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Author(s): Geoffrey A. Parker and Michael Begon

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OPTIMAL EGG SIZE AND CLUTCH SIZE:
EFFECTS OF ENVIRONMENT AND MATERNAL PHENOTYPE

GEOFFREY A. PARKER AND MICHAEL BEGON

Department of Zoology, University of Liverpool, P.O. Box 147, Liverpool L69 3BX,
United Kingdom

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Although the study of insect reproduction has long been neglected (but see Klomp and Teerink 1967; Price 1974, 1975), as early as 1950 Thorson provided an interesting discussion of reproductive strategies in marine invertebrates, and there exists a considerable body of literature on the evolution of clutch size in birds, stemming from the pioneering work of Lack (1947). There has, however, been a recent surge of interest in the evolution of insect clutch size (Charnov and Skinner 1984, 1985; Courtney 1984; Iwasa et al. 1984; Parker and Courtney 1984; Skinner 1985; Smith and Lessells 1985; Waage and Godfray 1985). The recent work on insect clutch size assumes that egg size is constant and independent of clutch size. A more likely proposition is that there is an inverse relationship between clutch size and egg size; for a given reproductive output, a female could produce a few large eggs or many small ones (though in practice, individuals with large amounts of reproductive resources may produce both larger eggs and larger clutches than those with a smaller total reproductive output). In the present paper, we examine the optimal allocation of reproductive reserve into eggs and clutches.

Previous work on optimal egg size (Williams 1966; Gadgil and Solbrig 1972; Sibly and Calow 1983, 1985; Sibly and Monk, MS), in line with previous work on life histories generally, has been based on the assumption that a single, optimal egg size is appropriate under a given set of environmental conditions. By contrast, we believe that the optimal allocation between egg size and number may depend critically on the female's phenotype and should alter in relation to the conditions she encounters during the current season. In other words, we are interested in the evolution of phenotypic plasticity in oviposition strategies relating to clutch size and egg size. In particular, we anticipate that larger females may have a larger overall capacity for egg production within a clutch; and it is on this intrapopulation effect that we focus. However, we also show that the differences between large and small females may be parallel to other intrapopulation differences.

For simplicity, we have concentrated in our model on the trade-offs between clutch size and egg size, both of which may in practice be affected by further trade-offs between growth and reproduction. Such interactions are beyond the

scope of the present analysis, which we regard as a necessary preliminary to a more extensive study.

Invertebrates show such a wide variety of life history patterns that no single model can be generally representative. The model outlined below is designed specifically for an insect that first becomes gravid with eggs at a feeding site and then travels to an oviposition site. Such patterns are common in species for which the adult and larval food sites are separate. The model is designed to serve only as a vehicle, however, and the specificity is more apparent than real. The general approach should apply to a wide range of organisms.

THE MODEL

We analyze the optimal reproductive pattern of an insect having the following characteristics. The adult female forages in a feeding habitat to gather resources for egg production. After a time she stops provisioning her clutch of eggs and leaves the feeding habitat to search for an oviposition site. On reaching the oviposition site she lays a single clutch of eggs and then returns to the feeding site to begin production of the next clutch.

We assume that selection acts to maximize the reproductive success of the female parent. Following Lack (1947), we expect that reproductive success is proportional to the rate of production of the surviving progeny. Two variables can be altered by selection to optimize the outcome of two "decisions" by the female: the time spent gathering the resources for each clutch (t), which corresponds to the egg-dependent time costs of Parker and Courtney (1984); and the amount of resource spent on each individual egg (m). Suppose that a total amount of gametic resources, M , is gathered by the female during time t . Then, in making the decision to forage for time t and to lay eggs of size m , a female is also making the decision to lay a clutch of $M(t)/m$ eggs.

We examine how these decisions about foraging time, egg size, and clutch size are optimized in relation to three separate components of larval success: (1) the absolute effect of egg size on larval (or, more generally, preadult) viability; (2) the effect of the initial number of other larvae, from the same or other clutches, on the survival probability of a given larva; and (3) the effect of relative egg size on larval success. In order to present the model in the simplest way, we begin by examining the effect of the first component (absolute effect of egg size). We then add the other two components in order to increase the model's complexity.

LARVAL SUCCESS DEPENDENT ONLY ON ABSOLUTE EGG SIZE

The Model

The simplest form of relationship between M (gametic resources gathered) and t (foraging time) is shown in figure 1. The female transfers resources into gametic mass at a constant rate until she becomes full of eggs and contains M_{\max} gametic mass. The relationship $M(t)$ depends on the female's phenotype; small females become full at a lower value of M_{\max} , gaining M at the same rate as or at a different rate from large females.

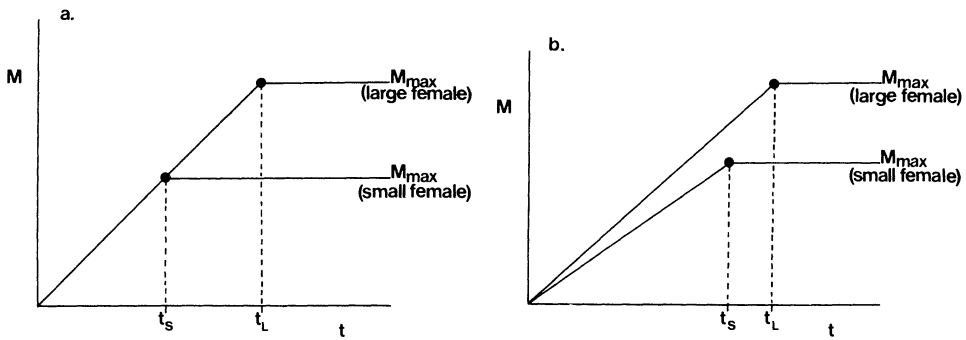


FIG. 1.—The amount of resources accumulated for eggs, M , depends on the time, t , spent foraging. Larger females reach their maximum capacity at a higher value of M than small females. *a*, Foraging efficiency is equal for each female size. *b*, Large females are more efficient foragers than small females. For further explanation, see text.

Assume now that the viability or “fitness” f of a larva depends only on the absolute amount of resources, m , provided in the egg by its mother. We follow Smith and Fretwell (1974), Brockelman (1975), and Parker and Macnair (1978) in assuming that $f(m)$ increases monotonically up to some asymptote, and that a certain minimal provisioning is necessary to ensure that the larva can develop at all (fig. 2*a*).

Let a constant time, d , be spent between leaving a feeding site to oviposit and returning to a feeding site after oviposition. Thus, time d is the average time taken to find an oviposition site, oviposit, and then find another feeding site. If we assume that the oviposition duration is trivial compared to the time spent searching for the oviposition site and the feeding site, then d corresponds to the egg-independent time cost of Parker and Courtney (1984).

Maternal fitness w is equivalent to the gain per unit of time and is dependent on

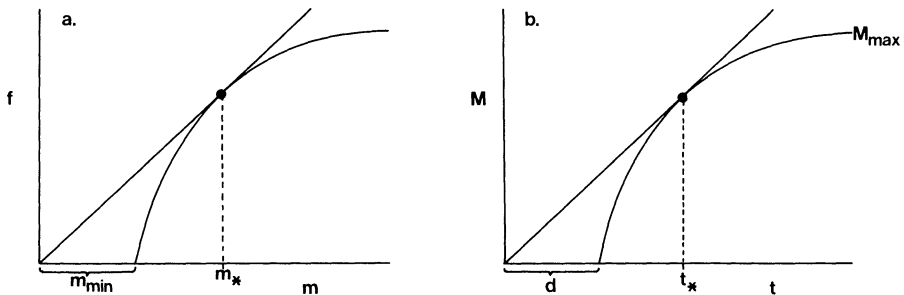


FIG. 2.—*a*, The optimal egg size, m_* , is given by the marginal-value solution when the fitness (survival prospects times relative reproductive success as an adult) of an individual larva increases with m , the investment in an egg. *b*, The optimal foraging time, t_* , is also given by the marginal-value solution when resources for eggs accumulate after the law of diminishing returns. If d , the time taken to find an oviposition site and return to a foraging site, is increased, t_* will increase.

the "decisions" about m and t : $w(m, t) = M(t)f(m)/m(t + d)$. To find the optimal foraging time, t_* , set $\partial w(m, t)/\partial t = 0$, which gives

$$M'(t_*) = M(t_*)/(t_* + d); \quad (1)$$

and to find the optimal egg size, m_* , set $\partial w(m, t)/\partial m = 0$, which gives

$$f'(m_*) = f(m_*)/m_*. \quad (2)$$

Equations (1) and (2) are the familiar marginal-value solutions (Charnov 1976), shown graphically in figure 2. In figure 2*b*, $M(t)$ has a continuously decreasing gradient rather than the discontinuous gradient shown in figure 1. The optimal foraging time, t_* , is given by the line tangent to $M(t)$ from the origin, which includes the time between foragings, d , on the abscissa. Similarly, the optimal egg size, m_* , is given by the tangent to $f(m)$ as first deduced by Smith and Fretwell (1974).

Conclusions

Egg size and foraging time are independent.—Egg size, m , and foraging time, t , are optimized independently of each other. Changing the form of $M(t)$ does not affect m_* , and altering $f(m)$ does not affect t_* .

Larger females lay larger clutches.—Since differences in female size are expressed as differences in $M(t)$ and since m_* is independent of $M(t)$, all females should lay eggs of equal size. Hence, bigger females (with higher M) should lay larger clutches. A number of invertebrates show this pattern (e.g., *Scatophaga*, Parker 1970; *Asellus*, Ridley and Thompson 1979; *Gammarus*, Birkhead and Clarkson 1980).

Foraging time increases with time to find an oviposition site.—If the uptake of resources for gametes shows diminishing returns, as in figure 2*b*, then the optimal foraging time, t_* , increases if the time d spent moving between feeding and oviposition sites increases. In the simpler case of a linear uptake of resources (fig. 1), increasing d does not affect the optimal foraging time, which always occurs when M reaches M_{\max} (the female becomes full of eggs).

Larger females have a longer interclutch time.—If resource uptake, $M(t)$, is linear at equal rates for large and small females, large females will spend longer foraging (time t_L , fig. 1*a*) than small females (time t_S , fig. 1*a*). However, if large females are more efficient at foraging than small females, the difference between t_L and t_S can be much smaller (fig. 1*b*). If large females are very efficient foragers, they may even have a shorter foraging time than small females. Thus, the interclutch interval of different-sized females depends on their foraging efficiency; large females have a longer interclutch interval than small females, unless large females are much more efficient foragers.

More generally, the optimal foraging time, t_* (and thus the interclutch interval), and the clutch output (M at t_*) depend on the precise form of $M(t)$ for different-sized females. For instance, if small females have a smaller reproductive capacity (M_{\max}) but a greater foraging efficiency (higher initial $M'[t]$), then they might produce larger clutches though with a longer interclutch interval or even larger clutches with the same interval (fig. 3). It is of interest, therefore, that Banks

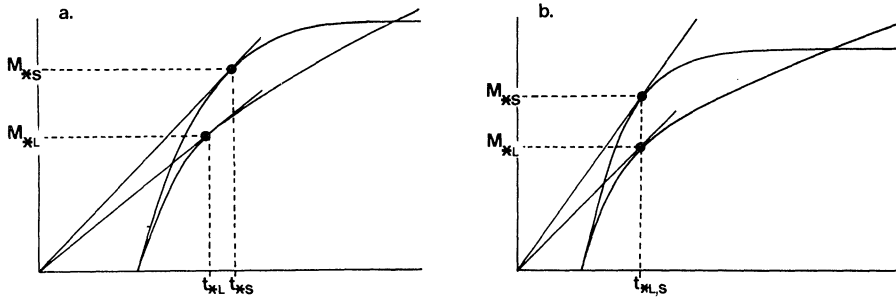


FIG. 3.—Smaller females may produce larger clutches than larger females if they are more efficient foragers (a higher initial value of $M'[t]$). *a*, Smaller females produce larger clutches but with a larger interclutch interval. *b*, Smaller females produce larger clutches with the same interclutch interval.

(1985) found small females of the damselfly *Coenagrion puella* producing significantly larger clutches, with an almost significantly longer interclutch interval ($P < 0.1$). Banks suggested, from a consideration of insect flight dynamics, that smaller damselfly females may be able to fly more efficiently and therefore forage more productively than larger females.

LARVAL SUCCESS AFFECTED BY COMPETITION BETWEEN SIBLINGS

The Model

We now investigate the case in which competition among members of the same clutch reduces the prospects of a given larva (see Charnov and Skinner 1984; Parker and Courtney 1984; Skinner 1985). Let $s(n)$ be the component of success of a larva (product of survival and relative reproductive success as an adult) that declines with increasing clutch size n . It is assumed that $s(n)$ decreases monotonically (fig. 4), though in some cases $s(n)$ rises to a peak and then declines, showing the "Allee effect" (Allee 1931; see also Parker and Courtney 1984).

We have chosen $s(n)$ rather than $s(M)$ to measure the intensity of sibling competition, because competition will typically become important only after a considerable amount of growth beyond the egg stage has occurred. Competition will therefore vary with the number of competitors (broadly, n) rather than with small differences in the provisioning of eggs before growth (M). The effects of size differentials, or "hierarchies," on competition will be discussed later.

Female fitness is now $w(m, t) = [ns(n)f(m)]/(t + d)$. Setting $\partial w/\partial t = 0$ gives the optimization for t_* ,

$$M'(t_*) = \frac{M(t_*)}{t_* + d} \left[\frac{s(n)}{s(n) + ns'(n)} \right], \quad (3)$$

in which $n = M(t_*)/m$. Equation (3) should be compared directly with equation (1). Setting $\partial w/\partial m = 0$ gives the optimization for m_* ,

$$f'(m_*) = \frac{f(m_*)}{m_*} \left[\frac{s(n) + ns'(n)}{s(n)} \right], \quad (4)$$

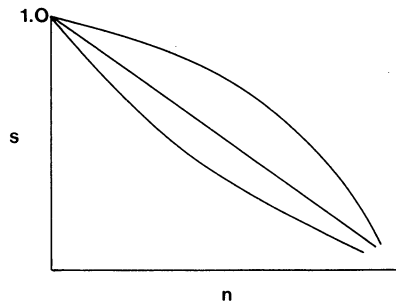


FIG. 4.—Decrease in an individual offspring's success (survival times reproductive success as an adult) in relation to clutch size, n . After Charnov and Skinner (1984); Parker and Courtney (1984).

in which $n = M(t)/m_*$. Equation (4) should be compared with equation (2). Clearly, if both t and m are to be optimized, then equations (3) and (4) must be satisfied simultaneously, with $n = M(t_*)/m_*$.

Conclusions

Competition reduces foraging time and increases egg size.—Unlike the preceding case, m_* and t_* are now interdependent through their effects on clutch size, $M(t_*)/m_*$. The intensity of sib competition is measured by the gradient $s'(n)$, which is negative (fig. 4). The denominator of the part of equation (3) in square brackets reduces below $s(n)$ as $s'(n)$ reduces below 0; the bracketed part of equation (3) is therefore always greater than 1. The bracketed part of equation (4) is the reciprocal of that in equation (3) and is therefore always smaller than 1. The effects of such constraints on marginal-value optima are well known (see, e.g., Parker 1985). A constraint value greater than 1 tends to decrease the optimum; a value less than 1 tends to increase the optimum. Thus, sib competition tends to reduce the foraging time, t_* , and to increase the egg size, m_* . This result is intuitively obvious. If increasing clutch size leads to losses through sib competition, it becomes optimal to compensate by reducing the time spent gathering resources for the clutch of eggs, leading to a smaller clutch (egg size times number) and also by laying larger (and hence even fewer) eggs. In contrast, when sib competition plays a negligible role, $s'(n)$ approaches zero and equations (3) and (4) reduce to equations (1) and (2).

Bigger females lay bigger eggs.—In order to investigate the effects of sib competition in their own right, we can isolate them by assuming temporarily that absolute egg size exerts a trivial effect on larval success. In short, $f'(m_*)$ approaches zero and equation (4) reduces to

$$-s'(n_*) = s(n_*)/n_*, \quad (5)$$

in which n_* is the clutch size that has maximum fitness (the Lack clutch size; Lack 1947). This indicates that clutch size tends to be conserved, irrespective of the amount of egg material, M . Thus, sib competition, when considered in isolation, can be seen as a force favoring the same clutch size in all females. This conclusion

contrasts markedly with the previous case, in which only egg size was important and was conserved so that bigger females laid bigger clutches. Here we predict that bigger females lay bigger eggs, as Klomp and Teerink (1967) found for the parasitoid *Trichogramma embryophagum*, which experiences competition predominantly between sibs.

Note, in passing, that Parker and Courtney (1984) and Charnov and Skinner (1984) sought optimal clutch sizes, assuming that egg size was fixed. Implicitly, therefore, they assumed that $f(m)$ was at a maximum and that $f'(m)$ was therefore zero. Both studies derived versions of equation (5) from their models, without considering the conservation of clutch size among different females.

Bigger females lay bigger eggs and bigger clutches.—If sib competition and egg size are both important components of larval success, both egg size and clutch size are expected to vary with female size. To obtain a feel for how m_* and n_* change with the total reserve for eggs, M , we have iterated solutions for m_* (and hence n_*) from equation (4), using the following explicit functions:

$$f(m) = 1 - \exp[-(m - m_{\min})]$$

$$s(n) = 1 - kn.$$

Constant m_{\min} is the smallest egg size necessary for survival, and increasing m_{\min} causes $f(m)$ to rise more sharply toward the asymptote; k is a positive constant specifying the rate of decline of s with n . Results are shown in figure 5. As would be expected, m_* increases more steeply with M when egg size is less constrained (m_{\min} low) than when it is more constrained (m_{\min} high). In contrast, the rise in clutch size approaches linearity when egg size is sharply constrained. In conclusion, in species that lay a single clutch per cycle, if sib competition and egg size both exert important influences on larval success, bigger females lay both bigger eggs and bigger clutches.

Species that lay several clutches per cycle.—Note that at very large M , clutch size approaches an asymptote (fig. 5*b*). This arises because the effects of larval

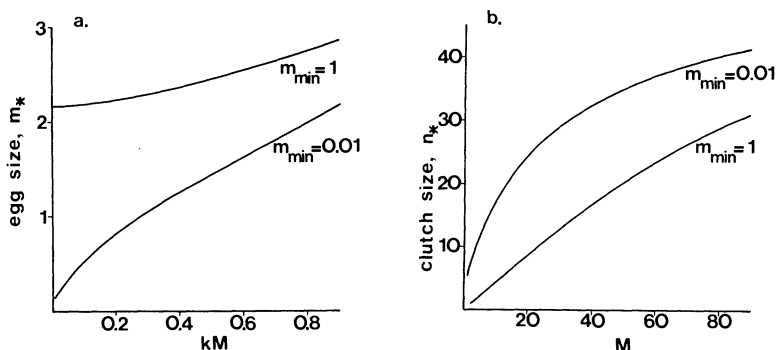


FIG. 5.—Single-clutch species: results obtained by iteration after substituting the explicit functions described in the text into equation (4). *a*, Relationship between optimal egg size, m_* , and total egg resources contained by a female, M . *b*, Relationship between optimal clutch size, n_* , and M , when $k = 0.01$.

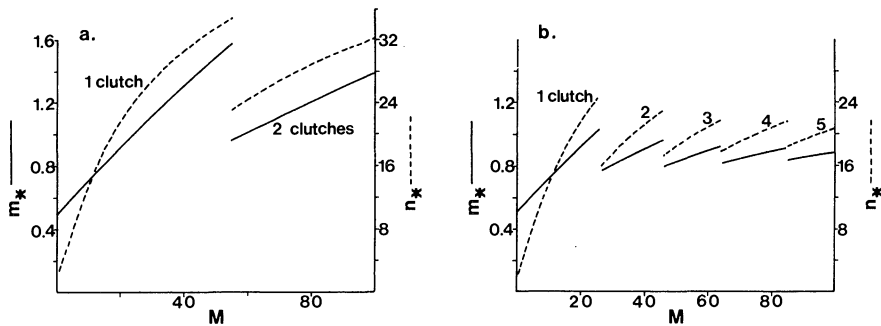


FIG. 6.—Multiple-clutch species: results obtained in a similar fashion to figure 5, but for the case where females can lay several clutches per cycle, although they pay a cost (decrement in M) for each journey between oviposition sites. For a given value of M , the curves show the combinations of egg size, clutch size, and clutch number that maximize fitness. *a*, High journey costs: the largest females have $M = 100$ and each female pays $M = 10$ for each journey. *b*, Low journey costs: each female pays $M = 2$. In each case $m_{\min} = 0.1$.

competition eventually become paramount, such that the priority is to conserve clutch size at the expense of producing eggs larger than the optimal size. At some threshold of increasing M , the strategy of producing one clutch per feeding cycle will be abandoned in favor of producing two clutches; the exact value of this threshold depends on the cost of searching for a second oviposition site. Indeed, at large M or with low search cost, we should expect to see patterns of multiple clutches (i.e., > 2). In order to demonstrate this effect, we used the same explicit functions of $f(m)$ and $s(n)$ as for figure 5, and calculated the optimal oviposition pattern, assuming that the cost of searching for a further oviposition site is experienced as a decrement in M . For a given range of M , if the search cost is relatively high, a single- or double-clutch pattern is likely (fig. 6*a*), whereas if the search costs are low, a multiple-clutch pattern occurs in females with high M (fig. 6*b*). Note in figure 6*b* that females laying small numbers of clutches exhibit more variation in egg size and clutch size than females laying large numbers of clutches. However, there is no overall trend by which clutch size or egg size varies with increasing numbers of clutches. Thus, in species that lay several clutches per cycle, there is no obvious correlation between egg and clutch size and female size, though bigger females lay more clutches per cycle.

For simplicity, we have assumed in our analyses that all oviposition sites are of equal quality. Variation in site quality would further complicate oviposition decisions by adding an optimal foraging dimension. In particular, we would expect greater investment in higher-quality patches.

LARVAL SUCCESS AND RELATIVE EGG SIZE: COMPETITIVE LAYING

The previous models have assumed that competition from larvae of other females is unimportant. We now investigate the case in which F females oviposit simultaneously at the same site, so that the larvae from F clutches scramble for the available food. A competitive advantage can be gained by producing eggs that

are bigger than average; larvae that begin with a size advantage do disproportionately well because the initial disparity becomes amplified during the competition. Such effects are well known: for example, the “jumper” effect in fish cohorts (Moav and Wohlfarth 1974) and the “hierarchy” effect (Begon 1985).

The Model

The success of a given larva now depends on three fitness components resulting from the absolute investment in the egg, $f(m)$; the total number N of competitors in the larval food patch, $s(N)$; and the size of the egg relative to the average size of other eggs. To investigate this effect we use a third function, $c(m_i/\bar{m})$, which is the relative competitive success of an egg of size m_i against eggs of average size \bar{m} (fig. 7). Larval success is proportional to the product of all three components. Thus, if the egg has size $m_i = \bar{m}$, then $c = 1$, and it neither gains nor loses through competition. If $m_i > \bar{m}$, the resulting larva has enhanced success (since $c > 1$; see fig. 7).

Assume that each female lays all her eggs in the larval food patch. To simplify the analysis, we first consider the case in which the reserve M available for eggs is constant for all females. This assumption will be relaxed later when we investigate specifically the effects of variance in M . We seek a stable egg size, m_* .

The best strategy for egg size depends on the strategies of the other females in the population. We therefore need an evolutionarily-stable-strategy (ESS) approach (see Maynard Smith 1982) rather than a simple optimization. For m_* to be an ESS, any mutant females playing $m \neq m_*$ must experience a lower payoff than an m_* female in a population playing m_* . The payoff of a mutant playing m against the m_* population is $w(m, m_*) = Mf(m)s(N)c(m/\bar{m})/m$, in which the total number of eggs laid, N , is $M(F - 1)/m_* + M/m$ and the average egg size is $\bar{m} =$

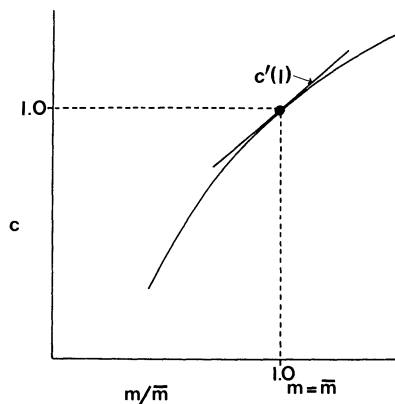


FIG. 7.—The hierarchy effect: competitive success, c , of an egg as a function of its size, m , relative to the average size, \bar{m} , of other eggs that will compete with it for food resources at the oviposition site. The tangent line shows the gradient $c'(1)$, that is, the gradient of c when $m = \bar{m}$. Since c is a multiplicative component of fitness, when $m = \bar{m}$, $c = 1$.

MF/N . We find the ESS by the usual technique of setting $\partial w(m, m_*)/\partial m = 0$ for $m = m_*$ (see Maynard Smith 1982). This results in

$$f'(m_*) = \frac{f(m_*)}{m_*} \left[\frac{s(N) + Ns'(N)/F}{s(N)} - \frac{c'(1)}{c(1)} \frac{(F-1)}{F} \right] \quad (6)$$

(see eqs. 2 and 4). In equation (6), $N = FM/m_*$, that is, the total number of eggs laid by the F females at the ESS. The gradient $c'(1)$ is the gradient of $c(m/\bar{m})$ at the point where $m = m_* = \bar{m}$ (fig. 7); it is the change in competitive success caused by a marginal deviation from the mean egg size.

Conclusions

The joint effect of the two types of competition increases egg size.—If both types of competitive effect are unimportant, such that $s'(N) \rightarrow 0$ and $c'(1) \rightarrow 0$, equation (6) reduces to equation (2) and egg size is optimized solely with respect to the absolute effect of size on larval success, $f(m)$. If both types of competitive effect are present, the part of equation (6) in square brackets is always less than 1 because $s'(N)$ is negative and $c'(1)$ is positive; following previous arguments, the joint effect of both types of competition tends to increase egg size.

Increased density leads to smaller clutches of larger eggs.—Consider the effects of competition that act solely through $s(N)$, the effect of competitor density. The term in equation (6) differs slightly from the corresponding $s(N)$ term in equation (4) in that the gradient $s'(N)$ is divided by F , the number of females. Further, note that $N_* = Fn_*$; that is, N is the total eggs from F clutches, each containing n_* eggs.

It is easiest to see the effects of $s(N)$ when other components of fitness are unimportant, such that $f'(m_*)$ and $c'(1)$ both approach zero. Then, equation (6) yields

$$-s'(N_*) = Fs(N_*)/N_* \quad (7)$$

(see eq. 5). Using the explicit function $s(N) = 1 - kN$, equation (5) yields $N_* = 1/2k$, whereas equation (7) gives $N_* = F/(1 + F)k$. Thus, as F becomes large, N_* converges to $1/k$; that is, competitive laying can double the number of eggs laid in the patch (Smith and Lessells 1985). But each female lays fewer and hence bigger eggs than before; because $N_* = n_*F$, the ESS clutch size contains $n_* = 1/(1 + F)k$ eggs. At high F , $n_* = 1/Fk$, much less than when only one female lays her eggs in the patch. In conclusion, competitive laying leading to increased larval density tends to cause females to lay smaller clutches of larger eggs.

The hierarchy effect increases egg size.—Consider the effects of competition that act through $c(m_i/\bar{m})$, the size of the egg relative to its competitors. Equation (6) reduces to equation (4) when there are no competitors (i.e., $F = 1$). But as F increases, there is a sharply increasing importance of the term $c'(1)(F-1)/c(1)F$ in equation (6), which quickly reaches an asymptote at $c'(1)/c(1)$ for high F . This term is negative, increasing egg size. If this term exceeds the magnitude of the $s(N)$ term, the bracketed part of equation (6) becomes negative. The best strategy then is for each female to lay a single egg (or larva) of size M . In conclusion, the hierarchy effect tends to increase egg size. Its effect is weakest when there are few

competing clutches, quickly increasing to an asymptote so that any number of clutches beyond seven or eight have a marginal effect. In cases of extreme hierarchy effects, single eggs or larvae should be produced.

Generalization for Females Having Different Amounts of Gametic Resource

We now consider the same model, but allow each female to have a different amount of resources for gametes. Assume for simplicity that at each oviposition site there are always F females having $M_1, M_2, \dots, M_i, \dots, M_f$ amounts of resource. We seek an ESS egg size, m_{i^*} , for female i that has an amount M_i of resource for eggs. Call

$$I = \{m_{1^*}, m_{2^*}, m_{3^*}, \dots, m_{i^*}, \dots, m_{f^*}\}$$

the ESS set of phenotype-dependent strategies present in the population. Against an I population, a single mutant female i that plays $m_i \neq m_{i^*}$ will experience a payoff $w(m_i, I) = (M_i/m_i)f(m_i)s(N)c(m_i/\bar{m})$, in which the total eggs laid at the site containing the mutant female is $N = (M_1/m_{1^*}) + (M_2/m_{2^*}) + \dots + (M_i/m_i) + \dots + (M_f/m_{f^*})$ and the average egg size is $\bar{m} = \bar{M}F/N$. As before, we find the ESS m_{i^*} by setting $\partial w(m_i, I)/\partial m_i = 0$ for $m_i = m_{i^*}$. Remembering that $N_* = F\bar{M}/\bar{m}$, this gives the result that

$$f'(m_{i^*}) = \frac{f(m_{i^*})}{m_{i^*}} \left[\frac{s(N_*) + s'(N_*)M_i/m_{i^*}}{s(N_*)} - \frac{c'(m_{i^*}/\bar{m})}{c(m_{i^*}/\bar{m})} \left(\frac{m_{i^*}}{\bar{m}} - \frac{M_i}{FM} \right) \right], \quad (8)$$

where N_* is the number of eggs at each oviposition site at the ESS I (see eq. 6). Equation (8) differs from the non-phenotypic equation (6) mainly in the last term, involving $c(m_{i^*}/\bar{m})$. Note that this term is no longer constant as in equation (6); it includes the phenotypic parameter M_i and the phenotype-limited ESS for egg size, m_{i^*} .

Unfortunately, it is extremely difficult to make deductions about m_{i^*} by simple inspection of equation (8). Further, we cannot isolate the effect of hierarchy by assuming that both other components are unimportant, such that $s'(N)$ and $f'(m)$ must simultaneously approach zero. For this to occur, the hierarchy effect alone would have to be able to optimize egg and clutch size, an impossibility if c is solely a function of relative and not absolute egg size, as seen for the non-phenotypic case (eq. 6). Here, optimization with $s'(N)$ and $f'(m)$ simultaneously approaching zero would require the tangent line equal to $c'(1)$ (fig. 7) to pass through a point $1/F$ on the abscissa. This could arise trivially by chance, but $1/F$ is only one of an infinite set of possible values. Alternatively, the intercept could be constrained to equal $1/F$ by a change in the form of $c(m/\bar{m})$ with a change in the absolute level of investment in each egg, \bar{m} . However, this would violate our assumption that c depends strictly on relative rather than absolute egg sizes.

As currently envisaged, the hierarchy effect therefore adjusts optimization against the other two constraints, $f(m)$ and $s(N)$, rather than acting as an optimizer in its own right. To analyze how the hierarchy effect influences phenotypic strategies, we examine separately the cases in which the density effect, $s(N)$, is unimportant, and in which the absolute effect of egg size, $f(m)$, is unimportant. Throughout, the hierarchy effect is modeled explicitly as the linear form $c(m_i/\bar{m})$

$= a(m_i/\bar{m}) + 1 - a$; that is, it has slope a and intercept $1 - a$, and it meets the requirement that $c(m_i/\bar{m}) = 1$ when $m_i = \bar{m}$.

First, consider the case in which the density effect is unimportant, such that $s'(N) \rightarrow 0$. Using, as before, the explicit function $f(m) = 1 - \exp[-(m - m_{\min})]$, we get

$$m_{i^*} = [\exp(m_{i^*} - m_{\min}) - 1] \left\{ \frac{m_{g^*}[1 - a(1 - M_i/F\bar{M})]}{am_{i^*} + m_{g^*}(1 - a)} \right\} \quad (9)$$

$$m_{g^*} = [\exp(m_{g^*} - m_{\min}) - 1][1 - a(1 - M_g/F\bar{M})], \quad (10)$$

where $m_{g^*} = \bar{m}$. In words, it is the ESS egg size of phenotype g , which has reserves M_g and produces eggs of exactly average size. Thus, g is an average phenotype in that it plays $m_{g^*} = \bar{m}$, but note that it does not necessarily have an average amount of reserve for gametes (M_g need not equal \bar{M}). This technique (see Parker and Knowlton 1981) is useful for deducing ESS's limited by phenotype; in the present case, a large female will have $M_i > M_g$, and a small female $M_i < M_g$. Equation (10) and hence (9) can easily be computed iteratively for given values of the constants m_{\min} , a , and $F\bar{M}$.

Some numerical results are shown in figure 8. First, note that when a approaches zero (hierarchy effect is unimportant), equations (9) and (10) converge, as expected, to equation (2); all phenotypes should produce the same egg size. When a is greater than zero (hierarchy operates), all females should increase egg size. However, paradoxically, the hierarchy effect causes bigger females to lay smaller eggs than small females (fig. 8). The reason for this counterintuitive prediction is that a large female ($M_i > M_g$) exerts a greater effect on the mean egg size \bar{m} at the oviposition site than does a small female ($M_i < M_g$). Hence, although

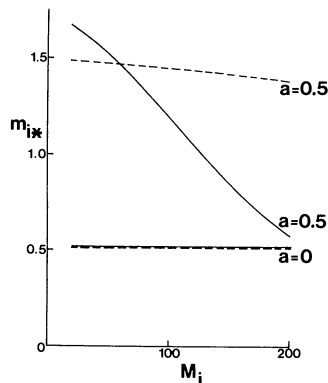


FIG. 8.—Results obtained by iteration of equations (9) and (10), in which $M_g = 100$ and $m_{\min} = 0.1$. Continuous lines are for $F\bar{M} = 500$ (few competing females); broken lines are for $F\bar{M} = 5,000$ (many competing females). In the absence of the hierarchy effect ($a = 0$), egg m_{i^*} is independent of female phenotype M_i . The hierarchy effect leads to an increase in egg size for all females. With few females, larger females produce smaller eggs; but with many females, egg size is similar for all females.

both large and small females produce larger eggs under the influence of the hierarchy effect, the advantage of an increase in egg size can be offset significantly in large females by the consequent increase in \bar{m} (since they tend to dominate the value of \bar{m}), whereas for small females, increases in the egg size hardly affect \bar{m} .

If F is large (many ovipositing females), all values of m_i tend to be similar, irrespective of differences in M_i (fig. 8). Hence, under high competition, the hierarchy effect tends to conserve egg size. In both *Drosophila melanogaster* (Warren 1924) and the dungfly *Scatophaga stercoraria* (Parker 1970), egg size remains constant irrespective of female size; in both cases, competitive laying is common.

We believe that optimizing with $c(m_i/\bar{m})$ against the constraint of $f(m)$ reveals the possible consequences of the hierarchy effect. It is biologically realistic to envisage advantages accruing through differences in egg size being moderated or constrained by other forces that act to conserve absolute egg size. In contrast, optimizing with $c(m_i/\bar{m})$ against the constraint of $s(N)$ is biologically unrealistic. This is apparent if we investigate the effect of density, $s(N)$, on females of different phenotypes by assuming that both $f'(m_i)$ and $c'(m_i/\bar{m})$ approach zero in equation (8), which then reduces to $-s'(N_*) = s(N_*)(m_{i^*}/m_i)$ for any i . Since N_* is constant, then M_i/m_{i^*} must also be constant for all i . Thus, clutch size ($n_{i^*} = M_i/m_{i^*}$) must be independent of female size, and egg size must therefore increase in strict proportion to female size. (Note that this prediction of the density effect is exactly opposite to that suggested by the hierarchy effect.) In other words, the density effect acting alone optimizes clutch size, such that egg size varies passively with the phenotype of the ovipositing female. Hence, if we optimize with $c(m_i/\bar{m})$ against the constraint of $s(N)$ alone, then the effects on differences in egg size are not constrained by any forces acting on absolute egg size alone.

Nevertheless, optimizing against $s(N)$ may shed light on systems in which all three fitness components operate simultaneously. Using the explicit function $s(N) = 1 - kN$, we obtained patterns diametrically opposed to those for optimization against $f(m)$; namely, larger females produce even larger eggs, and this difference increases as the number of females increases. These effects could act to balance those observed for optimization against $f(m)$.

BIOLOGICAL VARIATION IN THE FORM OF $f(m)$

Finally, it is possible to use variants of the simplest models examined here (eqs. 1 and 2) to investigate the likely effects of habitat variation on egg size by specifying a precise function for $f(m)$. For example, suppose that a species has a season of fixed length, T , within which preadult development and reproduction must occur. Many temperate-region poikilotherms, whose season length is determined largely by climatic factors, must conform to this description. Suppose, further, that preadults need to reach a size, A , for successful reproduction, and that it takes a time, $h(m)$, for an egg of size m to reach this size. The reproductive output of an individual may be assumed to depend directly on the length of the reproductive period; that is, $f(m) = T - h(m)$, but $h(m)$ will depend on egg size.

In broad terms, larger eggs can be expected to develop more rapidly to reproductive maturity. More specifically, the preadult growth curve can be assumed to be increasing at an accelerating rate (Sibly et al. 1985); for simplicity we assume that growth is exponential, terminating at size A . Individuals enter the growth curve at different points depending on their own initial size, m . The growth curve starts from an arbitrary minimum egg size, m_0 , such that

$$A = m_0 \exp[bh(m_0)] \quad \text{and} \quad h(m_0) = \ln(A/m_0)/b,$$

where b is the growth rate. The time taken to reach A from an egg size m is $h(m_0)$ less the time that would have been taken to reach m from m_0 ,

$$h(m) = \ln(A/m_0)/b - \ln(m/m_0)/b \quad \text{or} \quad h(m) = \ln(A/m)/b.$$

Therefore, $f(m) = T - \ln(A/m)/b$.

Optimal egg size, m_* , is given by the application of equation (2):

$$1/m_*b = [T - \ln(A/m_*)/b]/m_*,$$

which, on rearrangement, gives $\ln m_* = \ln A - bT + 1$.

It is possible to predict, therefore, that in a seasonal environment of the type envisaged here, egg size should be larger in environments where the rate of preadult development is slower, the season as a whole is shorter, and the size necessary for successful breeding is larger. Similar conclusions have been derived by alternative means for preadult development and season length in a seasonal environment (Sibly and Monk, MS), and for preadult development in general (Sibly and Calow 1985). Sibly and Calow (1985) found a negative correlation between egg size and the rate of preadult development, and Sibly and Monk (MS) showed a negative correlation between egg size and season length in the grasshopper *Chorthippus brunneus* in a seasonal environment.

A more general approach to the effect of the form of $f(m)$ on optimal egg size is shown in figure 9. In figure 9a, the two $f(m)$ curves differ by a constant multiplier. This is equivalent to saying that all individuals in the lower curve are subject to an additional source of mortality not affecting individuals in the upper curve, and that the force of this mortality is independent of phenotype (i.e., egg size). It is a well-known marginal-value result that for two curves differing in this way, the solution (i.e., the optimal egg size) is the same (Parker and Stuart 1976). By contrast, in figure 9b the individuals in the lower curve are subject to an additional source of mortality, the force of which varies with phenotype. Specifically, small individuals are disproportionately adversely affected, causing an increase in the optimal egg size.

The significance of these results can be understood by reconsidering some of the conventional wisdom of life history theory, namely, that intense preadult competition favors the production of fewer, larger offspring or, conversely, that an environment dominated by density-independent mortality favors the production of more, smaller offspring (Pianka 1970; Stearns 1976). The results derived here, however, show that the intensity of competition per se is not the important issue. What matters is the extent to which mortality is phenotype-specific. Consider figure 9b. Competition will promote the production of fewer, larger offspring

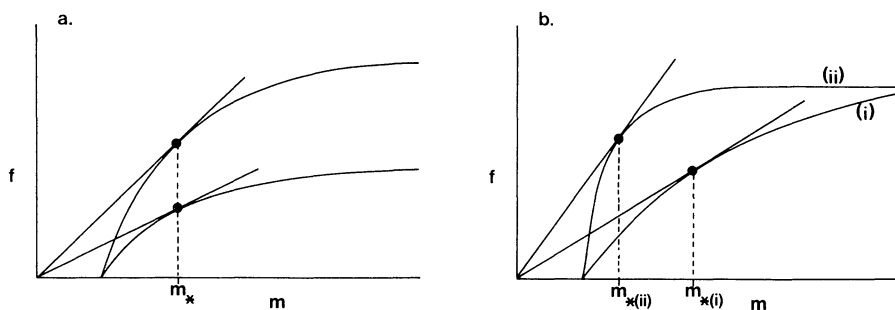


FIG. 9.—*a*, Two $f(m)$ curves for which the upper curve differs from the lower curve by a constant multiplier and the predicted optimal egg size, m_* , is the same. This could apply to two environments differing in the intensity or relative importance of competition or density-independent mortality, as long as the differences were independent of phenotype. *b*, In the lower curve, (i), mortality disproportionately affects the smallest individuals, but in the upper curve, (ii), mortality is independent of phenotype over most of the range. Optimal egg size is therefore smaller for curve (ii) than for curve (i). Thus, dependence of mortality on phenotype rather than on density affects egg size.

only if larger individuals tend to be better competitors (as in curve (i)). Density-independent mortality will promote the production of more, smaller offspring only if the mortality is also independent of phenotype. The conventional wisdom only appears to be true because density-independent mortality is typically independent of phenotype, and because competition does typically affect the smallest individuals disproportionately. However, if two environments differ in the intensity of competition they impose, but all individuals are equally affected because they compete in a scramble, there will be no consequential difference in the optimal egg size (fig. 9*a*). This result clearly changes the emphasis of the conventional wisdom, but does not contradict it outright.

GENERAL DISCUSSION

The results of our models can be divided into those relating to the environments experienced by developing young and those relating to the phenotypes of the ovipositing females. In the first case, we suggest, along with previous workers (see Stearns 1976), that increasing intensities of sib competition among developing young select for the production of fewer, larger eggs and that non-sib competition selects for even fewer, even larger eggs. We also show, however, that the dependence of competition on phenotype rather than on density is important in such cases. In addition, we suggest that in seasonal environments, the production of fewer, larger eggs is favored by slower rates of preadult development and shorter overall season lengths.

The main results relating to the sizes of ovipositing females are summarized in table 1 for the typical case in which larger females have greater gametic reserves and forage at least as efficiently as small females. By noting individually the effects of different environmental components, table 1 allows us to predict the dependence of egg size and clutch size on female size in environments dominated

TABLE 1

SUMMARY OF THE MAIN EFFECTS OF MATERNAL PHENOTYPE ON CLUTCH SIZE AND EGG SIZE, UNDER THE INFLUENCE OF VARIOUS COMPONENTS OF FITNESS

Fitness Component	Notation	General Effect	Reproductive Prediction for Larger Females
Intrinsic effects of egg size	$f(m)$	Egg size constant for all females	Larger clutches
Sib competition	$s(n)$	Clutch size constant for all females	Larger eggs
Sib competition with high M and/or low search costs for further oviposition sites	$s(n)$	Egg and clutch size variable with respect to female size (see fig. 6)	More clutches per oviposition cycle
Non-sib competition acting through total competitor density	$s(N)$	Clutch size constant for all females	Larger eggs
Non-sib competition acting on egg size relative to the sizes of others' eggs (hierarchy effect)	$c(m,/\bar{m})$	Egg size approximately constant for all females (particularly constant when there are many competing females)	Larger clutches (and smaller eggs when there are few competing females)

by these different components; but even in environments where many factors act, it allows us to see the parts played by the various components in forging an overall strategy. Thus, for example, where competition with non-sibs is important, the density of competitors per se plays no part in favoring the production of larger clutches by larger females. However, the hierarchy effect does tend to conserve egg size and perhaps even favor the production of smaller eggs by larger females, thereby favoring the production of larger clutches by larger females. In addition, the intrinsic effects of egg size on larval viability also favor the production of larger clutches by larger females. The production of larger eggs by larger females is predicted for those cases in which sib competition is an important factor.

Although our model is designed for the specific case of an organism that alternates between two localities, one for feeding and one for laying, it is clear that the approach could be applied with little modification to several other systems. Consider, for example, the case in which oviposition sites can be encountered in the same habitat as food items, such that searching for food and searching for an oviposition site are not mutually exclusive activities (see Skinner 1985). The main difference is that in Skinner's model, the amount of resource gathered, M , may depend strongly on the interval between leaving one oviposition site and finding the next. An important point is that whereas a clutch size can be "chosen" by a female as she encounters an oviposition site, egg size cannot; it must be fixed previously. Many of our conclusions about egg size may therefore remain unchanged and related to the distribution of intervals between successive encounters of oviposition sites (i.e., to the distribution of M). Differences between phenotypes relate mainly to differences in the rates of gathering resources, and to

differences in the absolute capacity for storing eggs (because sometimes females become "full" before an oviposition site is located). Because of the sib-competition density component, $s(n)$, an adaptive strategy would be to produce smaller eggs initially, and larger eggs later in the interval between ovipositions. We know of no evidence with which to test this prediction; an investigation along these lines might prove fruitful.

In contrast, clutch size can readily be "chosen" at the oviposition site. The female can select any number of eggs up to (but not more than) that which will maximize clutch fitness (the "Lack number"); and Skinner (1985) has shown by simulation that a good rule of thumb is for the female to lay all her mature eggs, up to the Lack number.

Clearly, the case in which feeding and laying opportunities occur in the same habitat could lead to complex strategies and there is much scope for further models. However, selection is likely to favor a preference for feeding early after oviposition and to favor seeking oviposition sites later as M increases. Such characteristics would converge toward the assumptions of our model. Furthermore, contrary to our intuition that clutch size can be facultative, in many insects the decision about the next clutch size seems to be set immediately after laying. Potential oviposition sites are then ignored until the clutch is matured. The present models appear to apply directly to such cases.

A second obvious application of our models concerns cases of semelparity, especially those in which all the resources M are collected during the larval stage and are later spent as an adult. This becomes equivalent to a single cycle of "gathering" and "spending." The difference between such systems and those envisaged in the present paper relates mainly to the time scale and hence to the mortality risks during the expenditure of M . In the present models we regard oviposition time and risk as insignificant (though other studies have used oviposition time to optimize clutch size; e.g., Charnov and Skinner 1984). With semelparity, age-independent mortality during the expenditure of M would be extensive and might alter considerably the conclusions (Parker and Courtney 1984; Begon and Parker 1986).

Regrettably, we were able to find few data sets with which to test our models. Relatively few studies have examined variations in egg size, and hardly any appear to have measured egg size in relation to female size. Although many studies show that larger females contain larger gametic masses, there have been relatively few attempts to examine the allocation of these resources between individual clutches and individual eggs in females of different size. We hope that our models provide a number of testable hypotheses that will stimulate further empirical study of this neglected area.

Our models are particularly testable because many of the predictions from them concern differences between phenotypically distinct individuals within species rather than simple differences between species. Testing predictions about interspecific differences is almost invariably difficult, because a multiplicity of factors (not necessarily those being modeled) can affect the difference under consideration. Hence, it is very easy to get the predicted difference but for some other reason, or not to get the difference because some other factor has con-

founded the comparison. However, if the interspecific difference concerns the nature of individual variation within each species, then the comparison is much less likely to be affected by the confounding effects of other factors. One species may have larger eggs or larger clutches than another species for an unknown reason, but the species may still be compared in terms of the differences between large and small females in each. This is true for many of the predictions of our model.

Ideally, one should compare closely related species that nonetheless exhibit ecological differences suggesting that $f(m)$, $s(n)$, and/or $c(m/\bar{m})$ are of differing importance. If, for example, $f(m)$ was most important in one species, the model would predict that large females should differ from small females mostly in terms of the number of eggs in each clutch, whereas in another species the females would differ more in terms of egg size. The data collected should include the egg and clutch sizes of different-sized females in the species considered, and also the density dependence of larval mortality and the probability of competition with sibs and non-sibs, in order to assess more precisely the relative importance of the different components of the model.

SUMMARY

In this paper, we develop a series of models for predicting optimal egg size and clutch size in different environments and for different maternal phenotypes. The models investigate the interaction between three components of fitness: (1) the intrinsic effect of egg size, (2) the density effect, the effect of the density of competing offspring (including competition with sibs and with non-sibs), and (3) the hierarchy effect, the effect of egg size relative to the sizes of competing eggs laid by other females. The environmental effects that we consider are the intensities of sib and non-sib competition, the number of egg-laying females, and some aspects of seasonal development. The particular aspects of maternal phenotype examined are foraging efficiency and the gametic reserve available at the time of egg laying (broadly equivalent to female size).

Regarding environmental effects, increasing intensities of sib competition select for the production of smaller clutches of larger eggs, and increasing intensities of non-sib competition select for even smaller clutches of even larger eggs. We show, however, that this occurs because viability depends on egg phenotype, not because competition depends on density. In addition, we show that in seasonal environments the production of smaller clutches of larger eggs is favored by slower rates of preadult development and shorter overall season lengths.

Regarding maternal phenotype, we derive the following conclusions. The intrinsic effects of egg size promote the production of eggs of a constant size by all females, so that larger females lay larger clutches. Sib competition (considered a density effect with no hierarchy component) favors constancy of clutch size for all females, so that larger females lay larger eggs. If, however, sib competition is coupled with circumstances in which females have high gametic reserves and/or low search costs for future oviposition sites, egg size and clutch size should vary with respect to female size, but larger females should lay more clutches. Non-sib

competition acting through total competitor density (the density effect) favors the production of a constant clutch size by all females, such that larger females lay larger eggs. The action of non-sib competition on egg size relative to the sizes of others' eggs (the hierarchy effect), although tending to increase egg size overall, may cause smaller females to produce eggs larger than those produced by larger females. This latter effect, however, is confined to cases in which there are few competing females; typically, the hierarchy effect will favor approximately constant egg sizes for all females, so that larger females lay larger clutches.

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