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Double Jeopardy and the Parameterization of Brood Reduction Models: A Comment on Mock and Forbes (1994)

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Hatching asynchrony in birds has puzzled ornithologists for years because it presents a paradox: Parental behavior appears to produce a hatching pattern that frequently results in the death of the last-hatched offspring (Magrath 1990). Lack (1947, 1954) proposed that asynchrony allows parents to reduce brood size to track unpredictable variations in food supply (the Brood Reduction Hypothesis). However, experimental tests of this hypothesis generally have found that fledging success of artificially synchronized broods was equal to or greater than that of asynchronous broods (32 of 34 tests; Stoleson and Beissinger 1995).

Mock and Forbes (1994) recently argued that effects on long-term fitness should be considered in studies of hatching asynchrony. They pointed out that, by using fledging success as the sole criterion for evaluating different hatching strategies, most authors have failed to recognize or assess possible differences in reproductive costs. Mock and Forbes suggested that in the absence of a mechanism to reduce brood size to available resources, parents at experimental synchronous nests may invest an imprudent level of effort in raising all their young, with a consequent reduction in future survival. Thus, asynchronous hatching may be favored over synchronous hatching if any long-term gain in adult survival compensates for any short-term losses in reproduction.

The tradeoff of fecundity and survivorship (hence, future reproduction) is central to studies of life-history evolution (e.g. Williams 1966, Charnov and Krebs

1974, Reznik 1985) but has been neglected in studies of hatching asynchrony. As Mock and Forbes (1994) noted, the effect of hatching patterns on the future survival of parents is poorly known. Few studies have quantified parental effort as an approximation of reproductive costs. Of 34 field studies reviewed recently, only six measured parental provisioning effort directly (Stoleson and Beissinger 1995), and one used an indirect measure (Gibbons 1987). Thus, the approach of Mock and Forbes in identifying life-history consequences of hatching asynchrony is particularly relevant and valuable.

To illustrate their argument graphically, Mock and Forbes (1994) presented a simple model that compares the relative fitness (measured as expected lifetime reproductive success) of a "brood-survival" strategy (i.e. synchrony) with that of a "brood-reduction" strategy (i.e. asynchrony). Synchronous and asynchronous hatching are preferable terms for the two strategies because they do not presume an adaptive function, but for the sake of clarity I will follow the usage of Mock and Forbes. Their model is meant to illustrate the effects on lifetime reproductive success of two different hatching strategies in relation to the frequency of good and bad food years. They presented two basic conclusions from their model results. First, a brood-survival strategy is less likely to prevail when good years are rare. Second, long-lived species are especially sensitive to survival penalties for using the brood survival strategy in bad years.

These conclusions, however, are to some extent dependent on the values used to parameterize the model. Mock and Forbes set the reproductive success of

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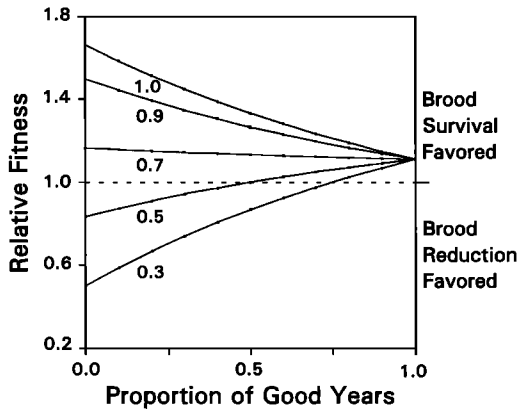
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Fig. 1. Relative fitness of brood-survival to brood-reduction hatching strategy with respect to proportion of good years (P) and expected recruitment of young from parents employing the brood-survival strategy in bad years (w[s,b]). Lines represent different levels of recruitment of young for adults using brood-survival strategy in bad years (1.0, 0.9, 0.7, 0.5, 0.3), and may be considered as representing different fecundity penalties. Expected recruitment values used in generating these curves were 1.0 for brood-survival strategy in good years (w[s,g]), 0.9 for brood-reduction strategy in good years (w[r,g]), and 0.6 for brood-reduction strategy in bad years (w[r,b]). Dotted line represents where the two strategies deliver equal fitness payoffs; above this line brood-survival is favored, below the line brood-reduction is favored.

parents adopting a brood-survival strategy in a good year at unity (i.e. w [s, g] = 1). Parents using the brood-reduction strategy were assigned a slightly lower success to represent the frequent occurrence of incidental mortality of youngest chicks even with abundant food. The values for reproductive success in bad years were chosen so that payoffs for the two strategies were equal when good and bad years were equally probable. As a result, parents adopting the brood-survival strategy in bad years had the lowest success. However, Mock and Forbes neglected to explain their rationale for these recruitment values. Without any *a priori* reason to assume equal payoffs with an equal probability of good and bad years, these values must be regarded as arbitrary. And because recruitment was the one component of the model that was kept constant throughout the analysis, their results represent a subset of the possible range of results and may not be generally applicable.

By analyzing the model with these recruitment values, Mock and Forbes (1994) appeared to contradict their original verbal argument. They suggested that parents incur a survival penalty when they adopt the brood-survival strategy in bad years because, without a means to adjust brood size to available food con-

ditions, they must invest an inordinate level of effort to raise an entire brood. Yet, the analysis of the model was based on the use of low reproductive success for these parents. Thus, parents using the brood-survival strategy in bad food years were placed in double jeopardy: They were penalized in both survivorship and reproductive success. Whereas parents of synchronous broods in bad years may invest enough additional effort to reduce their future survival, but not enough to raise most of the young successfully, it is not the only possible scenario and may be the least likely alternative. Of six experimental studies that measured parental effort directly, only one (Mock and Ploger 1987) found both higher parental effort and lower fledging success in synchronous broods (Stoleson and Beissinger 1995).

To better understand the consequences of the costs of reproduction on hatching strategies, it may be preferable to analyze the effects on lifetime reproductive success of either a survival penalty or reduced fecundity for parents rearing a synchronous brood in bad years, but not both simultaneously. I examined these two factors separately, using a different set of parameters for recruitment than that used by Mock and Forbes. This analysis is not intended to be thorough, but rather is presented to illustrate how parameterization of the model can affect its results.

I used the same mathematical model as Mock and Forbes to calculate the ratio of fitness payoffs for parents using a brood-survival strategy versus a brood-reduction strategy, based on the tradeoff in survival and reproduction in relation to the frequency of good and bad food years (Mock and Forbes 1994: equation 8 in appendix). I also examined the model using two levels of maximum adult survival, 0.95 and 0.50. Except where noted, the methods, symbols, and parameters used follow Mock and Forbes (1994).

If parental survival costs are ignored, the brood-survival strategy always will be favored when reproductive success under that strategy is equal to or greater than that of a brood-reduction strategy in a bad year (i.e. w[s, b] ≥ w[r, b]; Fig. 1). Also, the relative fitness of the brood-survival strategy will increase with a greater proportion of bad years. As the value for reproductive success of the brood-survival strategy in bad years (i.e. w[s, b]) declines, the proportion of good years necessary to favor the brood-survival strategy increases. Note that because parental survival costs are ignored here, the results are identical for high and low maximum adult survival.

To examine the effects of survival penalties for parents adopting the brood-survival strategy, I followed the argument that these parents lack a mechanism to reduce the size of their broods, and so increase their effort to raise the whole brood. Therefore, their reproductive success was set at unity (w[s, b] = 1). Although this value admittedly is arbitrary, and will probably vary with the severity of the year and other factors, it serves to illustrate the problem with con-

clusions drawn from parameterized models. The relative fitness of this brood-survival strategy was examined using various levels of survival penalties to represent the additional costs incurred (Fig. 2).

Results suggest that as adult survival penalties increase in severity, the relative fitness of the brood-survival strategy generally decreases. However, which strategy is favored depends on the severity of the penalty, the maximum adult survival, and (sometimes) the proportion of good years. When maximum parental survival is low, brood reduction is favored only when adults that adopt the brood-survival strategy incur extreme reductions in survival in bad years—at least with these recruitment values (Fig. 2). Thus, the conclusion that brood-survival becomes less likely as the proportion of good years decreases is not as general as might be inferred from Mock and Forbes (1994). Survival penalties for using the brood-survival strategy in bad years have a much greater influence on long-lived than on short-lived species. This makes intuitive sense because, in long-lived species, residual reproductive value composes a greater portion of total reproductive value than in short-lived species. This supports Mock and Forbes' (1994) second conclusion.

Differences between my results and those presented by Mock and Forbes (1994) illustrate clearly that the values used to parameterize a model may determine the conclusions drawn from its analysis. A thorough analysis requires not only that the values used are appropriate and empirically meaningful, but that a sample of the full range of such values is used. Because Mock and Forbes used only a single set of values for recruitment, their analysis examined only a fraction of the possible interactions of survival, reproduction, and the frequency of good years. However, their basic argument remains extremely apropos: Any attempt to understand brood reduction should include a life-history perspective and consider long-term effects of hatching patterns. Therefore, it is critical for field studies to incorporate an assessment of the costs of reproduction, and not rely solely on a tally of fledglings for comparing different hatching strategies.

By considering long-term effects in their analysis of brood reduction, Mock and Forbes provide an explanation for the apparent lack of support for the brood-reduction hypothesis provided by field studies using short-term measures (Stoleson and Beissinger 1995). Of course, adaptive brood reduction is just one explanation proposed for hatching asynchrony. To explore the adaptive significance of hatching asynchrony fully, it is essential to assess other potential costs and benefits of both hatching patterns and the early onset of incubation. A total of 17 hypotheses has been proposed to explain asynchrony in birds, and many suggest an adaptive function to early incubation, with the resulting asynchronous hatching considered merely a consequence (Stoleson and Beissinger 1995). The life-history approach suggested by
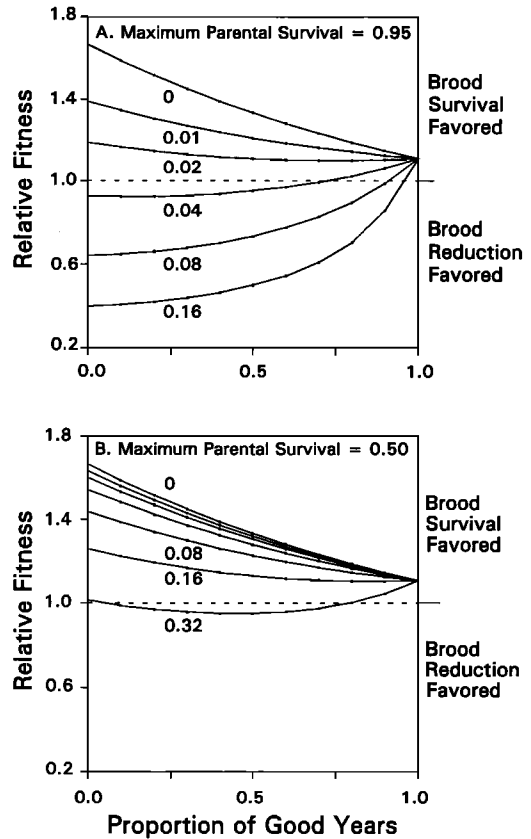

Fig. 2. Relative fitness of brood-survival to brood-reduction hatching strategy with respect to proportion of good years (P) and survival penalty to adults that employ a brood-survival strategy in bad years, for cases where maximum survival of parents is high (A) (0.95), and (B) low (0.50). Curves in each figure represent effects of various reductions in adult survivorship on fitness of parents using the brood-survival strategy in bad years, specifically, 0.00 (no penalty), 0.01, 0.02, 0.04, 0.08, and 0.16 (plus 0.32 in panel B only). These values were subtracted from maximum adult survival values in calculations of fitness. Dotted line represents where the two strategies have equal fitness payoffs; above this line brood-survival is favored, below the line rood-reduction is favored. Expected recruitment values for brood-survival strategy in bad years ($w[s,b]$) was 1.0; others as in Figure 1.

Mock and Forbes should prove valuable in assessing these alternative hypotheses in future studies.

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Abiotic Factors and Preroosting Behavior of Greylag Geese: A Comment

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In a paper on the preroosting behavior of Greylag Geese (*Anser anser*), Schmitt (1994) concluded that "abiotic factors determine departure time but do not disturb flock cohesion" (p. 763) and that "none of the variation in departure time is due to variation in social interactions leading to flock synchronization" (p. 762). Here, I argue that Schmitt (1994) has not convincingly shown that abiotic factors have no influence on flock cohesion during departure to the roost, that he has not clearly shown which abiotic factors influence departure time, and that he has not really shown a lack of correlation between departure time and flock synchronization.

Schmitt's conclusion that abiotic factors do not influence flock cohesion is at odds with his results (p.760) that "synchronization was lower on rainy than on cloudy and sunny evenings (both $P < 0.001$), but cloudy and sunny evenings did not differ." Schmitt went on to say that rainy evenings were colder and darker than cloudy and sunny evenings. Therefore, it is likely that temperature and/or light intensity, if not rain itself, affected synchronization. Unfortunately, no figures or tables with flock synchronization as the dependent variable were presented. Schmitt reported that a multiple regression analysis (on data from only one season) failed to correlate any abiotic factor with synchronization, but rainfall apparently was not included as an independent variable. More-

over, the power of the statistical test was not given. Forbes (1990) made a convincing argument that conclusions based on negative results (lack of statistically significant effects) should be accompanied by power analyses.

Schmitt stated that abiotic factors influence departure time, a conclusion that has been reached in many other studies (see references in his paper). However, it is not clear exactly which factors were involved in the case of Greylag Geese. The multiple regression analysis in Schmitt's table 1 shows that "illumination decrease" is the main factor. But a footnote to table 1 reveals that "illumination decrease" was calculated as the "difference between values at sunset and take off of flock." Obviously, a parameter closely related to the dependent variable (departure time) was used in the calculation of "illumination decrease," and therefore, departure time and "illumination decrease," from the start, were not independent from each other. Thus, it is not surprising that illumination decrease explained as much as 92% of the variation in departure time. It is obvious that the later the departure time, the lower the light intensity at that time, and the more positive (less negative) the illumination decrease, as defined. Later in the discussion, Schmitt seemed to redefine illumination decrease as how quickly light intensity changed, but there is no mention of how and at what time of day this rate was calculated. The argument of inherent relatedness between independent and dependent variables also could be used for other "independent" variables used

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