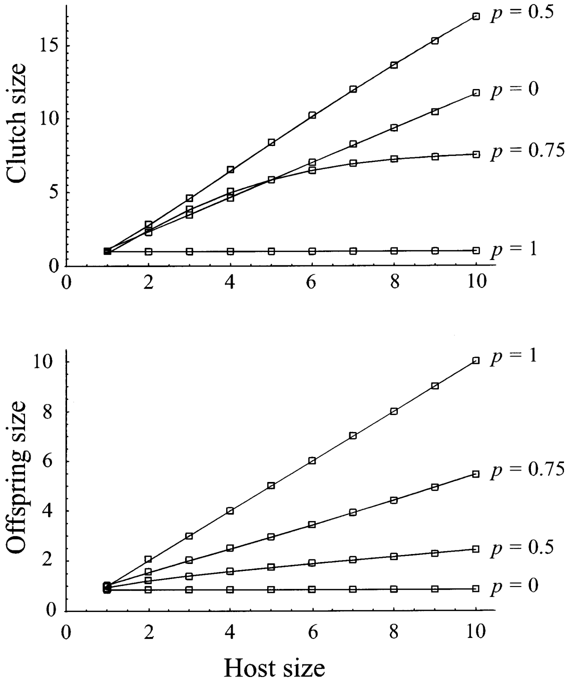

Fig. 3. Optimal clutch size and offspring size within a population as a function of host size for different levels of contest competition, p. Host sizes are uniformly distributed and parameters are $a = 0.01$, $t_0 = 5$, $m_0 = 0.1$. When no contest competition occurs ($p = 0$), the model reduces to Eq. 7 and offspring size is constant. As p increases towards 1 (solitary parasitoids), offspring size tends to increase more with host size.

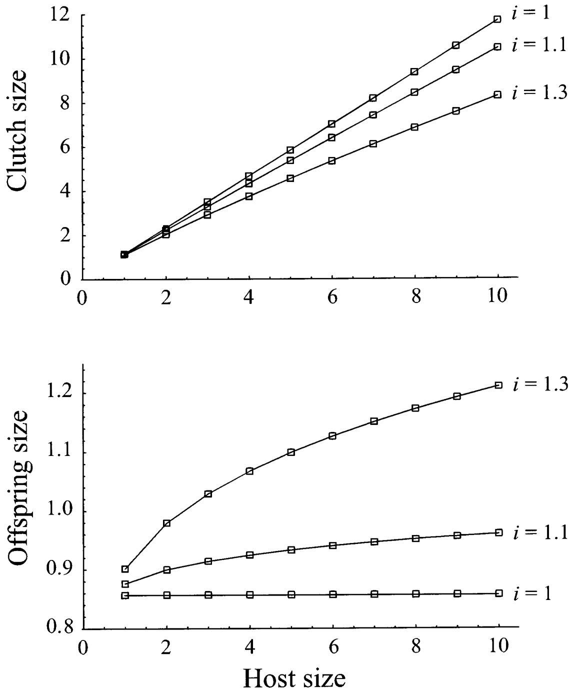

Fig. 4. Optimal clutch size and offspring size within a population when the magnitude of the lifetime trade-off varies with clutch size according to Eq. 9. Lines show different values of i. When the magnitude of the trade-off is constant for each egg ($i = 1$), offspring size is constant. When successive eggs in a clutch take longer to be laid ($i > 1$), larger hosts receive proportionally less eggs, and offspring size becomes an increasing function of host size.

larger offspring (Fig. 4). We do not expect the above assumptions to provide the sole explanation for such trends in parasitoids, and indeed they are obviously incorrect for many pro-ovigenic endoparasitoids. They do however provide one plausible explanation for the particular natural histories for which we have empirical data, and illustrate general principles required to explain the body size trends of interest.

Our brief reconsideration of existing clutch size models in the light of empirical studies of body size variation has suggested several specific reasons for such variation, which now require explicit testing:

1. Body size can increase with host size across populations or species as a result of larger body size carrying greater fitness when larger hosts are attacked, or as the result of a time-related fitness trade-off, the strength of which is affected by host size.
2. Body size can increase with host size within populations as a result of contest competition between larvae in combination with lifetime trade-offs, or if the severity of a time-related fitness trade-off increases with clutch size.

We emphasize that different parasitoid natural histories may require alternative explanations, but the search for such explanations should enhance our understanding of parasitoid reproductive decisions. Our approach of adding explicit assumptions about body size to existing clutch size models produces models which optimize two life history parameters simultaneously. In our opinion, any comprehensive evolutionary explanation of parasitoid body size or clutch size would have to consider both parameters, and it is only because of their roots in ornithology that previous theoretical models have failed to do so. Considering parasitoid body size explicitly forces this development upon us, and points to specific evolutionary assumptions which would not have come from studying qualitative variation in clutch size alone. Parasitoids also force us to take a rather unusual, though ecologically important, approach to body size evolution; that of optimal partitioning of resources amongst offspring rather than that of optimal maturation time. We consider both the use of existing theory to explore new questions, and the development of integrated theory to be desirable directions in life history studies.

Acknowledgements – PJM was supported by a William and Mary Leverhulme fellowship through the Royal Society of London, UK. OG was supported by the Fonds National Suisse de la Recherche Scientifique. We thank Richard Law for comments.

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