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Natural selection for reproductive optima

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**Summary. Clutch size has long been considered the most funda-
mental of life history traits. Theorists have argued that an evo-
lutionarily optimal brood size reflects a balance of tradeoffs be-
tween juvenile and adult survival. But several recent studies
have failed to document a consistent relationship between num-
ber of young and parental mortality. Natural selection may
operate instead on parental investment, and any selection for an
optimum clutch size would be incidental to its function of opti-
mizing this investment among offspring.**

For forty years, ecologists studying the evolution of life
histories have concentrated on the number of young
produced and the timing of reproduction (Lack 1947,
Cole 1954, Cody 1966, Williams 1966, Gadgil and Bos-
sert 1970, Charnov and Schaffer 1973, Stearns 1976).
This is logical because population dynamics is the even-
tual product of individual fecundity and survival proba-
bilities, eloquently shown in Lotka's characteristic
equation

$$1 = \int_0^\infty l_x m_x e^{-rx} dx$$

where l_x and m_x equal survival and rate of reproduction
at age x respectively, and e^{-rx} is a correction term for
changes in population size. Natural selection acting

within the competitive milieu of population density
should favour those genotypes which maximize lifetime
production of breeding adults. These maxima will in
turn represent optimal tradeoffs between the produc-
tion of young, and both juvenile and parental survival
(Charnov and Krebs 1974). The assumption has been
that brood size has evolved to reflect these tradeoffs.
An alternative explanation argues that brood size is in-
stead largely under the proximate control of other se-
lective forces.

An offspring's chances of survival to breeding age will
often be some function of parental investment. To maxi-
mize the production of offspring reaching breeding age,
parents must optimize the costs and benefits of invest-
ment in terms of offspring survival. There is still an opti-
mum brood size, but it serves principally to maintain an
optimum investment per offspring in response to
changes in the total investment available (Ricklefs 1968,
Smith and Fretwell 1974, Brockelman 1975, Drent and
Daan 1980, Högstedt 1980). For example, as parents
grow and mature, their total investment for any given
reproduction may increase, and if the investment per
offspring remains more or less constant, brood size will
also increase. There is no evolutionarily optimal brood
size because selection is operating primarily on the in-
vestment ratio per offspring. Variation in brood size is
the mechanism by which organisms optimize that ratio

290

in response to changing environmental or physiological conditions.

Tentative support for this view of life history evolution comes from several sources. First, size of eggs or newborn appears to be a more conservative trait than the number of young produced (Brockelman 1975). Second, there is some evidence that the probability of juvenile survival is constant over a wide range of brood sizes in both birds and mammals (Alerstam and Högstedt 1983a,b). Yet for any given parent, there must be some upper threshold brood size where this rule of constant brood survival no longer applies (Ricklefs 1983). Third, many recent studies have failed to find tradeoffs between current fecundity and future reproductive success of parents (De Steven 1980, Smith 1981, Nur 1984, Bell 1984a,b) even though this prediction is the foundation of classical models of life history evolution (Williams 1966). If brood size responds mainly to the total investment available as a mechanism to optimize that investment among offspring, the costs of reproduction are standardized across all brood sizes, and there is no tradeoff between current fecundity and future success.

On the other side, the strongest evidence in support of natural selection operating directly on brood size would seem to come from the observation that brood size is fixed in a number of organisms. Many marine birds lay one or two eggs, hummingbirds and most pigeons and doves lay two eggs, most whales and bats produce a single offspring, armadillos produce four and so on. But even these examples can be viewed as selection operating on optimal investment ratios.

In the optimal investment model, selection favours some constant value of investment per offspring (IO), such that

$$IO = TI_x/b_x$$

where b_x is brood size of the parent aged x, and TI_x is the total investment available for reproduction at that age. With IO constant, it follows that brood size will also be constant if

$$TI_x + VAR\ TI_x < IO(b_x + 1)$$

where $VAR\ TI_x$ is a measure of variation in total investment of parents aged x. Similar arguments apply for a reduction in brood size. Brood size is heritable, and under these conditions could become genetically fixed, but again, incidental to its function of optimizing parental investment among offspring.

Brood size is not the only mechanism which can optimize investment ratios. Delays in development or increased duration of parental care can also act to effectively increase investment per offspring produced (Ricklefs 1968, Smith and Fretwell 1974, Brockelman 1975). Such delays are likely to be constrained by the temporal demands of an iteroparous life history. Migration following fledging in birds and post-partum es-

trus in mammals are two examples of severe constraints to prolonged development. Despite its adaptive significance, uncontrolled variation in brood size will mean that some individuals in a population will have under or over corrected their investment per offspring. Behavioural and developmental plasticity would enable these individuals to compensate for the 'error' in optimal brood size.

The search for an evolutionarily optimal brood size in iteroparous species may be the philosopher's stone of evolutionary ecology. The same may be true of the search for reproductive costs in terms of parental survival and fecundity. If offspring fitness is in large part determined by parental investment, then the optimum life history is a tradeoff between the costs and benefits of that investment. The benefit is increased survival of young to reproductive age, the cost is fewer young produced and the risk of doing otherwise is reduced offspring survival with declining investment. Costs in terms of parental survival and future fecundity refer only to the total investment made by the parent. There will no doubt be an optimal age or stage-specific strategy of total parental effort (Schaffer 1974), but this is unlikely to be revealed by simply looking at brood size.

Tests of the optimal investment hypothesis would seem to rely on clever ways of 'tricking' parents into making sub-optimal investments per offspring (Pianka 1976). Brood size manipulations hold promise as long as they carefully control for age and physiological differences between parents, and environmental influences on post-manipulation investment capability. Costs and benefits are estimated solely in terms of offspring recruitment. Parents must be monitored to see if they increase total investment, and thereby maintain more or less constant investment ratios. If so, the experiment is no longer a test of optimal investment (though it is circumstantial support), but rather a test of tradeoffs in total reproductive effort against future parental survival and reproduction (e.g., optimal working capacity of Royama 1966). An alternative would be to hold parental investment constant, but manipulate the investment ratio among offspring. Such experiments could be performed in the laboratory by suitable manipulations of brood size while holding food resources constant, or by biasing in some way, parent-offspring conflict over parental investment (Trivers 1974). By removing the organism from its selective mosaic, such experiments will always be open to counter-interpretation, unless heritabilities for investment traits and brood size are contrasted.

No-one should interpret the optimal investment hypothesis to mean invariant investment ratios. These ratios, like all quantitative traits, will vary, and that variability may be adaptive in certain environmental contexts. What the model does predict is that, within species, variation in investment ratios should be substantially less than variation in brood size. Comparisons among species will document apparent patterns of adap-

tive variation in brood size (Stearns 1980), which in reality reflect differing rewards of investment ratios in alternative environmental contexts (Brockelman 1975, MacArthur and Wilson 1967).

Past studies of life history evolution appear to have over-emphasized reproductive rate and parental survival. To point out the need for considering offspring recruitment, we could modify Lotka's equation by introducing an explicit term for juvenile survival. Such an approach may be of value in understanding patterns of parent-offspring conflict over investment, but would unnecessarily complicate virtually all models of population dynamics. The characteristic equation is valuable because it is a simplified model of population performance. Over-emphasis on brood size and adult survival has made it less suitable as a model for evolution by natural selection.

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