

LIFE-HISTORY CONSEQUENCES OF AVIAN BROOD REDUCTION

DOUGLAS W. MOCK¹ AND L. SCOTT FORBES²

¹*Department of Zoology, University of Oklahoma, Norman, Oklahoma 73019, USA; and*

²*Department of Biology, University of Winnipeg, 515 Portage Avenue,
Winnipeg, Manitoba R3B 2E9, Canada*

ABSTRACT.—Studies of avian brood reduction characteristically focus on the short-term consequences of hatching asynchrony for offspring (e.g. number and sizes of fledglings), but a truly comprehensive brood-reduction theory needs to incorporate long-term fitness effects for parents if trimming family size leads to lessened parental effort thereafter. A simple model shows that a brood-reduction strategy is more likely to be favored by natural selection when early losses of one or more brood members in poor years (expedited by parental manipulation of hatching asynchrony) lead to significantly diminished parental work levels. Field workers should design experiments to assess the effects of brood reduction on parental work levels, parental survivorship, and/or future fecundity; they could do so simply by borrowing the experimental field techniques already employed in studies of avian reproductive costs. Received 9 February 1993, accepted 10 May 1993.

DAVID LACK (1947, 1954) suggested that parent birds may create more offspring than they can normally rear as a hedge against uncertain food. By starting incubation before laying has been completed, parents handicap last-hatched offspring, facilitating their selective elimination if food proves short. Conversely, when food is bountiful, the full brood may be reared.

Lack's hypothesis has attracted considerable attention in recent years. Field tests are easily performed, usually involving experimental manipulation of the normal pattern of hatching intervals followed by measurement of the consequences for number and quality of surviving offspring. The results of such work appear uneven and have spawned considerable controversy (Clark and Wilson 1981, Amundsen and Stokland 1988, Magrath 1990, Amundsen and Slagsvold 1991, Pijanowski 1992, Konarzewski 1993, Forbes and Mock 1994).

Experiments on the value of hatching asynchrony have focused mostly on how differing reproductive strategies affect recruitment from the current brood. In this regard they parallel the literature on another classic Lack hypothesis, his model of optimal clutch size. There he suggested that parent birds should not maximize the number of nestlings in each breeding attempt, but rather should maximize the number of offspring surviving to recruit into the breeding population (Lack 1954, 1966, 1968). Fundamental to this argument is a trade-off between the number and quality of offspring in a given brood. Although few would argue that Lack's clutch-size model did not represent an

important conceptual development, it was quickly recognized as being incomplete. In part, its failure to account for all observed variation inspired refinements of the basic model, most notably recognition that parental reproductive costs may favor smaller clutch sizes (Williams 1966a, b, Charnov and Krebs 1974).

Although Lack's hatching-asynchrony hypothesis (usually called the brood-reduction hypothesis, following Ricklefs 1965) predates his clutch-size model, it has not undergone similar scrutiny and amendment. Indeed, the brood-reduction hypothesis per se received little formal theoretical attention until relatively recently (Temme and Charnov 1987, Forbes 1991a, b, Forbes and Ydenberg 1992, Pijanowski 1992, Konarzewski 1993). These contributions have added much-needed mathematical rigor to the original argument, while exploring the roles of environmental variability, sibling rivalry, predation, and egg failure, as well as the cost of tracking variable resources on the evolution of brood-reduction strategies.

Not surprisingly, field studies of hatching asynchrony and brood reduction have maintained the same short-term focus. Lack's brood-reduction hypothesis is characteristically tested by perturbing the degree of hatching asynchrony (the presumed parental manipulation), then assessing how broods with trimmed (and sometimes exaggerated) hatching spreads compare with sham-manipulated control broods in terms of fledgling production. The rationale for this protocol is simple: the Lack argument predicts that synchronized broods should exhibit

greater nestling mortality and/or lower fledging mass (parents being less able to satisfy demands of evenly matched siblings during periods of food shortage) than normally asynchronous broods (reviewed in Magrath 1990; Amundsen and Slagsvold 1991, Pijanowski 1992, Konarzewski 1993).

One problem with this approach is that, while hatching asynchrony certainly facilitates brood reduction when food is short, it also has the potential to trigger brood reduction unnecessarily, when food is relatively abundant, which led Amundsen and Slagsvold (1991) to question whether such a brood-reduction pattern is adaptive or maladaptive. Most recently, Pijanowski (1992) pointed out that deleterious brood reduction may be an unavoidable cost of a mechanism needed for tracking variable food, a cost that is repaid when food is short.

In general the life-history consequences of avian brood-reduction strategies remain virtually unexplored. For example, the effects of manipulating hatching asynchrony on the future success of parents have not been measured directly. The closest indirect approximations of this dimension have involved measuring parental effort during the period of offspring provisioning. Of the 30 experimental field studies reviewed by Amundsen and Slagsvold (1991), only three measured parental delivery rates (Fujioka 1985, Gibbons 1987, Mock and Ploger 1987); the rest tacitly assumed parental effort to hold steady.

Only modest empirical consideration has been given to the postfledging survival of the offspring themselves. Husby (1986) found that postfledging survivorship of Black-billed Magpies (*Pica pica*) declined when the normal course of brood reduction was thwarted by replacing dying or ejected chicks. He suggested that early brood reduction diminished the parents' burden, thus enhancing the quality of subsequent parental care. Gibbons (1987) found that hatching asynchrony accelerated the onset of brood reduction in Jackdaws (*Corvus monedula*), thereby truncating "wasted" parental investment. Hahn (1981) similarly argued that hatching asynchrony promotes early brood reduction, lessening the cost of sibling rivalry in Laughing Gulls (*Larus atricilla*), although she addressed only the benefits for current reproduction.

In Japan, Cattle Egret (*Bubulcus ibis*) parents brought considerably more food (about 30% more) to artificially synchronized broods than

to broods with normal asynchrony, which presumably helped the synchronized chicks grow as rapidly as the privileged senior members of control (normal) broods (Fujioka 1985). In a Texas colony, although Cattle Egret parents similarly brought more food (again about 30% more) to artificially synchronous and asynchronous broods than to broods with normal asynchrony, fledging success was highest in broods with normal asynchrony (Mock and Ploger 1987). The natural (1.5-day) hatching interval apparently promoted higher reproductive efficiency (fledged chicks per unit of food) for the parents than either a doubled interval (3 days) or complete hatching synchrony (0 days).

The roles of offspring synchrony on begging competition and on parental responses remain little explored, but may be a key dynamic. Of direct interest is Smith and Montgomerie's (1991) study of nestling American Robins (*Turdus migratorius*), confirming the game-theory prediction that offspring escalate begging intensity to the level of their siblings (Parker and Macnair 1979, Harper 1986). Also, Slagsvold and Lifjeld (1989) reported that the body mass of female (but not male) Pied Flycatcher (*Ficedula hypoleuca*) parents with asynchronous broods was heavier at the end of the nestling period than that of mothers with more synchronized broods, perhaps reflecting reduced work levels.

Considerably more data underscore the relationship between offspring size at fledging and their probability of recruitment as breeders. Because even slight increments of fledging mass sometimes correlate with significantly enhanced long-term survivorship (Perrins 1964, Gustafsson and Sutherland 1988, Smith et al. 1989, Magrath 1991), one is tempted to infer that larger size is generally better. However, because the effect of fledging mass on offspring fitness logically must be a decelerating function, identifying the precise functional relationship between body mass and postfledging survivorship is key to measuring the relative success of different brood-reduction strategies. Ideally, the effects of hatching asynchrony on offspring via variation in offspring size at independence (which may occur well after fledging) would be measured directly by following offspring until they recruit into the breeding population.

Collectively, these results suggest a life-history dimension to Lack's brood-reduction hypothesis, the potential effects on the future re-

productive potential of parents. Some explanation is required for the fact that in many brood-reducing species, parents appear to expend submaximal effort, even while some members of the their current brood are dying. That parents are, in a sense, withholding critical resources is evidenced by their demonstrated ability to increase food deliveries dramatically under some experimental circumstances; even if they are being "tricked" (at the proximate level) by the test procedure, their enhanced performance betrays a higher investment capacity in the short run. Here we present a verbal and mathematical model that revises Lack's hypothesis to incorporate these parental patterns, and use it to explore the consequences for brood-reduction strategies.

A MODEL

We explore two parental reproductive strategies, which we shall refer to as brood survival and brood reduction. Under the former, all offspring are created equal (i.e. they are identical in size and hatch simultaneously) and one imagines that parents are attempting to raise all brood members to independence. This idealized strategy approximates the pattern of synchronous hatching observed in many birds (although in some species siblings develop various competitive asymmetries thereafter). By contrast, under a brood-reduction strategy, disparities in the timing of hatching and/or egg size result in mismatches and, hence, a competitive hierarchy among brood members. Here the parents are viewed as leaving open the option of a downward adjustment in family size at some point in the rearing process.

There are many variations on the theme of hatching spread. Perhaps the most common avian pattern, observed in many passerines, is intermediate: incubation commences with the penultimate egg, resulting in the final chick hatching a day or two after its elder siblings ("semiasynchrony" of Mock and Schwagmeyer 1990). Often, the last-hatched chick in such a brood suffers relatively retarded growth and/or elevated pre fledging mortality. More extreme patterns of hatching asynchrony also occur. For example, Green-rumped Parrotlets (*Forpus passerinus*) lay clutches of 5 to 10 eggs that hatch over an average span of 8.7 days (Beissinger and Waltman 1991). In any case, it is beyond the scope of our present treatment to consider the effects of differing magnitudes of offspring asynchrony. Rather, we simply contrast synchronous and asynchronous offspring strategies in a dichotomous fashion.

Lack (1947, 1954) surmised that a measure of hatching asynchrony should facilitate adaptive brood reduction during periods of food shortage. Insofar as asynchrony is under parental control, its degree should

serve parental interests. Here we offer a layered verbal argument, a conceptual model (presented more formally in Appendix) that explores how parental costs of reproduction can affect the payoffs available from this parental strategy dichotomy (brood reduction vs. brood survival).

Our model can be summarized verbally as a five-point argument: (1) We use parental lifetime reproductive success (LRS) as our surrogate for fitness (eq. 1 in Appendix); we assume that any behavior tending to increase LRS will be favored by selection. (2) LRS is the product of two factors, average annual reproduction and average annual survival (eq. 2-4 in Appendix). This tacitly assumes no variation in reproductive success or survival as a function of adult age (see Gustafsson and Pärt 1990). (3) Both of these factors (annual reproductive success and survival) depend, in turn, on two other facets of interest: (a) the proportion of "good" versus "bad" years; and (b) the parental strategy being used (brood reduction vs. brood survival). This is spelled out in eq. 5-8. (4) In comparing these two parental strategies, then, the brood reduction option is favored if the LRS realized by adopting it is greater than that obtainable via the brood-survival alternative (inequality 9). (5) The brood-reduction strategy, thus, can be favored by two routes: it can win outright (if bad years are so common that facultative pruning of family size actually yields the higher average annual reproduction success) or it can win in the long run by delivering a proportional gain in adult survival that compensates fully for any short-term losses in annual reproduction (inequality 10).

MODEL ANALYSIS

A simple numerical analysis of the model can illustrate the argument's properties graphically. The reproductive success of parents adopting a brood-survival strategy in a good year was set at unity; presumably this delivers the best possible annual success. We assumed that the next-best score would also occur during favorable conditions (by parents playing the brood-reduction strategy), but that bad-year conditions give an advantage to brood-reducing parents. In the Appendix model's terminology, $w(s, g) > w(r, g) > w(r, b) > w(s, b)$. The values for these parameters (see Fig. 1 legend) were chosen so that the payoffs for brood reduction and brood survival are identical when good and bad years are equally probable (the probability of good years, P , is 0.5), if we ignore parental survival costs (i.e. brood survival is favored when good years predominate [$P > 0.5$]; brood reduction favored when bad years predominate [$P \leq 0.5$]). We now examine the effect of a sur-

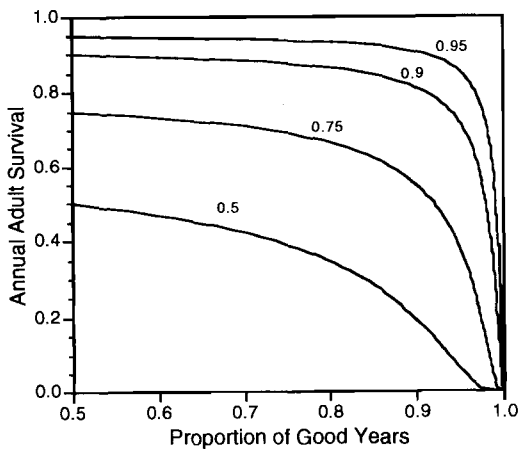


Fig. 1. Proportion of good years, P , required to sustain a brood-survival strategy, given that parents incur a mortality penalty for using that strategy in all $(1 - P)$ bad years. Four levels of maximum adult survival are shown (0.5, 0.75, 0.90, and 0.95), values that are realized only if all years are good ($P = 1$). The survival penalties $f(s, b) < f(s, g) = f(r, b) = f(r, g)$ are those used in Appendix eq. (9). Isopleths indicate combinations of good-year frequencies (P) and survival penalties ($f[s, b]$) at which the parental strategies of brood reduction and brood survival yield equivalent fitnesses. Expected recruitment parameter values used in generating these curves are: $w(s, g)$, for brood-survival strategy in good years, set at 1.0 (see text); $w(r, g)$, brood-reduction strategy in good years, 0.9; $w(r, b)$ brood-reduction strategy in bad years, 0.6; and $w(s, b)$, brood-survival strategy in bad years, 0.5. As the adult survival penalty for playing brood survival in bad years declines, there is a sharp rise in frequency of bad years required to keep fitness payoff of brood reduction as high as that for brood survival.

vival penalty imposed upon parents having the misfortune (in the context of our model) to adopt a brood-survival strategy in a bad year.

For simplicity, we assume that parental survival is compromised only by attempting the labor-intensive brood-survival strategy when conditions are bad—formally, when $f(r, g) = f(s, g) = f(r, b) > f(s, b)$. Four levels of maximum annual parental survival were examined (0.50, 0.75, 0.90, and 0.95), bracketing the range of adult survival rates for most birds (Lack 1966, Botkin and Miller 1974). The penalty to parents, expressed as a mortality cost for employing the brood-survival strategy in lean times, was examined as departures from these maximum values.

In the first analysis, we calculated the proportion of good years at which brood reduction

and brood survival yielded equivalent fitness as the penalty for adopting a brood-survival strategy in a bad year rose from zero (Fig. 1). Across all levels of maximum adult survival, the level of P at which brood reduction and brood survival yield equivalent fitness rose sharply as this penalty declined. That is, a steep increase in the frequency of good years is required to sustain a brood-survival strategy if there is a significant penalty for using that strategy in bad years.

In the second analysis, we examined the relative fitness payoff for brood survival (W_s) versus that for brood reduction (W_r) across varying frequencies of good years. A simple ratio, W_s/W_r , combines the payoffs, such that values greater than 1.0 represent an advantage for brood survival and those less than 1.0 indicate brood reduction's superiority. Two levels of maximum survival ($f[r, g] = f[s, g] = f[r, b]$) were examined: 0.95 (an annual survival rate corresponding to long-lived seabird) and 0.50 (corresponding to short-lived passerine). Five levels of additive mortality costs were examined for parents using the brood-survival strategy during bad years (calculation explained in Fig. 2 legend).

This analysis reveals two main points (Fig. 2). First, brood survival is less likely to prevail when good years are rare (i.e. when P is low). As the penalty for choosing the wrong (=brood-survival) parental strategy in a bad year (i.e. $f[s, b]$) declines, good years need not be so frequent to sustain the brood-survival strategy. That is, the threshold value of P (where fitnesses for brood reduction and brood survival are equivalent) rises. Second, long-lived parents may pay an especially steep fitness penalty for adopting the survival strategy in bad years. Conversely, such penalties are less important when adult survival is low anyway. As Bob Dylan put it succinctly, "when you ain't got nothin' you got nothin' to lose." So, short-lived parents (e.g. small passerines) are likely to find additional mortality more affordable than parents of longer-lived taxa (seabirds, large raptors, herons, etc.).

DISCUSSION

Several general facets of parental strategy in an uncertain world merit special consideration: (1) the potential penalty parents may pay for being overly conservative when conditions prove to be good (e.g. hatching asynchronously

and suffering unnecessary offspring losses); (2) the potential current-brood benefit parents can reap from the same measure when conditions prove bad; and (3) the benefits that asynchrony can confer to parental survivorship. As the first two have been explored extensively, both theoretically (Temme and Charnov 1987, Pijanski 1992, Konarzewski 1993) and empirically (e.g. see review by Magrath 1990), we shall focus on the third.

Where the effects of variation in parental effort between brood-reduction and brood-survival strategies are ignored, brood reduction is favored by selection only when the net effects on recruitment from the current brood are positive (i.e. the left-hand side of Appendix eq. 7 is greater than 1.0). However, when the effects of decreased work levels associated with offspring asynchrony are considered, we see that such a strategy can be favored, even when the net effects on recruitment from the current brood are negative, so long as this cost is counterbalanced by enhanced parental survivorship. Moreover, the simple numerical analysis suggests that associating even slight mortality costs to a brood-survival strategy may have dramatic effects on the relative payoffs for brood-reduction versus brood-survival strategies, particularly in taxa with normally high adult survival rates.

The framework developed here suggests two further questions. First, how hard should parents work under differing environmental conditions? Second, how do differences in parental work levels influence a parent's opportunities for future reproduction?

No detailed empirical information exists relevant to the first question. Certainly, parents are known to abandon broods entirely when conditions are disastrous (e.g. Kahl 1964), but it would be of great interest to know if parents adjust their efforts on a continuous scale, working somewhat harder when food is moderately short (e.g. Wright and Cuthill 1989). If so, do parental costs of asynchrony manifest themselves only under bad conditions? Alternatively, do differences in work levels between synchronous and asynchronous strategies extend across all food conditions?

The second question has not been addressed directly either, although useful inferences can be drawn from the burgeoning literature on clutch size and costs of reproduction (e.g. Williams 1966a, b, Charnov and Krebs 1974, Good-

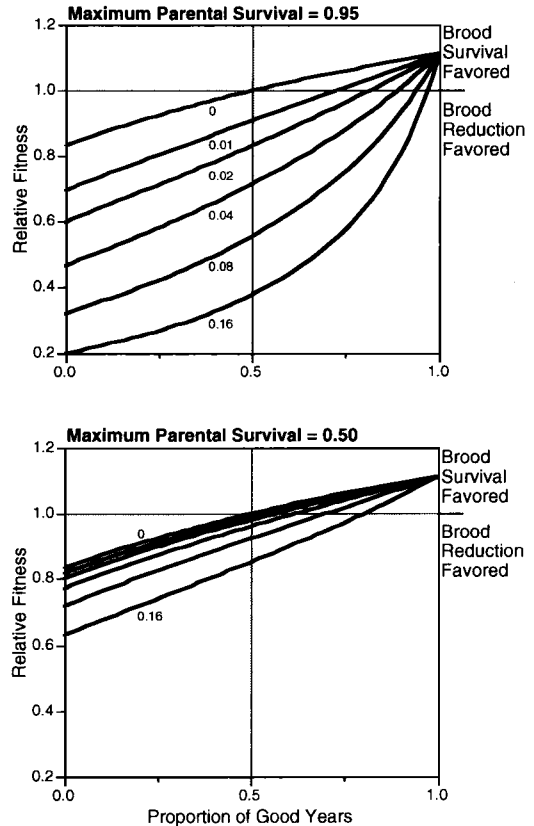


Fig. 2. Relative fitnesses of brood-survival and brood-reduction strategies (W_s/W_r) with respect to the proportion of good years (P) and the adult survival penalty paid by parents trying brood-survival strategy in bad years. When this relative fitness ratio is greater than 1.0 brood survival is favored (upper zones); when less than 1.0, brood reduction is favored (lower zones). Top panel shows case where maximum survival for parents is very high (0.95, comparable to that reported for large raptors and seabirds), while bottom panel shows parental survival rate typical of passerines (0.50). The five curves in each figure represent impacts of various mortality penalties on parents endeavoring to use the brood-survival strategy in bad years (i.e. $f[s, b]$), namely 0.0 (no penalty), 0.01, 0.02, 0.04, 0.08, and 0.16. These penalties are subtracted from maximum adult survivorship value (e.g. a passerine incurring a penalty of 0.08 for trying the brood-survival strategy in a bad year achieves a net survival rate of $0.5 - 0.08 = 0.42$). In both panels, increased survival penalties enhance attractiveness of brood reduction, but this is especially true in the upper graph (long-lived parents have more to lose). In general, as these penalties rise, the proportion of good years required to sustain a brood-survival strategy increases.

man 1974, Nur 1984, 1988, Reid 1987, Gustafsson and Sutherland 1988, Lindén and Møller 1989, Dijkstra et al. 1990, Magnhagen 1991, Hochachka 1992). Parents with experimentally increased clutches work harder, which may result in reduced parental survivorship and/or future fecundity. Whether increased parental work levels associated with offspring synchrony yield similar effects remains to be established.

Exploring stochastic systems, such as the brood-reduction mechanism proposed by Lack, presents formidable challenges to field workers. Without knowledge of the explicit relationship between the food supply/demand dynamic and the optimum clutch size, short-term studies can generate results that appear to be firmly in support of, or equally antagonistic to, Lack's hypothesis. The chief benefits of brood reduction are realized only when food is short relative to brood needs, which may themselves vary stochastically (e.g. due to capricious weather; Sullivan and Weathers 1992). A comprehensive test of the brood-reduction hypothesis requires simultaneous proof that food is indeed both short and unpredictable (lest parents make the necessary adjustments to clutch size). At present, it is customary merely to assume these conditions (but see Magrath 1989). Accordingly, reliance on natural variation in food supplies to provide critical tests of the brood-reduction hypothesis is risky in short-term studies, although such problems diminish over the course of long-term studies.

Experimental enlargement of brood size is one technique used to dodge the tricky issue of measuring the relationship between food supplies and brood demands, the rationale being that food shortage is more likely for larger broods. While this assertion is undoubtedly true on average, brood enlargement by no means guarantees the desired effect. Parents may still be able to compensate by escalating their efforts so as to meet the food demands of enlarged broods in a good (or even average) food year. Thus, parents may confound such experiments by stepping up the rate of food deliveries to enlarged broods (see review in Martin 1987) or by transferring the intended costs of food shortfalls to themselves (e.g. by drawing down fat reserves). Unless one takes the extra trouble to assess parental effort and body condition, cautious interpretation must prevail.

A further disquieting feature of brood-

enlargement experiments is that the manipulation may render the brood-reduction mechanism impotent. The adding of offspring is likely to have a greater relative impact on small broods than on large broods (see O'Connor 1978). For example, increasing a sibship from 2 chicks to 3 creates roughly a 50% jump in total brood needs, while increasing from 9 to 10 adds only 11%. If a brood-reduction strategy were pre-set for an expected range of supply/demand ratios, an experiment grossly exceeding that range might easily produce dramatic, but totally spurious, results.

CONCLUSIONS

A life-history framework adds an important dimension to the study of avian brood reduction, but it also makes the task for field workers more complex. It is increasingly clear that fitness estimates based solely on short-term studies (e.g. assessing only success of current brood) are inadequate. They cannot account for potentially important effects of intrabrood differences in nestling condition on the recruitment prospects for individual offspring (see reviews in Smith et al. 1989, Magrath 1991), nor can they account for effects on parental survivorship and/or future fecundity. The latter set of problems is easily addressed, however, by adopting the field techniques employed in studies of avian reproductive costs (e.g. Nur 1984, Reid 1987, Gustafsson and Sutherland 1988, Dijkstra et al. 1990, Martins and Wright 1993).

In short, brood reduction represents but one mechanism for matching variable food supplies and demands, with parental effort being an integral component of such systems (at least for care-providing taxa like birds). Insufficient food may impose costs for either parents or offspring (or both). The extent to which hatching asynchrony provides relief to parents during periods of food shortage by facilitating early brood reduction, however, remains little explored. We see this as a natural, albeit somewhat overdue, extension of Lack's original ideas on clutch size and brood reduction; addressing these issues will require the study of avian brood reduction to be woven into the fabric of research on reproductive costs and clutch-size optimization. Doing so will be an essential step in the development of a comprehensive, stochastic theory of avian clutch size.

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- reproductive success of parents, $E[\text{LRS}]$, where E denotes mathematical expectation, as our surrogate for fitness. A parent's lifetime reproduction can be approximated as

$$E[\text{LRS}] = \sum_{x=1}^n l(x)m(x), \quad (1)$$

where $m(x)$ represents expected recruitment from the current brood in year x , and n is the expected adult longevity. For simplicity we shall assume that parents breed annually, although more complex permutations could easily be developed. $l(x)$ is simply the product of parents' annual survival probabilities to year x , or

$$l(x) = \prod_{k=1}^{x-1} l(k). \quad (2)$$

In the spirit of Lack's original brood-reduction hypothesis, we assume that recruitment from the current brood is a function of: (1) environmental variability (e.g. food conditions); and (2) the brood-rearing strategy adopted. Following Temme and Charnov (1987) and Pijanowski (1992), we characterize environmental conditions as either good or bad, denoting the probabilities of such years as P and $(1 - P)$, respectively. We acknowledge that this dichotomy is artificial, as in nature food supplies are likely to vary widely across years in a continuous fashion; we adopt this approach for simplicity. We now set $m(x)$, the expected reproductive success in a given breeding attempt, equal to a parent's reproductive success in good and bad years, discounted by their probability of occurrence:

$$m(x) = w(i, g)P + w(i, b)(1 - P), \quad (3)$$

where $w(i, j)$ is the reproductive success of parents adopting strategy i in year type j (*type* being denoted by g for good years and b for bad years). From the field studies of Fujioka (1985), Gibbons (1987), Mock and Ploger (1987), and others, we expect that parents will generally work harder to rear synchronous broods under a brood-survival strategy.

Survivorship of parents to year x , $l(x)$, will be some function, f , of the strategy adopted and year quality. On average, parental survivorship to year x will be

$$l(x) = f(i, g)^{xP} f(i, b)^{x(1-P)}. \quad (4)$$

Substituting equations (3) and (4) into equation (2) yields

$$E[\text{LRS}] = \sum_{x=1}^n \{w(i, g)P + w(i, b)(1 - P)\} f(i, g)^{xP} f(i, b)^{x(1-P)}, \quad (5)$$

which rearranges to

$$E[\text{LRS}] = [w(i, g)P + w(i, b)(1 - P)] \sum_{x=1}^n f(i, g)^{xP} f(i, b)^{x(1-P)}. \quad (6)$$

APPENDIX. The formal model.

Because the strategies of interest are behavioral phenotypes of the parents, we use expected lifetime

The second term on the right-hand side of equation (6) is the sum of a geometric progression. As $n \rightarrow \infty$, this converges to

$$\sum_{x=1}^{\infty} f(i, g)^{xp} f(i, b)^{x(1-p)} = 1/[f(i, g)^p f(i, b)^{1-p}]. \quad (7)$$

Of course, parents do not live forever (as $n = \infty$ implies), but this approximation introduces only a small error because the terms on the left-hand side of equation (7) become very small as n increases. Such an allowance has the advantage of greatly simplifying the algebra.

Substituting equation (7) into equation (6) yields

$$E[LRS] = \frac{w(i, g)^P + w(i, b)(1 - P)}{1 - f(i, g)^p f(i, b)^{1-p}}. \quad (8)$$

We can now substitute for the parental strategy [rep-

resented as i in equation (8)], denoting the brood-reduction alternative as r and the brood-survival alternative as s . Brood reduction will be favored over brood survival when

$$\frac{w(r, g)^P + w(r, b)(1 - P)}{1 - f(r, g)^p f(r, b)^{1-p}} > \frac{w(s, g)^P + w(s, b)(1 - P)}{1 - f(s, g)^p f(s, b)^{1-p}}, \quad (9)$$

which rearranges to

$$\frac{w(r, g)^P + w(r, b)(1 - P)}{w(s, g)^P + w(s, b)(1 - P)} > \frac{1 - f(r, g)^p f(r, b)^{1-p}}{1 - f(s, g)^p f(s, b)^{1-p}}. \quad (10)$$