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Source: Ardea, 55(1–2) : 155-168

Published By: Netherlands Ornithologists' Union

URL: https://doi.org/10.5253/arde.v76.p155

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THE COST OF REPRODUCTION IN BIRDS: AN EXAMINATION OF THE EVIDENCE

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Received 18 June 1987, revised 17 September 1987

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1. INTRODUCTION

'Is the cost of reproduction important in understanding the evolution of avian reproductive strategies?' At first, this question had the attention of theorists, especially in the early-mid 1970's, when the theory of life history strategies (LHS) developed (*e.g.* Pianka & Parker 1975, Stearns 1976). In fact, the central assumption of LHS theory is that the cost of reproduction is an important force of the moulding of life histories, through the action of natural selection. More recently, the cost of reproduction has been studied in the field. Here the record has been mixed: often, results have been inconclusive. On this basis, a number of recent studies and reviews have suggested that the cost of reproduction might play only a minor role in the evolution of avian reproductive strategies (De Steven 1980, Smith 1981, Bell 1984, Horn & Rubenstein 1984, Alerstam & Högstedt 1984).

Because the cost of reproduction plays such a prominent role in theories of LHS, I examine the empirical record, to determine whether the importance of the cost of reproduction is affirmed or whether, as some have suggested, the notion should be relegated to the background, out of the spotlight it has enjoyed for the past several decades. By 'cost of reproduction' I refer here to a cost with regard to Darwinian fitness, which might be expressed as a reduction in survival or future fecundity (*i.e.* breeding success at the next breeding opportunity). I restrict attention to clutch size or brood size leaving aside other considerations such as whether an animal breeds at all, how many broods it has, or how much is invested in each young. I restrict myself to clutch and/or brood size mainly because it is with respect to this aspect of reproduction that the greatest amount of data and controversy has accumulated (for a more wide-ranging review, see Reznick 1985).

An important point to keep in mind is that though it may be difficult to demonstrate the statistical significance of small differences in survival probabilities, such differences may nevertheless be evolutionarily significant. If one class of individuals, say one genotype, survives 10% better than another class (*e.g.* with probability = 0.44 rather than 0.40), sample sizes of 1000 individuals for each class (genotype) would be insufficient to establish that the difference was significant at the 0.05 level. Yet survival differences of this magnitude can influence the evolution of brood size. To demonstrate this point I make use of a hypothetical example (Fig. 1), based on reasonable values for tit (*Parus*) species. With no effect of brood size on parental survival or subsequent fecundity, natural selection should favour the brood size that maximizes the number of young surviving to breed, symbolized b_p; in the example (Fig. 1) $b_p = 11$. However, if parental mortality increases with increasing brood size, b_p will not generally be the optimal brood size, as demonstrated by Charnov & Krebs (1974). With adult mortality as shown in Fig. 1, the optimal brood size (according to the Charnov-Krebs model) is 9, not 11. That is, small differences in adult survival probabilities (here 40% *vs.* 44%), which often will not attain statistical significance in field studies, can have a large effect on the evolution of brood size.

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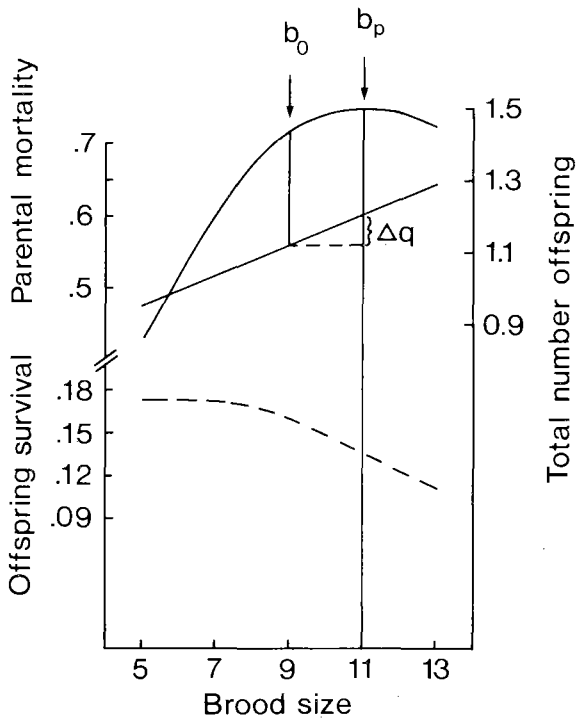

Fig. 1. Charnov & Krebs' (1974) model of optimal brood size. Non-linear solid curve, number of offspring surviving to breed (m) as a function of brood size (see right-hand y-axis); m equals brood size x per-offspring survival rate (shown as dotted line; lower left-hand y-axis). Linear solid curve, parental mortality (q). If adult survival is independent of brood size, then natural selection favours the brood size maximizing m, b_p. However, if adult survival varies with brood size then natural selection favours brood size which maximizes $\lambda = \frac{1}{2}m + (1-q)$, shown as b_o. The difference in adult survival (Δq) is enough to shift the optimum from 11 to 9.

2. REVIEW OF FIELD STUDIES: EXPERIMENTAL MANIPULATIONS

Investigators have sought to draw inferences regarding the cost of reproduction from two types of studies: (1) those that have compared adult survival rates in relation to natural variation in brood size and (2) those that have manipulated brood size and then compared observed survival rates. The difficulty with the first method is that adults rearing broods of different size tend to differ in other respects besides brood size. For example, clutch size (and brood size) tends to vary with age of the parent, time of breeding, habitat, territory quality (Perrins 1979, Högstedt 1980), etc.; these factors might themselves influence observed survival rates. The solution of the problem is to manipulate brood size. I review here six experimental studies (all the published ones I am aware of) before considering non-manipulative studies.

In the first, Askenmo (1979) enlarged brood sizes of Pied Flycatchers *Ficedula hypoleuca* breeding in Sweden to 9 young in 5 years and compared return rates with parents rearing unmanipulated broods (brood size from 3 to 7, mostly 5 and 6). Males rearing broods of 9 were recaptured significantly less often than those rearing unmanipulated broods. As for females, their return rate was too low to allow good estimates of survival.

Högstedt (1981) argued that the low return rate of males rearing enlarged broods may reflect the fact that these broods were not very successful, fewer young actually fledged from them than from normal broods. Low reproductive success may have caused the experimental males to disperse farther between years (Harvey *et al.* 1979), and this may account for their low rate of return.

The second study was carried out by De Steven (1980) on Tree Swallows *Tachycineta bicolor* in Canada. In one year some broods were enlarged by two nestlings (resulting in broods of 7–9 young). De Steven compared the recapture rate of females rearing enlarged broods with those rearing unmanipulated broods (5–7 young). 58% of unmanipulated females were recaptured compared with 67% of the 'experimental' females. The difference is not significant and is actually in the direction opposite that predicted by a cost of reproduction hypothesis.

Are these results fatal to the notion of a cost of reproduction in Tree Swallows? Perhaps, but the results also point out several ways in which the experimental design could be improved: (1) The mean difference in brood size between the two groups was small, just two nestlings. In fact, females rearing broods of seven were to be found in both the experimental and control group, making it difficult to detect a difference between the two groups if there was one. (2) The sample size was relatively small (a total of 40 females for the two groups). (3) The manipulation was carried out in only one year. As De Steven points out, that year seemed unusual (*e.g.* offspring survival was unusually high). Finally one piece of evidence supports the idea of a cost of reproduction in this population: females rearing reduced broods (3–5 young) survived better (78%) than those rearing unmanipulated broods (58%). The difference approaches statistical significance at the 0.05 level (Fisher exact probability test, one-tailed).

The third study is one I carried out on Blue Tits *Parus caeruleus* in Wytham Wood, England (Nur 1984a, 1988). Pairs were randomly assigned broods of 3, 6, 9, 12 and 15 nestlings. Fig. 2 shows recapture rates (an index of survival) for females (data pooled over 3 years, 1978–1980). No relationship was evident between brood size and male recapture rate. For females, the relationship of brood size and survival differed significantly (analysis of covariance, $p < 0.05$) from year to year: In both 1978 and 1980 female survival declined significantly ($p < 0.05$) with increasing brood size, but in 1979 survival was independent of brood size. In the pooled results survival dropped significantly, and in a linear fashion, with increasing brood size. The apparent effect of brood size is substantial; females rearing broods of 3 survived more than twice as well as those rearing 15.

The criticism Högstedt (1981) made regarding Askenmo's (1979) finding (see above) is not applicable here: (a) the largest Blue Tit broods were the most successful and (b) dispersal of

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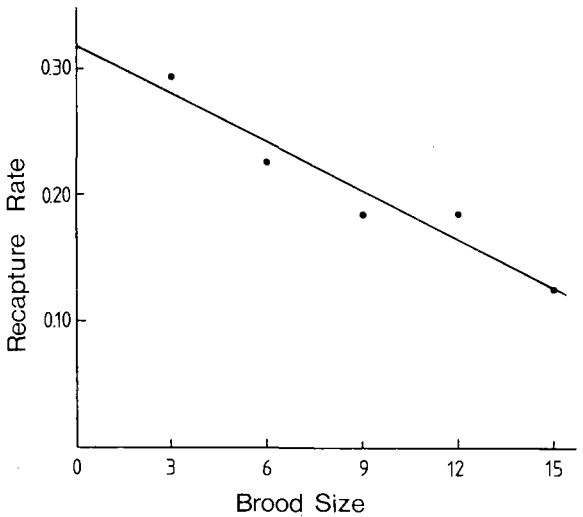

Fig. 2. Female survival (as inferred from recapture) in relation to experimental brood size in the Blue Tit (data from 1978–1980, combined) (from Nur 1987a). The relationship is significant ($p < 0.01$, linear regression analysis) and does not deviate significantly from linearity.

even moderate distances (⩾ 300 m) was apparently rare among females (Nur 1988).

In the fourth study, Boyce & Perrins (1987) manipulated Great Tit *P. major* brood size, also in Wytham Wood, England. Over the course of 12 years, 527 broods were manipulated, either enlarged or reduced (by 3 or 4 nestlings). The results are not clear-cut: whereas survival of females whose broods were enlarged by 4 (+4 treatment) was significantly lower than the −4 treatment (0.40 *vs.* 0.63), females in the +3 treatment actually survived slightly (but not significantly) better than the −3 treatment (0.45 *vs.* 0.42). Only the former result supports the cost of reproduction hypothesis. Furthermore, females in the −4 treatment survived better than those in the −3 treatment ($p < 0.02$) and females whose broods were enlarged by 3 survived better than those whose broods were enlarged by 4 (NS); both results are consistent with the cost of reproduction hypothesis. These results lend themselves to two contrasting interpretations: (1) survival of females in the −3 treatment is anomalous, in other ways the data show evidence of a cost of reproduction; or (2) survival of females in the −4 treatment is anomalous, in other ways the data do not demonstrate a cost of reproduction. The fact that of the six possible comparisons amongst the four experimental treatments, five are in the direction predicted by a cost of reproduction hypothesis and that three of the differences are significant, supports interpretation (1). A firm conclusion awaits further analysis of the data. No significant differences were observed with respect to male survival and brood size treatment.

The cost of reproduction may be manifest as a reduction in future reproductive success of the adults as well as a reduction in survival prospects. Slagsvold (1984) manipulated brood size among Norwegian Great Tits; on day 15, the nest and brood were removed from all pairs. Pairs which had reared enlarged broods (10–11 young) took slightly but significantly longer to lay a replacement clutch than pairs which had reared diminished broods (3–4 young). Moreover, fledging success of the replacement brood was significantly greater for parents which had initially reared a small brood. In other words, Great Tits rearing larger broods suffered a cost in that, had their nests been taken by a predator, they would have been less successful at replacing the initial brood than would tits which initially reared smaller broods.

For birds which do not have a second brood (even if the first one perishes) we might ask whether the effect of rearing a large brood in one year influences breeding success the next year. To investigate this question, Røskaft (1985) performed a study on a Norwegian population of Rooks *Corvus frugilegus*: some pairs were manipulated (brood size was enlarged), others were not (control pairs). In the following year, he compared the reproductive success of the two groups, which had otherwise been matched as closely as possible: control pairs fledged significantly more young than pairs which had reared enlarged broods the year before. This effect was due principally to a difference in hatching success between the two groups.

The Blue Tit study cited above (Nur 1988) also revealed an effect of brood size on future reproductive success of adults: the number of offspring produced that survived at least 3 months after fledging was inversely proportional to the experimental brood size the year before ($p < 0.05$). This effect was expressed in both males and females and in each year of the study (Nur 1988). For adults which had reared large broods, future fecundity was reduced, not because clutches or broods were smaller in the year following the manipulation but because the offspring survival rate was lower. In other words rearing a large brood had consequences for adults not expressed until more than a year later!

To summarize the results from experimental studies, the evidence for a cost of reproduction seems good. This is not to say that each species necessarily manifests all possible costs of reproduction. Rooks might demonstrate a future fecundity cost but not a survival cost (Røskaft 1985); other species may show an effect of brood size on subsequent survival but not future reproductive success. Nor is it necessarily the case that the cost of reproduction is manifest in every year. For example in one out of three years, Blue Tit females did not demonstrate an effect of brood size on their subsequent survival. Large degree of year-to-year variability in the manifestation of an effect does not make the cost of reproduction less important evolutionarily but it makes it more difficult to demonstrate in the ecological world. Such variability should make us wary of studies which attempt to draw conclusions from the data of just one year. Even a threeyear study (*cf.* Nur 1988) is of uncomfortably short duration (Nur 1986).

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3. PHENOTYPIC ADJUSTMENT OF CLUTCH SIZE: A MODEL

What of non-manipulative field studies, studies correlating subsequent survival with size of the clutch or brood naturally reared? Because clutch size varies with many factors, and in general in such a way that females tend to rear the largest clutches under the best conditions, we might elect to ignore any non-manipulative study which purports to cast light on the nature of the cost of reproduction (Reznick *et al.* 1986). I have chosen not to follow this course because many workers have tried to draw inferences regarding the cost of reproduction from correlative studies and therefore it is worthwhile to examine more carefully what can (and cannot) be inferred from such a study (see also Van Noordwijk & De Jong 1986).

To analyze data from non-experimental studies requires that we tackle the problem of the phenotypic adjustment of clutch size, what has been referred to as phenotypic plasticity (Nur & Hasson 1984). My approach has been to develop a model which explores two questions: (1) If females can adjust their clutch to suit their own condition or the environmental conditions, how should they adjust clutch size, and (2) what effect will the resulting correlation of clutch size and condition have on actual, observed survival rates for females rearing different-sized broods?

The first step in building the model is to consider optimal brood size and how that should differ with the condition a female finds herself in. To determine optimal brood size requires a criterion of fitness: here I use lifetime reproductive success, *i.e.* the expected number of offspring (which survive to reproduce) that an individual produces in its lifetime. For populations that are neither growing nor shrinking in size, lifetime reproductive success is generally considered a suitable measure of fitness (Schaffer 1983). Most avian populations (especially those of hole-nesters) are considered to be rather stable.

Lifetime reproductive success can be expressed as the product of two components: breeding longevity ('longevity' for short, S, the number of seasons a given animal breeds) and effective fecundity ('fecundity' for short, F, the number of offspring produced per breeding season which survive to a given age, *e.g.* breeding age). Where an animal breeds more than once, F must be weighted by the proportion of individuals which reach their second, third, etc. breeding season. Because differences in longevity necessarily imply differences in survival probability, I will sometimes use the term longevity and survival interchangeably.

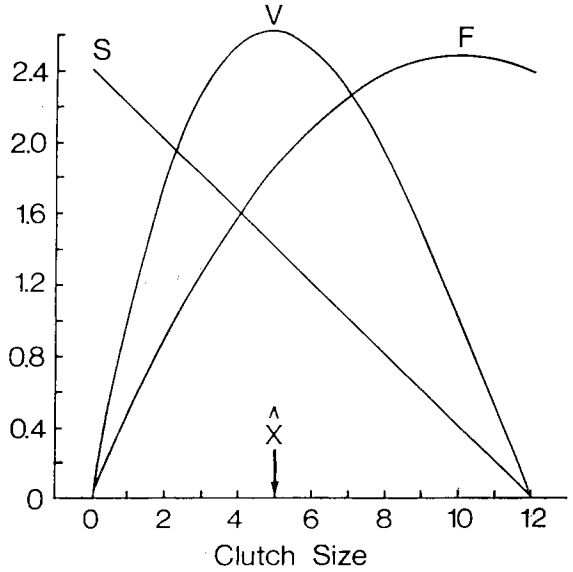

Fig. 3. Model of optimal clutch size. Fitness (V) equals the product of longevity (S, number of breeding seasons) and fecundity (F, expected number of offspring surviving from a given breeding season). The optimal clutch size ($\hat{x}$) maximizes V.

The crux of the model is that with increasing clutch size fecundity increases but survival (hence, longevity) decreases. In Fig. 3 I show a generally accepted shape (*e.g.* Perrins & Moss 1975) for the fecundity function: with increasing clutch size, the number of surviving offspring increases but the relationship shows diminishing returns. With a large enough clutch, the number of surviving offspring actually begins to decrease. (For simplicity I assume only one clutch per breeding season.) The survival function in Fig. 3 shows a linear decrease in longevity with an increase in clutch size. $S = 1$ refers to an individual which survives that breeding season but does not survive to the next breeding season; $S < 1$ implies that a proportion of individuals do not even survive the current breeding season. There is little published evidence as to the shape of the survival function, so the function shown in Fig. 3 is necessarily speculative. Note that, as demonstrated below, the shape of F

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and S is not critical to the conclusions of the model; many functions of different shape (linear, convex, concave) yield similar qualitative results. For example, the same qualitative results emerge if survival (not longevity) declines in a linear fashion with increasing clutch size.

The product of longevity (S) and fecundity (F) is lifetime reproductive success (symbolized V). The clutch size (X) which maximizes V is the optimal clutch size ($\hat{X}$).

We are now ready to consider the impact of individual differences (Fig. 4). Individual differences may be traced to differences in environment (*e.g.* characteristics of the habitat or territory) or the internal state of the individual. Differences in the latter may reflect genetic or environmental factors (*e.g.* different nutritional histories). Even environmental differences may have a genetic basis if genotypes assort themselves differently across environments. The model is concerned with either exogenous or endogenous differences; these may have a genetic basis if some individuals are in better condition (or in a better environment) than others as a result of their genotypic constitution. For the sake of simplicity, however, the model does not incorporate a direct effect of genotype of clutch size, but allows an indirect effect through the action of genotype on condition. What is important for the model is that individuals differ in a way which affects their own survival probability. I shall use the word condition to represent any relevant difference. For simplicity, I consider three conditions, i = 0,1,2, where i = 0 is the worst condition and i = 2 the best. A crucial aspect of the model is that for females rearing the same size clutch, the best condition females survive best. In Fig. 4 the longevity functions for the three conditions are shown as parallel curves (the difference in longevity is constant with clutch size), but this is not essential. For now, I assume that fecundity depends on clutch size, but is not related to condition of the female. Relaxation of this assumption is discussed below.

First, we can ask how optimal clutch size varies with condition. The result is that optimal clutch size increases with improved condition (Fig. 4). This prediction seems to be well-supported by the available data (*e.g.* Perrins 1979).

Secondly, we can ask what the actual longevities will be for females of each condition-class, if each

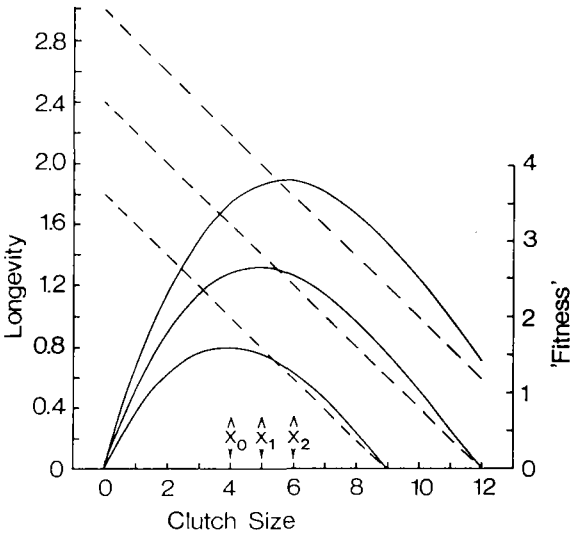

Fig. 4. Model of optimal adjustment of clutch size in relation to condition. Longevity (dashed lines) is assumed to depend on condition. Three classes of condition (i = 0, 1, 2) are shown. Fecundity is as in Fig. 3 and is not dependent on condition. The product of S and F = V ('Fitness') is shown for each condition class (solid curves). $\hat{x}_2$, $\hat{x}_1$ and $\hat{x}_0$ are optimal clutch sizes for the respective condition classes.

is producing an optimal size clutch. The result of the model is that (at the optimal clutch size) females in the best condition survive best (greatest longevity, hence highest survival rate). This is the case even though such females are producing the largest clutches, which in itself tends to depress their survival compared to what it would have been with a smaller clutch. In other words, females in the best condition are predicted to invest in large clutches, but not so large that their survival is depressed below that of females in poorer condition.

These results, that optimal clutch size and longevity at the optimal clutch size should be greatest for females in the best condition, appear to be generally applicable: Fig. 5 demonstrates that different combinations of linear, convex and concave fecundity functions and linear, convex or concave longevity functions yield the same qualitative results. The final prediction is that if females adaptively adjust clutch size according to condition then clutch size and adult female survival should be positively correlated. The correlation arises because females in the best condition have the largest clutches and yet (according to the model) survive best. In other words, the model predicts that if

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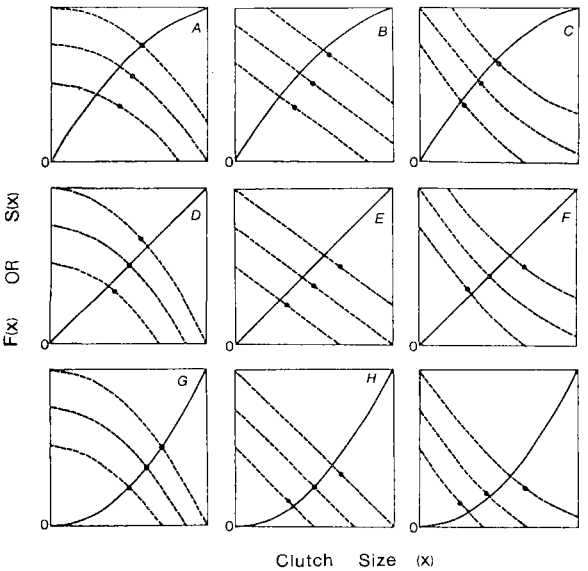

Fig. 5. Demonstration of different shapes and combinations of S- and F-curves, yield increasing optimal clutch size and increasing longevity at optimal clutch size with improvement in condition. S-curves (dashed lines) for each condition class (i = 0, 1, 2) are depicted as either linear (B, E, H), convex (A, D, G) or concave (C, F, I). F is shown as a linear (D, E, F), convex (A, B, C) or concave (G, H, I) function. Concave and convex curves are shown as parabolas (*i.e.*, quadratic functions) but this is not essential. For each condition and each combination of F- and S-functions, $\hat{x}_i$ and longevity at $\hat{x}_i = S(\hat{x}_i, i)$ are graphed as the points (x_i, y_i) where $x_i = \hat{x}_i$ and $y_i = S(\hat{x}_i, i)$. Note that for all 9 combinations $\hat{x}_2 > \hat{x}_1 > \hat{x}_0$ and $y_2 > y_1 > y_0$.

females adjust clutch size in an optimal fashion, the result of such adjustment will mask the deleterious effect of clutch size on female survival. Conversely, if females do not adjust clutch size according to condition (clutch size is independent of condition), then the cost of reproduction will not be masked, and a negative correlation between brood size and female survival will result.

The above predictions of the model rely on two important assumptions: first, an adult's condition affects its survival (hence S), not the survival of its offspring (a component of F). Suppose we assume, instead, that condition affects offspring survival rate but not adult survival, *i.e.* with better condition, offspring survives better. The model still predicts that clutch size should increase with increase in condition (an intuitively reasonable result), but now, because adult survival is independent of condition, adults in the best condition will not survive best, rather they will survive worst (because they are rearing the largest clutches). A negative correlation between clutch size and adult survival arises because the cost of reproduction is not being masked. Howevere, it seems most reasonable (and realistic) that condition would affect both offspring and adult survival rates. The outcome in these circumstances depends on the strength of the effects of condition on offspring and on adult survival. In general, the original predictions of the model are upheld, except where the effect of condition on adult survival is much weaker than the effect of condition on offspring survival (see Appendix). For example, even if offspring survival is 80% greater for broods reared under good rather than poor conditions, adult survival differences of 6% (between good and poor condition individuals) can be enough to bring about a positive correlation between clutch size and adult survival at optimal clutch size.

The second assumption is that females are able to optimize clutch size to suit their condtion(s). While evidence that birds may adjust their clutch size in an adaptive direction has been accumulating (Perrins & Moss 1975, Högstedt 1980, Nur 1986, 1987b) we do not yet know how commonly or with what accuracy such adjustments occur. If optimization were complete, then according to the model, a positive correlation between survival and clutch (brood) size should result. Therefore we can regard the observation of a positive correlation as evidence that adaptive adjustment of clutch size is occurring (especially if other, corroborative evidence were adduced) and that adjustment is related to adult survival probabilities. A positive correlation between survival and clutch size does not tell us whether or not there is a cost of reproduction. Only experimental manipulations could provide that information. Nevertheless, if we observe among unmanipulated clutches a negative correlation, this provides evidence for a cost of reproduction. Such an inference is valid on the grounds that the adaptive adjustment of clutch size can turn a negative correlation between clutch size and female survival into a positive correlation, as demonstrated by the model, but cannot turn a positive correlation into a negative one.

A negative correlation between clutch size and adult survival might mean that adjustments in clutch size are relatively weak (optimization is less than complete) or that condition affects offspring

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survival but not adult survival and females adjust clutch size accordingly. If the latter is the case then we expect clutch size to increase with improved condition(s); if the former, then there is no reason to expect such a relationship.

We should keep in mind that differences in clutch size may reflect constraint rather than individual adaptation: individuals in poor condition may simply be unable to produce a large clutch. For example, the same factors which may lower an individual's survival chances may prevent it from laying a large clutch (such factors may be genetic). Under such circumstances a positive correlation between clutch size and survival may arise. We can test the constraint hypothesis by determining whether individuals can lay more eggs than they usually do (*e.g.* by removing all or part of a clutch). Table 1 summarizes possible observations and the inferences that can be drawn from them.

4. NON-EXPERIMENTAL STUDIES: THE EVIDENCE

I turn now to the empirical evidence. Rather than review every published study regarding clutch size and survival I focus instead on four studies, the principal criterion for selection being whether the published results have previously been cited as evidence for or against the manifestation of a cost of reproduction.

The first study is that of Smith (1981) on Song Sparrows *Melospiza melodia* breeding on Mandarte Island, Canada. In this population females often raised two, sometimes three, broods per year. Since brood size and brood number are negatively correlated (Smith & Roff 1980), it is best to compare total egg or nestling production for the breeding season with annual survival. Females which survived from one year to the next produced more eggs per season (8.52 *vs.* 7.62) and more nestlings surviving to the following week (5.62 *vs.* 4.69) than females not surviving to the following year. These differences were significant ($p < 0.05$, two tailed t-test) for nestling production but not for egg production. These data represent results from several years which were lumped together.

What is particularly interesting is that females which laid 7–9 eggs survived best of all; for those laying 10–12 eggs there was a slight drop in survival and for those laying 12 eggs, a considerable drop in survival. As egg number decreased from 7–9 to 4–6 and then to 0–3, female survival decreased as well. That is, rather than there being a continuous increase or decrease in survival with increasing egg number per year, the data show a peak in survival at an intermediate value of egg number.

The second study was carried out on Magpies *Pica pica* in Sweden. Högstedt (1981) compared breeding longevity with the average clutch size in an adult's lifetime. Data for males and females were pooled. The results (Table 2) were similar to the pattern observed for Song Sparrows: (1) a trend for increasing mean clutch size with increasing longevity ($p < 0.05$, linear regression analysis)

Table 1. Possible interpretations regarding observations of the correlation between adult survival and clutch size.

Observation	Interpretation	
Positive correlation between survival and clutch size	1.a. Clutch size is adjusted to condition(s) and this (these) influence(s) adult survival	Can be tested by manipulating clutch/brood size and observing consequences to parents and young
	or	
	b. Clutch size constrained such that poor quality individuals cannot lay large clutches	Can be tested to determine whether individuals can lay more eggs
Negative correlation between survival and clutch size	2. Cost of reproduction expressed	Can be confirmed by manipulating clutch/brood size
	3.a. Adjustment of clutch size if any is less than optimal	Can be tested as with 1.a.
	or	
	b. Adjustment of clutch size is not to condition-dependant parental survival probabilities but to offspring survival probabilities	Supported if clutch size and condition are positively correlated

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Table 2. Longevity (number of breeding seasons alive for) and average clutch size in lifetime for the Magpie (data from Högstedt 1981).

Longevity	Clutch size	(n)
1	5.60	5
2	6.06	8
3	6.20	5
4	6.88	2
5	6.65	4
6	6.61	3
7-8	6.65	4

and (2) clutch sizes less than maximum were associated with the greatest longevity. Those living for 4–5 breeding seasons had the largest average clutches ($\bar{X} = 6.72$, $n = 6$), while those living for more than 5 breeding seasons had slightly smaller clutches ($\bar{X} = 6.63$ eggs, $n = 7$). However as longevity (lifespan) increased from one season only to exactly two, three and four seasons, clutch size increased continuously from 6.50 to 6.88 eggs. The non-linearity in the observed relationship of longevity to clutch size, *i.e.* that it peaks at an intermediate value, was confirmed with polynomial regression analysis: a quadratic regression provides a significantly better fit ($p < 0.05$) than does a linear regression.

The third study is that of Kluyver (1971) who presented data on survival of adult Great Tits (males and females not distinguished) breeding on the island of Vlieland, The Netherlands. In this population a sizeable proportion of breeders have a second brood. If we are to relate survival probabilities for adults to a single measure of fecundity then the best measure is the total number of offspring which parents raised, or attempted to raise in a breeding season. Table 3 shows that adults rearing the most offspring were least likely to be present the following October-December. Because the entire island's population was intensively studied, and because movement onto or off the island from one year to the next was rare, mortality could be safely inferred on the basis of the disappearance of an adult the following winter. As offspring production increased from 11–12 to 17–21, survival decreased from 60% to 24%. This drop in survival probability, which is significant ($p < 0.05$), can be contrasted with survival of adults rearing 12 or fewer young. Among the latter there was a weak tendency for survival to increase with increasing offspring number, but this trend was not significant. Thus the pattern for Vlieland Great Tits was similar to that of Swedish Magpies in that survival peaked at an intermediate value of offspring production, but in the Great Tits the initial rise is slight, beyond which the drop in survival is substantial, whereas for the Magpies the pattern is reversed.

One difficulty with the above interpretation is that Kluyver lumped data from a number of years. It may be that years in which overall nestling production was high are years in which subsequent adult survival was low, *e.g.* due to intraspecific competition (Tinbergen *et al.* 1985). We do not know whether a negative correlation between offspring production and adult survival is to be found within one or more years. A reanalysis to tease out within-year effects from between-year effects would be valuable. Furthermore, Tinbergen *et al.* (1985), analyzing a larger data set, which included Kluyver's, found that survival of adults was low only in years in which many fledglings were produced in the previous breeding season and the winter's beech crop was low. This suggests that a cost of reproduction might only be manifest when the environment is harsh (in this case a large number of competitors and a poor food supply).

The last study concerns a population of Pied Flycatchers breeding in the Forest of Dean, England, studied by Campbell from 1948–1964. Lack (1966) originally analyzed the data, comparing the survival of females rearing 7 and 8 young with those rearing: 1–6 young (median brood size = 6; there are almost no second broods) in seven of those years. His analyses, which were far from straightforward (data from some classes of breed-

Table 3. Survival of adults (both sexes) to the following Oct.-Dec. in relation to number of young reared per year (first and second broods added) among Great Tits breeding on Vlieland, Holland (data from Kluyver 1971). Data from a large number of years, not differentiated by year.

Number of young	Number of adults		Per cent surviving	
	surviving	total		
0	0	3	0%	48%
1- 4	21	41	51%	
5- 6	43	70	61%	55%
7- 8	68	131	52%	
9-10	40	74	54%	56%
11-12	24	40	60%	
13-14	14	31	45%	39%
15-16	8	25	32%	
17-21	5	21	24%	24%

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ers were excluded in some years but not in others, etc.), showed that in five out of seven years large-brooded females survived more poorly; in the two other years they survived better. Overall, the survival of females rearing large broods was 39% compared to 45% for those rearing smaller broods. These data suggest there is a cost of reproduction associated with brood size, yet Lack concluded from the data that the cost of reproduction could be safely ignored. Lack's negative conclusion has been cited more often than the data themselves, which favour a different interpretation.

To try to resolve the issue of whether this population demonstrates an apparent cost of reproduction, I have re-analyzed the original data, with the kind assistance of B. Campbell, P. Harvey and M. Stenning. A more complete treatment will be presented elsewhere. I present here the results of the analysis of the fate of all females which bred in 1950–1962, inclusive. The four variables of concern are: (1) brood size, (2) clutch size, (3) survival of breeding females (a female survived if she was recaptured whilst breeding in any subsequent year) and (4) breeding experience. Experience was determined on the basis of capture at the study site during previous breeding attempts. Thus a female which bred outside the study site would not have been considered to have had breeding experience that year when in fact it had. Overall, 96% of all females breeding in the study area were caught and identified at the nest.

The first result is that, on average, female survival declined with increasing brood size (Table 4). The relationship was linear and significant ($P < 0.05$; $n = 9$, weighted by sample size in each year). The second result is that the relationship of survival to brood size varies from year to year. Comparing the survival of females rearing moderate-sized broods (5 and 6) with females rearing large broods (7-9) indicates that in 6 years large-brooded females survived better, in 6 years they survived worst and in one year the survival percentages were equal. (Averaging over all years survival declined with increasing brood size because in some years large-brooded females survived much more poorly than other females, but never did they survive substantially better.) This year-to-year variability was statistically significant as demonstrated by analysis of covariance: the slopes of the regression lines of survival on brood size, fitted for each of the 13 years, differed from one another ($p < 0.01$).

The final result, more tentative than the first two, is that breeding experience plays a role in the relationship of survival to brood size. Table 5 demonstrates that among first-time breeders those rearing large broods (7–9) survived more poorly than those rearing moderate-sized broods (5–6) in 8 out of 13 years, while for the most experienced breeders, those rearing large broods survived worse in only 1 out of 6 years (excluding ties and years with too few data). Second-time breeders were intermediate between the two extremes. This trend, that years with positive correlations of survival and brood size become more common with increasing breeding experience, is significant ($p < 0.05$, Everitt 1977).

I interpret this result as experienced breeders tending to have a large brood only under good conditions, with the association between large

Table 4. Relation of brood size and clutch size to female survival in the Forest of Dean Pied Flycatcher population (1950-1962). Unpublished data of B. Campbell.

Brood Size	Number Survived	Total	Proportion	Clutch Size	Number Survived	Total	Proportion
1	13	26	0.500	1	–	0	
2	10	24	0.417	2	0	1	0.500
3	18	44	0.409	3	4	7	
4	26	77	0.337	4	7	25	0.280
5	58	150	0.387	5	34	77	0.442
6	85	216	0.394	6	69	181	0.381
7	84	237	0.354	7	146	404	0.361
8	22	69	0.319	8	58	170	0.341
9	1	6	0.167	9	4	12	0.333
Statistics	$r = -0.682$, $n = 9$, weighted by sample size, $p < 0.05$				$r = -0.564$, $n = 8$, weighted by sample size, $p > 0.1$		

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broods and good conditions being weak or non-existent among first-time breeders. Under this interpretation first-time breeders often attempt to rear large broods under average (or even below-agerage) conditions. The results, for this experience class, is no (or a weak) correlation between brood size and condition, and therefore no masking of the cost of reproduction. Another explanation is that individuals genetically predisposed to rearing large broods in their first year are weeded out by selection, and thus less likely to be found among experienced breeders. This explanation cannot be discounted, but we must still explain why, if this is so, a substantial segment of the population has a small brood in its first year and a larger brood subsequently (Harvey *et al.* 1985). The interpretation offered here is that experienced birds tend to be breeding under better conditions or are in better condition.

To summarize, the reanalysis of Campbell's data demonstrates the importance of year-to-year variation in the relationship of survival to brood size (*cf.* Boyce & Perrins 1987, Clobert *et al.* 1987). Such inter-annual variation might reflect: (1) yearly fluctuation in the cost of reproduction, or (2) yearly fluctuation in the adaptiveness of the phenotypic variation in clutch size. Possibility (1) is supported by the experimental demonstration that the cost of reproduction in the Blue Tit varies from year to year (see above). The density of competitors (intra- and inter-specific), predators, and the abundance of food are all factors, likely to vary from year to year, which would modulate the impact of rearing additional young on the parents' survival. An example is provided by Tinbergen *et al.*'s (1985) work on the Vlieland Great Tit population, discussed above. Possibility (2), that variation in clutch size is sometimes not adaptive, is a bit more speculative. Recall that predictions of the model follow on the assumption that females are able to optimally adjust clutch size to condition; it would be unrealistic to expect perfect adjustment in every case. Females must use cues in order to assess condition, which cues would be related (though not necessarily directly) to a female's survival prospects. If in a particular year a given cue is not reliable (not correlated with survival prospects) yet females respond to the cue, this would result in variation in clutch size which is not adaptive; together with a cost of reproduction, the result is a negative correlation between clutch size and adult survival.

Table 5. Comparison of survival of females rearing broods of 7-9 with those rearing broods of 5 or 6 in the Pied Flycatcher, 1950-1962. Data as in Table 4.

Breeding experience	Number of years in which females rearing 5-6 survives better		Number of years in which females rearing 7-9 survived better	
First time breeder	8	(62%)	5	(38%)
Second time breeder	5	(38%)	8	(80%)
Breeding 3rd time	1*	(20%)	5*	(80%)

* in 2 yrs, survival was equal; in 5 yrs, too few data ($n \leqslant 2$ for at least one of the group).

Reanalysis of Campbell's data also suggests the importance of breeding experience. It could be that females acquire the ability to adaptively adjust clutch size with breeding experience, or it could be that previous experience in the breeding area allows the female to make the proper adjustments. Optimal adjustment might be particularly difficult for a bird like the Pied Flycatcher which begins egg-laying so soon after arriving in the breeding area (in contrast with resident species like tits).

To summarize the four non-manipulative studies, both negative and positive trends are apparent in the data. In the Pied Flycatcher population, negative correlations characterized some years and, in general, first-time breeders; positive correlations characterized other years and, in general, the most experienced breeders. To what extent these two variables (inter-annual variation and breeding experience) play a role in the other three populations is not known since the reported data were not differentiated with respect to these two factors. Nevertheless, in the three populations there was evidence of both positive and negative trends: in each case, survival increased as brood or clutch size increased from the smallest to an intermediate value and declined thereafter. Such a peaked survival function may be quite common in birds: Oystercatchers *Haematopus ostralegus* demonstrate such a relationship for survival in relation to egg production per season (Safriel *et al.* 1984) as did Starlings *Sturnus vulgaris* with respect to brood size in one out of two years (Clobert *et al.* in press).

The peak in the survival function may reflect constraints on the adaptive adjustment of clutch

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size, *i.e.* it is easier to adjust clutch size down than to adjust it up. Poor condition females are easily able to adjust brood size in a downward direction: they need only lay fewer eggs. However, females in good condition may find it difficult to rear a larger brood, because this would require both laying more eggs and also extending the laying period (either getting an earlier start or finishing egg-laying later), which may be difficult (Nur 1984b). In this case, females breeding in good condition(s) may not necessarily be laying larger clutches than those in average condition(s). If so, then the cost of reproduction is not being masked and this accounts for the observation that adults rearing larger than average broods survive more poorly than those rearing average-sized broods (Safriel *et al.* 1984, Ekman & Askenmo 1986, Clobert *et al.* in press).

5. CONCLUSIONS

I conclude that the evidence is rather good that birds rearing larger broods suffer an enhanced cost of reproduction. This conclusion differs from that of Bell (1984) and Horn & Rubenstein (1984) who reviewed the literature. Bell, for instance, concluded: 'The evidence from birds... clearly... does not constitute solid, unarguable support for the cost hypothesis.' (1984:302). Others have been even more negative in their assessment, believing the empirical record to seriously call into question the evolutionary significance of a cost of reproduction (*e.g.* Alerstam & Högstedt 1984).

The difference in conclusions can be traced to several factors: (1) Several experimental studies (Nur 1984a, 1987a; Slagsvold 1984; Røskaft 1985) and non-experimental studies (Ekman & Askenmo 1986, Clobert *et al.* in press) which demonstrate or imply a cost of reproduction have only recently appeared. (2) One study, that of Campbell on the Pied Flycatcher, has been cited several times as demonstrating a lack of correlation between brood size and female survival; my reanalysis demonstrates instead a significant negative correlation. (3) We should be wary of drawing conclusions stemming from the inability to demonstrate that an observed difference in survival rates is statistically significant. The danger is of accepting the null hypothesis when it is not in fact true (type II statistical error). (4) Life history theory requires not that a population demonstrate all possible costs of reproduction, only that it demonstrate at least one cost (*e.g.* reduction in survival or future fecundity). Few studies have examined the effects of brood size on future fecundity. My own work demonstrates that the effect of brood size may not be apparent until more than a year after a given brood is reared. (5) Workers have not always sufficiently appreciated the significance of adjustment of clutch size (*i.e.* phenotypic response or plasticity) in relation to individual condition or environmental conditions (but see Perrins & Birkhead 1983). The model introduced in this paper predicts that if birds optimally adjust clutch size to condition, a positive correlation between clutch size and survival may result, even though a strong cost of reproduction is expressed within condition-class. For this reason, the observation of positive correlations between clutch size and survival, though it may provide evidence about the possible adaptive adjustment of clutch size, says nothing about the presence or absence of a cost of reproduction. The adaptive adjustment of clutch size and the cost of reproduction are not mutually exclusive (*cf.* Högstedt 1981).

The model presented here provides, I hope, a tool in understanding how and to what extent birds adjust their clutch size (or brood size) in response to condition or conditions, as well as the consequences of such phenotypic responses. I stress that in applying the model to the question on the determination of clutch size in birds I have not assumed that individual birds are optimizing clutch size. Rather the model provides a yardstick against which the actual performance of birds can be judged.

Negative correlations between brood size and survival provide support for the cost of reproduction hypothesis but it would be premature to conclude that positive correlations demonstrate adaptive adjustments in clutch size. Other explanations should also be considered, *e.g.* that poor quality individuals (which tend to survive poorly) are constrained to lay small clutches. Demonstrating adaptive adjustments in clutch size would require additional, experimental work, *e.g.* modifying clutch/brood size and observing the consequences for parents and young.

6. ACKNOWLEDGEMENTS

I was supported by a NATO Fellowship in Science (awarded

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1984) during the genesis of this paper and by an Alexander von Humboldt Research Fellowship during the final stages of preparation. Dr. Bruce Campbell, Dr. Paul Harvey and Mr. Martyn Stenning kindly provided access to the Forest of Dean Pied Flycatcher data. The Computer Unit and Department of Biological Science (Stirling University) and Abteilung Verhaltensphysiologie (University of Tübingen) provided technical assistance. The organizers of the Conference of Casual and Evolutionary Aspects of the Determination of Bird Numbers (1985) provided an opportunity to develop these ideas and conference participants, D. Bryant, T. Clutton-Brock, N. Davies, A. Grafen, P. Harvey, and A. Kacelnik provided helpful discussion. D. Unger and the editors provided valuable suggestions on the manuscript. To all I am grateful.

7. SUMMARY

The cost of reproduction plays a critical role in theories of the evolution of life history strategies, yet several recent reviews conclude that good evidence is lacking that, in particular, survival decreases with an increase in clutch or brood size. Some have therefore minimized the importance of the cost of reproduction as an evolutionary force. I review six studies which manipulated brood size, five of which provide evidence of a cost of reproduction (reduced survival or future fecundity); the experimental design of the sixth was such that an effect of brood size on survival, if there was one, would be difficult to detect.

Correlations of adult survival with natural (unmanipulated) brood size are difficult to interpret owing to the likelihood that females respond to environmental condition or their own condition by altering clutch size. As a result of the phenotypic adjustment of clutch size, the largest clutches tend to be reared under the best conditions and the latter influence observed survival. I present a model which predicts that if females optimally adjust clutch size to condition(s) then there will often (but not always) arise a positive correlation between clutch size and observed survival, even though a cost of reproduction is present.

I review four nonmanipulative studies each of which provides support for the existence of adaptive adjustment of clutch size and/or the manifestation of a cost of reproduction. Campbell's data on Pied Flycatchers are re-analyzed; they demonstrate a significant negative correlation between brood size and female survival and significant year-to-year variation in this relationship. Adaptive adjustment in clutch size may be more significant among older breeders than among first-time breeders. I conclude that the empirical record supports well the hypothesis of a cost of reproduction associated with rearing larger broods.

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APPENDIX

If condition affects both adult survival aand offspring survival, the correlation arising between optimal clutch size ($\hat{X}$) and longevity at $\hat{X}$ can be either positive or negative, depending on the exact parameters used. To illustrate this point, three quantitative examples (A, B and C) are presented below. In A) and B) condition weakly affects longevity, S; in C) it affects S to a greater degree. In B) and C) condition strongly affects offspring survival; in A) offspring survival is less strongly affected. Note that in A) and C) positive correlations arise between $\hat{X}$ and longevity at $\hat{X}$; in B) a negative correlation arises.

In the three examples I assume that S and the offspring survival rate (R) decrease linearly with increasing clutch size (just as in Fig. 3 and 4), that condition has an additive effect on longevity (just as in Fig. 3 and 4) and that condition has an additive effect on R. The quantitative results are sensitive to these assumptions. More precisely, $R_i = mx + b_i$ and $S_i = dx + c_i$, where x = clutch size, m = –0.01, d = –0.1 and b_i and c_i are constants which depend only on condition, i. (b_i and c_i are the R_i and S_i values, respectively, where x = 0.) As in the body of the paper, $\hat{X}$ maximizes S_iF_i where $F_i = xR_i$. If adult survival rates (p) are age-constant and clutch size influences parental survival in the current breeding season (as well as subsequent survival) than p = S/S+1). Also shown are S_i, p_i and R_i at a standardized X (symbolized S_i*, p_i* and R_i*).

Example A

Parameters			Results		Standardized		Values
i	b_i	c_i	$\hat{X}_i$	S at $\hat{X}_i$	S_i*	p_i*	R_i*
2	0.24	2.1	7.5	1.35	1.43	0.585	0.173
1	0.20	2.0	6.7	1.33	1.33	0.571	0.133
0	0.16	1.9	5.8	1.32	1.23	0.552	0.093

(N.B. $R_2^*/R_0^* = 1.86$; $p_2^*/p_0^* = 1.06$)

Example B

Parameters			Results		Standardized		Values
i	b_i	c_i	$\hat{X}_i$	S at $\hat{X}_i$	S_i*	p_i*	R_i*
2	0.26	2.1	7.70	1.330	1.43	0.585	0.193
1	0.20	2.0	6.67	1.333	1.33	0.571	0.133
0	0.14	1.9	5.32	1.368	1.23	0.552	0.073

(N.B. $R_2^*/R_0^* = 2.64$; $p_2^*/p_0^* = 1.06$)

Example C

2	0.26	2.15	7.8	1.37	1.48	0.597	0.193
1	0.20	2.00	6.7	1.33	1.33	0.571	0.133
0	0.14	1.85	5.3	1.32	1.18	0.541	0.073

(N.B. $R_2^*/R_0^* = 2.64$; $p_2^*/p_0^* = 1.10$)

* – S_i, p_i and R_i at a standardized X (X = 6.7, *i.e.*, the optimal clutch size for intermediate condition individuals.

9. SAMENVATTING

In theorieën over de evolutie van life history strategies spelen de kosten van voortplanting een belangrijke rol. Deze kosten zijn gedefinieerd als verminderde overlevingskans van de ouder of als verminderde toekomstige produktie van jongen bij een volgend legsel. Verscheidene auteurs van overzichtsartikelen op dit gebied hebben echter geconcludeerd dat in het bijzonder de idee dat de overlevingskans afneemt indien het legsel groter wordt of indien het aantal jongen toeneemt, zonder substantieel bewijs is. Dientengevolge heeft een aantal van hen de mate van belangrijkheid van de voortplantingskosten als selectiefactor in de loop van de evolutie in hun verklaringsmodellen geminimaliseerd. De auteur bespreekt zes studies waarin broedselgrootte experimenteel werd gemanipuleerd, waarvan vijf aanwijzingen geven over die voortplantingskosten; van de zesde studie was de experimentele opzet zodanig dat het eventuele effect van de broedselgrootte op de overlevingskans moeilijk te ontdekken zou zijn geweest.

Het is moeilijk om correlaties tussen de overleving van volwassen individuen en natuurlijke (ongemanipuleerde) broedselgrootte te interpreteren omdat het waarschijnlijk is dat vrouwtjes hun legselgrootte veranderen als reactie op omstandigheden in hun omgeving of op veranderingen in hun lichamelijke conditie. Tengevolge van deze fenotypische aanpassing van legselgrootte is er een tendens dat de grootste legsels worden grootgebracht onder de beste condities en juist dit laatste beïnvloedt ook de waargenomen overleving. De auteur presenteert een model dat voorspelt dat als de vrouwtjes hun legselgrootte optimaal aanpassen aan de omstandigheden (extern of lichaamsconditie) er een positieve correlatie ontstaat tussen legselgrootte en waargenomen overleving, zelfs als er sprake is van voortplantingskosten.

De auteur bespreekt vervolgens vier studies waarin niet ingegrepen werd in legsel- of broedselgrootte. Alle vier studies

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wijzen erop dat er een adaptieve aanpassing is wat betreft legselgrootte en/of dat er kosten zijn verbonden aan de voortplanting. Campbell's gegevens over de Bonte Vliegenvanger zijn opnieuw geanalyseerd, en zijn gegevens tonen nu een significante negatieve correlatie tussen broedselgrootte en de overleving van het vrouwtje en ook een significant variatie van jaar tot jaar wat betreft deze correlatie. Het zou kunnen zijn dat de adaptieve aanpassing van de legselgrootte belangrijker is voor oudere broeders dan voor vogels die de eerste keer broeden. De auteur trekt de conclusie dat de hypothese dat het grootbrengen van grotere broedsels geassocieerd zou zijn met (hogere) voortplantingskosten, goed wordt ondersteund door empirische gegevens. – H. H. T. Prins

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