

Clutch size, offspring performance, and intergenerational fitness ¹¹² *corrected*

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It is now generally recognized that clutch size affects more than offspring number. In particular, clutch size affects a suite of traits associated with offspring reproductive performance. Optimal clutch size is therefore determined not by the numerically most productive clutch but by the clutch that maximizes collective offspring reproductive success. Calculation of optimal clutch size thus requires a consideration of ecological factors operating during an intergenerational time frame, spanning the lifetime of the egg-laying adult and the lifetimes of her offspring. The optimal clutch cannot define reproductive values in advance, but instead requires that the strategy chosen is the best response to the set of reproductive values that it itself generates. In this article, we introduce methods for solving this problem, based on an iterative solution of the equation characterizing expected lifetime reproductive success. We begin by considering a semelparous organism, in which case lifetime reproductive success is a function only of the state of the organism. For an iteroparous organism, lifetime reproductive success depends upon both state and time, so that our methods extend the usual stochastic dynamic programming approach to the evaluation of lifetime reproductive success. The methods are intuitive and easily used. We consider both semelparous and iteroparous organisms, stable and varying environments, and describe how our methods can be employed empirically. *Key words:* intergenerational fitness, lifetime reproductive success, offspring performance, optimal clutch size. [*Behav Ecol* 5:412–417 (1994)]

The systematic study of clutch size, initiated by David Lack (1946, 1947, 1948) in his study of birds, remains a keystone in the behavioral and evolutionary ecology of birds (Dhondt et al., 1990) and other taxa, ranging from insects to mammals (Godfray et al., 1991). Clutch or litter size is an easily measured trait with direct fitness consequences that has been used to investigate trade-offs between offspring size and offspring number, present and future reproduction, and parental and offspring interests (Godfray et al., 1991; Lessells, 1991; Roff, 1992; Stearns, 1992). Clutch size was recently reviewed by Godfray et al. (1991) and Lessells (1991), who considered mainly empirical aspects of clutch size. Here we provide a theoretical development of the subject, accessible to a general readership. We focus on parasitic wasps, but the concepts that we develop are broadly applicable to birds, fish, and mammals (where the analog is litter size). Thus, we use "clutch size" to mean the number of eggs deposited in a single reproductive bout.

We begin with a brief review of the classic approach before presenting a new approach that incorporates the effects of intergenerational fitness. Lack (1947, 1948) proposed that females would lay the number of eggs that resulted in the most offspring from that clutch. That is, if c is the clutch and $p(c)$ is the probability that an offspring from a clutch of size c reaches independence (or recruitment when considering birds, fish, or mammals) from a clutch, then the optimal clutch size c would be determined by

$$\max_c [c p(c)] \quad (1)$$

where \max_c means to maximize over choices of c .

The trade-off is thus between clutch size and the probability of juvenile survival to independence.

However, it has become increasingly apparent that clutch size may affect more than offspring survivorship—it can affect a number of other components of offspring performance (such as size, attractiveness to mates, foraging ability) that directly or indirectly affect reproductive success (examples of such effects, for a wide variety of taxa, can be found in Beacham and Murray, 1993; Boutin et al., 1988; Bradshaw and Holzapfel, 1992; Brody and Lawlor, 1984; Calder, 1984; Clutton-Brock, 1991; de Steven, 1980; Dobson and Murie, 1987; Ford and Siegel, 1989; Hard and Bradshaw, 1993; Janzen, 1993; Johnsgard, 1973; Landa, 1992; Luxford and Beilharz, 1990; McGinley et al., 1987—especially Tables 3–7; Morris, 1986; Mousseau and Dingle, 1991a,b; Pettifor et al., 1988; Schluter and Gustafsson, 1993; Sinervo, 1990; Smith et al., 1989; Thornhill and Alcock, 1983; Tinbergen and Daan, 1990). In addition, it has recently been emphasized that the condition of the mother affects components of fitness (e.g., Price and Liou, 1988; Price et al., 1988; Rowe et al., 1994).

When clutch size affects other attributes of offspring performance we must include the expected lifetime reproductive success, $LRS(c)$, of an offspring that reaches independence from a clutch of size c and modify Equation 1 to

$$\max_c [c p(c) LRS(c)]. \quad (2)$$

This modified version of the clutch size producing the greatest gain in parental fitness from a single clutch is still called the "Lack clutch size" (Godfray

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et al., 1991) and is an important benchmark because it represents the optimal clutch size in the absence of costs associated with reproduction. The rest of this article discusses how we deal with this modification.

Charnov and Skinner (1984), Hardy et al. (1992), and many others (reviewed in Hardy et al., 1992) have proposed that a proxy for the expected lifetime reproductive success could be used. Possibilities include offspring longevity, egg producing ability, or realized lifetime reproductive success under laboratory conditions. As noted by those authors, the difficulties with using such proxies are that different proxies may lead to different predictions of the optimal clutch and that it is not clear how such proxies are connected to actual offspring reproductive success in nature. We shall see that new theoretical methods are required, and that they are intuitive and easily used.

The semelparous case

Lack worked with iteroparous organisms but, by considering only a single clutch, essentially analyzed his birds as if they were semelparous. We focus on a female whose "state" can be characterized by a variable X , with particular value x , measured in some equivalents of "eggs." We understand that X could be a vector of traits or a single trait such as size of a parasitoid. We let

$X(c)$ = State (measured in egg equivalents)
of an offspring emerging from a clutch of
size c . (3)

Suppose that $F(x)$ is the optimal fitness accrued to the mother when her state is x . Then from Equation 2 we have the relationship

$$F(x) = \max_{c \leq x} \{c p(c) F[X(c)]\}. \quad (4)$$

Because $F(x)$ appears on both sides of Equation 4, we are actually treating all generations at once (i.e., the unending sequence of Mother \rightarrow Daughter \rightarrow Mother . . .).

Equation 4 is more complicated than Equation 1 because fitness appears on both sides of the equation. That is, to evaluate the fitness associated with a particular size x , we need to know fitness associated with offspring sizes for all possible clutches up to x . We can solve this equation by an iterative method by letting $F_n(x)$ and $F_n[X(c)]$ denote the values of fitness on the n^{th} iteration and setting

$$F_n(x) = \max_{c \leq x} \{c p(c) F_{n-1}[X(c)]\} \quad (5)$$

where, for example, the value maximizing $cp(c)$ can be employed as a seed value for the iteration. That is, $F_0(x)$ is determined by maximizing $cp(c)$, constrained by $c \leq x$. As n increases, the solution of Equation 5 converges to produce stationary behavioral strategies and population growth rate (McNamara, 1991), measured by $F_n(x_{\text{max}})/F_{n-1}(x_{\text{max}})$ where x_{max} is the maximum value of the state variable. Thus, for example, we can use the solution of Equation 5 to determine the growth rate of a population of individuals following the optimal behavior. However, $F_n(x)$ described by Equation 5 does not converge, but grows, because it measures total number of offspring produced after n generations. This problem can be averted by recognizing that fitness is a *relative* measure of perfor-

mance. Thus, for $F_n(x)$ to converge, we must scale the right hand side of Equation 5. For example, replacing $F_{n-1}[X(c)]$ with $(F_{n-1}[X(c)])/(F_{n-1}[X(c_{\text{max}})])$ where c_{max} is the maximum possible clutch size leads to excellent numerical convergence. We then have

$$F_n(x) = \max_{c \leq x} \left\{ cp(c) \frac{F_{n-1}[X(c)]}{F_{n-1}[X(c_{\text{max}})]} \right\}. \quad (6)$$

This modification of Equation 5 solves the theoretical problem raised by Tinbergen and Daan (1990: 183) who used the proxy of fecundity in their attempt to couple parent and offspring reproductive success.

Alternatively, this scaling can be thought of as follows. Every reproductive strategy (rule for setting clutch size as a function of state) generates a stable distribution of offspring states, X , and thus a relative reproductive value for each offspring state. For every set of offspring reproductive values there is a strategy that maximizes the total payoff to a parent. The iterative method does not define reproductive values in advance but, instead, requires that the strategy chosen is the best response to the set of reproductive values that it itself generates. The feasibility of carrying out this program for animals as complicated as birds is demonstrated by the work of Tinbergen and Daan (1990).

To illustrate our method, we adopt the following parameterizations. First, we set

$$p(c) = 1 - \frac{c^g}{(c_{\text{max}} + 1)^g} \quad (7)$$

where c_{max} is the maximum clutch size (because $p(c_{\text{max}} + 1) = 0$), and g is a "shape parameter" determining how additional eggs affect the probability of survival. For example, if $c_{\text{max}} = 8$ and $g = 2$, we find that the most productive clutch is 5, expected to produce 3.45 offspring on average.

To relate clutch size to offspring performance, we use the data of Rosenheim and Rosen (1991). The size (in mm) of an emerging parthenogenetic parasitoid wasp (*Aphytis lingnanensis*) is related to clutch size by

$$S(c) = 0.245 - 0.0223(c - 1) \quad (8)$$

and the number of eggs to size by

$$X(c) = \max[0, -26.7 + 181.8 S(c)]. \quad (9)$$

The optimal clutch is found by solving Equation 6 with state $X(c)$ given by Equation 9. The numerical solution Equation 6 proceeds by first specifying $F_0[X(c)]$, which we choose to be $\max_{c \leq x} \{cp(c)\}$. For $n > 1$, we determine $F_n[X(c)]$ from the right-hand side of Equation 6. As n increases, the ratio on the right-hand side of Equation 6 rapidly converges and we consider $F_n[X(c)]$ defined in this way to be the solution. The results of such computations (Table 1) show that the most productive clutch is $c_{\text{mp}} = 5$ and that the optimal clutch is $c^* = 4$, assuming that $X > 3$. Because there is an inverse "mapping" between clutch size and offspring state affecting offspring reproductive success, we are naturally led to clutches that will be smaller than that which produces the largest number of offspring. If we adopted the proxy of offspring fecundity instead of offspring reproductive success, then we would choose the clutch to maximize $cp(c)X[S(c)]$ and predict optimal clutches of size 2 rather than 4.

Table 1
Optimal clutch size in the semelparous case

Step 1: Relate clutch size c to size of emerging offspring and then to eggs

c	Size	Eggs
1	0.245	17
2	0.2227	13
3	0.2004	9
4	0.1781	5
5	0.1558	0
6	0.1335	0
7	0.1112	0
8	0.0889	0

Step 2: Determine the numerically most productive clutch by maximizing $c p(c)X(c)$

c	$p(c)$	$cp(c)$	$cp(c)X(c)$
1	0.987654	0.987654	16.7
2	0.950617	1.90123	24.7*
3	0.888889	2.66667	24.0
4	0.802469	3.20988	16.0
5	0.691358	3.45679**	10.4
6	0.555556	3.33333	0.0
7	0.395062	2.76543	0.0
8	0.209877	1.67901	0.0

Step 3: Determine the optimal clutch by solving Equation 5 to find that the optimal clutch using offspring reproductive success is 4.

* The optimal clutch for the fecundity proxy is 2.
** The most productive clutch is 5.

The iteroparous case

For iteroparous organisms, the situation is more complicated because of the opportunity for more than one reproductive event. Such organisms face fundamental uncertainties and fundamental realities. The fundamental uncertainties are survival from one reproductive age to the next and the probability of a reproductive opportunity at the next age. The latter is important only through its interaction with the former. The fundamental realities are senescence and physiological state. Senescence implies there is an age or time, A , after which no more reproduction occurs. Mortality implies that there is only a chance of surviving to the

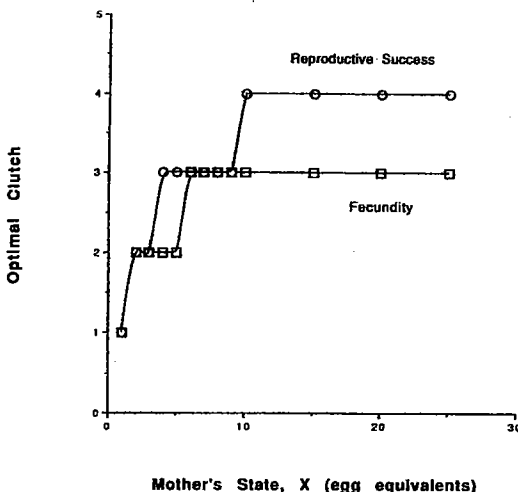


Figure 1
Optimal clutches at $t = 1$ (also the stationary clutches, Mangel and Clark, 1988) as a function of state of the mother X (measured in egg equivalents) for the case in which offspring fecundity is maximized and the case in which offspring reproductive success is maximized.

next age and that this might depend upon the "reproductive effort" at the current age. We assume that $s(c)$ is the probability that the mother survives to the next age, given a clutch of size c now, that λ is the probability that the female has a reproductive opportunity at age a and that m_0 is the probability of surviving to the next age in the absence of current reproduction.

We now replace $F(x)$ by $F(x, a)$, which is the maximum expected future fitness for a female with state, x , whose current age is, a . To compute $F(x, a)$, we must add to the current reproduction the expected future reproduction. We thus replace Equation 4 with

$$F(x, a) = (1 - \lambda)(1 - m_0)F(x, a + 1) + \lambda \max_{c \leq x} \{ c p(c)F[X(c), 1] + s(c)F(x - c, a + 1) \}. \quad (10)$$

Equation 10 has the same problem as Equation 4: it involves expected reproductive success at age $a = 1$ as well as age $a + 1$ on the right hand side, and thus cannot be solved by the usual method of backward induction (Mangel and Clark, 1988). We can, however, solve the associated equation by an iterative procedure analogous to the one used to solve Equation 4. On the n^{th} iteration we write

$$F_n(x, a) = (1 - \lambda)(1 - m_0)F_n(x, a + 1) + \lambda \max_{c \leq x} \left\{ cp(c) \frac{F_{n-1}[X(c), 1]}{F_{n-1}[X(c_{\max}), 1]} + s(c)F_n(x - c, a + 1) \right\}. \quad (11)$$

Equation 11 is solved in a manner similar to, but more complicated than, Equation 6. First, we specify $F_0(x, a)$ as the solution of Equation 10 with $c p(c) F[X(c)]$ replaced by $cp(c)$. Thus, $F_0(x, a)$ is the maximum expected production of offspring from age a onward for an individual whose current state is x . Then, for $n > 0$, we obtain $F_n(x, a)$ by solving Equation 11 as if it were a standard equation of stochastic dynamic programming (Mangel and Clark, 1988). Once again, as n increases, the ratio on the right hand side of Equation 11 converges and $F_n(x, a)$ defined in this way is the solution.

The solution of Equation 11 yields optimal clutch sizes that are completely defined neither by current reproductive opportunities nor by the condition and expectations of the parent. Rather, the clutch size that maximizes fitness also responds to the ecological conditions, such as host availability and mortality rates, expected to exist during the lifetime of the offspring. Thus far, we have considered only stable environments, in which conditions influencing the mapping of an individual's state, $X(c)$, to its fitness are constant; below, we suggest how this assumption can be relaxed.

To illustrate Equation 11, we use Equation 7, with $g = 3$, $c_m = 10$, assume that $x_{\max} = 25$ eggs, that $X(c) = \text{number of eggs of an individual emerging from a clutch of size } c = x_{\max}(1 - [c/c_{\max} + 1])$, that $A = 20$, $m_0 = s(c) = 0.1$ and that $\lambda = 0.4$. For these parameters, $cp(c)X(c)$ is maximized by clutches of size 5, but the optimal clutches taking only offspring fecundity into account are smaller

because of the cost of reproduction (Figure 1). If we use offspring reproductive success rather than the proxy of fecundity, the optimal clutches are generally larger.¹

Variable environments

Equation 11 is based on the assumption that expected conditions for the offspring match those experienced by the parent. When fluctuations of the environment are predictable, as with bivoltine parasitoids in a seasonal environment, our model could be expanded to predict optimal clutches as a function of season. Clutches might change over the course of the year in response to the environment expected for offspring rather than to that experienced by the parent. In general, we would specify a conditional distribution of the possible environments [characterized by m_0 , $s(c)$ and λ] that the offspring would experience, given the environment the parent experiences. We then replace $F_n(x, a)$ by $F_n[x, a | m_0, s(c), \lambda]$ and the analog of Equation 11 is now

$$F_n[x, a | m_0, s(c), \lambda] = (1 - \lambda)(1 - m_0)F_n[x, a + 1 | m_0, s(c), \lambda] + \lambda \max_{c \leq x} \left\{ cp(c) \mathcal{E} \left[\frac{F_{n-1}[X(c), 1 | m_0', s(c)', \lambda']}{F_{n-1}[X(c_{\max}), 1 | m_0', s(c)', \lambda']} \right] + s(c)F_n[x - c, a + 1 | m_0, s(c), \lambda] \right\} \quad (12)$$

where \mathcal{E} denotes the average of the possible environments that the offspring will experience, given that the mother currently experiences an environment characterized by m_0 , $s(c)$ and λ . The computations associated with Equation 12 are no more complex than those associated with Equation 11, once the distribution of environments is specified.

To illustrate this idea, assume that there are only two environments and that the difference between the two environments is that the host encounter rate is larger in environment 1 than in environment 2. If E_i denotes the environment, we must now specify two fitness functions $F_n(x, a | E_1)$ and $F_n(x, a | E_2)$ and transition densities between the two environments of the form $p_{ij} = \text{Prob}\{E_i \rightarrow E_j \text{ in the next generation}\}$. The analog of Equation 12 is then

¹ Empirical measurements of $F[X(c), 1]$ requires a more detailed examination of lifetime success. Suppose that a_c, c denotes the number of offspring in clutches of size c' produced on average over the lifetime of an individual derived from a clutch size c . It can be determined empirically by following the reproductive success of individuals and their offspring. Consider the matrix A with elements a_c, c , and a vector S representing the size structure of the population (indexed by clutch size) in the current generation. In the next generation, the size structure is determined by $S' = AS$. The right eigenvector (Caswell, 1989) satisfies $S' = rAS$ where r is the population growth rate. The relative reproductive value of an offspring derived from a clutch of size c is then an element in this right eigenvector of the matrix A . Thus, iterated single host maximum clutch thus maximizes the reproductive value of a brood, rather than the number of eggs produced in some future generation.

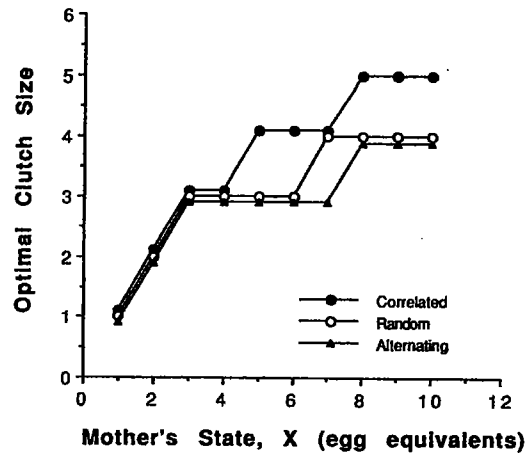


Figure 2
Optimal clutch size for parasitoids inhabiting a host poor environment, given that a host poor and a host rich environment are temporally correlated, random, or alternating across generations.

$$F_n(x, a | E_1) = (1 - \lambda)(1 - m_0)F_n(x, a + 1 | E_1) + \lambda \max_{c \leq x} \left\{ cp(c) \left[p_{11} \frac{F_{n-1}[X(c), 1 | E_1]}{F_{n-1}[X(c_{\max}), 1 | E_1]} + p_{12} \frac{F_{n-1}[X(c), 1 | E_2]}{F_{n-1}[X(c_{\max}), 1 | E_2]} \right] + s(c)F_n(x - c, a + 1 | E_1) \right\} \quad (13a)$$

$$F_n(x, a | E_2) = (1 - \lambda)(1 - m_0)F_n(x, a + 1 | E_2) + \lambda \max_{c \leq x} \left\{ cp(c) \left[p_{21} \frac{F_{n-1}[X(c), 1 | E_1]}{F_{n-1}[X(c_{\max}), 1 | E_1]} + p_{22} \frac{F_{n-1}[X(c), 1 | E_2]}{F_{n-1}[X(c_{\max}), 1 | E_2]} \right] + s(c)F_n(x - c, a + 1 | E_2) \right\} \quad (13b)$$

To illustrate Equation 13, we use the same parameterizations as in Figure 1, except that $g = 2$ and $m = 0.05$, and we assume that in the better environment $\lambda = 0.6$, that in the poorer environment $\lambda = 0.1$. Now consider three scenarios: (1) correlated environments, where the probability that offspring will be found in the same environment type as their mother is $p_{11} = p_{22} = 0.9$ and the probability that offspring will be found in the environment type different from that occupied by their mother is $p_{12} = p_{21} = 0.1$; (2) random environments, and $p_{11} = p_{12} = p_{21} = p_{22} = 0.5$; and (3) alternating environments, where $p_{11} = p_{22} = 0.1$ and $p_{12} = p_{21} = 0.9$.

Optimal clutch size decisions for parasitoids encountering a host in the poorer environment now depend on whether the environments are temporally correlated, randomly varying, or alternating (Figure 2). Mothers choose larger clutch sizes, thereby producing smaller, less fecund offspring,

when their offspring will inhabit a poor environment (where fecundity is unlikely to limit reproductive success because hosts are rare). On the other hand, mothers choose smaller clutches (thereby producing larger, more fecund offspring) when their offspring will inhabit a good environment (where fecundity is likely to define reproductive success). These results suggest that optimal clutch sizes, including Lack clutch size, are only clearly definable if future conditions can be defined.

Conclusion

The natural generalization of Lack's hypothesis that clutch size has evolved to correspond with the maximum number of offspring that the parents can rear to independence is to focus on the fitness associated with some number of offspring. Indeed, Godfray et al. (1991: 411) define "the Lack clutch size as the clutch size that leads to the greatest gain in parental fitness, irrespective of the biological mechanisms relating clutch size to offspring fitness." Implementing this definition is a non-trivial task, as Tinbergen and Daan (1990) noted.

In this article, we have introduced a method for determining optimal clutch size in terms of the expected relative lifetime reproductive success of offspring. For semelparous reproduction, our method is not much more complicated than the simpler ones that maximize the product of clutch size and survival to independence. For iteroparous reproduction, our method generalizes the techniques of stochastic dynamic programming (Mangel and Clark, 1988) as applied to behavioral ecology. In both cases, the essence of the method rests on the recognition that fitness is a relative measure. The numerical techniques for implementing our approach are straightforward.

The focus on the lifetime reproductive success of offspring, rather than offspring number, forces one to explicitly consider intergenerational phenomena. In particular, clutch sizes deposited by mothers will be directly affected by the environment experienced by their offspring. We have illustrated this (Equations 13a,b) with an example based on two environments, but the idea is fully general and raises an entire suite of new questions: If parents are selected to adjust clutch sizes in response to conditions projected to exist during the offspring lifetimes, how might such projections be made? Is there any evidence that parents indeed make such projections and modulate clutch sizes accordingly? Although there is some evidence that this occurs (Landa, 1992; Sinervo et al., 1992), the broad treatment of these questions remains to be addressed in experimental studies. Equations 12 or 13 thus focus attention on a range of biological problems hitherto unaddressed within experimental studies of clutch size. Optimal clutch sizes, including the Lack clutch size for semelparous organisms or iteroparous organisms not experiencing a cost of reproduction, can now be defined only if future conditions can be defined. Environments that fluctuate in an unpredictable manner may select for "bet hedging" reproductive behavior (Stearns, 1992). Our models can be extended in a natural way to assess the effects of between-generation variance in fitness by replacing Equation

12 with one that maximizes the expectation of the logarithm of total reproduction (Mangel and Clark, 1988). This may be important if aspects of the environment that influence offspring reproductive opportunities are rapidly fluctuating. For example, among insect parasitoids, offspring size is usually highly correlated with offspring fecundity. Under conditions of high host availability, large parasitoids may realize substantially higher levels of lifetime reproductive success than small parasitoids because the fitness of small parasitoids is constrained by their ability to produce eggs. Optimal clutch sizes may thus be smaller to produce a smaller number of larger offspring. Under conditions of low host availability, however, both large and small parasitoids may be unable to find enough hosts to exhaust their egg producing abilities; thus, there may be no fitness penalty associated with small size, and parents may be selected to produce large clutches of small offspring. Given this underlying theoretical framework, it should now be possible to most profitably pursue empirical studies.

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