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## EVOLUTION OF LIFE HISTORIES IN RESPONSE TO AGE-SPECIFIC MORTALITY FACTORS

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It has become increasingly common to view the life-history statistics of an organism as a coevolved unit. Regarded as an adaptation, these statistics summarize a good deal about the selective constraints "experienced" by the organism. Consequently, the  $l_x$  and  $m_x$  distributions reflect past environments in the sense that they have been molded by natural selection. As a result of MacArthur and Wilson's book (1967), an overemphasis was placed on density dependence as the main selective constraint molding the life history. This preoccupation with  $r$  and  $K$ -selection obscured some biological reality, and more recently writers have emphasized other constraints. For example, Wilbur et al. (1974) initiated a more community oriented perspective, while Istock, Zisfein, and Vavra (1976) and Istock, Vavra, and Zimmer (1976) emphasized environmental variation. Slobodkin (1957, 1959, 1961, 1968, 1972, 1974) initiated a theory of prey evolution, "prudent predation," which focused on the prey's life history. These papers, along with many others, are important because they help to identify a sufficient set of parameters which constrain the evolution of life histories.

The motivation for the present work stems from the recurring interest in the literature about the relationship between age-specific mortality and Fisher's age-specific reproductive value (RV) function (e.g., Fisher 1958; Medawar 1952; Slobodkin 1968, 1974; Caughley 1966). These authors, among others, have either called attention to or suggested a mechanism for the commonly observed inverse relationship of RV and mortality. Questions concerning this relationship are contained in the more general problem of the evolution of life histories in response to age-specific extrinsic mortality factors or factors which originate outside of the organism (e.g., predators).

### THEORY

A large body of theory has been developed in the area of life-history evolution. For a review of the nongenetic aspects see Stearns (1976). Many of these ideas have been extended to include genetic factors by a variety of authors. In particular, Charlesworth (1976) has summarized his contributions to the genetical aspects of the theory.

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In this paper a familiar life-history model (Schaffer 1974; Charlesworth and Leon 1976) is mobilized to provide a logical framework to investigate the evolution of life histories in response to age-specific mortality factors. These references, along with Gadgil and Bossert (1970), should be consulted for the biological motivation behind the model since only the mathematical framework will be given here.

Assume  $n + 1$  discrete age classes indexed 0 through  $n$  and let  $E_x$  denote the reproductive effort at age  $x$ . Reproductive effort (RE) is the fraction of available energy allocated to reproduction. The allocation of energy to reproduction diverts energy from growth and maintenance (for examples in plants see Harper and White 1974 and in animals see Comfort 1964). For each age  $x$ , the energy budget of an organism is represented by the "allocation functions"  $b_x(E_x, D)$ ,  $p_x(E_x, D)$ , and  $s_x(E_x, D)$  which relate, respectively, fecundity per unit size, probability of survival, and growth increment to RE and density ( $D$ ). Growth can be thought of as any increase in reproductive efficiency with age and is calculated in size units at birth. Density is taken to mean the density of the "critical age group" (Charlesworth 1972), that group of age classes to which the mechanisms of density regulation respond. From these basic variables it is possible to construct the quantities in table 1.

A problem in constructing evolutionary models is that one is often forced to specify an explicit functional relationship between the variables. This is usually necessary for mathematical solutions; however, such an explicit representation of the allocation functions is more than any biologist would be ready to assume. In addition, this assumption would seriously limit the applicability of the model, since any results obtained would then be dependent upon the explicit functions assumed. This criticism is very often directed at models which build upon the logistic formulation of density dependence. Since evolutionary models are mainly of heuristic value, generality must be preserved. This may be accomplished by placing constraints only on the first and second derivatives of the allocation functions, thereby assuming that these functions are monotonic and either convex or concave. Such constraints are much less restrictive than assuming an explicit functional form of the energy budget, and it should be obvious when they do not hold.

For obvious reasons, this model is of an iteroparous organism. It is well known theoretically (Gadgil and Bossert 1970; Schaffer 1974; or for a more intuitive approach see Pianka and Parker 1975) that repeated reproduction makes sense when the allocation functions are concave (downward) functions of RE,  $E_x$ . To my knowledge there is no data bearing on this assumption, yet it is justified theoretically. Consequently, the allocation functions are assumed to be monotonic functions of both variables and concave (downward) functions of RE:

$$\begin{aligned} \frac{\partial p_x}{\partial E_x} < 0, \quad \frac{\partial^2 p_x}{\partial E_x^2} < 0, \quad \frac{\partial p_x}{\partial D} < 0, \quad \frac{\partial^2 p_x}{\partial E_x \partial D} \leq 0, \quad \frac{\partial b_x}{\partial E_x} > 0, \\ \frac{\partial s_x}{\partial E_x} < 0, \quad \frac{\partial^2 s_x}{\partial E_x^2} < 0, \quad \frac{\partial s_x}{\partial D} < 0, \quad \frac{\partial^2 s_x}{\partial E_x \partial D} \leq 0, \quad \frac{\partial b_x}{\partial D} < 0. \end{aligned}$$

The constraints on the mixed partials mean that an increase in density increases the sensitivity of growth or survival to RE. It may be that any second order effects of density are negligible, in which case these derivatives would be zero.

TABLE 1  
DEFINITIONS OF TERMS AND SYMBOLS USED IN THE MODEL

*	Denotes the value of a life history variable evaluated at the ESS
$j$	Age class of increased mortality
$z$	Age of onset of reproductive activities
$D$	Density of the "critical age group"
$E_x$	Reproductive effort (RE) at age $x$
$b_x(E_x, D)$	Fecundity per unit size at age $x$
$p_x(E_x, D)$	Probability of survival through age $x$
$s_x(E_x, D)$	Growth rate at age $x$
$S_x = \prod_{i=0}^{x-1} s_i$	Size at age $x$ in size units at age one
$l_x = \prod_{i=0}^{x-1} p_i$	Probability of survival from birth to age $x$
$m_x = b_x S_x$	Fecundity of a female aged $x$
$v_x = l_x^{-1} \sum_{i=x}^n m_i l_i$	Fisher's reproductive value (RV) in a stationary population
$R_0(E, D) = \sum_{i=0}^n m_i l_i$	Net reproductive rate
$P_x = \frac{p_x s_x}{x-1}$	Defined for notational convenience
$L_x = \prod_{i=0}^{x-1} P_i$	
$RVM_x$	Reproductive value modifier at age $x$ . (Eq. [8])
$RVM_x^{evol}$	Evolutionary terms of $RVM_x$ (eq. [10])
ESS	Evolutionary stable strategy (eqq. [3])
$DD_x$	$= \frac{\partial b_x}{\partial D} L_x + \sum_{i=x+1}^n \left\{ \frac{\partial b_i}{\partial D} L_i + m_i l_i \sum_{k=x}^{i-1} \frac{\partial P_k}{\partial D} \frac{1}{P_k} \right\}$ A weighted measure of the density regulation experienced from age $x$ on.
$R_x$	$= \sum_{i=x}^n e^{-r(i+1)} m_i l_i$ ( $r = 0$ in stationary populations)
EST <sub><math>x</math></sub>	Evolutionary sensitivity weighting terms for age $x$ (see text for explanation)

The population and the evolutionary dynamics envisioned are as follows. The evolutionary variables are the age specific RE fractions and a phenotype is specified by the vector

$$\mathbf{E} = (E_z, E_{z+1}, \dots, E_{n-1}, 1),$$

where  $z$  is the age at which reproduction begins. Total RE during the last age class is lethal and is required for consistency. Selection coefficients are assumed to be small. Consequently the population dynamics, which involve changes in absolute numbers, are assumed to occur much more rapidly than the evolutionary dynamics, which involve changes in the vector  $\mathbf{E}$ . This means that for any given phenotype  $\mathbf{E}^*$  the population is assumed to be in ecological equilibrium where the density of the critical age group is equal to  $D^*$ , defined implicitly by

$$R_0(\mathbf{E}^*, D^*) = 1. \quad (1)$$

A nice example of this type of dynamics is provided in Nicholson's experiments (Nicholson 1959, p. 483). These time dynamics are different from those assumed in

the "genetic feedback" models of Pimentel (1961), for there ecological and evolutionary dynamics occur on the same time scale.

It is now assumed that the population will evolve until it reaches an "evolutionary stable strategy" or ESS (Maynard Smith and Price 1973; Maynard Smith 1976). In this model an ESS is a phenotype, a vector of age specific RE's, which, when common, eliminates rare mutant phenotypes. If a phenotype  $\mathbf{E}^*$  is an ESS, then any mutant phenotype,  $\mathbf{E}'$ , must be at a selective disadvantage when rare. Since a mutant is rare by definition, it is assumed to have a negligible effect on the factors regulating density. All this can be expressed by

$$R_0(\mathbf{E}', D^*) < R_0(\mathbf{E}^*, D^*). \quad (2)$$

For the remainder of the paper a superscript \* indicates a life-history variable evaluated at an ESS. Note that density in the mutant life history is held constant at the value  $D^*$  determined by the predominant phenotype  $\mathbf{E}^*$  via equation (1). Equation (2) can be translated into local stability criteria for perturbations to  $\mathbf{E}^*$  by applying the usual partial derivative criteria for local maxima. These equations (Charlesworth and Leon 1976, eq. (9), (10), and (11) where their  $V_x = v_x S_x^{-1}$ ) define the evolutionary stable vector,  $\mathbf{E}^*$ :

$$\begin{aligned} R_0(\mathbf{E}^*, D^*) &= 1, \\ \frac{\partial R_0}{\partial b_x} &= 1 + \frac{\partial P_x}{\partial b_x} (v_{x+1}/S_{x+1}) = 0, \\ \frac{\partial^2 R_0}{\partial b_x^2} &= \frac{\partial^2 P_x}{\partial b_x^2} (v_{x+1}/S_{x+1}) < 0, \quad x = z, z + 1, \dots, n - 1, \\ \frac{\partial^2 R_0}{\partial b_x \partial b_y} &= 0, \quad x \neq y. \end{aligned} \quad (3)$$

All partial derivatives are to be evaluated at the ESS  $\mathbf{E}^*, D^*$ . The previous two equations are always satisfied for all ages. Note that in translating the ESS condition (2) into criteria for a local maximum in  $R_0$ , the partial derivatives of  $R_0$  are taken with respect to  $b_x$  and not  $E_x$ . This is a matter of mathematical convenience and is justified, since  $b_x$  is a monotonically increasing function of  $E_x$  for each age  $x$ . Consequently, the allocation functions are regarded as similarly constrained functions of  $b_x$  and not  $E_x$ . It is important to understand why the partials of  $R_0$  are only taken with respect to  $b_x$ . As noted in Lawlor and Maynard Smith (1976), this procedure reflects the concern in comparing individual organisms and not populations. If the total derivative of  $R_0$  were taken then populations with different  $R_0$ 's would be compared, and the argument would essentially be one of group selection. As a technique the ESS is not concerned with total maximization of some quantity, yet it expresses the condition that mutations be disadvantageous.

The analysis so far has been patterned after Charlesworth and Leon (1976). They used equations (3) to provide criteria for the increase or decrease of RE with age. This paper concerns ways organisms compensate for age-specific mortality factors and the effects of this compensation on RV.

Consider, initially, mortality factors which act during only one age class  $j$ . It will be

shown in a later section that the analysis here extends naturally to mortality factors which act differentially during many age classes. Rewrite the probability of survival through age class  $j$  as  $p_j(E_j, D) = \tilde{p}_j \cdot p'_j(E_j, D)$ . This simply recognizes the fact that there is some extrinsic probability of survival through age class  $j$ , namely  $\tilde{p}_j$ , which is independent of RE or density. The extrinsic survival probability depends upon the ecological context of the population, for example, the presence or absence of predators. The total survivorship is partitioned in this way only to emphasize that  $E_j$  and  $D$  are held constant when evaluating the partials with respect to  $\tilde{p}_j$  in equations (5) and (6) below. Comments later in this paper concerning the effects of  $\tilde{p}_j$  on the dynamics of RE and RV actually hold for total  $p_j$  as well. The question now is, "How does the ESS change with respect to changes in  $\tilde{p}_j$ ?"

Define the vector function

$$\mathbf{F} = (F_0, F_z, \dots, F_x, \dots, F_{n-1})$$

where

$$F_0 = R_0(\mathbf{b}^*, D) - 1 = 0,$$

$$F_x = 1 + \frac{\partial P_x}{\partial b_x} (v_{x+1}/S_{x+1}) = 0, \quad x = z, z+1, \dots, n-1. \quad (4)$$

Now, the ESS is considered a function of  $\tilde{p}_j$ , which was previously (3) a constant. Application of the implicit function theorem yields the derivatives of the ESS with respect to  $\tilde{p}_j$  (see Appendix A for details).

$$\frac{db_x^*}{d\tilde{p}_j} = \left( \frac{\partial F_x}{\partial b_x} \right)^{-1} \left( \frac{\partial F_0}{\partial \tilde{p}_j} \left( \frac{\partial F_x}{\partial F_0} \frac{\partial D}{\partial D} \right) - \frac{\partial F_x}{\partial \tilde{p}_j} \right), \quad x = z, z+1, \dots, n-1. \quad (5)$$

$$\frac{dD^*}{d\tilde{p}_j} = -\frac{\partial F_0 / \partial \tilde{p}_j}{\partial F_0 / \partial D} > 0 \quad \left( \text{since } \frac{\partial F_0}{\partial \tilde{p}_j} > 0 \text{ and } \frac{\partial F_0}{\partial D} < 0 \right). \quad (6)$$

The partials are to be evaluated at the point  $(\mathbf{E}^*, D^*)$  defined by equations (3).

### Equilibrium Density

A general result which is independent of the nature of density regulation is  $dD^*/d\tilde{p}_j > 0$ ; in other words, a decrease in survival results in a decrease in the equilibrium density of the critical age group. This is a direct result of the initial constraints assuming monotonic density dependence. This result says nothing about the equilibrium density of other age groups or total prey density, unless the critical age group includes all the age classes. The magnitude of decrease in density depends (i) directly upon the proportion of  $R_0$  realized after age  $j$ , as has been shown experimentally for *Daphnia* (Hairston and Pastorok 1975; Slobodkin 1959), (ii) inversely on the intensity of density dependence, and (iii) inversely on  $\tilde{p}_j$ . Clearly, for a given increase in extrinsic mortality, there is a greater effect on  $R_0$  when a greater proportion of  $R_0$  has yet to be realized. The more sensitive the mechanism of density regulation is to changes in density, the greater the effect on growth, survival, and fecundity of a given decrease in density. The inverse dependence on  $\tilde{p}_j$  is more interesting and considerations of  $\tilde{p}_j$  will reappear in the analysis. Biologically, this

dependence means that equilibrium density is more sensitive to mortality factors which affect age classes already plagued by high mortality. Age classes which are already "bottlenecks" for survival, for example, the "critical phase" when the yolk sacs of floating larvae of many ocean fish are used up (Hjort 1914; May 1973), are critical in their effects on the overall life-history table. Mathematically, this is due to the fact that the survival probabilities enter multiplicatively. It is for a similar reason that a geometric average is especially sensitive to low entries.

### *Reproductive Effort*

The derivatives in (5) are most interesting. They represent the direction and magnitude of the evolutionary dynamics of RE in response to age-specific mortality factors which act during age  $j$ . This technique could provide the sensitivity, in an evolutionary sense, of the evolutionary variables with respect to any of the parameters in the model. Notice that the technique provides no information on the transient dynamics, yet it provides qualitative information on how an ESS would change if one of the parameters were to vary.

To determine the evolutionary dynamics of RE, calculate the needed partials in (5) and rearrange to obtain

$$\frac{db_x^*}{d\tilde{p}_j} = R_{j+1} \frac{\left[ (\partial^2 P_x / \partial b_x \partial D) R_{x+1} - (\partial P_x / \partial b_x) \left( \delta_{x \leq j} DD_0 - DD_{x+1} \right) \right]}{\tilde{p}_j (\partial^2 P_x / \partial b_x^2) R_{x+1} DD_0}, \quad (7)$$

where

$$\delta_{x \leq j} = \begin{cases} 1 & x \leq j \\ 0 & x > j. \end{cases}$$

For  $x \leq j$ , (7) is negative. Consequently RE always increases for those age classes prior to  $j$  (since  $\tilde{p}_j$  is decreasing due to the new mortality factor). Examination of (7) results in the following additional remarks. The exact magnitude of  $db_x^*/d\tilde{p}_j$  depends upon the values taken by the first and second degree partials of  $P_x(b_x, D)$  when evaluated at the ESS defined by (3). Obviously, since these functions are never specified, the value of these partials cannot be obtained. Consequently it is impossible to say in any mathematically rigorous sense whether the magnitude of  $db_x^*/d\tilde{p}_j$  increases or decreases with age  $x$ . This problem, which will reappear, results from the desire not to explicitly specify the allocation functions. Later, when RV is considered, these partials will often cancel. It will be convenient to notate the other terms which weight these partials in the expression for  $db_x/dp_j$ . They will be referred to as the evolutionary sensitivity weighting terms for age  $x$  ( $EST_x$ ), since, in conjunction with the partials of  $P_x$ , they determine the evolutionary sensibility of RE. The  $EST_x$  equal  $db_x^*/dp_j$  if the partials of  $P_x$  appearing in  $db_x^*/dp_j$  are set equal to one. Note that  $EST_x$  depend only on the algebraic sums involved, while the partials of  $P_x$  are peculiar to the particular physiology and energy budget of the organism. Inspection of the  $EST_x$  in (7) for  $x \leq j$  indicates that their magnitude increases monotonically as  $x$  increases to  $j$ . Consequently these terms contribute to an increased sensitivity of RE to mortality at age  $j$  as age increases up to  $j$  (fig. 1).

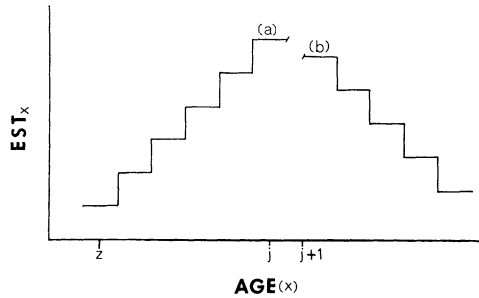


FIG. 1.—The absolute value of  $EST_x$  plotted as a function of age. These terms, in conjunction with the partials of  $P_x$ , determine the evolutionary sensitivity of age-specific RE to changes in extrinsic mortality during age class  $j$ . The relative positions of (a) and (b) depend upon the specific  $I_x$  and  $m_x$  distributions. However, the earlier in life age  $j$  is, the more likely  $EST_j \leq EST_{j+1}$ . See text for further explanation.

For  $x > j$  the sign of (7) is ambiguous. If there were some age  $k$  ( $k > j$ ) beyond which there were no density effects, then (7) would equal zero for  $x > k$  and RE would not change for these age classes. However, for age classes between  $j$  and  $k$  the sign of this expression depends upon the relative magnitudes of  $\partial^2 P_x / \partial b_x \partial D$  and  $\partial P_x / \partial b_x$ . Again, since the functions are never specified, these values cannot be obtained. However, it seems unlikely that the second order effects of density would exceed the first order effects of RE. Assuming this to be the case, RE would always decrease for those age classes between  $j$  and  $k$  (since  $db_x^* / d\tilde{p}_j$  (7) would now be positive). The magnitude of  $db_x^* / d\tilde{p}_j$  ( $x > j$ ) again depends upon the values taken by the partial derivatives in (7) as modified by the  $EST_x$ . The only  $EST_x$  which change with age are  $DD_{x+1}$  and  $R_{x+1}$ , both of which decrease with age. Algebraically, there are  $I_x$  and  $m_x$  schedules and schemes of density regulation for which the ratio of the magnitudes of  $DD_{x+1}$  and  $R_{x+1}$  could behave in almost any conceivable way as  $x$  changes. Consequently, nothing can be said about the behavior of the  $EST_x$  ( $x > j$ ) unless these things are known.

However, as density is known to affect the relative allocation of resources to growth and reproduction in at least one case (Ogden 1974), there is the possibility that for some age classes of some organisms  $|\partial^2 P_x / \partial b_x \partial D| > |\partial P_x / \partial b_x|$  consequently, (7) could be negative for some  $x > j$  and RE would increase for these age classes. This is due to the fact that along with the decrease in density,  $|\partial P_x / \partial b_x|$  has decreased. The allocation functions are now less sensitive to RE and consequently RE can increase.

### Reproductive Value

It is also possible to monitor variables which are themselves functions of the ESS. In particular consider RV,  $v^*(\mathbf{b}^*(\tilde{p}_j), D^*(\tilde{p}_j))$ . Its total derivative indicates how the evolutionary dynamics of RE, the ecological changes in equilibrium density (both which result from changes in  $\tilde{p}_j$ ), as well as direct changes in  $\tilde{p}_j$  itself, affect the RV of age class  $x$ . However, the direct partial,  $\partial v_x^* / \partial \tilde{p}_j$ , is not included in the following equations. We are interested in changes in RV which result from the response of the



model to mortality factors, not from the mortality factor itself. Now, since the population is at the ESS, the RV functions are always evaluated there. The derivative of  $v_x$  can be calculated from (4) to be ( $z < x < n$ )

$$\frac{dv_x^*}{d\tilde{p}_j} = v_x^*(\text{RVM}_x^{\text{ecol}} + \text{RVM}_x^{\text{evol}}) = v_x^* \text{RVM}_x. \quad (8)$$

From (8) one can see that the sensitivity of  $v_x$  to changes in  $\tilde{p}_j$  is proportional to the  $v_x$  as modified by the bracketed terms, which will be referred to as the RV modifier (RVM). The  $\text{RVM}_x$  equals the proportionate change in RV of age  $x$  and will be used to compare proportionate changes in RV across age classes ( $z < x < n$ ). The more positive it becomes, the greater the proportionate withdrawal of RV from age  $x$ . It captures both the ecological as well as the evolutionary dynamics of RV and can be partitioned accordingly. Due to the decrease in density (6), those life-history variables which are density dependent will change. The proportionate change in RV of age  $x$  due to this immediate density release,  $(\partial v_x^*/\partial D)(dD^*/d\tilde{p}_j)/v_x^*$ , is described by the ecological terms

$$\text{RVM}_x^{\text{evol}} \equiv \sum_{i=0}^{x-1} \frac{\partial s_i}{\partial D} \frac{dD^*}{d\tilde{p}_j} \frac{1}{s_i} - \left( \frac{\partial P_{x-1}}{\partial b_{x-1}} \right)^{-1} \left( \frac{\partial^2 P_{x-1}}{\partial b_{x-1} \partial D} \frac{dD^*}{d\tilde{p}_j} \right). \quad (9)$$

The change in RV of age class  $x$  due to evolutionary changes in RE,

$$\sum_{i=z}^n (\partial v_x^*/\partial b_i)(db_i^*/d\tilde{p}_j)/v_x^*,$$

is described by the evolutionary terms

$$\text{RVM}_x^{\text{evol}} \equiv \sum_{i=z}^{x-1} \frac{\partial s_i}{\partial b_i} \frac{db_i^*}{d\tilde{p}_j} \frac{1}{s_i} - \left( \frac{\partial P_{x-1}}{\partial b_{x-1}} \right)^{-1} \left( \frac{\partial^2 P_{x-1}}{\partial b_{x-1}^2} \frac{db_{x-1}^*}{d\tilde{p}_j} \right). \quad (10)$$

The RVM is partitioned in this way to distinguish between two quite different effects of age-specific mortality. First, the ecological terms given in (9) describe the immediate effects on RV of decreased density. Second, the decrease in density (6) along with the decrease in  $\tilde{p}_j$  change the selection pressures on RE. Changes in RV which result from the evolution of RE (5) are given by the  $\text{RVM}_x^{\text{evol}}$  in (10). It is these changes which are of primary interest, for they are a result of the intrinsic dynamics of the model and not some external constraint. There are many schemes of density regulation possible, and once one is determined by specifying which age-specific life-history variables are density dependent, the changes in RV which will occur once density decreases (9) have been built into the model. Presumably in nature the mechanism (which variables of which age classes) of density regulation itself is under some evolutionary control; however, this model is not designed to take this into account. Since the question of interest concerns the way in which the evolutionary variables compensate for mortality factors, we should concentrate only on those changes in RV which result from the dynamics of the evolutionary variables. Concentrating on the evolutionary terms (10) does not mean that density dependence is irrelevant. Density dependence is taken into account in the evolutionary dynamics of RE (5) and appears explicitly when the  $\text{RVM}^{\text{evol}}$  (10) is written out (e.g., [11]).

Equations (8)–(10) provide information only on RV of age classes that come after the age of onset of reproductive activities,  $z$ . Differentiating the recurrence relation for RV in stationary populations ( $v_x = v_{x+1} p_x + m_x$ ), it can be seen that as age increases from birth to age  $z + 1$ , so does  $dv_x^*/d\tilde{p}_j$ .

Note that nothing has been said about the sign of these derivatives. A positive sign would indicate withdrawal of RV while a negative sign would indicate an increase. However, since RV is a relative quantity (usually RV of the first age class is set equal to 1), the change in RV can be expressed relative to the change of any chosen age class. Since it is clear from the previous paragraph that RV is increasingly withdrawn as age increases up to  $z$ , the change in RV of age classes which come after  $z$  will be expressed relative to the change for age  $z$ . Hence these age classes will be thought of as gaining or losing RV relative to age  $z$ . As already shown, changes in RV for these ages depend upon the original RV curve as modified by the RVM. We now focus attention on the RVM and in particular on its evolutionary components,  $\text{RVM}^{\text{evol}}$ .

The behavior of (10) as age changes depends in part upon the values taken by the partials of  $P_x$ . Consequently, there is no general result. However, consider those forms of density regulation in which the second order effects of density are negligible ( $\partial^2 P_x / \partial b_x \partial D \approx 0$ ). Examples include any form of solely density dependent fecundity or prereproductive density dependence in which the mechanisms regulating density act prior to the onset of reproductive activities. This latter form may actually be fairly common in nature. For example, seedling mortality seems to be the main source of population regulation in many pasture plants (Putwain et al. 1968; Sarukhan and Harper 1973; Law et al. 1977). Goodman (1974) argues for this form of density regulation in *Sula sula*, an offshore-feeding sea bird. Cushing (1973) argues for both density dependent survival and growth during mainly the juvenile stages of many commercial marine fishes. Indeed, this assumption underlies a common technique of estimating natural mortality by fisheries biologists (Ricker 1954; Murphy 1967). Also density dependent mortality and growth are concentrated in the larval stages of many insects. Note that this form of juvenile density dependence does not preclude density effects on adult fecundity, as many density effects are mediated through juvenile growth rates.

The assumption that  $\partial^2 P_x / \partial b_x \partial D \approx 0$ , means that the partials of  $P_x$  cancel in (10) and the evolutionary terms become:

$$\text{RVM}_x^{\text{evol}} = \sum_{i=z}^{x-1} \frac{\partial s_i}{\partial b_i} \frac{db_i^*}{d\tilde{p}_j} \frac{1}{s_i} + R_{j+1} \left( \frac{\delta}{x \leq j+1} DD_0 - DD_x \right) / (\tilde{p}_j R_x DD_0) \quad (11)$$

$$x = z + 1, \dots, n - 1.$$

These equations are independent of the partial derivatives of  $P_x$  and are not as forbidding as one might suspect, for as age changes, their sum displays the qualitative dynamics shown in figure 2.

The peak at  $j + 1$  instead of  $j$  is a direct result of the sequence of life history events assumed in Leslie matrix models. Immediately upon entry into an age class reproduction occurs, and subsequently mortality factors act. Consequently, the increased mortality during age  $j$  has no effect on the chances of producing offspring during age class  $j$ . The important effect of unrealized births begins with age class  $j + 1$ .

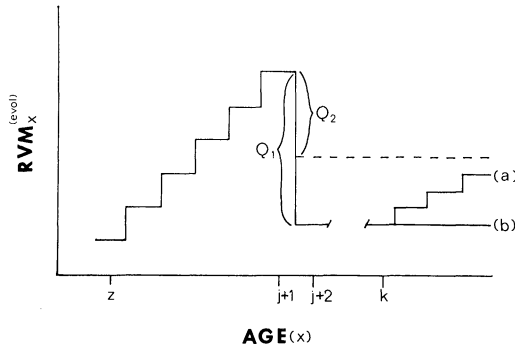


FIG. 2.— $RVM_x^{evol}$  plotted as a function of age for adult age classes. It presents the proportionate change in RV of age class  $x$  due to the evolutionary dynamics of RE. The more positive it becomes the greater the proportionate withdrawal of RV. See text for further explanation.

It is worth noting that if growth were to cease before age  $j$  these qualitative dynamics would hold for the complete RVM (still assuming  $\partial^2 P_x / \partial b_x \partial D \approx 0$ ). In many organisms, growth will cease even before age  $z$ . From figure 2, it is seen that as the model evolves the proportionate withdrawal of RV is greatest for that age class suffering increased mortality. The difference  $Q_1$  (fig. 2) is

$$Q_1 = -\frac{\partial s_{j+1}}{\partial b_{j+1}} \frac{db_{j+1}^*}{d\tilde{p}_j} \frac{1}{s_{j+1}} + \frac{1}{\tilde{p}_j} \left( 1 - \frac{DD_{j+1}}{DD_0} + \frac{R_{j+1} DD_{j+2}}{R_{j+2} DD_0} \right).$$

Consequently, the peakedness at age  $j+1$  depends to a great extent on  $\tilde{p}_j$ , as the bracketed terms weighting  $1/\tilde{p}_j$  will often be close to one. The smaller the age-specific survivorship is, the greater the withdrawal will be.

The qualitative behavior of the  $RVM_x^{evol}$  for  $x > j+1$  is generally ambiguous and depends upon the age specific growth rates and the elusive ratio  $DD_x/R_x$ . However, it is generally true that the  $RVM_x^{evol}$  ( $x > j+1$ ) is bounded above by the dotted line in fig. 2, which lies at a distance of  $Q_2 = Q_1 - (R_{j+1} DD_{j+2} / \tilde{p}_j R_{j+2} DD_0)$ . Also, if there were some age  $k$  beyond which there were no density effects, then the  $RVM_x^{evol}$  would behave as depicted by (b) in figure 2.

In general we may expect  $\partial^2 P_x / \partial b_x \partial D$  not to be zero (though the arguments above depend upon  $|\partial^2 P_x / \partial b_x \partial D|$  being small relative to  $|\partial P_x / \partial b_x|$ ). As one example of a form of density regulation in which  $\partial^2 P_x / \partial b_x \partial D$  is not zero, consider the case of age-independent, density-dependent growth and survival. This form can be interpreted biologically to mean that density effects are mediated through the same limiting resource irrespective of age:  $b_x = b_x(E_x)$ ,  $s_x = s_D(D)s_x(E_x)$ , and  $p_x = p_D(D)p_x(E_x)$ . The  $p_D$  and  $s_D$  are age-independent functions of density. Substitution of these functions into equations (5)–(10) results in the following conclusions. The  $db_x^*/d\tilde{p}_j$  is negative for  $x \leq j$  and positive for  $x > j$ , and consequently RE increases for age classes which come before  $j$  (as it always does) and decreases for those which come after. The magnitude of the  $EST_x$  behaves as in figure 1 for all ages. The  $RVM_x^{evol}$  displays the same qualitative dynamics described in figure 2, and if growth were to cease before age  $j$  curve (a) would begin at age  $j+2$ ; these dynamics would apply as well to the complete RVM.

*Density Independent Populations*

In this case the allocation functions depend only on RE (or  $b_x$ ) and are not functions of density. Evolution acts by weeding out phenotypes (i.e., vectors of age specific RE's) with a lowered intrinsic rate of increase (Charlesworth 1973). The ESS is defined by a system of equations (Charlesworth and Leon 1976, eq. [2] and [3]) which again define the ESS as an implicit function of  $\tilde{p}_j$ . Implicitly differentiating this system yields the derivatives

$$\frac{db_x^*}{d\tilde{p}_j} = \frac{(dP_x/db_x)R_{j+1}}{(d^2P_x/db_x^2)\tilde{p}_jR_{x+1}} \left[ \frac{\sum_{i=x+1}^n (i-x)e^{-r(i+1)}m_i l_i}{\sum_{i=0}^n (i+1)e^{-r(i+1)}m_i l_i} - \delta_{x \leq j} \right] \quad (12)$$

The sign of  $db_x^*/d\tilde{p}_j$  changes from negative for  $x \leq j$  to positive for  $x > j$ , and consequently the evolutionary response to increased mortality during age  $j$  is to increase RE before age  $j$  and decrease it after. The magnitude of the  $EST_x$  behaves as in figure 1. Consequently, as was observed in the density dependent cases, as age gets closer to age  $j$  these terms contribute to an increasing evolutionary sensitivity of RE.

As with the density dependent case, we can monitor the change in the RV function evaluated at the ESS,  $dv_x^*[\mathbf{b}^*(\tilde{p}_j)]/d\tilde{p}_j$  ( $z < x \leq n$ ). Again by differentiating the recurrence relation for RV, the derivatives of RV with respect to  $\tilde{p}_j$  increase during prereproductive life. The total derivative of  $v_x^*[\mathbf{b}(\tilde{p}_j)]$  with respect to  $\tilde{p}_j$  is  $dv_x^*/d\tilde{p}_j = v_x^*RVM_x$ , where

$$RVM_x = RVM_x^{\text{evol}} = \sum_{i=z}^{x-1} \frac{ds_i}{db_i} \frac{db_i}{d\tilde{p}_j} \frac{1}{s_i} + \frac{R_{j+1}}{\tilde{p}_j R_x} \left[ \frac{\sum_{i=x}^n (x-i-1)e^{-r(i+1)}m_i l_i}{\sum_{i=0}^n (i+1)e^{-r(i+1)}m_i l_i} + \delta_{x \leq j+1} \right]$$

Again the explicit dependence on  $\tilde{p}_j$  has not been included, and all changes in RV now occur because of evolutionary changes in the vector of RE's. This  $RVM_x$  again behaves qualitatively as in figure 2, where now

$$Q_1 = -\frac{ds_{j+1}}{db_{j+1}} \frac{db_{j+1}^*}{d\tilde{p}_j} \frac{1}{s_j} + \frac{1}{\tilde{p}_j} \left[ 1 - \frac{\sum_{i=j+1}^n (i-j)e^{-r(i+1)}m_i l_i}{\sum_{i=0}^n (i+1)e^{-r(i+1)}m_i l_i} + \frac{R_{j+1} \sum_{i=j+2}^n (i-j-1)e^{-r(i+1)}m_i l_i}{R_{j+2} \sum_{i=0}^n (i+1)e^{-r(i+1)}m_i l_i} \right],$$

and

$$Q_2 = Q_1 - \frac{R_{j+1} \sum_{i=j+2}^n (i-j-1)e^{-r(i+1)}m_i l_i}{\tilde{p}_j R_{j+2} \sum_{i=0}^n (i+1)e^{-r(i+1)}m_i l_i}$$

Again the peakedness depends mainly on  $\tilde{p}_j$ , as the bracketed terms in the expression for  $Q_1$  will often equal one. For ages after  $j$  the qualitative behavior is again ambiguous; however, if there were some age  $k$  at which growth stopped, the  $RVM_x$  would behave as indicated by curve (a) (fig. 2) for subsequent ages. If  $k < j$ , then curve (a) would begin immediately at age  $j + 2$ .

### *Prereproductive Mortality*

Many mortality factors act during the prereproductive life stages. Unfortunately a RE model seems unsuited for their analysis. Variables concerning growth rates or parental expenditure in caring for the young seem to be the more relevant evolutionary responses, and such evolutionary behavior is not within the scope of this model. However, RE does respond to such mortality factors, as can be seen from the above analysis.

As commented on above, (7) ( $j < z < x$ ) would be positive for most organisms and zero for those age classes beyond which there exist no density effects. It is interesting to note that if all density regulation occurs during the juvenile stage, (7) and (11) are both zero and there is no evolutionary response of RE or RV during any adult age class. The new mortality factor ( $j < z$ ) is simply replacing some of the density-dependent mortality (Errington 1946). For the density independent case, (12) would be positive for all reproductively active age classes and the magnitude of the  $EST_x$  now decreases monotonically as age increases from  $z$ . Hence, in both cases an increase in mortality during the prereproductive life stages selects for decreased RE later in life.

As one may suspect, considerations of RV fail to yield the dynamics observed above for adult mortality. RV by definition increases during prereproductive life (assuming  $r > 0$  in the density independent case) and the absurdity of withdrawing RV from these age classes has been pointed out by Mertz and Wade (1976).

### *Multiple Age Classes*

In the previous sections it was assumed that the new mortality factors acted during only one age class. That framework is now extended to the more general case of mortality factors which act during any number of age classes with any relative degree of severity. The formalities are given in Appendix B, but the idea is fairly simple. The population is thought of as a point in  $n$  dimensional space. This point  $\tilde{\mathbf{p}} = (\tilde{p}_0, \tilde{p}_1, \dots, \tilde{p}_{n-1})$  characterizes the extrinsic survival probabilities for all the age classes. Again, the ESS is thought of as an implicitly defined function of  $\tilde{\mathbf{p}}$  but now a directional derivative is computed at the point  $\tilde{\mathbf{p}}$ . The direction is determined by a "mortality vector," or  $\mathbf{w}$ , which indicates the age classes which experience a change in mortality as well as the relative severity of this change. A theorem from advanced calculus provides the following directional derivatives:

$$\mathcal{D}_{\mathbf{w}} b_x^*(\tilde{\mathbf{p}}) = \sum_{j=0}^{n-1} w_j \frac{\partial b_x^*}{\partial \tilde{p}_j}, \quad x = z, z + 1, \dots, n - 1,$$

where  $\mathcal{D}_{\mathbf{w}}$  denotes the directional derivative along the vector  $\mathbf{w}$ . The partials  $\partial b_x^*/\partial \tilde{p}_j$  are provided by equations (5). Likewise, to monitor the age specific RV functions evaluated at an ESS one obtains:

$$\mathcal{D}_{\mathbf{w}} v_x^*(\tilde{\mathbf{p}}) = \sum_{j=0}^{n-1} w_j \frac{\partial v_x^*}{\partial \tilde{p}_j}$$

where  $\partial v_x^*/\partial \tilde{p}_j$  are provided by (8). This can be rewritten as  $\mathcal{D}_{\mathbf{w}} \ln v_x^*(\mathbf{p}) = \text{RVM}_x$  where now  $\text{RVM}_x = \sum_{j=0}^n w_j \cdot \text{RVM}_x^j$  and  $\text{RVM}_x^j$  is the familiar bracketed terms in (8).

For the purpose of illustration, consider the following mortality vector,  $\mathbf{w}'$ , which has  $\gamma$  in the  $r$  position,  $\eta$  in the  $t$  position and zeros everywhere else;  $\{\gamma, \eta \in (0, 1]; z < r < t < n\}$ . The derivative which describes the change in equilibrium density  $\mathcal{D}_{\mathbf{w}} D^*(\tilde{\mathbf{p}})$ , is greater than zero irrespective of the mortality vector, which means that as the probability of survival decreases, so does density. The presence of other age classes experiencing increased mortality reinforces the dynamics of  $D^*$  which were described earlier. Concerning RE, there is no qualitative change in its behavior for  $x < r$  and  $x > t$  from what it would be if only one age class (either  $r$  or  $t$ ) were affected. The effects of mortality during the two age classes are reinforcing. However, for age classes between  $r$  and  $t$  the effects can be conflicting if the mechanism of density regulation is such that increased mortality during  $r$  and  $t$  selects for increased RE before and a decrease after both age classes  $r$  and  $t$ . The outcome of selection for these middle age classes will be a compromise resulting from the weighted average  $\gamma(\partial b_x^*/\partial \tilde{p}_r) + \eta(\partial b_x^*/\partial \tilde{p}_t)$ . To see how intricate the situation can now become, consider the following additional assumption that there is some age  $k$  between  $r$  and  $t$  beyond which there are no density effects on the life-history variables. Assume also that  $\gamma \gg \eta$  (or that  $\tilde{p}_r \ll \tilde{p}_t$ ). Then it is possible to create the following mosaic pattern of selection on RE,

$$z < (+) \leq r < (-) \leq k < (+) \leq t < (0) < n;$$

where a (+), (-) or (0) indicates, respectively, selection for an increase, decrease, or no change in RE during those age classes shown.

The additive nature of the selection pressures created by mortality during the different ages  $r$  and  $t$  applies to the withdrawal of RV as well. The increasing proportionate withdrawal of RV up to age  $r$  is reinforced by mortality during age  $t$ . However, now there is the possibility of getting a single peak either at age  $r + 1$  or at  $t + 1$ , or a double peak with a saddle somewhere between  $r$  and  $t$ . The actual outcome depends upon  $\gamma$ ,  $\eta$ ,  $\tilde{p}_r$ ,  $\tilde{p}_t$ , and the  $l_x$  and  $m_x$  distributions.

## DISCUSSION

A life-history model embedded in the literature has been extended to provide a framework for studying the evolution of life histories in response to age-specific mortality factors. In addition to the sufficiency of the net reproductive rate or the intrinsic rate of increase as measures of fitness, the main assumptions are as follows. Most importantly, it is assumed that the population evolves to an ESS. The

technique of ESS's considers genetics in part by asking whether a rare mutant phenotype can invade a population. However, the role of recombination is not considered by the ESS approach and polymorphic stable strategies may exist. Random effects as well as historical effects are also not considered.

As is true of any evolutionary model, the genetic variability needed for adaptation must exist in the right amount and proper form. Selection on life-history components has been successful in flour beetles (Mertz 1975), *Drosophila* (reviewed in Lewontin 1974), certain plants (Harper and White 1974) and the pitcher-plant mosquito (Istock, Zisfein, and Vavra 1976), to name a few. Indeed, the ease with which selection succeeds on such a great variety of characters has been commented on by Lewontin (1974, pp. 86-94). However, in other cases the absence of the required genetic variability may pose immediate limits on adaptation. For example, the variability needed for adaptation by some organisms with complex life cycles may simply not exist (Istock 1967, 1970, 1975).

For the most part, the above limitations stem from the strategic approach to evolution. Strategic arguments are used in hopes of understanding pattern in adaptation. Certainly the search for pattern must appear as futile to those who believe that nature is capricious, for counter examples always exist. While many questions can only be answered by an understanding of the historical events which constrain the present or by identifying the unique characteristics involved, perhaps there are other more general features of organisms which to a greater extent are independent of these bothersome details. Obviously, I have treated life histories in this way. This approach could be justified by pointing to the convergence of life-history strategies of different organisms. The search, mentioned in the introduction, for a sufficient set of parameters to analyze life histories depends upon this assumption, that the life history of an organism depends upon the general ecological context.

RE models have become quite popular in exploring both experimentally and theoretically the evolution of life histories. The problems associated with measuring RE in nature as well as a sketch of some theoretical results are provided by Hirshfield and Tinkle (1975). More references to experimental work can be found in Pianka and Parker (1975). The results obtained from the present analysis can be compared with those from other theoretical investigations. Concerning the effects of resource levels on the evolution of RE, the results confirm the arguments of Hirshfield and Tinkle (1975). Gadgil and Bossert (1970) argue that any density release would increase the amount of resources available and select for higher levels of RE. However, as shown previously, it is often advantageous for individuals who survive beyond the age of increased mortality to reduce RE in hopes of increased reproductive success later in life due to the "new" resources available. It is also interesting to note that as juvenile survival decreases (i.e.,  $j < z$ ), RE decreases, or in other words, the degree of iteroparity increases (Charnov and Schaffer 1973; but see Hirshfield and Tinkle 1975).

An interesting application of the theory of this paper is to Slobodkin's (1974) hypothesis of "prudent predation." This hypothesis recognizes that different age classes of the prey are more (or less) important to the reproductive maintenance of the prey population. Prudent predators are those which exploit age classes of low RV. Taken as a concept in applied ecology, prudent predation seems well defined.

Theoretically, there is no reason why a rational predator, like man, could not make the necessary calculations and decide on a prudent predation procedure. However, the concept has now been argued (Slobodkin 1968, 1972, 1974) to be of general relevance to the coevolution of predator-prey interactions. Slobodkin suggests that if predators were to preferentially take one age class, there would be a selective advantage to those prey which, by altering their life-history variables, withdrew RV from that age class. Consequently, evolution of the prey life history in response to predation makes the predator appear prudent. Viewed in this way, prudent predation is one aspect of the prey's life-history strategy.

Since predation is simply an added force of mortality, the results of this paper are applicable. It was consistently observed that evolution of RE indirectly led to the greatest withdrawal of RV, per unit RV, from those adult age classes experiencing mortality. The mechanism of density regulation could, in some cases, obscure this result though it would exist nevertheless. In any case, this result seems consistent with Slobodkin's hypothesis; however, note the sequence of logic used in this deduction. Selective advantage in withdrawing RV from age classes preferred by the predator per se was not assumed anywhere in the analysis. It was assumed that  $R_0$  (or  $r$  in the density independent case) was at a local maximum with respect to the RE variables and the withdrawal of RV is deduced mathematically from this assumption along with the other constraints. It is not clear if this withdrawal would occur had some other phenotype which was more of a function of time been chosen as the evolutionary "director" or if the  $l_x$  and  $m_x$  functions fluctuated in time. Notions of time drop out of the picture since stationary populations and stable age distributions are assumed to exist.

The withdrawal of RV from the exploited age class would tend to stabilize total population size and guard against extinction. The mechanism exposed in this paper would be most effective when the age of increased mortality coincides with the age of highest RV and hence could provide an important evolutionary safeguard. These stabilizing effects may precede other more difficult coevolutionary adjustments. However, in a predator-prey system there will be a need for other forces to operate in limiting the quantity of prey taken and not just the reproductive quality (Slobodkin 1974; Maiorana 1976). Whatever the relevance to the apparent stability of predator-prey interactions, the proportionate withdrawal of RV from adult age classes could potentially be an important evolutionary result, especially since the logic works both ways. In other words, the converse of the dynamics observed in this paper would occur if mortality factors had decreased for age class  $j$ . In this case age class  $j$  would obtain the greatest proportionate increase in RV.

It was Fisher (1958) who first called attention to the inverse relationship between RV and mortality in man. This relationship holds for a number of other mammals (Caughley 1966; Smith 1973) though not for all animals (especially fish, Michod 1978). Medawar (1952) later investigated this relationship by suggesting that RV was the sufficient parameter to analyze the problem of senescence. He suggested that the intensity of selection on an age class should be proportional to the RV of that age class. This reasoning is still common (e.g., Wilson 1975, p. 95; Cody 1971). Hamilton (1966) dismantled this notion by showing that the intensity of selection (as measured by effects on the intrinsic rate of increase) on age-specific, or age-of-onset, modifiers



of life-history variables decreases monotonically with age. RV of an age class  $x$  is not relevant, since selection on a gene expressed during the age class is diluted by a "poor penetrance" of the gene, for in a proportion of individuals  $(1 - l_x)$  the gene is never expressed; and RV is constructed so as to ignore this. Charlesworth (1973) justified the use of the intrinsic rate of increase as a measure of fitness by showing that the rate of incorporation of mutants into an age-structured Mendelian population was approximately proportional to their effects on  $r$ .

An inverse relationship between mortality and RV is expected on the basis of the work done here; however, it is unlikely that this provides the only causal mechanism for the relationship. Medawar (1952), in his analysis, viewed the RV curve of an organism as given and then reasoned how selection might push mortality factors to the extremes of the age distribution. The analysis here views the mortality factors as given and follows the evolution of the life history in response. Clearly, both approaches are too rigid. In reality organisms may respond by some morphological adaptation which would then feed back to soften the impact of the mortality factor. An energy budget model is clearly unsuitable for the analysis of morphological adaptation.

#### SUMMARY

A life-history model from the literature (Schaffer 1974; Charlesworth and Leon 1976) is extended to study the relationship of life-history evolution to age-specific mortality factors. It is shown that an increase in mortality during one age class ( $j$ ) selects for an increase in reproductive effort before and a decrease after the afflicted age class. However, density dependence in age classes subsequent to  $j$  could lead to an increase in reproductive effort for these ages. It is also shown that evolution of reproductive effort leads to the greatest proportionate withdrawal of reproductive value from those adult age classes plagued by new mortality factors. Hence, the commonly observed inverse relationship between reproductive value and mortality is provided with a theoretical underpinning. The smaller the existing survival through age  $j$ , the greater the evolutionary sensitivity of reproductive value and reproductive effort to changes in survival through age  $j$ . An application of the theory concerns Slobodkin's (1974) hypothesis of prey evolution, prudent predation, which is discussed. Extension of the results to mortality factors which affect multiple age classes is sketched.

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## APPENDIX A

The Jacobian matrix of  $F$  (4) is:

$$(A_1 \ A_2) = \begin{pmatrix} \frac{\partial F_0}{\partial \tilde{p}_j} & \frac{\partial F_0}{\partial b_z} & \dots & \frac{\partial F_0}{\partial b_{n-1}} & \frac{\partial F_0}{\partial D} \\ \vdots & \vdots & & \vdots & \vdots \\ \frac{\partial F_{n-1}}{\partial \tilde{p}_j} & \frac{\partial F_{n-1}}{\partial b_z} & \dots & \frac{\partial F_{n-1}}{\partial b_{n-1}} & \frac{\partial F_{n-1}}{\partial D} \end{pmatrix}.$$

Then by the Implicit Function Theorem:

$$\begin{pmatrix} \frac{db_z^*}{d\tilde{p}_j} \\ \frac{db_{z+1}^*}{d\tilde{p}_j} \\ \vdots \\ \frac{db_{n-1}^*}{d\tilde{p}_j} \\ \frac{dD^*}{d\tilde{p}_j} \end{pmatrix} = - \begin{pmatrix} -\frac{\partial F_z/\partial D}{(\partial F_0/\partial D)(\partial F_z/\partial b_z)} \\ -\frac{\partial F_{z+1}/\partial D}{(\partial F_0/\partial D)(\partial F_{z+1}/\partial b_{z+1})} \\ \vdots \\ -\frac{\partial F_{n-1}/\partial D}{(\partial F_0/\partial D)(\partial F_{n-1}/\partial b_{n-1})} \\ \left(\frac{\partial F_0}{\partial D}\right)^{-1} \end{pmatrix} \begin{pmatrix} \left(\frac{\partial F_z}{\partial b_z}\right)^{-1} & 0 & 0 & \dots & 0 \\ 0 & \left(\frac{\partial F_{z+1}}{\partial b_{z+1}}\right)^{-1} & 0 & \dots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 0 & \dots & 0 & \left(\frac{\partial F_{n-1}}{\partial b_{n-1}}\right)^{-1} & 0 \\ 0 & \dots & \dots & \dots & 0 \end{pmatrix} \\ \times \begin{pmatrix} \frac{\partial F_0}{\partial \tilde{p}_j} \\ \frac{\partial F_z}{\partial \tilde{p}_j} \\ \vdots \\ \frac{\partial F_{n-1}}{\partial \tilde{p}_j} \\ 0 \end{pmatrix} = A_2^{-1} A_1,$$

which are equations (5) and (6).

## APPENDIX B

In the more general case where any number of different age classes are afflicted with varying degrees of severity, the mathematical framework is analogous to that of Appendix A. The ESS is now regarded as an implicit function of the vector of age specific extrinsic survivals:  $\tilde{\mathbf{p}} = (\tilde{p}_0, \tilde{p}_1, \dots, \tilde{p}_{n-1})$ . The Jacobian matrix of  $F$  now becomes:

$$\begin{pmatrix} A_1 & A_2 \end{pmatrix} = \begin{pmatrix} \frac{\partial F_0}{\partial \tilde{p}_0} & \dots & \frac{\partial F_0}{\partial \tilde{p}_{n-1}} \\ \vdots & & \vdots \\ \frac{\partial F_{n-1}}{\partial \tilde{p}_0} & \dots & \frac{\partial F_{n-1}}{\partial \tilde{p}_{n-1}} \end{pmatrix} A_2$$

where  $A_2$  is given in Appendix A. By the Implicit Function Theorem the following equation is obtained;

$$B = A_2^{-1} A_1,$$

where the matrix  $B$  is defined

$$b_{ij} = \begin{cases} \frac{\partial b_{i+z-1}^*}{\partial \tilde{p}_{j-1}} & 1 < i < n - z + 1 \\ \frac{\partial D^*}{\partial \tilde{p}_{j-1}} & i = n - z + 1 \end{cases} \quad 1 < j < n.$$

From this equation the following gradient vector is obtained;

$$\begin{aligned} \nabla b_i^* &\equiv \begin{pmatrix} \frac{\partial b_i^*}{\partial \tilde{p}_0} \\ \vdots \\ \frac{\partial b_i^*}{\partial \tilde{p}_{n-1}} \end{pmatrix} \\ &= \begin{pmatrix} \frac{(\partial F_i / \partial D)(\partial F_0 / \partial \tilde{p}_j)}{(\partial F_0 / \partial D)(\partial F_i / \partial b_i)} - \frac{\partial F_i / \partial \tilde{p}_j}{\partial F_i / \partial b_i} \end{pmatrix} \leftarrow j + 1 \text{ entry}, \quad i = z, z + 1, \dots, n - 1, \\ \nabla D^* &\equiv \begin{pmatrix} \frac{\partial D^*}{\partial \tilde{p}_0} \\ \vdots \\ \frac{\partial D^*}{\partial \tilde{p}_{n-1}} \end{pmatrix} = \begin{pmatrix} -\frac{(\partial F_0 / \partial \tilde{p}_j)}{(\partial F_0 / \partial D)} \end{pmatrix} \leftarrow j + 1 \text{ entry.} \end{aligned}$$

The inner product of these gradients are taken with the mortality vector to obtain the directional derivatives.

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