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ON CLUTCH-SIZE AND FITNESS

Lack (1954) proposed that in nidicolous birds the survival rate of young is lower in larger broods, resulting in a clutch-size (b_0) that maximizes the number of young surviving to breed ('the most productive clutch'), and that selection should favour this clutch-size. Lack's hypothesis made no prediction about variations around the most productive clutch. Many workers have attempted to test the hypothesis (reviewed by Klomp 1970, Hussell 1972), and several studies have shown that the commonest clutch is in fact smaller than the most productive (e.g., Ward 1973). Mountford (1968) has proposed one possible explanation for these observations by developing a genetic model based on a particular pattern of inheritance.

Williams (1966) and Klomp (1970), among others, have pointed out that the number of young surviving to breed is an incomplete measure of fitness. Since many birds reproduce several times, adult survival must also be considered. We propose to introduce the concept of 'optimal clutch-size', defined as that which maximizes an individual's fitness.

In any annually reproducing species with a stable age distribution, if $N_{(T)}$ is the number of organisms alive in year T, counted just before reproduction but after the year's mortality, the rate of population growth (λ) is given by:

$$N_{(T+1)} = \lambda \, . \, N_{(T)}$$

For a perennial species reproducing for the first time at age one:

$$N_{(T+1)} = P \, . \, N_{(T)} + b \, . \, S \, . \, N_{(T)}$$
$$= (P + b \, . \, S) \, . \, N_{(T)}, \text{ or } \lambda = P + b \, . \, S$$

Where:

b = clutch-size

S = survival rate for the clutch for the first year

P = yearly adult survival rate.

Let:

$$a = \lambda - 1, \text{ then } a = b \,.\, S\text{-}q, \text{ where } q = 1 - P.$$

λ is the exponential form of Malthusian Fitness (Fisher 1958) which for our purposes may be taken to be a rate of increase for a phenotype (specified by b, S and P). Maximizing a is an equivalent to maximizing λ.

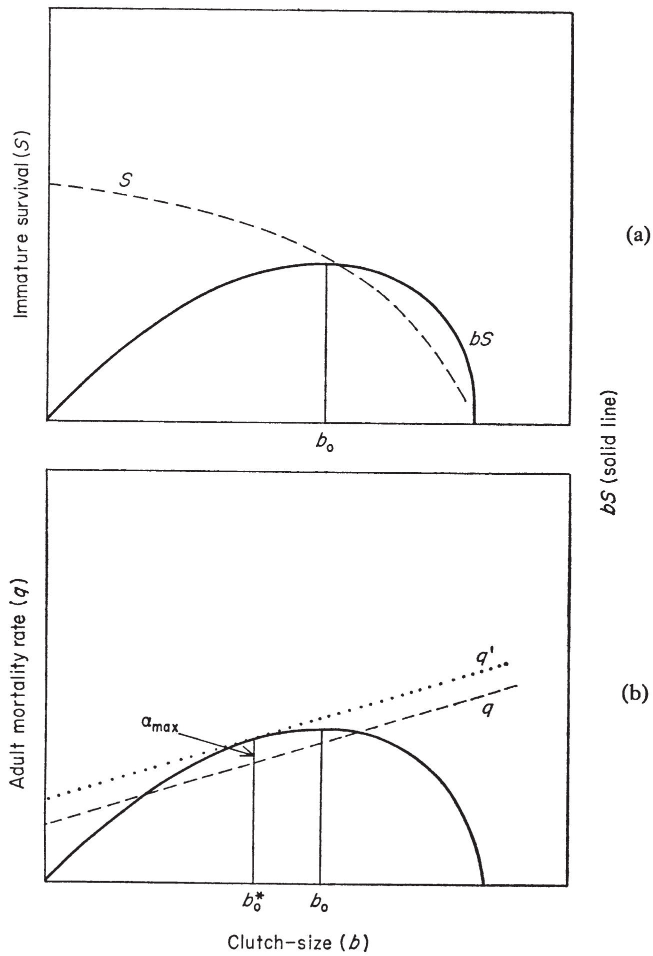

FIGURE 1. (a) The relationship between clutch-size (b) and survival rate for the first year of life (S) (broken line). The resulting b. S or production curve (solid line) has a single maximum at b_0. Under Lack's hypothesis this is the clutch favoured by natural selection. (b) If adult mortality (q) (dashed line) increases with b, the clutch (b_0^*) that maximizes the measure of fitness (a) is always smaller than b_0. The optimal clutch is found by constructing the line parallel to q(q'—dotted line) which just intersects the b. S curve (solid line). In general, clutches smaller than b_0 will have a higher fitness than those larger.

Figure 1a (broken line) shows the survival rate of young as a function of clutch-size, the shape of the curve being an approximation to that observed in nature (Klomp 1970). The mode of the resulting curve of productivity (b . S) is skewed to the right (solid line). Figure 1b shows the results arising if adult mortality (q) is an increasing function of clutch-size. The optimal clutch is found by drawing a line parallel to q which just intersects the productivity curve. The point of intersection gives the optimal clutch. As long as the increase in q begins to the left of the most productive clutch-size, the model predicts that the optimal clutch (b_0^*) will be less than the most productive clutch (b_0). The second prediction of the model is that deviations from the optimal clutch should be smaller than the most productive. This can be seen from figure 1b: a is in general larger for non-optimal clutches that are smaller than b_0 than for those greater than b_0. If the productivity curve is skewed to the right, this result will hold even if q is assumed constant (see also Mountford 1968).

The assumption of the model, that q increases with clutch-size, has not been demonstrated directly, although indirect evidence suggests that it is correct. Several studies have shown that parents raising larger broods 'work harder' (Klomp 1970, Cody 1971) and may loose weight during the breeding season (Hussell 1972). Perrins (1965) found a relationship between b and q in one year but not in another. The possibility that b and q are related is certainly not a new suggestion, and it or similar assumptions form the basis for much of the recent life history theory (Williams 1966, Schaffer in press). Lack (1966) discussed the idea, but did not stress its consequences.

Our model, then, does not present any totally new concepts, but it does emphasize that egg-addition experiments showing the commonest clutch to be smaller than the most productive do not necessarily show that the individual is not maximizing fitness. Perrins & Moss (in prep.), have shown that in the Great Tit *Parus major* the commonest clutch is smaller than the most productive in many years. They discussed a variety of possible explanations for their results, including the one we present here. It would seem likely that the effect of adult survival on fitness would be less important in a short-lived bird such as the Great Tit than in long-lived species such as gulls (Ward 1973).

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