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FRACTIONAL RESOURCE ALLOCATION INTO FEW EGGS: DAPHNIA AS AN EXAMPLE

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Most of our understanding of environmental effects on life history traits is based on models of continuous quantitative traits like age and body size. This approach has problems when discretely varying traits like clutch size or the number of broods in a breeding season are considered. For example, if total investment in a clutch is not some whole number multiple of the optimal egg size, production of either the next highest whole number of smaller than optimal eggs, or the next lowest whole number of larger than optimal eggs, is possible. This effect is particularly strong for small clutches. For a given reproductive investment, changing clutch size from one to two eggs is accompanied by a 50% decrease in investment per egg, while increasing a four-egg clutch by one egg reduces investment per egg only by 20%. Although species with small clutches are found in all groups of organisms, fractional

resource allocation into few eggs has been discussed only for birds and reptiles (Ricklefs 1968, Nussbaum 1981).

The Model

Offspring fitness is described by a positive convex function with zero fitness below a minimum offspring size (Fig. 1; Smith and Fretwell 1974). Under the assumption that a trade-off between offspring size and can be found that maximizes total clutch-fitness (product of offspring number and fitness). This level of investment can be found using the marginal value approach (Appendix: Part 1), here called marginal value solution (MVS). Since for most organisms resources invested into reproduction increase with environmental quality, I use reproductive investment as a measure of environmental quality.

Calculating the MVS implies that non-integer clutch sizes are possible. Since this is unrealistic, an alternative method is needed to find the offspring size and number which maximizes fitness. For any given clutch size, clutch fitness increases asymptotically as more resources are invested into each offspring (Fig. 1). Fig. 1 shows that the clutch size with the highest fitness for a given reproductive investment is the one that maximizes fitness (Appendix: Part 3). Dividing the reproductive investment by this fitness maximizing clutch size results in the corresponding “realizable offspring size” (ROS). Due to the discrete nature of clutch size, the ROS is sometimes larger and sometimes smaller than the MVS for the same amount of reproductive investment (Fig. 2a). The largest size differences can be found for the smallest levels of reproductive investment. From Figs. 1 and 2a it becomes clear that

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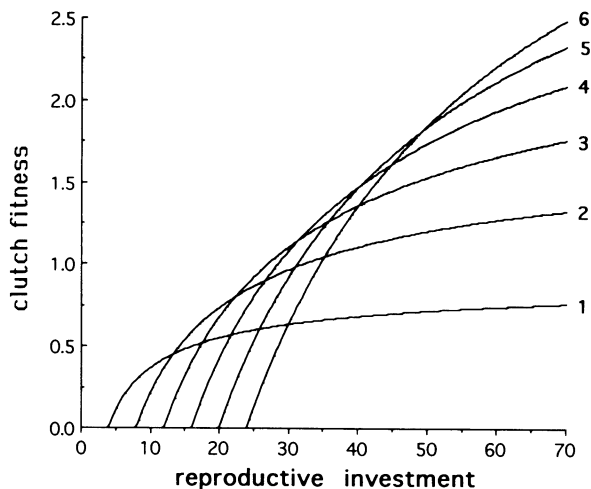


FIG. 1. Relation of clutch-fitness and invested resources for clutch sizes 1 to 6. The fitness curve for clutch size 1 represents the fitness function for offspring size. Clutch-fitness (= offspring fitness times clutch size) was calculated by converting offspring size (= reproductive investment divided by clutch size) into offspring fitness and then multiplying offspring-fitness by clutch size. The clutch size with the highest fitness for a given investment is the one that maximizes fitness. Parameters used: $a = 0.5$, $m = 2$, $K = 2$ (see Appendix: Part 1).

clutch-fitness increases with any small increase in reproductive investment. This is true independent of the difference between the ROS and MVS. Thus a small increase in reproductive investment increases clutch-fitness regardless of whether the difference between ROS and MVS becomes larger or smaller. It is often assumed that offspring under poor conditions should be larger than under good conditions (e.g., Hutchinson 1951, Green 1966). For this case the MVS and ROS can be calculated as before (Fig. 2b; Appendix: Part 2).

Since the production of few offspring of unusually large size (Fig. 2a and b) seems impractical, I analyze the effects of an additional assumption: an upper limit to offspring size. There could be different reasons for such a size limitation, for example a constraint (physiological constraint or space limitations) or a cost-benefit argument (e.g., the cost of producing and carrying ovaries that are able to produce unusually large eggs might be higher than the costs of sometimes producing eggs of sub-optimal sizes). In Fig. 2c and d the maximum size was set at 9.5 units. Thus, when the offspring size that maximizes clutch fitness is > 9.5 units, clutch size should be increased by one egg to reduce the mean offspring size. In particular, for small clutches (clutch sizes 1–3) this often leads to ROS's which are considerably smaller than the MVS (Fig. 2c and d) and by this might pull the mean offspring size far below the MVS.

Predictions. The model makes three predictions, which can be tested empirically. Suppose we measured offspring and clutch size under poor, medium, and rich food conditions and found clutch sizes of 1–3, 4–7, and 15–20 eggs, respectively. The model predicts larger offspring size variation among smaller clutches than among larger clutches. The variance of offspring size among clutches can be calculated for each clutch size and then tested against clutch size or reproductive investment across all food levels. In our dataset, clutches from the poor food environment should have the largest offspring size variance. Second, if an upper offspring size limit exists, the model predicts that offspring from poor conditions will often be smaller than those from the next larger clutch (Fig. 2d). Thus, we would expect the largest eggs under intermediate conditions (4–7 egg clutches) and smaller eggs under poor (1–3 eggs) and rich conditions (15–20 eggs), i.e., a hump- or dome-shaped reaction norm for offspring size. It is important to note that the model predicts that offspring will frequently, but not always, be smaller in small than intermediate clutches.

Third, for clutch sizes in which the upper offspring size is limited, the offspring size distributions should be skewed to smaller sizes. Thus, in our example the offspring size distribution in poor food conditions would be expected to be skewed to smaller sizes, i.e., sizes beyond the size limit would be cut off. If the offspring size limit is correlated with maternal size (e.g., Congdon and Gibbons 1987), it is necessary to correct for this before testing for skewness. If the first two predictions are fulfilled, the third prediction must also be fulfilled to distinguish between a hump-shaped reaction norm due to a size limit or due to an adaptation. In the latter case, one would not expect a skewed size distribution.

Daphnia as an Example

Recently the problem of optimal offspring size in the planktonic crustacean *Daphnia* and related cladocerans has received considerable attention (e.g., Perrin 1989, Tessier and Consolatti 1991, Glazier 1992, Gliwicz and Guisande 1992, and others). Here I use their results to justify assumptions and test predictions of the model.

The convex egg/offspring size fitness function. — Bell (1983) found that hatching probability increases asymptotically with egg volume and that eggs below a minimum size do not hatch at all. Threlkeld (1976) gave evidence that resistance to starvation increases asymptotically with offspring size. These results further suggest that smaller offspring under rich food conditions are adaptive for *Daphnia* (Gliwicz and Guisande 1992).

The offspring size-number trade-off. — Negative cor-

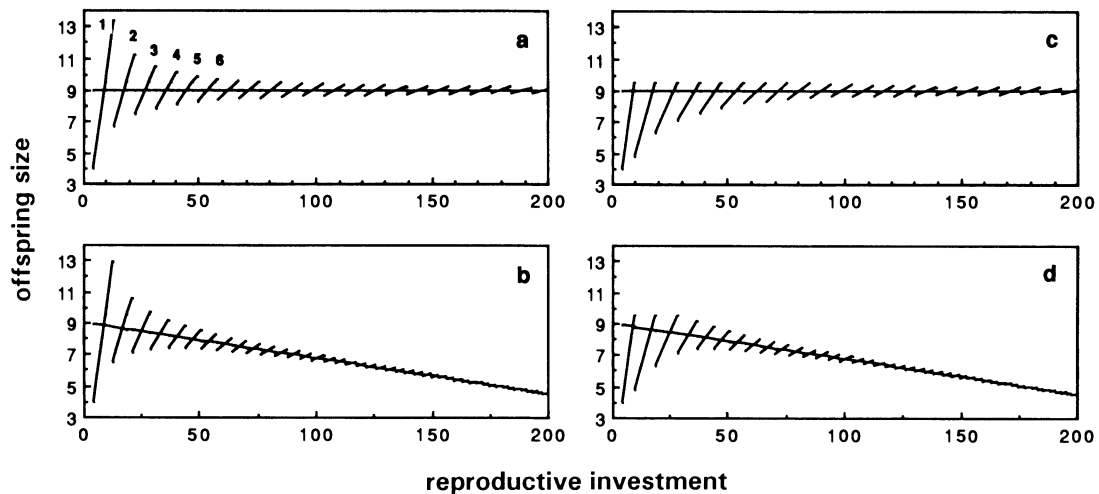


FIG. 2. For any level of investment the relative offspring size (ROS) and clutch size that maximize clutch-fitness are shown as short, positively sloped lines. Non-integer clutch sizes were not allowed. Each short, positively sloped line represents one clutch size, with clutch size increasing from left to right (see numbers for clutch sizes 1 to 6 in graph a). The long lines in each graph show the marginal value solution (MVS, see Appendix) for optimal offspring size. In parts c and d an upper offspring size limit of 9.5 size units is assumed. Parameters: $a = 0.5$, $m = 2$, $K = 2$ (parts a, c) or $K = 2 - 0.005 \cdot R$ (parts b, d).

relations between offspring size and number were often found under intermediate and poor conditions, but seldom under rich conditions (see Ebert 1993 for a review). Because the fractional resource allocation model is particularly relevant under poor conditions, the assumption of an offspring size–number trade-off in *Daphnia* seems justified.

Upper limit for egg size.—This assumption seems most plausible as a result of a morphological or physiological constraint. For example, for freshwater turtles it was shown that the pelvic girdle can constrain egg size (Congdon and Gibbons 1987). For cladocerans such a constraint has been discussed but not described (Perrin 1989, Glazier 1992).

Offspring size and number: testing the predictions.—The model predicts that when larger eggs in poor conditions are adaptive (Gliwicz and Guisande 1992), and when egg size has an upper limit, eggs of intermediate clutches (intermediate conditions) will be on average larger than eggs from large (rich conditions) and from small (poor conditions) clutches (Fig. 2d). The largest eggs were found in intermediate conditions several times in *Daphnia* (e.g., Urabe 1988, Tessier and Consolatti 1991, Lynch 1992). Where clutch sizes were given, the small, low-food eggs/offspring came indeed from very small clutches (1.55 eggs/clutch, Urabe 1988; 1.4–3.18, Tessier and Consolatti 1991). Tessier and Consolatti's detailed data show that egg sizes under poor conditions were usually, but not always, smaller than those from intermediate conditions. This fully agrees with the model.

Studies that compared egg sizes in only two food treatments further support a hump-shaped reaction norm for egg size in *Daphnia*. When clutches were very small in the low food treatment (<2.88 eggs/clutch, Brambilla 1980), average egg size was smaller in the low food treatment than in the high food treatment. Under less severe low food treatments, with slightly larger clutch sizes, average egg size in the low food treatment was greater than in the high food treatment (Glazier 1992, Ebert 1993). In summary, the largest eggs per offspring in *Daphnia* are often found when clutch size is ≈ 4 –7 eggs, while smaller as well as larger clutches have smaller propagules. The scenario of Fig. 2d agrees with these results. I could not find any data to test the model's predictions on enlarged variation and skewed distributions of offspring size.

An alternative model to explain the finding of smaller eggs under poorest conditions was proposed by Tessier and Consolatti (1991). They speculate that offspring of higher quality (more nitrogen) born in poor conditions allow a reduction of the minimum offspring size and thus of the optimal size. Existing data rather suggest that under starvation conditions relative nitrogen (protein) increases because lipids decrease (Lemcke and Lampert 1975). Since lipid content is positively correlated with the survival ability of newborn in poor conditions (Tessier et al. 1983), high nitrogen content seems to indicate lower, rather than higher, newborn quality.

The "fractional resource allocation egg size model" is meant to provide a framework for problems related

to small clutches. The model can be tested easily and might help to distinguish and to clarify problems related to the evolution of egg size.

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APPENDIX

Part 1. Calculation of the optimal offspring size. Assume offspring fitness (F) is a function of offspring size, s : $F(s) = 1 - (Km/s)^a$, when $s > Km$ and $F(s) = 0$ otherwise, where m is the minimum viable offspring size and a is a constant determining the rate of approach of F to its asymptote. K is a constant (> 1) that is positively related to the optimal offspring size. Fitness is maximized when the slope of fitness gain per resource unit is highest (Smith and Fretwell 1974). When non-integer clutch sizes are allowed the optimal offspring size, s^* is:

$$s^* = Km(1 + a)^{1/a} \tag{1}$$

Part 2. Optimal offspring size decreases with increasing investment. Some function is needed to represent the decrease in K with the resources invested, R . I used the following

function: $K = 2 - R \cdot 0.005$ ($0 < R < 200$). When this expression is substituted for K in Eq. 1, the optimal size for each investment is:

$$s^* = (2 - R \cdot 0.005) \cdot m \cdot (1 + a)^{1/a}$$

Part 3. Discrete clutch size. Reproductive investment can be divided into a discrete number of offspring c , of size s ($s = R/c$). The clutch-fitness P (= parental fitness) of clutch size c is given as $P_c = c \cdot F(s)$. The clutch size that maximizes fitness is given by:

$$P_{(c-1)} < P_c > P_{(c+1)}$$

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