The evolution of parasitoid egg load

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INTRODUCTION

Insect parasitoids lay their eggs in, on or close to their insect hosts. These eggs hatch into larvae that use a single host to complete their development. If the risk of parasitoid attack is substantial, the antagonistic interaction between the parasitoids and their hosts may lead to intense coevolution of attack and counterattack strategies. The hosts try to escape detection, and those that are nevertheless found and attacked may try to neutralize the parasitoid's eggs, e.g. by encapsulation. The parasitoids, in turn, will try to increase their searching efficiency and may develop countermeasures to overcome their hosts' defensive tactics (Carton & Nappi 1991 Kraaijeveld & van Alphen 1994, Kraaijeveld & Godfray 1997, Hochberg 1997, Chapter by Godfray).

From the viewpoint of the hosts, what is at stake is simple: their life. The risk of attack determines how well a host should be prepared; this will set an optimum balance of costs (allocation of resources to defense that could have been used otherwise) and benefits (probability of surviving parasitoid attack). For the parasitoids, however, what is at stake is less clear. If eggs were cheap and fast to produce, and if the time required to attack a host were minimal, a parasitoid may lose nothing by parasitizing any host she encounters. However, if the hosts evolve defense strategies, this is not likely to be the case. Expensive eggs that require substantial investment of resources (or hosts that are dangerous to attack) could imply a direct cost of parasitizing an encountered host. Thus, it is necessary to include the potential costs of parasitoid eggs (and/or attack) to understand host-parasitoid coevolution.

Traditionally, parasitoids are subdivided into ‘egg-limited’ and ‘time-limited’ species. Time-limited parasitoids have an ample supply of eggs or they can quickly mature new ones if their supply has become depleted so their fitness is proportional to the number of hosts they are able to attack during their lifetime. This type of parasitoid has been the paradigm of optimal foraging theory (Charnov & Stephens 1988, Stephens & Krebs 1986). In contrast, egg-limited parasitoids have a finite egg supply (‘egg load’), which sets an upper limit to their lifetime reproductive success. For such parasitoids eggs *must* be costly, and indeed, theory and observation suggest that such parasitoids are more choosy when presented with hosts of varying qualities (Iwasa *et al*. 1984, Roitberg & Mangel 1989, Mangel 1992).

This dichotomous view has been giving way to the more integrative view that time-limitation and egg-limitation are the extremes of a continuous spectrum, and that, given the stochasticity inherent in their way of life, parasitoids are to some extent subject to both (Minkenberg *et al*. 1992, Rosenheim 1996, Heimpel & Rosenheim 1998). Even when most individuals die without having depleted their egg load, some may have to spend their last hours or days (or a proportion of their time in the case of synovigenic parasitoids) in vain because they have no more eggs to deposit.

The evolutionary question is where on the spectrum we expect parasitoids to be and how this depends on the ecological characteristics of host-parasitoid interaction? On the one hand, a parasitoid’s investment in her capacity to go on searching for hosts is wasted once she has laid her last egg. On the other hand, preparing more eggs than the maximum number of oviposition opportunities a parastoid can expect is also wasteful. As Rosenheim (1996) has put it, parasitoids should strike the ‘optimal balance’ between being egg-limited (because it wastes foraging opportunities) and being time-limited (because this wastes eggs).

This gambling aspect of oviposition strategies has received recent attention by Rosenheim (1996) and Sevenster *et al*. (1998). In these studies, the stochastic component of the parasitoid's life history takes the form of stochastic survival: a parasitoid may die before she has depleted all her eggs. The unpredictability of the rate of host encounter has received less attention, but the effect is analogous. If a parasitoid is living in a completely predictable environment, she should never store more eggs than the number of hosts she is going to encounter. However, in unpredictable environments it is unlikely that the best strategy is to prepare eggs just for the expected number of hosts encountered. Even if the probability is low that a parasitoid will be lucky and encounter many hosts, the potential payoff may still be sufficiently high to be equipped for it (Godfray 1994).

Models that address optimum strategies for egg-limited parasitoids are generally based on a life-history framework (Iwasa *et al*. 1984 Mangel 1992, Roitberg & Mangel 1989, Minkenberg *et al*. 1992, Rosenheim 1996, Sevenster *et al*. 1998, Heimpel *et al*. 1998). This approach the assumes that the environment is constant: under such conditions the parasitoid should try to maximize the number of successful ovipositions given an unvarying mortality rate. From such studies it appears that it does not pay to economize on eggs if mortality rates are high: such parasitoids should therefore tend to be more time-limited. Dynamic programming models that keep track of the state of the egg complement of parasitoids throughout their life (Iwasa *et al*. 1984, Mangel 1992, Roitberg & Mangel 1989) show that optimum decisions depend on the age of the parasitoid. Young parasitoids should not waste eggs (behaving like egg-limited parasitoids) whereas parasitoids near the end of their life should be less choosy (behaving like time-limited parasitoids).

Models that have addressed the ecological consequences of egg limitation usually draw the analogy with handling time in predator foraging (Thompson 1924, cited in Getz & Mills 1996, Hassell & May 1973, Hassell 1978, Hochberg 1997, Chapter by Heimpel). If host density is low, parasitoid fitness is likely to be constrained by encounters with hosts, whereas 'saturation' will occur with higher host densities, *ergo* egg-limitation ensues. This approach is less satisfactory than an approach that explicitly models the condition of parasitoid females, because it is essentially *ad hoc*: there is no explicit relationship between egg load and fitness. Shea *et al*. (1996) analysed a population dynamical model that includes explicit oviposition dynamics. In contrast to what could be expected on the basis of the handling time analogy, they found no effect of egg limitation on population stability. This result is difficult to interpret because their model was based on a continuous-time Lotka-Volterra system of differential equations, whose dynamical behavior is very different from that of the discrete-time Nicholson-Bailey model that is usually taken to represent host-parasitoid dynamics (May 1974, Hassell 1978).

The evolution of egg limitation depends on the resource cost of an egg, which is an individual-level characteristic, as well as on the expected number of encounters with hosts, which is a population-level characteristic. This calls for an integrative aproach that links individual-level optimization and population-level consequences. There have been some approaches to integrate ecological and evolutionary models involving parasitoids (e.g. Driessen & Hemerik 1992, Hochberg & Holt 1995, Getz & Mills 1996, Shea *et al*. 1996, Hochberg 1997) but these are limited by the lack of a fitness measure for egg-limited parasitoids that is consistent with the Nicholson-Bailey model. The fitness concept underlying most life-history models *can* be integrated into a population dynamical setting, but typically it leads to a mathematical nightmare, characterized by a profusion of parameters, additional assumptions, and so on. Consequently, it is difficult to reassess the model results in terms of the ‘standard’ Nicholson-Bailey model. What I will do here is derive, from first principles, the per capita fitness of parasitoids with a finite egg supply in a classical Nicholson-Bailey setting. In contrast to the standard derivation, which is based upon the consideration of what can happen to individual hosts (escape from attack, being parasitized, etc.), I shall derive the model from the point of view of individual parasitoids (whether she encounters more or fewer hosts than her egg load, whether there is competition with conspecifics, etc.). For simplicity, the model is tailored to solitary parasitoids that lay only a single egg per host attacked.

As I will show, the model is essentially equivalent to the Nicholson-Bailey model. The merit of this approach is not that the Nicholson-Bailey model is realistic (it surely isn’t), but because it is the theoretical benchmark, and hopefully the modification that I will present leads to hypotheses that can be tested using more detailed models or experimental observations.

When the model derived from individual behaviour of the parasitoids is extended with an equation that describes the dynamics of the host population, the long-term consequences and possible evolutionary feedbacks that govern the selection of egg load can be investigated. I will discuss only a very simple example to illustrate the principles involved, leaving more complex cases for future analysis.

Parasitoid fitness in the absence of competition

I assume that the parasitoids have an ‘area of discovery’ of size a, and that they can detect and attack every host that is found within this area. Since this area is finite, and since hosts come in discrete units (e.g., eggs or larvae), there will be stochastic variation in the number of hosts encountered. I will begin by assuming an unspecified probability distribution ϕ_n for the number of hosts encountered $\underline{n}$. (The underline is to indicate that $\underline{n}$ is a stochastic variable.)

The model assumes also that parasitoids are proovigenic, that is, they have a fixed egg load of E eggs. If during her life-time, a parasitoid encounters fewer hosts than her egg load E, she can parasitize them all, but if she encounters more, some opportunities go unused. Therefore, the number of hosts attacked by a parasitoid (which may be called its ‘oviposition success’ or, more loosely, its ‘gain’ G) with E eggs that encounters n hosts is, in the absence of competitors,

$$G(n) = \begin{cases} n & (n < E) \\ E & (n \geq E) \end{cases} \tag{1}$$

The parasitoid’s expected gain, EG, is

$$\mathrm{E}G(\underline{n}) \quad = \sum_{n=0}^{\infty} \phi_n G(n) \tag{2}$$

This expression can be rewritten as

$$\mathrm{E}G(\underline{n}) \quad = \sum_{n=0}^{\infty} \phi_n\, n - \sum_{n=E+1}^{\infty} \phi_n (n - E)$$

$$= N - \sum_{n=0}^{\infty} \phi_{n+E}\, n \qquad (3)$$

where the first term gives parasitoid’s potential oviposition success (the expected number of hosts encountered) and the second term represents the opportunity cost of egg limitation (the opportunities that are unused for oviposition). An equivalent way of representing the parasitoid’s expected gain is

$$\mathrm{E}G(\underline{n}) \quad = E - \sum_{n=0}^{E} \phi_n (E - n) \qquad (4)$$

which shows that she can never be attack more than E hosts (Figure 8.1).

[Figure 8.1 about here]

The expected gain depends not only on the mean of the distribution of host encounters but also on the variance. This effect is demonstrated in Figure 8.2, which shows the expected gain as a function of egg load, E, for different values of the clumping parameter k of the negative binomial distribution (with the same mean host density). Such a clumped distribution of encounters can have multiple causes in nature. If the parasitoids have sophisticated foraging strategies, clumped encounter rates will follow (Chesson & Murdoch 1986). Nonetheless, here I will assume that parasitoids search randomly (which is the assumption underlying the Nicholson-Bailey model) in which case clumpedness is a direct consequence of the hosts’ spatial distribution.

The more clumped the hosts (the smaller k) the greater the variance in the number of hosts encountered. The greater the variance, the greater the relative probability for a parasitoid to encounter more hosts than her egg-load allows her to parasitize. Fitness therefore keeps increasing with egg load long past the mean host density, when the hosts are very clumped. In contrast, when the hosts are very homogeneously distributed, it does not pay to carry more than the mean host density. One obvious result is that it will never pay to carry more eggs than the maximum ever to be encountered. However, the Poisson and negative binomial distributions have no maximum, so for these distributions there is always an opportunity cost because there is always a chance that a parasitoid encounters more hosts that her egg load allows her to parasitize.

[Figure 8.2 about here]

Overcoming host defenses

If the hosts have defenses that allow them to encapsulate parasitoid eggs, the parasitoids are forced to take countermeasures (see chapter by Godfray). This may simply mean larger eggs but also eggs requiring more resources to equip them with anti-encapsulation properties (Kraaijeveld and van Alphen 1995). In any case, such countermeasures are likely to be costly. Suppose that parasitoids have allocated a fixed amount of resources to reproduction (R), but that they can subdivide this into larger or smaller units, so that size s is given by

$$s = R/E \,. \tag{5}$$

For simplicity, I will refer to s as egg size, though size does not necessarily refer to the eggs' physical size but could equally well apply to the amount of an 'anti-encapsulation agent' (for example polydnavirus, Fleming 1992, Godfray 1994) that is injected together with the egg. The crucial assumption is that a parasitoid's total supply of this agent is fixed so that more eggs means less per egg.

If the probability of successful development of a parasitoid egg is a function of its size, $c(s)$, then we have that expected fitness (EF) is the product of survival probability and expected gain:

$$\mathrm{E}F = c(R/E)\ \mathrm{E}G \tag{6}$$

To calculate the numerical examples I took the arbitrary function $c(x) = 1 - \exp(-x)$. Here I assume that the parasitoid does not self-superparasitize. However, if superparasitism occurs, the assumption that only one egg will survive to maturity produces the same equation.

[Figure 8.3 about here]

As can be seen in Figure 8.3, the optimum egg load depends on the expected host density. Since this particular model assumes a random (i.e., Poisson) host distribution, the variance increases with the mean, which implies that it pays to be prepared for encounters with large numbers of hosts when the mean increases. Since such preparedness requires increased egg loads, a fraction of each of these eggs survival chances has to be sacrificed.

Within-host competition

If parasitoid density is sufficiently high, a focal parasitoid will encounter hosts that are already parasitized by other females, and hosts parasitized by her may in turn be found by other females. We therefore have to incorporate competition for hosts into the model. Again, let n be the number of hosts in the patch, and let there be p competing resident parasitoids (each with an egg complement of E^* eggs). Then, there are $E + pE^*$ parasitoid eggs to be distributed over the n hosts. Assuming that the parasitoids can distinguish between parasitized and unparasitized hosts, every parasitoid can oviposit her entire egg load if $n \geq E + pE^*$, but if $n < E + pE^*$, there is competition for hosts. I assume that superparasitism will then occur, and that the ensuing survival probability of an egg is inversely proportional to the total number of eggs deposited in its host. Assuming no differences between parasitoids other than their egg load, the probability that an egg of the focal parasitoid will hatch on average is $E/(E + pE^*)$. Putting everything together, the expected gain of the focal parasitoid becomes

$$G(n,p) = \begin{cases} n\,\dfrac{E}{E+pE^*} & n < E+pE^* \\ E & n \geq E+pE^* \end{cases} \quad . \tag{7}$$

The focal parasitoid’s overall expected oviposition success is therefore

$$\mathrm{E}F = \sum_{p=0}^{\infty} \sum_{n=0}^{\infty} \phi_{n,p} G(n,p) \ , \tag{8}$$

where $\phi_{n,p}$ gives the joint probability of finding n hosts and p parasitoid competitors in the patch. As before, this can be rewritten as

$$\mathrm{E}G = E - \sum_{p=0}^{\infty} \sum_{n=0}^{E+pE^*} \phi_{n,p}\left(E - n\,\frac{E}{E+pE^*}\right) . \tag{9}$$

This expression requires the evaluation of an infinite sum that cannot be solved for finite egg complements E and E^*. However, as a check, it can be shown that if (i) the focal parasitoid has the same egg load as the resident parasitoids ($E = E^*$), (ii) E approaches infinity, and (iii) hosts and parasitoids are distributed over the patches according to a joint

Poisson distribution with means of aN hosts and aP parasitoids, then the expected gain of the focal parasitoid will be

$$\mathrm{E}G = \frac{aN(1 - e^{-aP})}{aP}, \qquad (10)$$

which is the expected gain of a parasitoid in the Nicholson-Bailey model. This is no surprise, of course, because the underlying assumptions are the same as those of the Nicholson-Bailey model.

[Figure 8.4 about here]

I have not been able to find a closed expression for expected fitness of egg limited parasitoids (Equation 9). Numerical exploration reveals that the effect of egg limitation decreases if the mean density of resident parasitoids increases (Figure 8.4). This is no surprise, as competition for hosts effectively decreases the number of available hosts. Figure 8.4 does not show an optimum; this is because I did not include a cost of larger egg complements. If such a cost is included (for example because larger egg complements are associated with smaller eggs that have smaller survival chances, as in Figure 8.3a), the curves would eventually decline for high enough parasitoid densities. Note also that to arrive at this figure, I assumed that hosts and parasitoids are randomly and independently distributed. It may well be that the results would be different if the parasitoids aggregate independently of host density, because this increases the variance in the number of hosts encountered by a parasitoid.

[Figure 8.5 about here]

Figure 8.4 shows the expected fitness of a resident parasitoid; it shows that the satiating effect of egg limitation decreases with mean parasitoid density. This effect that is not taken into account in the ‘handling time’ analogy used in previous models (Thompson 1924, cited in Getz & Mills 1996, Hassell & May 1973, Hassell 1978, Hochberg 1997, Chapter by Heimpel), because handling time only depends on host density. To calculate the force of selection on egg number, we have to compare this with the fitness of parasitoids having different egg loads. An example is shown in Figure 8.5. Here it becomes apparent that the benefit of an additional egg depends on the combination of host and parasitoid densities

(Figure 8.5a). If mean host density (*aN*) is larger than the egg complement, the benefit of an additional egg decreases with parasitoid density (Figure 8.5b). This is because competition with other parasitoids brings the number of available hosts within the range where the focal parasitoid does not ‘feel’ the consequences of egg limitation (and as a consequence, an additional egg is of little value). In contrast, if the mean host density is substantially less than the parasitoid’s egg complement, the value of an additional egg may actually *increase* with parasitoid density (Figure 8.5b). Under these conditions, parasitoids always encounter less hosts than their egg complement allows them to parasitize, but an increase in egg complement gives them an advantage over other parasitoids in when superparasitization is common (Ives 1989). Since it is assumed that host survival is not affected by the number of times they have been parasitized, an additional egg represents an extra ticket in the superparasitism lottery.

Note that the fitness benefit, depicted in Figure 8.5, does not yet take into account the costs associated with increased egg loads. To work out whether it is selectively advantageous to increase the egg complement, the decreased survival probabilities of every egg should be included.

In summary, analysis of the individual fitness of a focal parasitoid reveals that optimum egg load depends on the details of the interactions between host individuals and the parasitoids, and also on details of the interactions among the parasitoid larvae themselves in the case of superparasitism. However, the optimum egg load also depends on the densities and distributions of hosts and parasitoids. The latter are not fixed constants, but instead are set by the dynamics of the resident host-parasitoid system. The resulting population dynamical feedbacks have figured importantly in the chapters by Heimpel, Bernstein and Godfray. In the context of egg limitation, population dynamics mediates a feedback in the evolution of oviposition strategies of parasitoids. The next section aims to investigate this feedback in more detail.

POPULATION DYNAMICAL FEEDBACK

The environment that is faced by a focal parasitoid is determined by the interaction of the other parasitoids and the hosts. Because it leads to saturation of the parasitoid functional response, one would expect egg limitation to be a destabilizing factor analogous to the effect of a typeII functional response in Lotka-Volterra systems. This leads to the following speculative evolutionary scenario. Suppose the host population is at a stable equilibrium. This implies that to the parasitoids the availability of hosts is predictable, which favors increased egglimitation, because parasitoids are selected to carry no more eggs than necessary. Because egg limitation increases instability, the system may start to cycle. These cycles will decrease predictability: at some times the parasitoids will encounter large numbers of hosts whereas at other times hosts will be rare. If the cycles become too violent, selection pressure will favor less egg-limited hosts, decreasing the tendency of populations to cycle. Thus, ecology and evolution may interact to regulate egg limitation.

To explore this hypothesis more quantitatively, I will present some simulations of a simple host-parastoid model that is based on the Nicholson-Bailey framework. The model is chosen for its simplicity rather than its realism. Because its underlying assumptions are identical to the behavioural model presented in the last section, the fitness concept I have empoyed applies to population dynamical model as well.

A problem with the Nicholson-Bailey model is that its equilibrium is always unstable and, since no limit cylces occur, populations are non-persistent. To render the resident system persistent, I assume that a proportion α of the hosts is in a refuge and cannot be attacked by the parasitoids; in these refuges hosts can survive but not reproduce (for a discussion of this model see Hochberg & Holt 1995). For a model without egg limitation this leads to the following pair of recurrence equations:

$$N_{t+1} = (1-\alpha)\,\lambda\, N_t\, e^{-aP_t} + \alpha\, N_t \qquad (11a)$$

$$P_{t+1} = (1-\alpha)\, c\, N_t (1 - e^{-aP_t}) \qquad (11b)$$

where λ represents the host's finite rate of increase in absence of parasitism, and c is the probability of successful development of a parasitoid egg (note that any attacked host is killed, irrespective of parasitoid survival).

To introduce egg limitation in the model, we need to use expression (9) for a parasitoid's expected fitness, whence

$$N_{t+1} = \lambda\,[(1-\alpha)\,N_t - P_t\,\mathrm{E}G] + \alpha\,N_t \qquad (12a)$$

$$P_{t+1} = P_t\,c(R/E)\,\mathrm{E}G \qquad (12b)$$

Note that the host equation (12a) results from the assumption that every host that is not attacked reproduces.

[Figure 8.6 about here]

Numerical exploration of system (12) shows that depending on the egg load of the resident host population, the system cycles with varying mean and amplitude. As expected, the amplitude is largest with the most egg-limited parasitoids (Figure 8.6a). Note also that the mean density of the parasitoids decreases for larger egg loads whilst that of the host increases; this is a direct consequence of the survival cost of small eggs. For sufficiently large egg loads (resulting in small eggs with low survival chances) the resident parasitoid population may not be able to persist at all. For this simulation, parameters were chosen deliberately to emphasize the mechanism of egg limitation affecting population dynamics rather than to mimic some real system.

Using expression (9) to calculate the fitness of a focal parasitoid with an egg complement $E^* + 1$, we can get insight into the selective pressure on egg load. Figure 8.6b indicates that for low egg complements the selection differential is always positive (increasing egg load), whereas for for high egg loads it is always negative which indicates that lower egg loads are favored. Thus, some intermediate egg complement will be optimal. It is not possible to deduce the evolutionarily stable strategy (ESS) exactly from Figure 8.6b; for this, the geometric mean fitness differential should be calculated over the cycle (Holt & McPeek 1996, van Baalen & Sabelis 1999).

I refrain from analysing this model in too great detail because of the limited value of the underlying population dynamical model. Indeed, well over 100 studies have been dedicated to the question of host-parasitoid persistence, and many variants of the basic Nicholson-Bailey model have been considered (see Hochberg & Holt 1998 and chapter by Bernstein). The most promising approach is probably a model taking into account demographic stochasticity (such as analysed by Wilson & Hassell 1997) because this would give insight into how the population distributions (here embodied in the parameters $\phi_{n,o}$) depend on individual characteristics.

DISCUSSION

Most model studies of host-parasitoid interactions have been based on variants of the discrete-time Nicholson-Bailey model (Hassell 1978, but see Murdoch & Stewart-Oaten 1989, Shea *et al*. 1996, Hochberg & Holt 1998). There are good biological reasons for this. The nature of many host-parasitoid interactions implies that there will be a time delay between foraging and fitness return for the parasitoids: hosts parasitized in one generation will give rise to parasitoids in the next generation. This time delay turns out to be a strongly destabilizing mechanism. This has been the incentive to study the possible mechanisms that render the interaction persistent (Hassell & May 1973, Hassell 1978, van Baalen & Sabelis 1993, chapter by Bernstein).

The Nicholson-Bailey model and most of its variants are based on population-level bookkeeping. For the parasitoids, this usually leads to an equation of the form $P_{t+1} = cN_t$ [proportion of hosts attacked]. That is, the Nicholson-Bailey framework does not provide a natural per-capita fitness concept for an individual parasitoid of the form $P_{t+1} = P_t$ [per-capita fitness]. From the Nicholson-Bailey equations one can derive $aN/(1 - e^{-aP})$ as the per-capita fitness of the parasitoids, but here I have shown that this is only correct for time-limited parasitoids. For egg-limited parasitoids, I could not derive a simple expression for per-capita fitness.

In this respect it is perhaps ironic that parasitoids have been popular model organisms in more individual-based evolutionary ecology studies *because of* the clarity of the fitness concept. Indeed, for time-limited parasitoids, there is a consistent relationship between foraging behaviour and fitness (Stephens & Krebs 1986, Charnov & Stephens 1988).

Parasitoids must find their hosts in order to parasitize them, and given the vagaries of finding hosts, foraging optimization is not a trivial problem. Thus, much research has focused on aspects related to parasitoid searching (spatial distributions in population dynamical studies, foraging strategies in evolutionary ecology, see Stephens & Krebs 1986, Charnov & Stephens 1988, van Alphen & Visser 1990, Driessen & Visser 1993, Hochberg *et al*. 1996). Much of this work has been based on the standard assumption is that once a parasitoid has located and attacked a host, everything is determined. It is as if the parasitoids have a magic wand with which they only have to touch their victims in order to convert them into their own kind. In contrast, a growing number of studies into the defense mechanisms that are available to the hosts (see chapter by Godfray) shows that there may be more going on in host-parasitoid interactions. In particular, many hosts can encapsulate and thereby neutralize parasitoid eggs. There is evidence for spatial variation in the outcomes of the parasitoid attack/host defense outcome (Carton & Nappi 1991, Kraaijeveld & van Alphen 1995, Kraaijeveld *et al*. 1997).

My point is that if we want to understand the evolutionary outcome of parastoid attack and host defense, we need to have insight in the costs of an egg to a parasitoid. To this end, we need to be able to calculate per-capita fitness of parasitoids. In this chapter, I have indicated how such fitness measures can be derived from first principles, and I have tried to illustrate some of the basic aspects that are involved. As noted by Rosenheim (1996), egg limitation is an expected evolutionary outcome if there is a constraint relating egg survival and egg complement, and there is stochasticity in the number of reproductive opportunities that parasitoids have. Rosenheim (1996) and Sevenster *et al*. (1998) assume the stochasticity arises from random mortality of the parasitoids. Here I assumed that the stochasticity arises from variability in the distribution of the hosts. In reality, of course, both mechanisms may be important.

The ecological model that I analysed is a caricature: a constant proportion of hosts remains inert in refugia, and hosts and parasitoids are distributed randomly across space with encounter probabilities given by a joint Poisson distribution. In reality, many environmental aspects may be important, and moreover, the spatial distribution of the populations as well as the host's use of refuges are likely to be affected by all sorts of behaviors that are subject to evolution. Active searching by the parastoids will lead to population distributions that deviate from Poisson because they are likely to end up in locations of high host density. For this reason, however, hosts may be selected to avoid areas with high densities of conspecifics (van Baalen & Sabelis 1993, 1999). Depending on how behaviorally flexible hosts and parasitoids are, this may lead to spatio-temporal variation in host and parasitoid densities. I have argued that egg limitation may therefore be the result of a complex interplay of all these factors. To what extent the general hypothesis proposed in this chapter (increased egg limitation increases instability which in turn favors decreased egg limitation and more stability) holds in these more realistic settings remains open for investigation. How the evolution of egg limitation is correlated with the evolution of other parastoid traits is as yet an open question. It is conceivable, for example, that parasitoid populations may diverge into populations with different foraging-strategy/egg-load combinations, if different foraging strategies lead to different variances in the number of hosts encountered (see the chapter by Godfray).

To what extent would egg limitation affect the legitimacy of optimal foraging models based on gain rate maximization? Recently, Sevenster *et al*. (1998) have argued that because egg limitation occurs only infreqently, it is probably not important. However, this ignores the 'jackpot effect': if 90 patches contain ten hosts but 10 each contain a hundred, a parasitoid with an egg complement of 10 is only egg-limited in 10% of the cases, but it nevertheless foregoes almost half of its opportunities for reproduction (its expected gain is 10, whereas it *could* have been $0.9 \cdot 10 + 0.1 \cdot 100 = 19$). From the model that I analysed here it is clear that parasite fitness always increases with foraging efficiency, but at decreasing rates. It does not pay a parasitoid to search so efficiently that she is going to encounter more hosts than she can deal with. But at the same time, an increase in a will affect the optimum egg load. The only way to understand how egg limitation will affect rate maximization is therefore to consider joint models. This will require insight into possible trade-offs between foraging efficiency and other aspects of parasitoid life-history parameters. An example of such an analysis is given in Heimpel's chapter in this book.

Lastly, I want to briefly point out some interesting points of overlap of my analysis with other aspects of parasitoid biology. From the start, I assumed that the parasitoids are solitary parasitoids, that lay only one egg in each host they encounter. Many parasitoids are ‘gregarious’, depositing a clutch of eggs in every host. I am not aware of any studies that address this situation, but this might be a case where the parasitoid ‘swamps’ its host’s defensive abilities (see chapter by Strand). Whether or not this is the case, however, gregariousness gives an extra dimension to the distinction between egg-limited and time-limited parasitoids (see chapter by Heimpel).

Larger eggs may also be the consequence of within-host competition among the offspring of different parasitoid females, if superparasitism occurs. Then it may well be that larger eggs give rise to offspring that have greater competitive abilities. To understand this effect, we can no longer focus on the interaction between single hosts and single parasitoids, but we have to take into account the interaction among the different parasitoid individuals within a host. This involves a rather complicated bookkeeping of all singly and multiply parasitized hosts. Though an interesting extension, although it may yield new perspectives on the conditions favoring avoidance of superparasitim (Parker & Courtney 1984, Bakker *et al*. 1985, van Alphen & Visser 1990, Nagelkerke *et al*. 1996).

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FIGURES

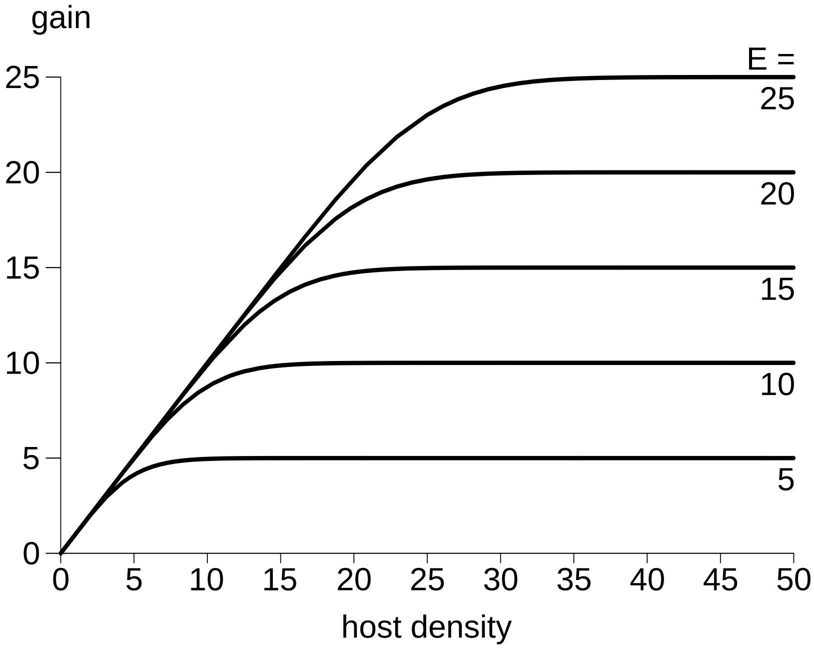


Figure 1. Parasitoid gain (lifetime number of hosts attacked) in absence of competition with other parasitoids, as a function of host density and egg load. The hosts are randomly encountered (i.e., according to a Poisson distribution).

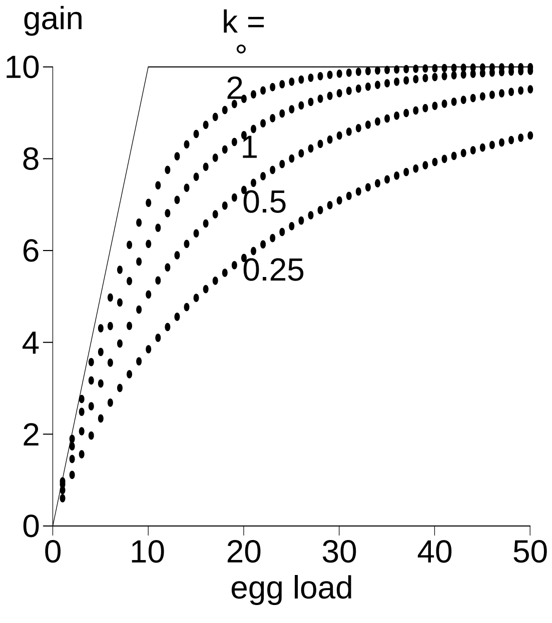
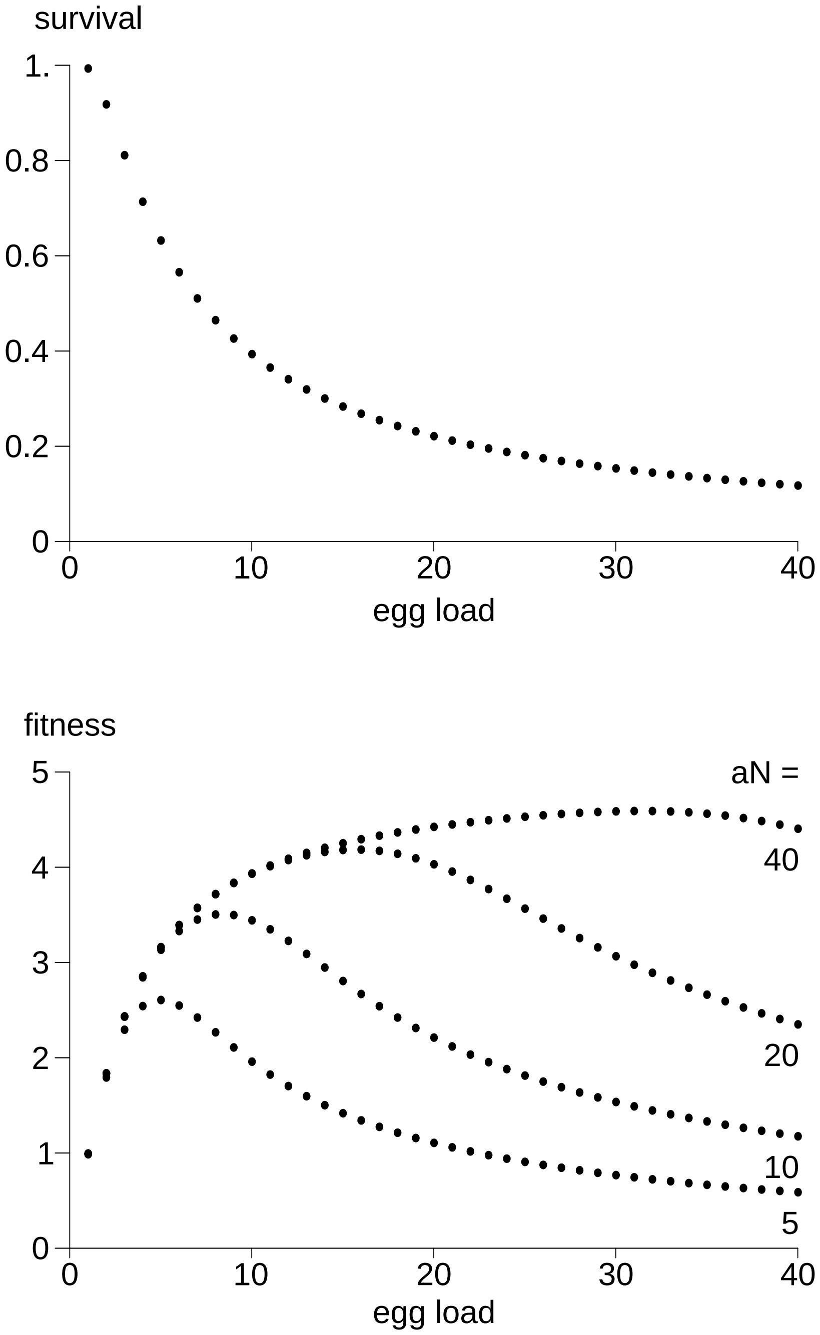


Figure 2. Expected parasitoid gain (lifetime number of hosts attacked) as a function of egg load *E*, when hosts are encountered according to negative binomial distributions with the same mean ($aN = 10$) but with different values of the clumping parameter k. The solid line shows expected gain when the variance in the number of hosts encountered is zero.



(a)

(b)

Figure 3. (*a*) Offspring survival and (*b*) expected fitness as a function of egg load E, when egg size is inversely proportional to egg load, $s = R/E$ with $R = 5$, and offspring survival is a function of egg size, taken arbitrarily to be $c(s) = 1 - \exp(-s)$. Expected fitness is shown for a range of mean host densities, indicated in the plot.

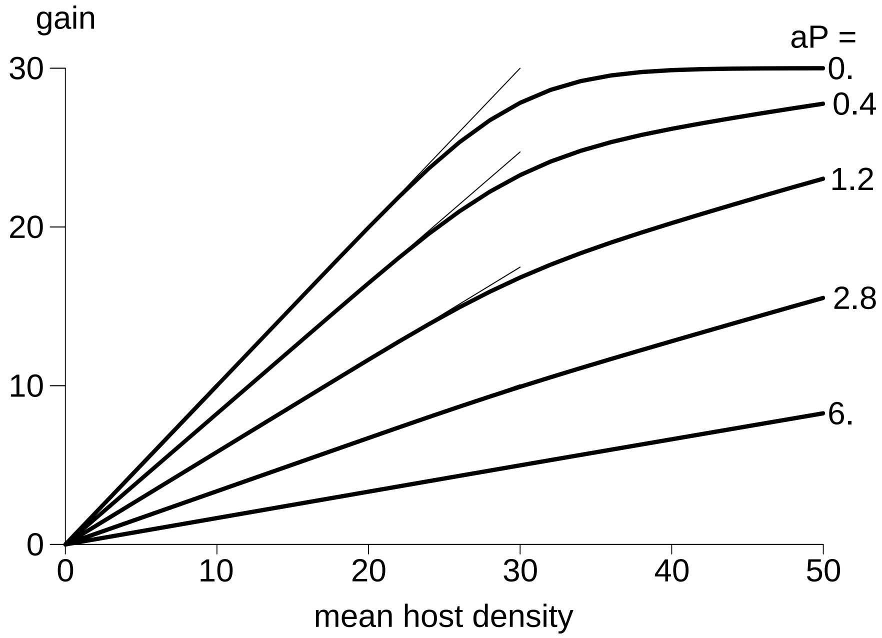
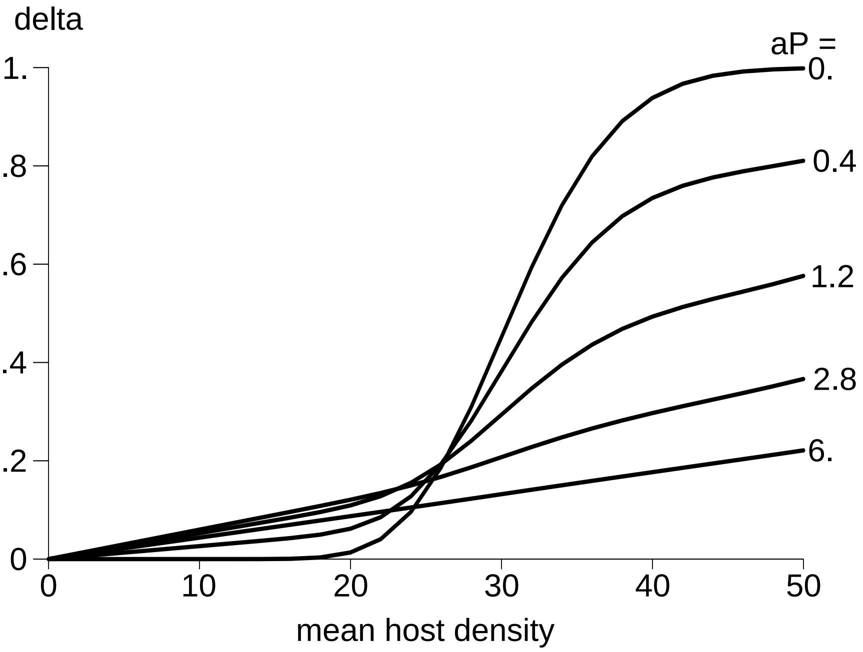
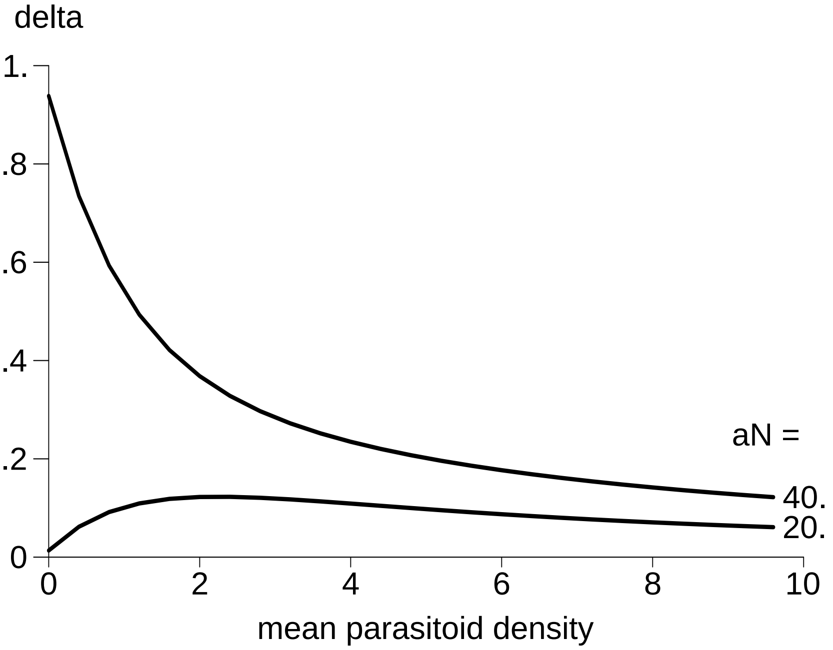


Figure 4. Expected fitness of an egg limited (E = 30) parasitoid as a function of mean host density (aN), for various values of resident (E^* = 30) parasitoid density as indicated in the plot. Encounters with parasitized and unparasitized hosts are assumed to be randomly distributed. The thin lines indicate per capita fitness in absence of egg limitation ($aN(1 - e^{-aP})/aP$).



(a)



(b)

Figure 5. Fitness benefit $\Delta = \mathrm{E}G(E^{*}+1) - \mathrm{E}G(E^{*})$ associated with an increased egg complement, as a function of (*a*) mean host density and (*b*) mean resident ($E^{*} = 30$) parasitoid density.

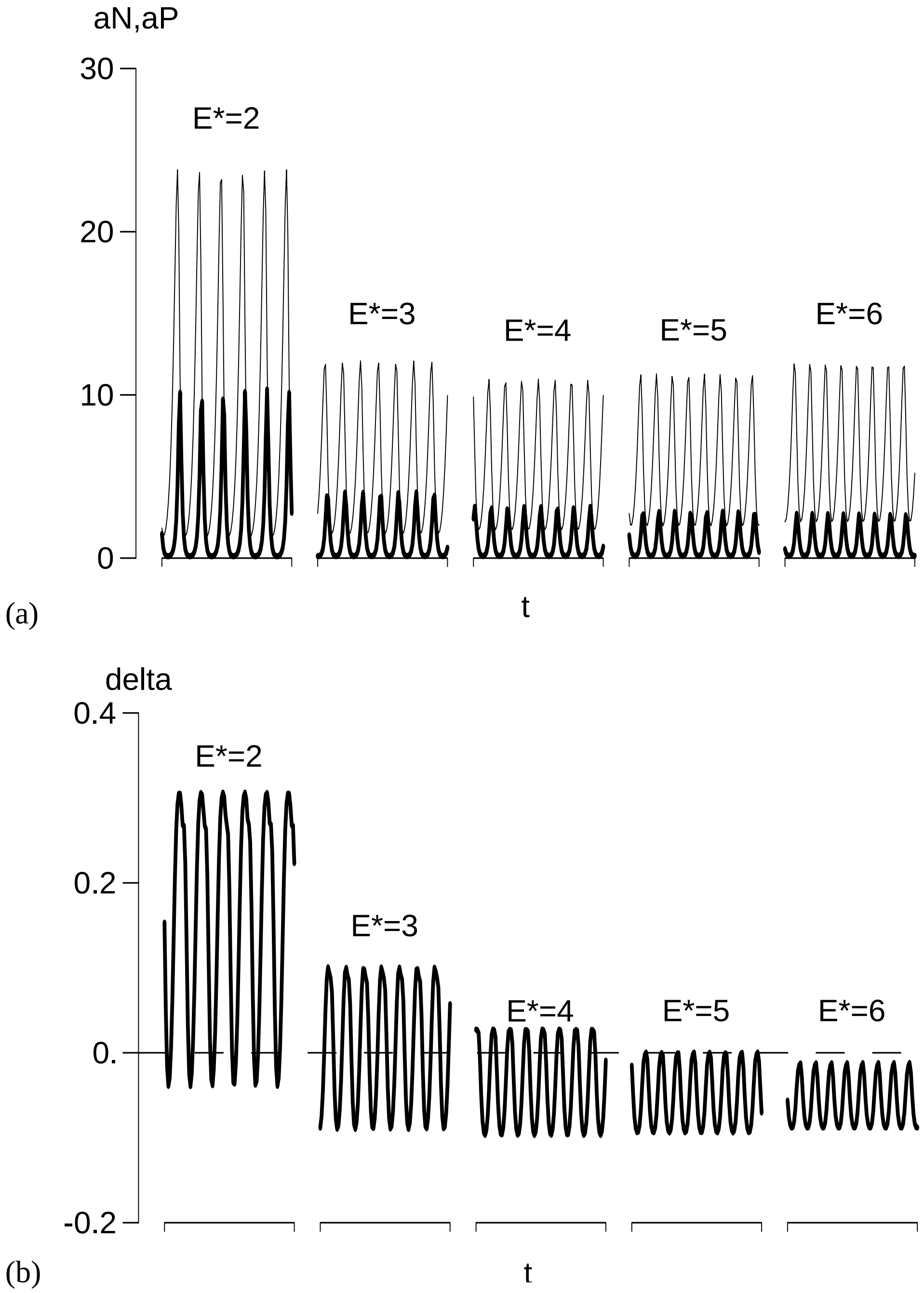


Figure 6. Population dynamics of hosts (thin lines) and parasitoid (thick lines) (a) and the resulting selection differrential on egg load (b). Parameters: $\lambda = 2$, $\alpha = 0.5$, $R = 5$. Displayed are the results over 100 generations, after the transients have disappeared.