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ON THE EVOLUTION OF REPRODUCTIVE STRATEGIES
IN BIRDS: REPRODUCTIVE EFFORT

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The evolutionary significance of variation in reproductive rate has been a concern of ecologists since Lack's (1947, 1948) first papers on clutch size in birds. Lack viewed clutch size as an evolved adaptation and directed his attention to factors in the environment, primarily food supply, that applied selection directly upon fecundity. In populations regulated by density-dependent factors, fecundity and adult survival are inversely related (Lack 1954, 1966; Wynne-Edwards 1962), but the possibility that this correlation could have an adaptive basis as well as being a direct consequence of density-dependent population regulation has been explored only recently. Although Lotka (1925, p. 128) stated the general principle that fecundity and mortality schedules are optimized with respect to each other as well as to the environment, most recent studies on the evolution of life-history strategies have a common origin in Cole's (1954) landmark paper on the optimization of life-table parameters.

Williams (1966*a*) applied Cole's approach to investigate the evolutionary significance of reproductive effort. He treated the reproductive strategy as a compromise maintained in a balance between the benefits of reproductive effort expressed as increased fecundity and the costs of reproductive effort expressed as increased adult mortality. Williams argued that a given level of commitment to reproduction (reproductive effort) more greatly jeopardizes future reproduction through increased parental risk of death in long-lived species than in short-lived species, and increasingly as organisms grow older. Williams's reasoning, applied to birds, leads to the prediction that species with low adult mortality should exhibit low reproductive risk whereby they can maintain a high expectation of future reproduction. Conversely, individuals with low probability of surviving to reproduce in the future should demonstrate great commitment to reproduction in the present.

Observations on birds are at least qualitatively consistent with Williams's model. Increased life span is paralleled by decreasing clutch size, deferred maturity, and, frequently, decreased reproductive success (Cole 1954; Lack 1954, 1966, 1968; Ashmole 1963, 1971; Williams 1966*b*; Cody 1966, 1971; Ricklefs 1973*b*; Goodman 1974). We should not, however, be easily persuaded to view adult mortality as the primary influence on the evolutionary optimiza-

tion of reproductive rate, especially to the exclusion of recognizing the direct influence of environment, as originally envisioned by Lack.

Williams fostered a new perspective on reproductive rate, more balanced than that of Lack, but because reproductive effort and its influence on fecundity and adult mortality have not been measured in any way meaningful to his model, Williams's conclusions cannot easily be verified. In particular, one cannot measure the relative contributions of direct and indirect influences in the environment to the evolution of reproductive rate. Gadgil and Bossert (1970) have incorporated the influence of reproductive effort on fitness into a more detailed model in which the trade-off between reproduction and growth, as well as the shape of the function relating fecundity and mortality to reproductive effort, is specified. Although Gadgil and Bossert's model is consistent with many observations, it, like Williams's model, can neither be tested nor verified, at least not in any practical sense. The more empirical approach taken by Tinkle and his co-workers (Tinkle 1969; Hirshfield and Tinkle 1975), who have measured the partitioning of energy by lizards between maintenance and growth on the one hand and formation of eggs on the other, provides an operational definition of reproductive effort, but their system is not suitable for measuring the cost of reproductive effort. In birds, reproductive effort may be manifested in subtle changes in behavior, particularly in brood protection and foraging effort, which defy practical measurement, but fecundity and mortality are more accessible.

In this paper, fecundity and adult mortality are related to each other directly, rather than indirectly through reproductive effort. In the model described below, reproductive rate and adult reproductive risk, both measurable expressions of reproductive effort in birds, are optimized with respect to environmental factors and with respect to each other by maximizing intrinsic rate of increase in population size. The model is used to answer the following question: To what extent is variation in the reproductive rate of birds due to (1) intrinsic physiological restrictions to reproductive rate (such as long development time in large species), (2) direct ecological influence of resources and other environmental conditions on reproduction, (3) indirect influence of adult mortality on reproduction through density-dependent responses of resources to population size, and (4) optimization of reproductive risk with respect to other life-history parameters? These factors may be interpreted loosely as (1) efficiency of resource utilization, (2) availability of resources (including the effects of interspecific competition), (3) effects of intraspecific competition, and (4) optimization of effort to procure resources and protect investment in reproduction. Although each of these factors influences reproductive rate, we do not know the degree to which each is responsible for variation in reproductive rate among species of birds.

PREMISES AND ASSUMPTIONS

As in the development of all models, some degree of reality has been sacrificed to construct relationships whose properties can be explored mathematically.

The basic premises, assumptions, and simplifications incorporated into the model are outlined briefly below. They are discussed more fully in Appendix A, where their influence on properties of the model is evaluated. Premises concerning the genetic bases of reproductive behavior are not necessary to evaluate optimization strategies but are needed if we are to have evolution transpose an abstract model into the adaptations of real organisms.

Taxonomic Restriction

This model was developed to be tested by data available for birds. The model may apply more widely, but its structure contains certain properties that are appropriate to bird populations but restrict its generality. First, adult body size varies little within populations of birds and does not vary with age after the onset of reproduction; the inverse relationship between growth and production, mediated through allocation of resources, that is characteristic of fish and lizards (Williams 1966b; Tinkle 1969) is not incorporated into the model. Second, reproduction is seasonal and generations overlap. Third, reproductive effort includes extensive parental care of eggs and young in most species. Fourth, adult mortality and fecundity are approximately constant after the onset of reproduction, which allows simplification of the model.

Premises

First, the reproductive strategy of an individual is assumed to be genetically determined and fixed. Second, the fitness of a genotype is assumed to be equivalent to the intrinsic population growth rate (λ) of individuals bearing that genotype. Therefore, individuals with genotypes having the highest λ are selected, and evolution tends to maximize λ . Effects of genotype frequency on fitness are ignored. Third, all possible phenotypes define a continuous variable, and phenotype bears a simple relationship to genotype. Fourth, populations are assumed to have discrete, overlapping generations. Intrinsic population growth rate (λ) is therefore determined by the equation

$$1 = \sum_{x=0}^{\infty} \lambda^{-x} l_x b_x \quad (1)$$

(Lotka 1956), where l_x is the survival to age x and b_x the fecundity at age x . Fifth, l_x and b_x schedules for a given genotype are assumed to be unvarying.

Simplifying Assumptions

To formulate the model in its simplest form, we assume that adult mortality and fecundity are constant after the onset of reproduction. Therefore, l_x of equation (1) is replaced by $l_x = l_\alpha(1 - M)^{x-\alpha}$, where M is the probability of death between one breeding season and the next, and α is the age of onset of reproduction. We further set b_x equal to B , where B is the number of young raised to independence annually and does not include eggs or young that die

or are killed prior to independence. Fecundity (B) is distinguished from survival of immature individuals between independence and the age of first reproduction (l_α) by being dependent on reproductive effort of the parents; l_α is not. Fecundity prior to the age of first reproduction is 0. With constant fecundity and mortality assumed, equation (1) becomes

$$1 = l_\alpha B \sum_{x=\alpha}^{\infty} \left(\frac{1-M}{\lambda} \right)^{x-\alpha},$$

which may be transformed to

$$\lambda^\alpha - \lambda^{\alpha-1}(1-M) - l_\alpha B = 0, \quad (2)$$

provided that $(1-M) < \lambda$. If $l_\alpha B$ is greater than 0, population growth rate (λ) will always exceed annual adult survival $(1-M)$; a population cannot decline more rapidly than individuals die.

When mortality (M) equals recruitment ($l_\alpha B$), equation (2) reduces to $\lambda = 1$ (constant population size). When age at first reproduction (α) is 1, equation (2) simplifies to $\lambda = l_\alpha B + (1-M)$.

STRUCTURE OF THE MODEL

Having derived λ as a function of M , B , α , and l_α , we now incorporate an expression relating M to B into the model. Adult mortality (M) is separated into two components: m , the risk of death resulting from reproductive activities that influence fecundity, and K , a component of adult mortality not influenced by reproductive activity. The K includes risk due to behavior preparatory to breeding (courtship, nest building, and so on) which does not directly bear on fecundity but is necessary for any level of reproductive output. In this model, m is related to B by

$$m = \left(\frac{B}{f} \right)^Z, \quad (3)$$

where f and Z are constants.

Equation (3) has several properties that are reasonable for a function relating risk to fecundity: when $B = 0$, $m = 0$; as B approaches f , m approaches 1, and so f represents an upper limit to fecundity; for positive Z , m increases as a monotonic function of B ; the shape of the function, which is determined by Z , is sufficiently flexible to provide approximate descriptions of many types of functions within a narrow range of B near the optimum. For a given level of reproductive risk (m), B varies in direct proportion to f . We may interpret f as a measure of resources, such as food availability or nesting-season length, that directly affect fecundity.

How we calculate annual adult survivorship $(1-M)$ from reproductive and nonreproductive components of mortality (m and K) depends upon the independence of the two probabilities of death. If an individual assumes reproductive and nonreproductive risk concurrently (Model I), the components

of mortality are additive and

$$(1 - M) = (1 - m - K). \quad (4)$$

If exposure to different sources of mortality is separated in time (Model II), the risks are independent and

$$(1 - M) = (1 - m)(1 - K). \quad (5)$$

Because exposure to nonreproductive risk occurs both during and outside the period of reproduction, both models apply to natural populations in some combination, and the most appropriate treatment of survivorship will lie somewhere between the extremes of Model I and Model II.

Optimization of Fecundity

Substituting expressions for $(1 - M)$ (4, 5) and m (3) into (2) yields an equation for population growth rate (λ) as a function of fecundity (B) and the variables f , K , l_α , and Z . Optimum fecundity is defined as that B which maximizes λ . Taking the derivative of the equation for λ with respect to B and solving for $d\lambda/dB = 0$ reveals a maximum at

$$\hat{B} = \left(\frac{l_\alpha f^Z}{Z \hat{\lambda}^{\alpha-1}} \right)^{1/(Z-1)}, \quad (Z > 1), \quad (6)$$

for Model I, and

$$\hat{B} = \left(\frac{l_\alpha f^Z}{(1 - K) Z \hat{\lambda}^{\alpha-1}} \right)^{1/(Z-1)}, \quad (Z > 1), \quad (7)$$

for Model II. The \hat{B} from Model II exceeds \hat{B} Model I by a factor of $[1/(1 - K)]^{1/(Z-1)}$. This factor is close to 1 for large Z ($Z \gg 1$) and small K ($0 < K \ll 1$), but it can become very large for large K , particularly as Z approaches 1. As we shall see below, empirically determined Z normally exceeds 4, and so optimum B calculated by the two models will normally differ by less than 20% for K as high as 0.5.

Properties of the Model

The relationships between optimum fecundity (\hat{B}) and the variables f , Z , l_α , and K (eqq. [6] and [7]) are complicated by the fact that λ incorporates each of the independent variables. The value of \hat{B} may be evaluated with the aid of a computer. If $\alpha = 1$, however, λ disappears from (6) and (7). In most of the derivations that follow, α is taken to be 1, but varying α does not qualitatively affect the results obtained here (Appendix A).

To examine the relationships between variables, equations (6) and (7) are first converted to their logarithmic forms:

$$\log \hat{B} = \frac{1}{(Z - 1)} (Z \log f + \log l_\alpha - \log Z), \quad (\alpha = 1), \quad (8)$$

for Model I, and

$$\log \hat{B} = \frac{1}{Z-1} [Z \log f + \log l_\alpha - \log Z - \log (1 - K)], \quad (\alpha = 1), \quad (9)$$

for Model II. Differentiating (8) and (9) with respect to l_α and f yields

$$\frac{\partial \log \hat{B}}{\partial \log l_\alpha} = \frac{1}{Z-1}, \quad (\alpha = 1), \quad (10)$$

and

$$\frac{\partial \log \hat{B}}{\partial \log f} = \frac{Z}{Z-1}, \quad (\alpha = 1). \quad (11)$$

Thus for large Z , \hat{B} is relatively insensitive to variation in prereproductive survival but varies in direct proportion to f . As Z approaches 1, \hat{B} becomes increasingly sensitive to both f and l_α . For Model II only, we obtain the relationship

$$\frac{\partial \log \hat{B}}{\partial \log (1 - K)} = -\frac{1}{Z-1}, \quad (\alpha = 1). \quad (12)$$

Optimum fecundity thus increases with increasing nonreproductive mortality (decreasing survivorship $[1 - M]$) but is relatively insensitive to K for large Z . Optimum fecundity is not related to K in Model I.

The optimum level of reproductive risk (\hat{m}) can be determined by substituting equation (3) into equations (6) and (7) and rearranging to obtain

$$\hat{m} = \frac{l_\alpha B}{Z\lambda^{\alpha-1}}, \quad (\text{Model I}), \quad (13)$$

and

$$\hat{m} = \frac{l_\alpha B}{Z\lambda^{\alpha-1}(1 - K)}, \quad (\text{Model II}). \quad (14)$$

Equations (13) and (14) indicate that optimum levels of reproductive risk vary in direct proportion to prereproductive survivorship (Models I and II) and inversely with adult nonreproductive survivorship (Model II only). To find the relationship between \hat{m} and f , we rearrange equation (6) to obtain

$$\frac{\hat{B}}{f} = \left(\frac{l_\alpha f}{Z\lambda^{\alpha-1}} \right)^{1/(Z-1)}, \quad (\text{Model I}),$$

and

$$\frac{\partial \log (\hat{B}/f)}{\partial \log f} = \frac{1}{Z-1}, \quad (\alpha = 1). \quad (15)$$

From equation (3) we obtain

$$\frac{\partial \log \hat{m}}{\partial \log (\hat{B}/f)} = Z, \quad (16)$$

and by multiplying (15) and (16) we obtain

$$\frac{\partial \log \hat{m}}{\partial \log f} = \frac{Z}{Z-1}, \quad (\alpha = 1). \quad (17)$$

A similar derivation for Model II is identical to (17). Equation (17) suggests that optimum reproductive risk increases as resources available to reproduction increase.

Density Dependence

The relationships among variables derived in the preceding section describe optimum levels of reproductive risk and resulting levels of fecundity for given prereproductive survivorship, nonreproductive adult mortality, resource availability (f), and relationship of risk to fecundity (Z). The slopes of the partial correlations among variables show the initial direction of evolutionary change in \hat{m} and \hat{B} with respect to changes in l_α , K , and f in a population with unrestricted growth (density independence). Under the more usual conditions of density-dependent regulation of bird populations (Lack 1966; Tanner 1966; von Haartman 1971; Ricklefs 1973b), environmentally induced changes in l_α , K , and f , as well as evolutionary responses of m and B to the environment, cause compensating adjustment of the life table so that population growth rate (λ) remains close to 1.

In a density-dependent system in which $\lambda = 1$, the reproductive-effort model developed above has the added constraint that recruitment ($l_\alpha B$) must equal mortality (M), a condition derived from (2) for the special case of $\lambda = 1$. The relationship among variables in the model under density-dependent restraints may be derived from equations (3), (4) or (5), and (6) or (7) with the restriction

$$M = l_\alpha B, \quad (\lambda = 1). \quad (18)$$

According to Model I (additive adult mortality components), equations (3), (4), and (18) may be combined to give

$$\left(\frac{B}{f}\right)^Z + K = l_\alpha B \quad (19)$$

which, expanded slightly, becomes

$$\frac{B}{f^Z} B^{Z-1} + K = l_\alpha B$$

which, with (6) substituted for \hat{B}^{Z-1} , yields

$$\hat{B} = \frac{K}{l_\alpha} \left(\frac{Z}{Z-1} \right). \quad (20)$$

A similar derivation for Model II gives the same result. Because f is allowed to vary, it absorbs density-dependent adjustments required by changes in the ratio of K to l_α . With this condition (eq. [19]), we see that $\partial \log \hat{B} / \partial \log K = 1$, and $\partial \log \hat{B} / \partial \log l_\alpha = -1$. Furthermore, because $B l_\alpha = M$, $K = M[(Z-1)/Z]$, $\hat{m} = \hat{M}/Z$, and

$$\hat{m} = \frac{K}{Z-1} \quad (21)$$

for both Model I and Model II.

When prereproductive survivorship (l_x) rather than f is unspecified in the equation for optimum B , we may evaluate the model as follows: for Model I, equation (19) is rearranged using the relationship, obtained from (6),

$$\hat{B} = \frac{Z}{l_x} \left(\frac{\hat{B}}{f} \right)^Z$$

to give

$$K + \left(\frac{\hat{B}}{f} \right)^Z = Z \left(\frac{\hat{B}}{f} \right)^Z,$$

which may be rearranged to give

$$\hat{B} = \left(\frac{Kf^Z}{Z - 1} \right)^{1/Z}. \quad (22)$$

Hence with l_x allowed to vary and thus absorb density-dependent adjustments required by changes in the product Kf^Z ,

$$\frac{\partial \log \hat{B}}{\partial \log K} = \frac{1}{Z}, \quad (23)$$

and

$$\frac{\partial \log \hat{B}}{\partial \log f} = 1. \quad (24)$$

Note that equation (21), relating \hat{m} to K , also applies here.

In the density-dependent system, optimum reproductive risk is always a constant fraction $[1/(Z - 1)]$ of nonreproductive mortality. The relationship of reproductive rate to nonreproductive mortality in an optimized system depends on whether density-dependent feedbacks required by variation in K are met through changes in resources for reproduction (f) or prereproductive survival (l_x). In the first case, \hat{B} varies in direct proportion to K ; in the second case, \hat{B} is relatively insensitive to K for large Z .

Calculation of Z

Because Z has a strong bearing on relationships among variables in the optimized model, it will be useful to derive an expression relating Z to quantities that can be estimated for natural populations. For Model I, we combine (3) and (4) to give $M = (B/f)^Z + K$, which, slightly expanded, becomes

$$M = \frac{BB^{Z-1}}{f^Z} + K. \quad (25)$$

From equation (6) we obtain

$$\hat{B}^{Z-1} = \frac{l_x f^Z}{Z \hat{\lambda}^{\alpha-1}}. \quad (26)$$

Substituting (26) into (25) and solving for Z yields

$$Z = \frac{l_x \hat{B}}{(\hat{M} - K) \hat{\lambda}^{\alpha-1}} \quad (27)$$

at optimum B . Substituting $l_{\alpha}\hat{B} = \hat{\lambda}^{\alpha-1}(\hat{\lambda} - 1 + M)$ (eq. [2]) and $\hat{m} = \hat{M} - K$ into (27) yields $Z = (\hat{\lambda} - 1 + \hat{M})/\hat{m}$, which reduces to

$$Z = \frac{\hat{M}}{\hat{m}} \quad (28)$$

for the special case of $\lambda = 1$. For Model II, the relationship of Z to annual adult mortality (M) and reproductive risk (m) is identical to that for Model I. Assuming constant population size, Z is the ratio of annual adult mortality to mortality related to reproduction.

ESTIMATION OF Z IN NATURAL POPULATIONS

The significance of Z for the evolution of reproductive effort can be seen in relationships among variables in the optimized demographic equation (6, 7, 20, 22). In a density-independent system, the sensitivity of \hat{B} to changes in prereproductive survivorship (l_{α}) (10), and adult nonreproductive mortality (K) (12), decreases with increasing Z . Among independent environmental variables, only f , acting directly upon fecundity, exerts a strong influence on \hat{B} at all levels of Z (11). In a density-dependent system, Z determines the sensitivity of \hat{m} (reproductive risk) to K (21), and of \hat{B} to K (23) when density-dependent responses to the population are absorbed by prereproductive survivorship (l_{α}) and not by f .

When reproductive risk is optimized, Z can be estimated by the ratio \hat{M}/\hat{m} (eq. [28]), that is, the ratio of total adult mortality to reproductive mortality. Annual adult mortality (\hat{M}) is well known for many species of birds, both from studies of survivorship in marked populations and from the recovery of individuals banded as nestlings (see, for example, Deevey 1947; Hickey 1952, 1955; Farner 1955; Lack 1954; Boyd 1962; Ashmole 1971; Henny 1972; Ricklefs 1973b), but mortality owing to reproductive effort is more difficult to ascertain.

In this study, the ratio of \hat{M} to \hat{m} is estimated from the annual distribution of deaths. When the disappearance of birds from local populations or the recovery of dead birds are tabulated on a monthly basis, one can differentiate mortality during the reproductive and nonreproductive seasons. Two estimates of reproductive mortality (\hat{m}) were used to calculate Z : (1) total deaths during the breeding season, and (2) excess of deaths during the breeding season over the average number of deaths for months immediately prior to and following the breeding season. In both cases, \hat{M} is the total of disappearances or recoveries. Therefore, estimates of \hat{M} and \hat{m} are normalized to $\hat{M} = 1$ and they do not reflect absolute mortality rates. Values of \hat{m} also can be estimated from differences in annual mortality rates of males and females when the relative reproductive effort of each sex can be guessed with confidence, as in cowbirds or species with precocious young.

In estimating Z from the monthly distribution of recoveries, we assume that the effects of reproduction on adult survivorship are felt immediately and that changes in mortality due to reproductive effort appear only during the breeding season. Birds may, however, subsequently suffer from depletion of nutrient

TABLE 1
ESTIMATED VALUES FOR *Z*

| SPECIES AND REFERENCE | BASIS FOR CALCULATION | VALUES FOR <i>Z</i> CALCULATED FROM <i>m</i> ESTIMATED AS | |
|--|------------------------------------|---|--------|
| | | Total | Excess |
| Sparrow hawk (Glue 1973) | Recoveries | 2.4 | 5.4 |
| California quail (Anthony 1970) | Sex ratio | ... | 6.0 |
| Great blue heron: | | | |
| (Owen 1959) | Recoveries | 3.5 | 12.0 |
| (Henny 1972) | Recoveries | 4.2 | 10.5 |
| Black-crowned night heron (Henny 1972) . . . | Recoveries | 2.3 | 4.1 |
| Silver gull (Van Tets 1968) | Recoveries | 5.6 | ... |
| Southern black-backed gull (Van Tets 1968) . | Recoveries | 6.7 | ... |
| Herring gull (Van Tets 1968) | Recoveries | 2.2 | 3.8 |
| Black-headed gull (Van Tets 1968) | Recoveries | 5.5 | ... |
| Glaucous-winged gull (Van Tets 1968) | Recoveries | 5.6 | ... |
| Barn owl (Glue 1973) | Recoveries | 3.2 | 7.4 |
| Little owl (Glue 1973) | Recoveries | 3.4 | 4.6 |
| Tawny owl (Glue 1973) | Recoveries | 1.6 | 4.3 |
| Robin (Farner 1949): | | | |
| 2+ yr | Recoveries | 2.6 | 9.6 |
| 1st year | Recoveries | 2.2 | 4.9 |
| English blackbird (Snow 1958 <i>b</i>): | | | |
| 2d calendar year | Recoveries | 1.8 | 6.7 |
| Later years | Recoveries | 1.8 | 4.6 |
| Starling (Fankhauser 1971) | Sexual differences in mortality | ... | 7.0 |
| House sparrow (Summers-Smith 1956): | | | |
| 1 | Recoveries | 1.9 | 2.9 |
| 2 | Returns | 1.8 | 3.9 |
| Cowbird (Fankhauser 1971) | Sexual differences in mortality | ... | 7.4 |
| Song sparrow (Nice 1937) | Returns | 3.5 | 7.0 |

NOTE.—For further details see Appendix B.

reserves at the end of the breeding season. Although many species lose weight during the breeding season (e.g., Richdale 1947; Nice 1937; Newton 1966), observations on female starlings (*Sturnus vulgaris*) indicate that weight loss results from the recrudescence of the ovary and oviduct and involves neither fat reserves nor somatic tissues (Ricklefs and Hussell, unpublished). In other species, however, adult weight loss during the nesting cycle may result in severe atrophy of some somatic tissue (Ankney 1974). Furthermore, weights of some species at the end of the nesting cycle have been shown to be inversely related to reproductive effort (Breitenbach and Meyer 1959; Breitenbach et al. 1963; Hussell 1972; Redfield 1973).

Estimated values of *Z* for 18 species of birds are presented in table 1. Most values of *Z* lie between four and 10, with an average of 6.2 ± 2.5 SD, when *Z* is calculated from excess mortality. Because many breeding activities not directly bearing on variation in fecundity must carry substantial risk, \hat{m} is

undoubtedly overestimated and Z underestimated in this study. Original data, calculations employed, and variation among species are discussed in Appendix B.

THE CAUSE OF HIGH Z -VALUES

The relationship between m and B becomes increasingly concave with higher Z , approaching what might be regarded as a threshold function in which m is negligible up to some critical value of B and then increases rapidly above that point. The B -axis should properly be regarded as a vector in a multidimensional space with as many axes as there are ways to alter fecundity (e.g., number of broods, development rate, egg size, clutch size, parental defense), each scaled by increments of contribution to B . Selection will inevitably extend reproductive effort in that direction which offers the least resistance, in terms of increased adult mortality.

Important components of fecundity are: (1) number of eggs laid and young successfully nourished, (2) length of breeding season, (3) length of nesting cycle, and (4) probability of survival of the offspring from egg laying to independence (Ricklefs 1969). Variation in clutch size and breeding-season length are tied to the adult's ability to exploit food resources and, to somewhat lesser degree, the efficiency with which the young utilize resources. Length of the nesting cycle derives from the development rate of the young and the duration of the period of parental care (relative to stage of development of the young). Nest success is influenced by antipredator adaptations of the parents and young, including nest construction, choice of nest site, defensive behavior, and even social organization. All these factors are interrelated, and all could be expected to result in high Z -values. For example, extension of the nesting season may cut into the adult molting period in late summer. Late nests are known to be unproductive in many species, and the increased parental risk resulting from a lengthened season may provide little gain in fecundity. In the extreme, extending reproductive effort to include winter breeding would surely result in high Z -values in most species because risk would increase with virtually no increment in fecundity. Increased foraging effort, undertaken to increase clutch size, could upset the heat balance or water balance of adults above a critical level of activity (Ricklefs and Hainsworth 1968; Ricklefs 1971) and create a true threshold function.

Foraging also reduces the wariness of the adults and increases their vulnerability to predators. Ashmole (1963) noted that cat predation on boobies (*Sula* spp.) on Ascension Island increased dramatically when the adults began to feed their chicks. Of 13 deaths of known cause of blackbirds (*Turdus merula*) in the Botanic Garden at Oxford, eight were due to predators, including five birds taken by tawny owls (*Strix aluco*) (Snow 1958b). Most deaths occurred during the breeding season. Summers-Smith (1956) noted that adult house sparrows (*Passer domesticus*) are most easily trapped during the breeding season. Of 21 birds banded as juveniles and later trapped as adults, 12 recaptures occurred at a time when the birds were feeding young in the nest, three when feeding

fledglings, and only two outside the breeding season. Similarly, Glue (1973) has noted that deaths in small raptorial birds caused by vehicles, telephone wires, shooting, and trapping occur at a disproportionately high rate during the breeding season compared to other causes of death.

Although shortening the development period would increase fecundity, growth rate is tied so closely to precocity of development and parental care (Ricklefs 1969, 1973a) that it is unlikely to be evolutionarily flexible and probably is beyond the influence of adult reproductive effort. Indeed, of all components of fecundity, the length of the nest cycle exhibits the least variation among species of birds.

Antipredator defenses are tied to other components of fecundity, and their relationship to reproductive risk is unclear: increased parental care of the young would reduce time for foraging; selection of less accessible nest sites could limit suitable habitat and increase intraspecific competition; construction of a less easily detectable nest could reduce its insulative qualities and therefore reduce nestling growth efficiency.

The construction of a nest and provision of parental care that are minimally sufficient for raising young would likely yield a substantial increment in fecundity compared to adult risk. But when adult time and energy are fully allocated, changes in behavior would likely require substantial changes in reproductive strategy and therefore might increase risk greatly with little gain in fecundity. A risk-fecundity function with a high value of Z may easily be envisioned. The complete resolution of this function is, however, clearly beyond the scope of this paper but nonetheless should receive more attention from field ecologists in the future.

DISCUSSION

Strategies of reproduction in birds are constrained by the opposing influences of reproductive effort on fecundity and adult survival. In an optimized system, reproductive effort should increase until the added mortality resulting from reproductive activities more than offsets the increment in lifetime reproductive output.

Among the diverse reproductive and life-history patterns of birds, breeding productivity is inversely related to life span. At one end of the demographic spectrum, annual survival of adult wandering albatrosses (*Diomedea exulans*) exceeds 95%. Age at first reproduction is delayed up to the tenth year, only one egg is laid, and adults breed every other year (Tickell 1968). At the other end of the demographic spectrum, many small, temperate zone songbirds exhibit annual mortality rates of 50% or more, but individuals breed at the age of 1 yr, commonly lay four to six eggs per clutch, and often attempt to raise two or three broods per season (e.g., Nice 1937).

The inverse relationship between fecundity and life span in birds is consistent with the idea that reproductive effort should be inversely related to life span (Williams 1966a, 1966b; Cody 1971), but the relationship could also be predicted from density-dependent adjustments of the life table in response to environ-

TABLE 2

DEMOGRAPHIC PARAMETERS M , B , AND l_x FOR REPRESENTATIVE SPECIES OF BIRDS

| Species and Source | Locality | M | B | l_x |
|--|-------------------|------|------|-------|
| Wandering albatross (Tickell 1968) | S. Georgia Is. | .043 | 0.17 | .25 |
| Gannet (Nelson 1964, 1966) | England | .061 | 0.40 | .15 |
| Black-and-white manakin (Snow 1962) . . . | Trinidad | .11 | 0.50 | .22 |
| Kittiwake (Coulson and White 1958, 1959) | England | .12 | 0.75 | .16 |
| Yellow-eyed penguin (Richdale 1957) | New Zealand | .16 | 0.81 | .20 |
| Shag (Potts 1969; Snow 1960) | England | .20 | 1.00 | .20 |
| Brown pelican (Henny 1972) | Southeastern U.S. | .20 | 0.43 | .47 |
| Scrub jay (Wolfenden 1973) | Florida | .20 | 0.57 | .35 |
| Great blue heron (Henny 1972) | Eastern U.S. | .22 | 1.00 | .22 |
| Red-shouldered hawk (Henny 1972) | Eastern U.S. | .31 | 0.94 | .33 |
| Barn swallow (Henny 1972) | Eastern U.S. | .43 | 2.99 | .14 |
| Black-capped chickadee (Henny 1972) . . . | Eastern U.S. | .50 | 3.00 | .17 |
| Robin (Henny 1972) | Eastern U.S. | .50 | 2.59 | .19 |
| Tree sparrow (Pinowski 1968) | Poland | .55 | 6.60 | .08 |

mental factors affecting either fecundity or mortality (see Lack 1966; Cody 1966). We must ask, therefore, to what extent life-history patterns represent the optimization of fecundity and survivorship with respect to each other or, conversely, the independent optimization of fecundity and survivorship with respect to ecological influences acting directly upon each, their relationship being determined either by density-dependent factors in the environment or fortuitously. Specifically, are the different reproductive rates of the albatross and sparrow the result of adaptations optimized with respect to factors in the environment that directly influence fecundity or with respect to the different life spans of the two species? Put another way, do albatrosses and sparrows assume different levels of reproductive risk, and if so, what is the resulting difference in fecundity? In a density-dependent system, fecundity (\hat{B}) and adult mortality (\hat{M}) are related by $\partial \log \hat{B} / \partial \log \hat{M} = 1/Z$ if the burden of density dependence is assumed by prereproductive survivorship (l_x), and they are related by $\partial \log \hat{B} / \partial \log \hat{M} = 1$ if density dependence is assumed by factors in the environment directly affecting fecundity through f . Remember that Z is the power of the relationship between reproductive risk (m) and fecundity in the expression $m = (B/f)^Z$. If l_x varied in a density-dependent manner and f were held constant, variation in \hat{B} would be caused solely by optimization with respect to prereproductive survival and adult mortality. If Z were large, the influence of adult mortality on optimum B would be small, even though reproductive risk is always a constant proportion ($1/Z$) of total adult mortality. If f varied in a density-dependent manner and l_x were held constant, the relationship between \hat{B} and \hat{M} would derive primarily from the relationship between B and f in the equation $B = fm^{1/Z}$ when Z is large. Reproductive risk, although varying in direct proportion to adult mortality, would exert little influence on \hat{B} .

Representative values of \hat{M} , \hat{B} , and l_x are listed in table 2. The term \hat{M} was determined from recoveries of banded birds, \hat{B} was estimated as the number of

young fledged per pair per season divided by two, and l_x was calculated indirectly from the relationship $l_x = M/B$. Although the sample presented in table 2 is small, the data reveal that $\log \hat{B}$ is related to $\log \hat{M}$ ($r = .91$, $p < .01$) with slope $1.14 \pm .15$ SE, which is much greater than a slope of .17 (1/Z) expected from demographic optimization in a density-dependent system in which f is held constant. The slope of $\partial \log \hat{B} / \partial \log \hat{M}$ suggests that, in response to variation in K , density-dependent factors alter f rather than l_x . In fact, $\log l_x$ and $\log \hat{M}$ are not correlated ($r = -.25$, $p \gg .05$), but $\log l_x$ is related to $\log \hat{B}$ ($r = -.64$, $p < .05$) with slope $-.28 \pm .10$ SE. We may conclude that (1) the optimization of B with respect to M and l_x is a minor demographic force; (2) the inverse relationship of \hat{M} and \hat{B} is the result either of fortuitous correlations between environmental factors influencing the evolution of M and B independently or of density-dependent relationships between these variables; and (3) variation in prereproductive survivorship (which includes variation in age at first reproduction) results from density-dependent response to variation in fecundity, not to variation in adult mortality.

Although the correlation between \hat{B} and \hat{M} suggests a direct link between population density and resources available to individuals for reproduction, we lack evidence that density and \hat{M} are inversely related. Enhanced adult survival would tend to increase the adult population, bringing increased pressure on food resources and favoring reduced territory size. The value of \hat{M} is lowest in many seabird populations. The open ocean could probably support greatly increased populations of oceanic species, but food resources near breeding colonies may be severely depleted by the great concentrations of birds (Ashmole 1963, 1971). Changes in \hat{M} in seabird populations undoubtedly affect competition for food near the breeding site and thus affect \hat{B} . By comparison to small land birds, however, the low fecundity and low mortality of seabird populations are certainly determined, in part, independently by the peculiar features of oceanic existence: low \hat{M} being related to the absence of predators and to the vast resources available to nonbreeding birds, low \hat{B} being related to the concentration of individuals onto a few small islands. Because annual production of offspring cannot be reduced further in species laying one egg, requirements of constant population size are apparently met by variation in age at first reproduction, hence in l_x .

If population size were limited by the environment independently of \hat{M} , f would also be determined independently of \hat{M} and the relationship of \hat{B} to \hat{M} would be mostly a fortuitous consequence of negative correlations between breeding and nonbreeding environments. For example, adult survivorship may be enhanced in the tropics by the favorable climate compared to temperate regions, but the lack of marked seasonality may also reduce the surplus of resources over adult requirements during the breeding season, and hence reduce \hat{B} .

If the relationship between \hat{B} and \hat{M} were not perfect, the density dependence observed among populations and required by population stability would be expressed in variation in the survival of young to reproduction (including deferred maturity). The burden of density dependence within populations is

known to fall on prereproductive individuals in many species (Tanner 1966; Watson 1967; Sadler 1969), but the weak correlation between l_x and \hat{B} and small slope $\partial \log l_x / \partial \log \hat{B}$ suggests that fecundity is the primary target of density dependence.

Although the model presented here relates fecundity to adult mortality only weakly through demographic optimization—the cause of the observed correlation between \hat{B} and \hat{M} lying elsewhere—reproductive risk (\hat{m}) is expected to vary in direct proportion to nonreproductive adult mortality (K) and total adult mortality (\hat{M}) (eq. [21]). If Z were reasonably constant among species, albatrosses would be expected to assume only one-tenth the risk in reproduction as sparrows. The difference in risk would not, however, be clearly reflected in fecundity if Z were great. Nor would differences in reproductive behavior causing a 10-fold change in risk necessarily be apparent if Z were large and the relationship between m and B therefore approached a threshold function. When Z is large, demographic optimization occurs within the region in which m rises steeply with increasing B , and small changes in behavior (for example, proportion of time spent feeding, length of nesting season, nest tenacity at the approach of predators) increase m rapidly.

The analyses presented in this paper advise caution in interpreting life-history patterns in birds as evidence for the different effects of r - and K -selection (Cody 1966; MacArthur and Wilson 1967; cf. Wilbur et al. 1974). Populations with relatively constant size maintained by intraspecific competition at or near the carrying capacity of the environment most of the time are said to be K -selected. Populations in variable and unpredictable environments, suffering catastrophic population crashes and thus frequently in a rapid growth phase of population recovery, are said to be r -selected. Pianka (1970) includes low fecundity, slow development, and deferred maturity as attributes of K -selected species; r -selected populations have opposite attributes. The model presented here suggests that optimum fecundity is relatively insensitive to variation in population growth rate when both Z is large and variation in population growth rate is caused by variation in adult mortality (Appendix A). Furthermore, fecundity is unrelated to population growth rate when age at first reproduction is 1 (eqq. [6] and [7]). It can be shown that changes in both adult mortality and population growth rate exert identical influences on fecundity when population growth rate is maintained at a constant level by density dependence. Under these conditions, variation in fecundity can be explained as well by variation in population turnover rate as by variation in population growth rate. Even for constant populations, fecundity will respond to variation in adult mortality among species.

The relationships among demographic parameters in populations of birds discerned in this study may be outlined as follows: The primary driving force in avian demography is seen as that aspect of the environment which influences adult self-maintenance, hence adult mortality. Fecundity is determined primarily by density-dependent response to adult mortality mediated through resources available for reproduction. A negative correlation between the environments separately influencing adult self-maintenance and breeding may

also be an important component of the observed negative correlation between survival and fecundity. Demographic optimization of m and B are of relatively little importance in bird populations, assuming a proportion of $1/Z$, perhaps 10%–25% of the correlation between survival and fecundity. Because prereproductive survivorship of fledglings (l_x) is correlated with fecundity but not adult mortality, variation in l_x is probably determined by breeding productivity. Indeed, one would expect conditions that enhance adult survivorship also to enhance prereproductive survivorship, balancing the relationship expected through density dependence and thereby obscuring the separate influences of fecundity and adult survival on prereproductive survivorship.

In conclusion, assuming the relationship between reproductive risk and fecundity used in this analysis, and values of Z estimated between four and 10, optimization of life-history parameters with respect to each other can account for only a small part of the diversity in the life histories of birds. The causes of this diversity must be sought primarily in environmental factors that directly influence fecundity, prereproductive survivorship, and adult mortality and in density-dependent or fortuitous relationships among these aspects of the environment.

SUMMARY

A model is developed for the optimization of fecundity (B) with respect to adult mortality (M) in populations of birds. Special assumptions of the model include constant age-specific survival and fecundity and adult risk due to reproduction (m) related to fecundity by the expression $m = (B/f)^Z$. The term f is interpreted as the level of resources available to reproduction. For large values of Z , optimized fecundity is insensitive to variation in M , although risk is always a constant proportion of $(1/Z)$ of M . Values of Z estimated for natural populations as the ratio of M to m were found to vary between four and 10 with an average of about six. The direct relationship between fecundity and adult mortality observed in natural populations is interpreted as reflecting primarily the density-dependent feedback of adult survival on resources for reproduction (f). Optimization of reproductive risk with respect to adult mortality exerts a minor influence on fecundity and explains little of the variation of reproductive rates among species of birds.

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APPENDIX A

EVALUATION OF PREMISES AND ASSUMPTIONS

Many of the premises and assumptions of the model presented here slightly misrepresent nature for the sake of simplification. In this appendix, I have not attempted so much to evaluate the quantitative effects of these simplifications on the model as to demonstrate that their influence is small.

1. *λ as a measure of fitness.*—Population growth rate (λ) can be calculated accurately from life-table data for a population when all individuals have the same expectations of age-specific survivorship and fecundity and the life table is unchanging. For two uniform populations with different genotypes, λ provides a valid measure of their relative fitness, but the replacement of one genotype by another due to natural selection necessarily occurs in a genetically heterogeneous population, unless one invokes group selection. Unique values of λ cannot strictly be calculated for different genotypes within a population because interactions between the genotypes vary with the frequency of the genotypes. Unless negative interactions, such as heterozygote inferiority, exist between genes, gene interactions will affect the rate of evolutionary change but not its final outcome. Thus λ calculated for the uniform population is probably a reasonable measure of the competitive status of a genotype at any frequency. Furthermore, the traits affecting life-table parameters probably have polygenic inheritance with each locus providing small additive effects. Interactions of the kind that would prevent the fixation of a superior allele are probably rare. Genes causing such interactions would presumably be removed by selection from a system which is genetically sensitive to small changes in the environment.

2. *Discrete generations.*—Most species of birds are seasonal breeders with annual cycles of reproductive behavior and physiology. Populations therefore have discrete age classes, as required by equation (1). Reproduction does, however, require considerable time, during which some adults die. This presents a problem for defining age-specific survivorship (l_x). For synchronized breeders that lay one clutch per year, one could measure survivorship and fecundity at the end of the period of parental care, thereby avoiding the complication of adult death during reproduction. With renesting and the raising of additional broods during the nesting season, natural populations deviate more widely from the premises of equation (1). At one extreme, we may imagine a population with continuous breeding and total lack of synchrony. This population can be modeled by the integral equation analogous to (1),

$$1 = \int_{x=\alpha}^{\infty} \lambda^{(x-\alpha)} l_x b_x dx,$$

which, assuming $b_x = B$ and $l_x = l_x(1 - M)^{(x-\alpha)}$, yields

$$\hat{B} = \left(\frac{l_{\alpha} f Z}{Z \lambda^{\alpha}} \right)^{1/(Z-1)}$$

for Model I. This result is identical to (6) except that $\lambda^{\alpha-1}$ becomes λ^2 . If $\alpha = 0$, or if $\lambda = 1$, the derivation of Z and the relationships among variables are identical to those of the discrete-generation case. A discrete-generation analogue (see Goodman 1967) of the continuous breeding model, whose solution is given here, yields the same result.

3. *Age at first reproduction* [$(\alpha) = 1$].—The discrete-generation model was evaluated at $\alpha = 1$ to simplify the expression for \hat{B} (6, 7). Changing the age at first reproduction distorts the time scale of the life table but does not substantially alter \hat{B} if age at first reproduction (α) is independent of l_x , K , f , and Z . The influence of α on \hat{B} in Model I can be evaluated by taking the logarithm of (6) and solving for

$(\partial \log B)/(\partial \alpha) = -[(\log \lambda)/(Z - 1)]$. For large Z or λ close to 1, α has little influence on optimum fecundity. In a growing population ($\lambda > 1$), \hat{B} decreases with increasing α (K also must decrease concurrently to maintain constant λ); in a declining population ($\lambda < 1$), \hat{B} increases with increasing α (and decreasing K).

4. *Population growth rate* [$(\lambda) = I$].—In the density-dependent model, we assumed constant population size. If a population were to increase or decrease at a constant rate, the influence of λ on \hat{B} can be evaluated by taking the logarithm of (6) or (7) and solving for

$$\frac{\partial \log \hat{B}}{\partial \log \lambda} = -\frac{\alpha - 1}{Z - 1} \quad (29)$$

when λ is altered by variation in K . For $\alpha > 1$, optimum B decreases with increasing λ (decreasing K), but the effect is diminished by large Z .

5. *Reproductive risk (m) equals (B/f)^Z*.—The relationship between m and B was chosen for its simplicity and flexibility of form. Using this relationship, the model predicts positive, finite values for optimum fecundity (\hat{B}) for all Z greater than 1. If increasing reproductive effort were to increase risk more rapidly than it increased fecundity—an application of the law of diminishing returns—the assumption of $Z > 1$ would be reasonable. Furthermore, the function is reasonable in that m increases monotonically with increasing B , and $m = 0$ when $B = 0$.

The relationship between risk and fecundity has no asymptotic upper bound and thus allows m to exceed 1 when B exceeds f . In a discrete-generation model, mortality cannot exceed 1, and B must therefore be less than f . If a continuous model is used, m has no upper bound in so much as mortality is an instantaneous rate.

If m is much less than 1, the behavior of the function $m = (B/f)^Z$ as it approaches and exceeds 1 may not be pertinent to the behavior of the model. The slope of the relationship between m and B , $dm/dB = (ZB^{Z-1})/f^Z$, evaluated at \hat{B} is

$$\frac{dm}{dB} = l_\alpha \quad (30)$$

for Model I and

$$\frac{dm}{dB} = \frac{l_\alpha}{1 - K} \quad (31)$$

for Model II, when $Z > 1$ and $\alpha = 1$.

If mortality is related to fecundity by a linear model, such as $m = c_1 + c_2 B$, $d\lambda/dB = 0$ when $c_2 = l_\alpha$ (Model I) or when $c_2 = l_\alpha/(1 - K)$ (Model II, $\alpha = 1$). Also, $dm/dB = c_2$. Furthermore, $d\lambda/dB > 0$ when $dm/dB < l_\alpha$, and $d\lambda/dB < 0$ when $dm/dB > l_\alpha$. Therefore, any model relating m to B will have a stable equilibrium point at $dm/dB = l_\alpha$, or $dm/dB = l_\alpha/(1 - K)$ if the second derivative of the relationship between m and B is positive at that point. A function for m which, for example, is asymptotic to $(1 - K)$ (Model I) or 1 (Model II) with increasing B , and which has an initial concave portion whose slope exceeds l_α or $l_\alpha/(1 - K)$ at some point, will yield a stable equilibrium value for optimum fecundity (\hat{B}). Large portions of such curves around the equilibrium point should reasonably be described by an equation of form $m = (B/f)^Z$.

6. *Independence of l_α and B* .—In the model presented here, the influence of parental care on the survival of the offspring is included in B and ceases abruptly at independence; l_α is independent of parental care. In natural populations, the influence of parental care clearly extends beyond the age of independence (Perrins and Moss 1974; Snow 1958a, 1958b), and many deaths prior to independence are clearly independent of parental care. Nonetheless, without parental care most species of birds cannot survive through the time of hatching, and many species cannot survive to the age at which the young begin to feed themselves. The influence of parental care on survival gradually diminishes thereafter.

We may ask whether separate components of mortality, one being dependent upon reproductive effort, the other unrelated, are truly independent. The term $l_{\alpha}B$ (recruitment) is equivalent to $C(1 - m_p)(1 - m_{np})$, where C = number of eggs laid, m_p = mortality related to lack of parental effort, and m_{np} = mortality unrelated to parental effort. Formulating recruitment thusly is suitable if m_p and m_{np} are independent. If young were susceptible to both types of mortality at the same time, recruitment should be reformulated as $C(1 - m_p - m_{np})$. Natural populations must lie somewhere between these extremes. Replacing $l_{\alpha}B$ by $C(1 - m_p - m_{np})$ has little influence on the model if m_p and m_{np} are small. Substituting $C(1 - m_p - m_{np})$ for $l_{\alpha}B$ in equation (2), we obtain $\lambda = 1 - M + C(1 - m_p - m_{np})$, ($\alpha = 1$). We again let $M = m + K$ (Model I). If adults incur reproductive risk only by altering number of eggs laid (C), we have $m = (C/f)^Z$, and the outcome of the model is changed only in that B becomes \hat{C} and l_{α} is replaced by $(1 - m_p - m_{np})$.

When adults incur reproductive risk by attempting to reduce the mortality of their young (m_p), the relationship between risk and survival of young, $s_p = (1 - m_p)$, may be described as $m = s_p^Z$ ($s_p < 1$). In this formulation, m approaches 1 as s_p approaches 1; Z determines the concavity of the function. Substituting $C(1 - m_p) \times (1 - m_{np})$ for $l_{\alpha}B$ in equation (2) and following the steps represented by equations (3)–(6) yield $\hat{s}_p = [C(1 - m_{np})/Z]^{1/(Z-1)}$, (Model I, $\alpha = 1$), ($Z > 1$ and $C[1 - m_{np}] < Z$), which is identical in form to (6). The expression for estimating Z and the relationships among variables remain unchanged, with the appropriate substitutions made. Interesting and testable predictions are that $(\partial \log \hat{s}_p)/(\partial \log C) = 1/(Z - 1)$, and $(\partial \log \hat{s}_p)/(\partial \log s_{np}) = 1/(Z - 1)$.

Assuming mortality components m_p and m_{np} to be additive and substituting $C(1 - m_p - m_{np})$ for $l_{\alpha}B$ in (2) yield $\hat{s}_p = (C/Z)^{1/(Z-1)}$, (Model I, $\alpha = 1$), ($Z > 1$ and $C < Z$). In this case, s_p is not related to $(1 - m_{np})$, except through demographic feedback imposed by density-dependent population regulation. When components of prereproductive mortality are additive, the constraint $C < Z$ is more stringent than when mortality components are independent [$C(1 - m_{np}) < Z$].

7. *Constant age-specific adult mortality.*—Birds are thought to be nearly unique among animals in that adult mortality remains constant with increasing age (Deevey 1947; Lack 1954; Farnier 1955; Henny 1972). Botkin and Miller (1974) have recently argued, however, that birds exhibit increasing mortality with age. Birds kept in laboratories or zoos do, in fact, demonstrate senescence (Comfort 1962), but few wild birds attain the age of captive individuals. This controversy cannot be resolved here. It would be informative, nonetheless, to evaluate the effect of an increasing mortality rate with age on the equilibrium value of B . Age-specific changes in fecundity (B_x) in response to increasing M_x will not be considered.

Hamilton (1966) derived an expression for evaluating the effect of a small step change in adult mortality M at age a on population growth rate. Restated in the symbols used in this paper, Hamilton's expression is

$$\frac{d \log \lambda}{d \log (1 - M)_{(a \dots \infty)}} = \frac{\sum_{a+1}^{\infty} (x - a) \lambda^{-x} l_x b_x}{\sum_0^{\infty} x \lambda^{-x} l_x b_x}.$$

Assuming M_x and b_x constant, we have

$$\frac{d \log \lambda}{d \log (1 - M)_{(a \dots \infty)}} = \frac{l_{\alpha} B \sum_{a+1}^{\infty} (x - a) \lambda^{-x} (1 - M)^x}{l_{\alpha} B \sum_0^{\infty} x \lambda^{-x} (1 - M)^x} = \left(\frac{1 - M}{\lambda} \right)^a.$$

Utilizing equation (29), $\partial \log \hat{B} / \partial \log \hat{\lambda} = -(\alpha - 1)/(Z - 1)$ (l_{α} , f , Z constant, K variable; Model I), we find that

$$\frac{d \log \hat{B}}{d \log (1 - M)_{(a \dots \infty)}} = \frac{d \log \hat{\lambda}}{d \log (1 - M)_{(a \dots \infty)}} \cdot \frac{d \log \hat{B}}{d \log \hat{\lambda}} = -\frac{\alpha - 1}{Z - 1} \left(\frac{1 - M}{\lambda} \right)^a.$$

Increasing adult mortality at age a (reducing $1 - M$) increases optimum fecundity in the absence of density-dependent effects of changed K on l_x and f , but the effect is small, and it is nought when $\alpha = 1$.

8. *Constant age-specific fecundity*.—Number of eggs laid per season and nesting success are known to increase with age in many species (for references see Lack 1966, 1968; Klomp 1970; Ainley and Schlatter 1972; Ricklefs 1973b; Perrins and Moss 1974). The influence of increasing age-specific fecundity on \hat{B} after fecundity levels off is negligible if feeding efficiency (f) rather than reproductive risk (\hat{m}) accounts for the increase in \hat{B}_x . In this case, we may treat the reduced fecundity of young birds as equivalent to an increase in age of first reproduction (α) which, as we have seen from (c) above, has little effect either on \hat{B} or on the general structure of the model.

APPENDIX B

SOURCES OF DATA

1. Sparrow hawk (*Accipiter nisus*): Data compiled by Glue (1973) from records of birds recovered in England by the British Trust for Ornithology (BTO); 118 adults at least 2 yr old; breeding season May–July.

2. California quail (*Lophortyx californica*): Data from Anthony (1970), gathered in southeastern Washington. Excess mortality of females over males, attributed to reproductive effort (primarily egg laying and incubation), was calculated from the change in sex ratio of the population among subsamples of immature and adult birds.

3. Great blue heron (*Ardea herodias*): Owen (1959) tabulated monthly recoveries of birds banded as nestlings and recovered throughout North America; 126 adults at an age of more than 1 yr; breeding season April–June. Henny (1972) tabulated monthly recoveries of birds banded as nestlings and found dead throughout North America; 68 adults at an age of more than 2 yr; breeding season April–June.

4. Black-crowned night heron (*Nycticorax nycticorax*): Henny (1972) tabulated monthly recoveries of birds banded as nestlings and found dead throughout North America; 134 adults more than 2 yr old; breeding season April–June.

5. Five species of gulls (*Larus*): Recoveries of birds banded as nestlings and found dead more than 1 yr after fledging, tabulated by Van Tets (1968). Silver gull (*L. novaehollandiae*), banded and recovered in southeastern Australia, 450 recoveries, breeding season August–October; southern black-backed gull (*L. dominicanus*), banded and recovered in New Zealand, 73 recoveries, breeding season October–December; black-headed gull (*L. ridibundus*), banded in the Netherlands, recovered in Europe and Africa, 155 recoveries, breeding season March–May; herring gull (*L. argentatus*), banded in the Netherlands, recovered in Europe and Africa, 295 recoveries, breeding season May–July, high reproductive mortality (low Z) may be due to poisoning programs during the breeding season; glaucous-winged gull (*L. glaucescens*), banded in British Columbia, recovered in western North America, 116 recoveries, breeding season May–July.

6. Barn owl (*Tyto alba*): BTO records of birds recovered in Britain tabulated by Glue (1973); 124 recoveries of birds 2 yr or older; young are fed July to October.

7. Little owl (*Athene noctua*): BTO records of birds recovered in Britain tabulated by Glue (1973); 101 recoveries of birds 2 yr or older; breeding season May and June.

8. Tawny owl (*Strix aluco*): BTO records of birds recovered in Britain tabulated by Glue (1973); 188 recoveries of birds 2 yr or older; breeding season March–July; total reproductive mortality may be low because adults do not breed in poor rodent years.

9. American robin (*Turdus migratorius*): Recoveries in North America tabulated by Farner (1949); 311 recoveries of adults found dead after their second January 1,

286 recoveries of immatures and adults found dead between their first and second January 1; breeding season April–June.

10. English blackbird (*Turdus merula*): BTO records of birds recovered in Britain tabulated by Snow (1958a); 209 immatures and adults found dead in their first calendar year (after their first January 1); 139 adults found dead in later calendar years; breeding season March–June.

11. Starling (*Sturnus vulgaris*): Z -value calculated from adult mortality rates for males (.546) and females (.588) presented by Fankhauser (1971); females were estimated to exert twice the reproductive effort of males, based on Kessel (1957) and unpublished observations of D. J. T. Hussell and R. E. Ricklefs; difference between mortality rates of sexes (.042) was therefore assumed to $\frac{1}{2}m$ ($m = .084$); Z was then calculated as the ratio $.588/.084 = 7.0$.

12. House sparrow (*Passer domesticus*): BTO records of birds recovered in Britain tabulated by Summers-Smith (1956); 359 birds recovered after their first January 1; breeding season April–July. Also, disappearances of color-marked adults from a local population studied by Summers-Smith (1956); 35 disappearances tabulated for birds after their first October 1; breeding season April–July; winter mortality may be low, and Z correspondingly low, due to abundance of food near human habitations.

13. Brown-headed cowbird (*Molothrus ater*): Z -value calculated from adult mortality rates for males (.515) and females (.596) presented by Fankhauser (1971); because males do not participate in reproduction beyond mating, the difference between male and female mortality rates (.081) was assumed to be equal to m ; Z was calculated as the ratio $.596/.081 = 7.35$.

14. Song sparrow (*Melospiza melodia*): Disappearances of individually marked birds from a local population studied by Nice (1937). Monthly mortality during the 2-mo breeding season was twice that during nonbreeding months. Total reproductive mortality was set at $2 \times 2 \text{ mo} = 4$, and nonreproductive mortality was set at $1 \times 10 \text{ mo} = 10$; Z was calculated as $14/4$ and $14/2$.

APPENDIX C

ALTERNATIVE LIFE-HISTORY MODELS

In his classic paper on life-history phenomena, Cole (1954) treated the demographic features of a population as a set of adaptations integrated by their common influence on population growth rate. Although Cole did not specifically consider the problem of reproductive effort, his elucidation of the relationship between fecundity and mortality led to a series of papers on the optimization of reproductive effort. The first of these was by Williams (1966a), who formulated the problem in terms of the trade-off between the risks and benefits resulting from small changes in reproductive effort. Williams considered optimum reproductive strategy as the sum of evolutionary choices made between increasing or not increasing effort by small increments of parental commitment.

Williams's result took the form $\hat{c} = [(a + b)\phi]/(\Phi - \phi)$, where \hat{c} is the barely justified cost, in terms of forfeited future (residual) reproductive output, of choosing to increase effort. The constants a and b are the magnitude of the opportunity for, and threat to, increasing reproductive value through increased fecundity; Φ is the reproductive value of the individual; ϕ is the portion of reproductive value at stake and thus influenced by the choice.

If \hat{c} is considered as an increment of cost to the individual measured in terms of potential future reproductive output and thus is analogous to dm in the terminology of this paper, and if $(a + b)\phi$ is considered as an increment of fecundity, analogous to dB , the expression analogous to equation (30)— $dm/dB = l_\alpha$ at \hat{B} and with λ or $\alpha = 1$ —would be, in Williams's terminology, $\hat{c}/[(a + b)\phi] = 1/(\Phi - \phi)$. We can

consider ϕ negligible compared to Φ . It is shown below that for a nonsenescent population (M_x and b_x constant), reproductive value is equal to $1/l_\alpha$. The term $\hat{c}/(a + b)\phi$ is thus equivalent to dm/dB evaluated at \hat{B} .

Reproductive value (V_a/V_0) at age a is defined as

$$\frac{V_a}{V_0} = \frac{\lambda^a}{l_a} \sum_{x=a}^{\infty} l_x b_x \lambda^{-x},$$

which, assuming $b_x = B$ and $l_x = l_\alpha(1 - M)^{(x-\alpha)}$, becomes

$$\frac{V_a}{V_0} = \frac{\lambda^a l_\alpha B}{l_\alpha (1 - M)^a} \sum_{x=a}^{\infty} \left(\frac{1 - M}{\lambda} \right)^{x-a},$$

or $V_a/V_0 = (B\lambda^{a+1})/(\lambda - 1 + M)$. For $\lambda = 1$, $V_a/V_0 = B/M$. Because, at $\lambda = 1$, $l_\alpha B = M$, $V_a/V_0 = 1/l_\alpha$. Hence, for λ close to 1, Williams's model and the model presented in this paper are consistent with each other. For nonsenescent species, \hat{c} (reproductive risk) is independent of age, and the acceptable increment of risk relative to increment of increased fecundity is equal to l_α , the survival from independence to first reproduction. We would expect, therefore, that reproductive risk would be greatest in species with the highest prereproductive survival, in spite of the negative correlation between l_α and B in table 2.

Goodman (1974) used an approach similar to that of Williams to model reproductive effort in long-lived seabirds. Assuming a nonsenescent life table, Goodman derived an expression for the relationship of cost to benefit that favors an increase in reproductive effort if $\Psi > \Psi'[(1/M) - 1]$, where Ψ is the fractional increment of prereproductive survival (l_α) due to added adult reproductive effort (clutch size is always 1 in Goodman's model), Ψ' is the decrement in fitness due to loss of expected future reproduction, and M is the annual adult mortality. For small changes in reproductive effort, we can consider Ψ as dB/B , and Ψ' can be shown to be approximately dm/M , giving

$$\frac{dm}{dB} = \frac{M}{1 - M} \quad (32)$$

at optimum B . In long-lived birds, selection to increase reproductive effort should, according to Goodman's model, proceed much less far than in short-lived birds along a curve of dm/dB that steadily increases with B . Goodman's result (32) greatly underestimates the justifiable cost of added fecundity for small M and overemphasizes the role of adult mortality in the optimization of reproductive output.

Goodman's model is not an optimization model and thus does not adequately reflect the process of natural selection. Evolution was constrained by $\lambda = 1$ and the resulting relationship $B = M/l_\alpha$. Because B was set at 1, increased prereproductive survivorship (l_α) is necessarily countered by an increase in adult mortality (M), hence the difficulty of increasing recruitment. The success of a novel genotype in natural populations is not, however, initially constrained by the density-dependent effects of its enhanced recruitment on the population as a whole because the genotype constitutes a small fraction of the population.

Gadgil and Bossert (1970) have constructed a model of optimal reproductive effort which specifies qualitative changes in fecundity and adult mortality with respect to reproductive effort. Their model maximizes λ , given fecundity and mortality as arbitrary functions of reproductive effort.

Simplifying Gadgil and Bossert's model by eliminating age dependence of fecundity, mortality, and body size after age α , yields

$$l_x = \prod_0^x c_1 f_1(\Theta) = [c_1 f_1(\Theta)]^x,$$

and $b_x = c_2 f_2(\Theta)$, where c_1 and c_2 are constants and f_1 and f_2 are functions relating annual survival and fecundity to reproductive effort, θ ($0 < \theta < 1$). These expressions are compatible with the model presented in this paper if we set c_1 and c_2 equal to 1, $f_1(\Theta) = 1 - \Theta^{Z_m}$, where $M = \theta^{Z_m}$, and $f_2(\Theta) = B = a\Theta^{Z_b}$. Because $\Theta = (B/a)^{1/Z_b}$, we obtain $m = (B/a)^{(Z_m/Z_b)}$, which is identical to equation (3).

Gadgil and Bossert explored many life-history phenomena, including the effect of uniform change in M_x . They concluded that "A change in mortality does not affect optimal reproductive effort. . . ." This conclusion was verified by Taylor et al.'s (1974) analysis of life-history strategies. In Model I of this paper, in which reproductive and nonreproductive components of mortality are additive, optimum fecundity is independent of K (eq. [6]). When the constraint of density dependence, which is not a feature of Gadgil and Bossert's model, is added, however, independence of B and K disappears (eq. [20]).

Schaffer and Tamarin (1973) employed an approach similar to that of Gadgil and Bossert (1970), except that they restricted themselves to a qualitative graphical analysis of expected direction of change in reproductive effort with varying density. Their model is thus not directly comparable to the analysis presented here.

Murphy (1968) has explored the consequences of year-to-year variation in l_x and B (M constant) on optimal reproductive effort and concluded that variable pre-reproductive survivorship (including that incorporated in B) favors increased life span and, presumably, reduced reproductive effort as a means of accomplishing this. The relative strength of selection on reproductive effort due to environmental variability compared to that due to changes in average demographic parameters has not been explored, but Murphy's analysis emphasizes the importance of stochastic properties of the environment to life-history models.

Green and Painter (1975) have devised equations relating the intrinsic rate of population increase to fertility and development time, using approaches similar to those outlined here. Their model employs a γ density function to describe the $l_x b_x$ curve of (1) and considers the trade-off between development time and total fertility (including adult survival) but does not incorporate density-dependent considerations.

Finally, Taylor et al. (1974) have derived a recursive formula for estimating optimum age-specific schedules of survivorship and fecundity. Their derivation is based on the principle that the optimum life-history strategy maximizes reproductive value at every age. Beginning with some small reproductive value at an arbitrarily old age, one can then work backwards through the life table to calculate optimum age-specific survivorship and fecundity. This technique promises to be a fruitful tool in population research.

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