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OPTIMAL LIFE HISTORIES UNDER AGE-SPECIFIC PREDATION

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If there is any generalization which can be made about predators, it is that they are selective in their choice of prey. From the broadest levels of preference for particular prey species, to finer levels of preferred shapes, sizes, colors, and palatabilities, predators are continually discriminating among potential prey victims. Of these wide ranging selective activities of predators, I focus on one particular kind in this paper: the choice of particular age groups as prey. It is hard to conceive of a predator in nature without some elements of age specificity in prey choice. Furthermore, man often acts as an age-specific predator on both natural populations and those kept under cultivation.

Recent research on the evolution of life histories has indicated ways in which some of the evolutionary consequences of age-specific predation can be analyzed. It is argued that, in the absence of a "Darwinian demon" which can maximize all aspects of fitness simultaneously, there is a cost to reproduction (e.g., Williams 1966; Gadgil and Bossert 1970). This cost is incurred in the form of reducing subsequent chances of survival and rates of reproduction at later ages. It is further argued that the relationship between the profits arising from immediate reproduction and the costs resulting from less reproduction later exert a strong influence over the patterns of age-specific reproduction which maximize the rate of increase (e.g., Schaffer 1974; Taylor et al. 1974; Charlesworth and Léon 1976).

Now, if a predator starts to crop particular age groups of a prey population it is likely to alter the costs of reproduction. For example, if it kills all individuals of a particular age class, there ceases to be any cost of reproduction for this age class because no individuals can survive to reproduce later. Some effects of age-specific predation have been briefly considered by Gadgil and Bossert (1970). They argued that increased mortality late in life would reduce the costs of reproduction earlier in life but would have no effect on the profits. Thus increased reproduction at early stages would be advantageous. But if mortality increased early in life, both the profits and costs of reproduction later would be reduced. They also suggested that changes in mortality to an equal degree at all ages would not change the relative contribution of each age class at all. Taylor et al. (1974) gave a formal proof of the same point. On the other hand, Schaffer (1974) argued that equal changes in mortality at all ages should lead to greater reproduction at all ages (in iteroparous organisms).

In this paper I consider the effects of some patterns of age-specific predation on optimal rates of reproduction in a prey population. There are several reasons for doing this. First, it allows some predictions about ways in which prey populations evolve under predation. Second, it provides information on some likely evolutionary changes in natural and cultivated populations exploited by man. Third, this may eventually allow the development of an evolutionary perspective on the management of exploited populations.

ANALYTICAL METHODS

Before considering any evolutionary effects of age-specific predation, it is necessary to modify some standard demographic equations so that they account explicitly for predation mortality. It is convenient to separate mortality due to predation from mortality due to other causes, so $1 - \theta_k$ is defined as the probability with which an individual aged k is cropped. The chance of an individual surviving from age k to $k + 1$ is now $p_k \theta_k$, where p_k is the probability with which an individual survives from k to $k + 1$ in the absence of predation. Notice also that if the equations are to correspond with previous work on life-history evolution (e.g., Schaffer 1974), some assumptions must be made about the kinds of populations to be considered. They must be isolated, with seasonal reproduction ("birth pulse" model of Caughley 1967), and they must be censused immediately before reproduction each year.

If such populations exist for long enough at steady state to achieve equilibrium proportions in each age class, they can be shown to satisfy the equation

$$1 = \theta_c \sum_{j=0}^m \lambda^{-(j+1)} L_j b_j \left(\prod_{k=0}^{j-1} \theta_k \right), \quad (1)$$

where there are $m + 1$ age classes and λ is the finite rate of population increase. Following Charlesworth and Léon (1976), L_j is defined as $\prod_{k=0}^{j-1} p_k g_k$, where g_k is the growth per unit size of an individual aged k between k and $k + 1$. The b_j is the rate of reproduction per unit size of an individual aged j , weighted by the chance of a newborn individual surviving death due to causes other than predation before reaching the age of first census. Newborn individuals are of course open to predation, so, if predation mortality is to be separated from mortality due to other causes, a term must be introduced to express the chance of loss of a newborn uncensused offspring by predation ($1 - \theta_c$). Note that $L_j = \prod_{k=0}^{j-1} \theta_k = 1$ when $j = 0$.

In the sections which follow, it will be necessary to make use of the reproductive value of an individual aged i . This will provide a measure of the contribution to future generations of an individual aged i relative to one aged 0 (Fisher 1930). For reasons mentioned by Schaffer (1974), it is convenient to use a modified reproductive value (V_i), which can be defined under predation as

$$V_i = \frac{\lambda^i \theta_c}{L_i} \sum_{j=i}^m \lambda^{-(j+1)} L_j b_j \left(\prod_{k=i}^{j-1} \theta_k \right), \quad (2)$$

where $\prod_{k=i}^{j-1} \theta_k = 1$ when $i = j$. This is in effect the reproductive value per unit size of an individual aged i .

In studies of the evolution of life histories, it is supposed that the parameters for

reproduction, growth, and survival in equations (1) and (2) are not constant. Instead I suppose that the resources available to an organism are limited and must be partitioned between reproduction, growth, and maintenance. This leads to a conflict in each age class. Allocation of resources to reproduction incurs a cost through reduced rates of growth to the next age class and/or a reduced chance of survival (through less resources being available to maintenance). It should be clear that the rate of increase (λ) will depend on the way in which the conflict is resolved, and that at each age there is likely to be a pattern of resource allocation which maximizes the rate of increase. This can be called the "optimal resource allocation at age i ," and to this there will be a corresponding "optimal rate of reproduction at age i " (b_i^*). If resource allocation is optimal in all age classes, we then have an "optimal life history."

Rates of increase provide us with measures of fitness. If a mutant arises in a population with an optimal life history, its rate of increase is less than that of the rest of the population and it should be eliminated (Charlesworth 1973). An optimal life history can therefore be envisaged as an evolutionarily stable strategy (Maynard Smith 1972).

To determine the optimal rate of reproduction at age i (b_i^*) it is convenient to make use of the following property. If resource allocation is held constant in all age classes except for i , b_i^* not only maximizes the rate of increase but also the reproductive value at age i (V_i). This allows us to find b_i^* from V_i . It is also convenient to write equation (2) in the form of a recurrence relation:

$$V_i = \frac{b_i \theta_c + p_i g_i \theta_i V_{i+1}}{\lambda}. \quad (3)$$

This serves to illustrate that there are two components to the contribution to future generations, reproduction at age i , and reproduction deferred to greater ages. It is the balance between these two components maximizing V_i which concerns us. This will depend on the relationship between reproduction (b_i), survival (p_i) and growth (g_i), expressed succinctly in the function $p_i g_i(b_i)$ (fig. 1). In general V_i is a function of b_i and the pattern and intensity of predation. But for any constant pattern of predation it is possible to find the optimal rate of reproduction by differentiating equation (3) with respect to b_i . The turning point for V_i can be shown to be a maximum as long as $d^2 p_i g_i / db_i^2$ is negative. If this condition is satisfied, the optimal rate of reproduction at age i (b_i^*) is defined by

$$\frac{dp_i g_i}{db_i} = \frac{-\theta_c}{\theta_i V_{i+1}} \quad \text{at } b_i^* \quad (4)$$

(see fig. 1).

Having defined the value of b_i^* under any constant pattern of predation, one can approach the central problem in this paper, the effect of changing the pattern and intensity of predation on b_i^* . By solving this problem, the effects of predation on optimal resource allocation at age i should be clarified. This in turn should permit prediction of the kinds of genetic change in life histories which occur under changing patterns of predation. The problem is much simplified by making certain assump-

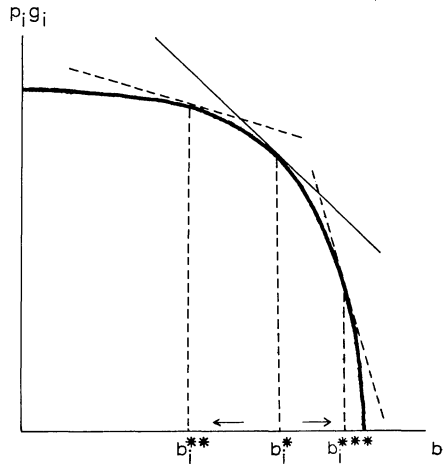


FIG. 1.—Concave form of the function $p_i g_i(b_i)$. Optimal rate of reproduction (b_i^*) defined by $dp_i g_i/db_i = -\theta_c/(\theta_i V_{i+1})$. If predation causes $f(b_i, \theta)$ (eq. [5]) to increase, the optimal rate of reproduction at age i decreases (b_i^{**}). If predation causes $f(b_i, \theta)$ to decrease, the optimal rate of rate of reproduction at age i (b_i^{***}) is given.

tions. I will suppose that, before the pattern of predation starts to change, the prey life history is optimal. As predation changes, I will hold all age classes except for i at their previous optima, so that age class i is the only one with variable resource allocation. It will also help to assume that the risk of predation is independent of any allocation of resources to escaping predation. Finally, I will suppose that if more than one age class is liable to predation, then the chance of predation is the same in each of them ($1 - \theta$). The V_i is now a function of two independent variables b_i and θ , and could take the form of the surface in figure 2.

To determine the effect of predation on b_i^* , ideally one would consider the function $b_i^*(\theta)$ as in figure 2. However, it is not possible to write an explicit function of this form; we only know that b_i^* satisfies equation (4). However, this suggests an alternative approach of studying the function

$$f(b_i, \theta) = \frac{\theta_i V_{i+1}}{\theta_c} \quad \text{at } b_i^*, \quad (5)$$

where $\theta_i = 1$, or $\theta_i = \theta$ and $\theta_c = 1$, or $\theta_c = \theta$ depending on whether age class i and newborn uncensused offspring experience predation. Suppose to begin with that this function increases as predation increases (i.e., as θ decreases). This will lead to a decrease in the optimal rate of reproduction at age i (b_i^*) (fig. 1). Suppose on the other hand that the function decreases as predation increases. The optimal rate of reproduction at age i will now increase (fig. 1). Analytically, the necessary information can be obtained by examining the effect of changes in θ on $f(b_i, \theta)$ at b_i^* . (To do this, one can make use of the fact that $f(b_i, \theta)$ depends on b_i only through λ . At b_i^* , $\partial \lambda / \partial b_i = 0$, by definition. Therefore at b_i^* $f(b_i, \theta)$ depends on θ only. Thus the problem is reduced to determining the sign of $df/d\theta$ at b_i^*).

It is worth noting that these arguments are in accordance with intuitive notions of

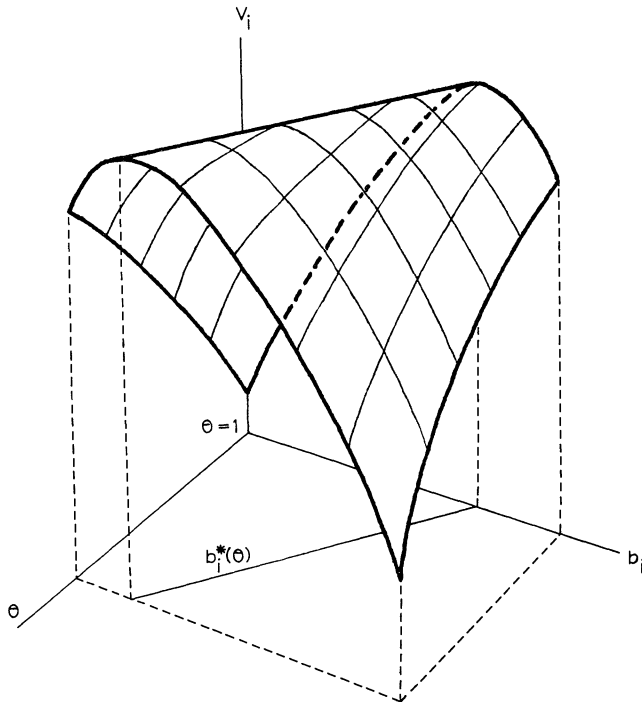


FIG. 2.—A possible form for the surface $V_i(b_i, \theta)$, showing the function $b_i^*(\theta)$.

the effects of predation on optimal resource allocation at age i . It should be clear from equation (3) that predation usually influences the balance between immediate and deferred reproduction through V_{i+1} . If predation leads to an increase in V_{i+1} , the balance is tilted in favor of deferred reproduction, and one can reasonably expect the optimal rate of reproduction at age i to decrease as resources are diverted towards growth and maintenance. Conversely, if predation leads to a decrease in V_{i+1} , the balance is tilted in favor of immediate reproduction and one can expect the optimal rate of reproduction to increase.

RESULTS

Using the method outlined in the last section, the direction of change in optimal rates of reproduction at age i (b_i^*) can be determined following changes in pattern and intensity of predation. This should allow prediction of the kinds of genetic change in resource allocation which occur following the onset of predation. There are obviously many different possible patterns of age-specific predation in an age-distributed prey population. I will confine my attention to four of the simplest patterns involving predation on (a) one age class, (b) a consecutive series of age classes, (c) two disjunct age classes, and (d) all age classes. To clarify the methods involved, I will consider the first pattern in some depth. For the others, I will only quote the main conclusions, relegating the essential analytical steps to the Appendix.

One Age Class Cropped

It is essential to appreciate that the kind of change in resource allocation at age i will depend on the age of the age class experiencing predation relative to i . Denoting the cropped age class as a , we can identify four different categories: $a = c$, $0 \leq a < i$, $a = i$, and $a > i$.

$a = c$.—Let us begin by supposing that predation is confined to newborn uncensused individuals. To find the effect of increasing predation on b_i^* it is necessary to find the sign of the derivative of $f(b_i, \theta)$ at b_i^* ; V_{i+1} can be obtained from equation (2) by putting in appropriate expressions for θ_c and θ_k ($\theta_c = \theta$, $\theta_k = 1$ for all k). Substituting for V_{i+1} in equation (5) gives

$$f(b_i, \theta) = \frac{\lambda^{i+1}}{L_{i+1}} \left(\sum_{j=1}^m \beta_j \right). \quad (6)$$

For notational convenience I write $\lambda^{-(i+1)} L_j b_j = \beta_j$ here and in all subsequent equations. Notice that, although equation (6) does not appear to contain θ , it is nonetheless a function of θ because the rate of increase (λ) is a function of θ ; i.e., $\lambda(b_i, \theta)$. So, differentiating $f(b_i, \theta)$ with respect to θ at b_i^* gives

$$\frac{df}{d\theta} = -\frac{\lambda^i}{L_{i+1}} \frac{d\lambda}{d\theta} \left[\sum_{j=1}^m (j-i)\beta_j \right] \quad \text{at } b_i^*, \quad (7)$$

bearing in mind that at b_i^* $df/d\theta = \partial f/\partial \theta$. To complete the function for $df/d\theta$, it is necessary to find $d\lambda/d\theta$. This can be obtained from equation (1) once appropriate expressions for θ_c and θ_k have been entered ($\theta_c = \theta$, $\theta_k = 1$ for all k). Equation (1) is an implicit function for $\lambda(b_i, \theta)$, and, like $f(b_i, \theta)$, $d\lambda/d\theta = \partial \lambda/\partial \theta$ at b_i^* . Using this information, $d\lambda/d\theta$ at b_i^* is found to be

$$\frac{d\lambda}{d\theta} = \frac{\lambda}{\theta} \frac{\left(\sum_0^m \beta_j \right)}{\left(\sum_0^m (j+1)\beta_j \right)} \quad \text{at } b_i^*. \quad (8)$$

Substituting for $d\lambda/d\theta$ in equation (7) gives

$$\frac{df}{d\theta} = - \left[\frac{\lambda^{i+1}}{\theta L_{i+1}} \right] \frac{\left[\sum_0^m \beta_j \right] \left[\sum_{i+1}^m (j-i)\beta_j \right]}{\sum_0^m (j+1)\beta_j} \quad \text{at } b_i^*. \quad (9)$$

Since all terms in brackets are positive, the derivative must be negative. Thus, as predation increases (i.e., as θ decreases), $f(b_i^*, \theta)$ also increases. Using equation (4) this change can be translated into change in the position of b_i^* . As predation increases the absolute value of the gradient of $p_i g_i(b_i)$ at b_i^* decreases. Therefore the optimal rate of reproduction at age i is reduced, by increasing predation on newborn uncensused individuals (see fig. 1).

$0 \leq a < i$.—If the age class which experiences predation lies at age 0 or between 0 and i , $f(b_i, \theta)$ remains exactly as in equation (6): Thus the derivative remains as in

equation (7). However, $d\lambda/d\theta$ at b_i^* is no longer as in equation (8) because the age class experiencing predation has been changed. To obtain $d\lambda/d\theta$, substitute the new expressions for θ_c and θ_k ($\theta_c = 1$, $\theta_k = \theta$ for $k = a$ otherwise $= 1$) into equation (1) and differentiate with respect to θ at b_i^*

$$\frac{d\lambda}{d\theta} = \frac{\lambda \sum_{a+1}^m \beta_j}{\sum_0^a (j+1)\beta_j + \theta \sum_{a+1}^m (j+1)\beta_j} \quad \text{at } b_i^*. \quad (10)$$

Then substitute for $d\lambda/d\theta$ in equation (7):

$$\frac{df}{d\lambda} = -\left(\frac{\lambda^{i+1}}{L_{i+1}}\right) \frac{\left(\sum_{a+1}^m \beta_j\right) \left[\sum_{i+1}^m (j-i)\beta_j\right]}{\sum_0^a (j+1)\beta_j + \theta \sum_{a+1}^m (j+1)\beta_j} \quad \text{at } b_i^*. \quad (11)$$

Like predation on newborn uncensused offspring, this pattern of predation gives a negative derivative. Thus, as predation increases so does $f(b_i, \theta)$; this leads to a reduction in the optimal rate of reproduction at age i .

$a = i$.—If the age class liable to cropping is also the age class with variable resource allocation, the function $f(b_i, \theta)$ is slightly altered. Substituting for V_{i+1} in equation (5), (using eq. [2] with $\theta_c = 1$, $\theta_k = \theta$ for $k = i$ otherwise $= 1$), $f(b_i, \theta)$ can be written as follows.

$$f(b_i, \theta) = \frac{\theta \lambda^{i+1}}{L_{i+1}} \left(\sum_{i+1}^m \beta_j\right). \quad (12)$$

Differentiating this with respect to θ at b_i^* gives

$$\frac{df}{d\theta} = -\frac{\theta \lambda^i}{L_{i+1}} \frac{d\lambda}{d\theta} \left(\sum_{i+1}^m (j-i)\beta_j\right) + \frac{\lambda^{i+1}}{L_{i+1}} \left(\sum_{i+1}^m \beta_j\right) \quad \text{at } b_i^*. \quad (13)$$

To find $d\lambda/d\theta$, enter the appropriate expressions for θ_c and θ_k into equation (1) and differentiate with respect to θ at b_i^* . This gives an equation similar to (10), where $a = i$ in the summations. Putting this into equation (13) gives, with some rearranging,

$$\frac{df}{d\theta} = \frac{\lambda^{i+1}}{L_{i+1}} \left(\sum_{i+1}^m \beta_j\right) \frac{\sum_0^i (j+1)\beta_j + \theta(i+1) \sum_{i+1}^m \beta_j}{\sum_0^i (j+1)\beta_j + \theta \sum_{i+1}^m (j+1)\beta_j} \quad \text{at } b_i^*. \quad (14)$$

Clearly, all components of this derivative are positive, so $df/d\theta$ is positive. Thus as predation increases (i.e., as θ decreases) $f(b_i^*, \theta)$ decreases. This means that the absolute value of the gradient of $p_i g_i(b_i)$ at b_i^* increases. Reference to figure 1 shows that this leads to an increase in b_i^* . Therefore predation on age class i brings about an increase in the optimal rate of reproduction at age i .

$a > i$.—It only remains to consider the possibility of an age class older than i experiencing predation. As before, put appropriate expressions for θ_c and θ_k into

equation (2) ($\theta_c = 1$, $\theta_k = \theta$ if $k = a$ otherwise $= 1$) and substitute for V_{i+1} in equation (5), obtaining

$$f(b_i, \theta) = \frac{\lambda^{i+1}}{L_{i+1}} \left(\sum_{j=i+1}^a \beta_j + \theta \sum_{j=a+1}^m \beta_j \right). \quad (15)$$

Differentiating this function with respect to θ at b_i^* :

$$\frac{df}{d\theta} = -\frac{\lambda^i}{L_{i+1}} \frac{d\lambda}{d\theta} \left[\sum_{j=i+1}^a (j-i)\beta_j + \theta \sum_{j=a+1}^m (j-i)\beta_j \right] + \frac{\lambda^{i+1}}{L_{i+1}} \left(\sum_{j=a+1}^m \beta_j \right) \quad \text{at } b_i^*. \quad (16)$$

To find $d\lambda/d\theta$, once again the appropriate expressions for θ_c and θ_k are entered into equation (1). The derivative is then the same as equation (10). Substituting for $d\lambda/d\theta$ in equation (16) and rearranging, gives

$$\frac{df}{d\theta} = \frac{\lambda^{i+1}}{L_{i+1}} \left(\sum_{j=a+1}^m \beta_j \right) \frac{\sum_0^i (j+1)\beta_j + (i+1) \sum_{j=i+1}^a \beta_j + \theta(i+1) \sum_{j=a+1}^m \beta_j}{\sum_0^a (j+1)\beta_j + \theta \sum_{j=a+1}^m (j+1)\beta_j} \quad \text{at } b_i^*. \quad (17)$$

All components of this derivative are positive, so the derivative itself is positive. Therefore predation on an age class older than i brings about an increase in the optimal rate of reproduction at age i .

This analysis of predation on single age classes therefore demonstrates two contrasting effects on the optimal rate of reproduction at age i . If the individuals liable to predation are younger than i , the optimal rate of reproduction at age i decreases. On the other hand, if they are equal or older than i the optimal rate of reproduction at age i increases.

Consecutive Series of Age Classes Cropped

Many patterns of predation involve the removal of a consecutive series of age classes, particularly when the predator is man. For example, one might expect such patterns to be typical of fish populations harvested by man. By making the assumption that the risk of predation is the same in all age classes liable to predation ($1 - \theta$), it is possible to use $f(b_i, \theta)$ to find the effect of these patterns on b_i^* . As before, one can expect the effects of predation to depend critically on the age of cropped age classes relative to i . Denote the youngest of a series of cropped age classes as a , and the oldest as a' . There are three general categories to be considered: all cropped age classes younger than i ($0 \leq a < a' < i$), all cropped age classes older than i ($i < a < a' < m$), cropped age classes both younger and older than i ($a < i < a'$).

$0 \leq a < a' < i$.—If all predated age classes are younger than i , it can be shown that the derivative of $f(b_i, \theta)$ with respect to θ at b_i^* is negative (eq. [A2]). Such patterns must therefore lead to a decrease in the optimal rate of reproduction at age i . A similar proof can be used to show that this still applies if the series is extended to include newborn offspring ($c = a < a' < i$, eq. [A3]).

$i < a < a' < m$.—On the other hand, if all cropped age classes are older than i $df/d\theta$ is positive at b_i^* (eq. [A6]). Under these patterns, then, there is an increase in the optimal rate of reproduction at age i as predation increases. The same change occurs if the series of cropped age classes is extended to include even the oldest age class ($i < a < a' = m$) (eq. [A7]).

$0 \leq a < i < a' < m$.—However, if the series of predated age classes spans over i the sign of $df/d\theta$ at b_i^* cannot be unambiguously determined (eq. [A10]). There are both positive and negative components to the derivative, so the optimal rate of reproduction at age i may increase or decrease with increasing predation depending on the relative magnitude of the life-history parameters.

It is worth noting, though, that both the positive and negative components of equation (A10) decrease as i increases relative to a and a' , as long as perturbations in θ from unity are small. So, if most cropped age classes are older than i , b_i^* is more likely to increase than if most cropped age classes are younger than i . This might be expected intuitively if a balance exists between the conflicting forces of predation on age classes younger and older than i . We have already seen that increasing predation on younger age classes reduces the optimal rate of reproduction and that on older age classes it increases the optimal rate of reproduction. Thus, the smaller the proportion of cropped age classes younger than i , the more likely it is that the optimal rate of reproduction will increase.

There are two circumstances in which the direction of change of b_i^* can be unambiguously determined. If the youngest cropped age class is also the age class with variable resource allocation ($a = i < a' < m$), $df/d\theta$ at b_i^* is positive (eq. [A12]); so in this case the optimal rate of reproduction at age i increases as predation increases. A similar result is obtained if the series of cropped age classes is extended to include even the oldest individuals ($a < i < a' = m$, eq. [A11]). This pattern is of particular interest as it is likely to occur in many fish populations harvested by man. On the other hand, the ambiguity still remains for the two analogous cropping patterns on younger age classes. If the series is extended to include even newborn offspring before they reach the age of first census ($c = a < i < a'$) there are both positive and negative components to $df/d\theta$ at b_i^* (eq. [A13]). A similar result is obtained if the oldest cropped age class is also the age class with variable resource allocation ($0 \leq a < i = a'$, eq. [A14]).

Two Disjunct Age Classes Cropped

Patterns of cropping involving removal of individuals from two disjunct age classes are of particular interest. Such patterns are known to maximize sustainable yields from a wide range of prey populations (Beddington and Taylor 1973), so their evolutionary consequences are of some applied importance. It might also be argued that they approximate common patterns in predator-prey systems where youngest and oldest individuals are easiest to catch. If it is assumed, as before, that the risk of predation is the same in both age classes liable to predation ($1 - \theta$), once again it is possible to use $f(b_i, \theta)$ to determine the effect of increasing predation on b_i^* . Again, the effect of predation depends critically on the age of the cropped age classes relative to i . Calling the younger cropped age class a and the older a' , three general categories

can be defined: both age classes younger than i ($0 \leq a < a' < i$), both older than i ($i < a < a' < m$), and one younger and the other older than i ($a < i < a'$).

$0 \leq a < a' < i$.—If both cropped age classes are younger than i , it can be shown that the derivative of $f(b_i, \theta)$ with respect to θ at b_i^* is negative (eq. [A16]). Therefore, as predation increases the optimal rate of reproduction at age i decreases. The same conclusion holds if the younger cropped individuals are newborn uncensused offspring ($c = a < a' < i$, eq. [A17]).

$i < a < a' < m$.—If both cropped age classes are older than i the direction of change is reversed, the optimal rate of reproduction at age i tending to increase as predation increases (eq. [A20]). This result still holds if the older cropped individuals are the oldest in the population ($i < a < a' = m$), since the problem simplifies to one in which a single age class is cropped (eq. [17]).

$0 \leq a < i < a' < m$.—However, if one cropped age class is younger than i and the other older, the optimal rate of reproduction at age i can either increase or decrease as predation increases, since $df/d\theta$ contains both positive and negative components (eq. [A23]). Notice, though, that the negative part of this equation increases (becomes less negative) as i becomes closer to a' . Thus, if i is close to a' , b_i^* is more likely to increase than if i is close to a . Intuitively, such a result can be expected if the influence of a cropped age class on b_i^* depends on how close the class lies to i . Since predation on older age classes tends to increase b_i^* , the closer i is to a' the greater the force tending to make b_i^* increase.

There are two conditions under which the effects of predation on b_i^* can be found without ambiguity. First, if $a' = m$, the problem becomes the same as cropping a single age class younger than i , for which it is already known that b_i^* tends to decrease (eq. [11]). Second, if the younger cropped age class is the same as i ($a = i < a' < m$), b_i^* increases as predation increases (eq. [A24]). Two other cases should also be mentioned, although in both of them b_i^* can either increase or decrease. These are $c = a < i < a' < m$ (eq. [A25]) and $0 \leq a < i = a'$ (eq. [A26]).

All Age Classes Cropped

It is conceivable that predation might take place without any age specificity at all. Let us suppose that all individuals including newborn uncensused offspring experience the same chance of predation ($1 - \theta$). In these circumstances it can be shown that $df/d\theta$ at b_i^* is zero (eq. [A30]); that is, there is no change in the optimal allocation of resources at age i . This is in accordance with the results of Gadgil and Bossert (1970) and the proof of Taylor et al. (1974). It differs from Schaffer's (1974) result, as he did not take into account cropping of newborn individuals (see his eq. [A3.2]).

DISCUSSION

The effects of various patterns of age-specific predation on optimal rates of reproduction at age i are summarized in figure 3. Several points emerge from this figure. First, b_i^* decreases as predation increases only if all cropped individuals are younger than i . Second, b_i^* increases as predation increases only if all cropped individuals are equal to or older than i . Third, b_i^* may increase or decrease if individuals younger than and individuals equal to and/or older than i are cropped. (There are, however, two exceptions to this rule. If two disjunct age classes are

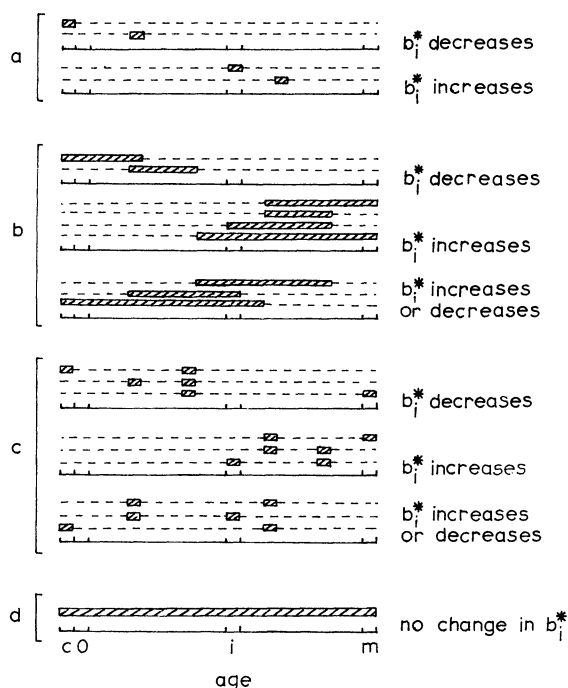


FIG. 3.—Patterns of predation as functions of age (predated age classes shown as hatched areas). *a*, Predation on one age only; *b*, Predation on a consecutive series of ages; *c*, Predation on two disjunct ages; *d*, Predation on all ages. In each case the effect of predation on the optimal rate of reproduction at age i (b_i^*) is given.

cropped, and the older one is the oldest age class in the population, b_i^* must decrease. Also, if all age classes starting from an age less than i experience predation, b_i^* must increase.) Fourth, it is only under rather unusual circumstances that predation does not bring about a change in b_i^* . Either all individuals would have to be open to predation, or if only some were, then the influence of predation on individuals younger than i would have to be exactly canceled out by the influence of those older than i .

One should however bear in mind the assumptions made in obtaining these results. They refer to isolated populations with seasonal reproduction, which are censused immediately before reproduction each year. It is assumed that the chance of an individual avoiding death due to causes other than predation depends on predation only through its influence on the rate of population increase. This assumption excludes an interesting class of prey which can reduce its chance of predation by expending resources. An analysis without this assumption could shed some light on optimal allocation of resources to preventing predation; for example, through escape behavior or production of toxic compounds. I have also assumed that predation has a direct influence only on the chance of survival, thereby excluding a large class of predators which crops without killing its prey. This includes many herbivores, whose influence on optimal resource allocation of plants would be better studied by supposing a direct effect on growth and reproduction rather than

survival. The results are also limited to populations with iteroparous optimal life histories in the absence of predation, and with the exception of i all age classes are constrained to remain at their previous optima. This excludes the possibility of coevolution of a series of age classes to meet the effects of predation. Finally, I have ignored the influence of predation on population density, which would be an additional factor in reshaping the life history of the prey.

Clearly, this analysis is a simplification of changes arising in a prey population which begins to experience predation. Nevertheless, if the factors I have considered are important, the results do predict the kind of genetic change to expect in a prey population following changes in a pattern of age-specific predation. It would be interesting, then, to see if any real populations show signs of changing in the directions predicted.

There have been two experimental studies, which although carried out for another purpose (investigation of evolution of senescence), provide us with information on the effects of age-specific predation. These are experiments of Sokal (1970) and Mertz (1975) on populations of flour beetles (*Tribolium castaneum*). In both experiments populations exposed to intense predation of young adults (by the investigators) were compared with populations in which adults could live out their full natural lifespan. Sokal found that mortality rates of adults from predated populations tended to be greater than those from unpredated ones when compared under standard conditions. Mertz found that rates of reproduction of young adults from predated populations were greater, again when compared under standard conditions. These results are compatible with the prediction that predation on adults should favor genotypes with greater allocation of resources to reproduction and less to growth and maintenance.

In natural populations it is more difficult to study genetic change in life histories under predation since other variables cannot be controlled. Predation almost always has other effects on prey populations, by changing their density and the behavior of the individuals they contain. So, for example, Paine's (1969) observation that the herbivorous gastropod *Tegula funebris* has greater rates of reproduction when experiencing predation by the starfish *Pisaster ochraceus* could be interpreted in several ways. It might be no more than a result of greater food availability due to lower population density, without any genetic change. If genetic change does occur, it might be due to a changing pattern of age-specific mortality as the constraints of density-dependent mortality are lifted through a reduction in population density. Alternatively, genetic change might occur for the reasons discussed in this paper. To distinguish this from the other alternatives, one must demonstrate first that the change is genetic and second that it is directly attributable to the age-specificity of predation. To my knowledge these requirements have never been satisfied.

The same problem applies to natural populations exploited by man. Like other animals, our patterns of predation usually have elements of age specificity; even if we have no direct knowledge of age, we select on the basis of characters associated with age, such as size. For example, in harvesting a fish population by netting, individuals greater than a minimum size are all liable to be cropped. If size is related to age, to a first approximation individuals greater than a minimum age are liable to be cropped. The results in this paper suggest that this will lead to selection for greater rates of reproduction in any age class with variable resource allocation. Yet, in spite of the

importance of understanding our influence on exploited populations, our role as an agent of selection has rarely been considered.

However, one exploited population which has been the subject of careful demographic analysis is a population of pike (*Esox lucius*) in Lake Windermere, U.K. This population has a history of intermittent exploitation, but large scale cropping of adults was started by the Freshwater Biological Association in 1944. Since 1963 estimates have been made of numbers of eggs per female, and results published for the first 4 yr showed a tendency towards increase (Kipling and Frost 1969). More recently the upward trend has continued, so that number of eggs per 3-yr-old female was about 80,000 in 1975 as opposed to about 50,000 in 1963 (Bagenal, personal communication). Such changes could of course be under direct environmental control, allowing greater rates of reproduction irrespective of genotype (although an appropriate environmental variable has yet to be demonstrated). On the other hand, such changes would be expected from selection for genotypes with greater rates of reproduction as a result of the pattern of age-specific predation. The implications of these changes in fecundity to commercial fisheries are of some importance, and it would be interesting to test the alternative interpretations.

The potential for genetic change in life histories as a result of predation has some bearing on the problem of maximizing the yield to the predator. Yield maximization has been extensively studied, and various solutions have been proposed, generally involving predation on no more than two age classes (e.g., MacArthur 1960; Beddington and Taylor 1973; Clarke et al. 1973; Doubleday 1975; Mendelsohn 1976; Law 1979). The results in this paper suggest that when such cropping patterns are applied to populations with genetic variation in resource allocation they will bring about genetic change. Consequently, the cropping pattern may cease to maximize the yield. It is a weakness of these management models that they do not take into account the potential for genetic change in prey populations. Ideally, our management models should tell us how to maximize the short term yield while selecting for genotypes which will give a greater yield in the long term.

Finally, it is worth mentioning that populations kept under cultivation by man are also likely to experience the effects of age-specific predation. There are strong elements of age specificity in our cropping patterns of most domesticated species, which may bring about genetic change irrespective of any artificial selection programs which may be practiced. Perhaps some of the differences observable between varieties could be due to their exposure to different patterns of age-specific mortality. For example, there are substantial differences in fecundity of Tasmanian Merino and Finnish Landrace sheep, the former producing no more than one lamb per litter and the latter as many as four or five (Land et al. 1974). Although these differences may have arisen partly from side effects of artificial selection, it would be interesting to know if differences in the mortality regimes to which they have been exposed could also have contributed.

SUMMARY

If a predator crops prey of certain ages in preference to others, it may be acting as an agent of selection, causing genetic change in the prey population. This paper adapts a model of life-history evolution to investigate some selective consequences of

several patterns of age-specific predation. The model allows allocation of resources to reproduction, growth, and maintenance in an age class i to be varied. Subject to several assumptions, it is shown that increasing predation on individuals younger than i leads to selection for lower rates of reproduction at age i . Conversely, increasing predation on individuals older than and/or equal to i leads to selection for greater rates of reproduction. If individuals from both these age ranges are cropped the optimal rate of reproduction may either increase or decrease. The only circumstance under which no change occurs arises if all individuals irrespective of age are liable to be cropped, or if the effects of predation on younger and older age classes exactly cancel one another. The implications of these results to the management of populations exploited by man are discussed.

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APPENDIX

DERIVATIONS FOR $df/d\theta$ AT b_i^* , FOR VARIOUS PATTERNS OF AGE-SPECIFIC PREDATION

Note that all symbols are as defined in equations (1), (2) and (5). All age classes liable to predation experience the same risk of predation. $\lambda^{-(j+1)}L_jb_j$ is written as β_j for the sake of brevity. Notice also that all derivatives are determined at b_i^* .

Predation on a Consecutive Series of Age Classes

Call the youngest age class to experience predation a , and the oldest a' .

i) $0 \leq a < a' < i$.— $f(b_i, \theta)$ is given by equation (6), and $df/d\theta$ by equation (7); $d\lambda/d\theta$ is found from equation (1) after entering appropriate expressions for θ_c and θ_k ($\theta_c = 1$, $\theta_k = \theta$ for $a \leq k \leq a'$ otherwise $= 1$).

$$\frac{d\lambda}{d\theta} = \frac{\lambda \left[\sum_{a+1}^{a'} (j-a)\theta^{j-a}\beta_j + (a'+1-a)\theta^{a'+1-a} \sum_{a+1}^m \beta_j \right]}{\theta \left[\sum_0^a (j+1)\beta_j + \sum_{a+1}^{a'} (j+1)\theta^{j-a}\beta_j + \theta^{a'+1-a} \sum_{a+1}^m (j+1)\beta_j \right]}. \quad (A1)$$

Substituting for $d\lambda/d\theta$ in equation (7) gives

$$\frac{df}{d\theta} = - \left[\frac{\lambda^{i+1}}{\theta L_{i+1}} \sum_{i+1}^m (j-i)\beta_j \right] \frac{\sum_{a+1}^{a'} (j-a)\theta^{j-a}\beta_j + (a'+1-a)\theta^{a'+1-a} \sum_{a+1}^m \beta_j}{\sum_0^a (j+1)\beta_j + \sum_{a+1}^{a'} (j+1)\theta^{j-a}\beta_j + \theta^{a'+1-a} \sum_{a+1}^m (j+1)\beta_j}. \quad (A2)$$

ii) $c = a < a' < i$.—With some small modifications to equation (A1), it can be shown that

$$\frac{df}{d\theta} = - \left[\frac{\lambda^{i+1}}{\theta L_{i+1}} \sum_{j=i+1}^m (j-i)\beta_j \right] \frac{\sum_0^{a'} (j+1)\theta^{j+1}\beta_j + (a'+2)\theta^{a'+2} \sum_{a'+1}^m \beta_j}{\sum_0^{a'} (j+1)\theta^{j+1}\beta_j + \theta^{a'+2} \sum_{a'+1}^m (j+1)\beta_j}. \quad (\text{A3})$$

iii) $i < a < a' < m$.—To find $f(b_i, \theta)$ enter appropriate expressions for θ_c and θ_k ($\theta_c = 1$, $\theta_k = \theta$ for $a \leq k \leq a'$ otherwise $= 1$) in equation (2), and substitute for V_{i+1} in equation (5):

$$f(b_i, \theta) = \frac{\lambda^{i+1}}{L_{i+1}} \left(\sum_{j=i+1}^a \beta_j + \sum_{a+1}^{a'} \theta^{j-a}\beta_j + \theta^{a'+1-a} \sum_{a'+1}^m \beta_j \right). \quad (\text{A4})$$

Differentiating with respect to θ gives:

$$\begin{aligned} \frac{df}{d\theta} = & -\frac{\lambda^i}{L_{i+1}} \frac{d\lambda}{d\theta} \left[\sum_{j=i+1}^a (j-i)\beta_j + \sum_{a+1}^{a'} (j-i)\theta^{j-a}\beta_j + \sum_{a'+1}^m (j-i)\theta^{a'+1-a}\beta_j \right] \\ & + \frac{\lambda^{i+1}}{L_{i+1}\theta} \left[\sum_{a+1}^{a'} (j-a)\theta^{j-a}\beta_j + (a'+1-a)\theta^{a'+1-a} \sum_{a'+1}^m \beta_j \right]. \end{aligned} \quad (\text{A5})$$

Substitute for $d\lambda/d\theta$ using equation (A1):

$$\begin{aligned} \frac{df}{d\theta} = & \frac{\lambda^{i+1}}{\theta L_{i+1}} \left[\sum_{a+1}^{a'} (j-a)\theta^{j-a}\beta_j + (a'+1-a)\theta^{a'+1-a} \sum_{a'+1}^m \beta_j \right] \\ & \times \frac{\sum_0^i (j+1)\beta_j + (i+1) \left(\sum_{i+1}^a \beta_j + \sum_{a+1}^{a'} \theta^{j-a}\beta_j + \theta^{a'+1-a} \sum_{a'+1}^m \beta_j \right)}{\sum_0^a (j+1)\beta_j + \sum_{a+1}^{a'} (j+1)\theta^{j-a}\beta_j + \theta^{a'+1-a} \sum_{a'+1}^m (j+1)\beta_j}. \end{aligned} \quad (\text{A6})$$

iv) $i < a < a' = m$.—With small modifications to equations (A1) and (A4), $df/d\theta$ is as follows.

$$\frac{df}{d\theta} = \frac{\lambda^{i+1}}{\theta L_{i+1}} \left[\sum_{a+1}^m (j-a)\theta^{j-a}\beta_j \right] \frac{\sum_0^i (j+1)\beta_j + (i+1) \left(\sum_{i+1}^a \beta_j + \sum_{a+1}^m \theta^{j-a}\beta_j \right)}{\sum_0^a (j+1)\beta_j + \sum_{a+1}^m (j+1)\theta^{j-a}\beta_j}. \quad (\text{A7})$$

v) $0 \leq a < i < a' < m$.—To find $f(b_i, \theta)$ enter appropriate expressions for θ_c and θ_k ($\theta_c = 1$, $\theta_k = \theta$ for $a \leq k \leq a'$ otherwise $= 1$) in equation (2), and substitute for V_{i+1} in equation (5):

$$f(b_i, \theta) = \frac{\lambda^{i+1}}{L_{i+1}} \left(\sum_{j=i+1}^{a'} \theta^{j-i}\beta_j + \theta^{a'+1-i} \sum_{a'+1}^m \beta_j \right). \quad (\text{A8})$$

Differentiating with respect to θ gives

$$\begin{aligned} \frac{df}{d\theta} = & -\frac{\lambda^i}{L_{i+1}} \frac{d\lambda}{d\theta} \left[\sum_{j=i+1}^{a'} (j-i)\theta^{j-i}\beta_j + \theta^{a'+1-i} \sum_{a'+1}^m (j-i)\beta_j \right] \\ & + \frac{\lambda^{i+1}}{L_{i+1}\theta} \left[\sum_{j=i+1}^{a'} (j-i)\theta^{j-i}\beta_j + (a'+1-i)\theta^{a'+1-i} \sum_{a'+1}^m \beta_j \right]. \end{aligned} \quad (\text{A9})$$

Substitute for $d\lambda/d\theta$ using equation (A1):

$$\frac{df}{d\theta} = \frac{\lambda^{i+1}}{\theta L_{i+1}} \left\{ \frac{\left[\sum_{i+1}^{a'} (j-i)\theta^{j-i}\beta_j + \theta^{a'+1-i} \sum_{a'+1}^m (j-i)\beta_j \right] \times \left[\sum_0^a (j+1)\beta_j + (a+1) \sum_{a'+1}^{a'} \theta^{j-a}\beta_j + \theta^{a'+1-a} \sum_{a'+1}^m (j+a-a')\beta_j \right]}{\sum_0^a (j+1)\beta_j + \sum_{a'+1}^{a'} (j+1)\theta^{j-a}\beta_j + \theta^{a'+1-a} \sum_{a'+1}^m (j+1)\beta_j} - \left[\theta^{a'+1-i} \sum_{a'+1}^m (j-a'-1)\beta_j \right] \right\}. \quad (\text{A10})$$

vi) $0 \leq a < i < a' = m$.—The negative component of the derivative in equation (A10) is lost, giving

$$\frac{df}{d\theta} = \frac{\lambda^{i+1}}{\theta L_{i+1}} \frac{\left[\sum_{i+1}^m (j-i)\theta^{j-i}\beta_j \right] \left[\sum_0^a (j+1)\beta_j + (a+1) \sum_{a'+1}^m \theta^{j-a}\beta_j \right]}{\sum_0^a (j+1)\beta_j + \sum_{a'+1}^m (j+1)\theta^{j-a}\beta_j}. \quad (\text{A11})$$

vii) $a = i < a' < m$.

$$\frac{df}{d\theta} = \frac{\lambda^{i+1}}{\theta L_{i+1}} \left[\sum_{i+1}^{a'} (j-i)\theta^{j-i}\beta_j + (a'+1-i)\theta^{a'+1-i} \sum_{a'+1}^m \beta_j \right] \times \frac{\sum_0^i (j+1)\beta_j + (i+1) \left[\sum_{i+1}^{a'} \theta^{j-i}\beta_j + \theta^{a'+1-i} \sum_{a'+1}^m \beta_j \right]}{\sum_0^i (j+1)\beta_j + \sum_{i+1}^{a'} (j+1)\theta^{j-i}\beta_j + \theta^{a'+1-i} \sum_{a'+1}^m (j+1)\beta_j}. \quad (\text{A12})$$

viii) $c = a < i < a' < m$.—

$$\frac{df}{d\theta} = \frac{\lambda^{i+1}}{\theta L_{i+1}} \left\{ \frac{\left[\sum_{i+1}^{a'} (j-i)\theta^{j-i}\beta_j + \theta^{a'+1-i} \sum_{a'+1}^m (j-i)\beta_j \right] \left[\theta^{a'+2} \sum_{a'+1}^m (j-a'-1)\beta_j \right]}{\sum_0^a (j+1)\theta^{j+1}\beta_j + \theta^{a'+2} \sum_{a'+1}^m (j+1)\beta_j} - \left[\theta^{a'+1-i} \sum_{a'+1}^m (j-a'-1)\beta_j \right] \right\}. \quad (\text{A13})$$

ix) $0 \leq a < i = a'$.—

$$\frac{df}{d\theta} = \frac{\lambda^{i+1}}{L_{i+1}} \left\{ \frac{\left[\sum_{i+1}^m (j-i)\beta_j \right] \left[\sum_0^a (j+1)\beta_j + (a+1) \sum_{a'+1}^i \theta^{j-a}\beta_j + \theta^{i+1-a} \sum_{i+1}^m (j+a-i)\beta_j \right]}{\sum_0^a (j+1)\beta_j + \sum_{a'+1}^i (j+1)\theta^{j-a}\beta_j + \theta^{i+1-a} \sum_{i+1}^m (j+1)\beta_j} - \left[\sum_{i+1}^m (j-i-1)\beta_j \right] \right\}. \quad (\text{A14})$$

Predation on Two Disjunct Age Classes

Call the younger of the two age classes to experience predation a , and the older a' .

i) $0 \leq a < a' < i$.— $f(b_i, \theta)$ is given by equation (6), and $df/d\theta$ by equation (7); $d\lambda/d\theta$ is

found from equation (1) after entering appropriate expressions for θ_c and θ_k ($\theta_c = 1$, $\theta_k = \theta$ for $k = a$ and $k = a'$ otherwise $= 1$):

$$\frac{d\lambda}{d\theta} = \frac{\lambda \left(\sum_{a+1}^{a'} \beta_j + 2\theta \sum_{a+1}^m \beta_j \right)}{\sum_0^a (j+1)\beta_j + \theta \sum_{a+1}^{a'} (j+1)\beta_j + \theta^2 \sum_{a+1}^m (j+1)\beta_j} \quad (\text{A15})$$

Substituting for $d\lambda/d\theta$ in equation (7) gives

$$\frac{df}{d\theta} = - \left[\frac{\lambda^{i+1}}{L_{i+1}} \sum_{i+1}^m (j-i)\beta_j \right] \frac{\sum_{a+1}^{a'} \beta_j + 2\theta \sum_{a+1}^m \beta_j}{\sum_0^a (j+1)\beta_j + \theta \sum_{a+1}^{a'} (j+1)\beta_j + \theta^2 \sum_{a+1}^m (j+1)\beta_j}. \quad (\text{A16})$$

ii) $c = a < a' < i$.—With appropriate modifications to equation (A15), it can be shown that

$$\frac{df}{d\theta} = - \left[\frac{\lambda^{i+1}}{L_{i+1}} \sum_{i+1}^m (j-i)\beta_j \right] \frac{\sum_0^{a'} \beta_j + 2\theta \sum_{a'+1}^m \beta_j}{\theta \sum_0^a (j+1)\beta_j + \theta^2 \sum_{a+1}^m (j+1)\beta_j}. \quad (\text{A17})$$

iii) $i < a < a' < m$.—To find $f(b_i, \theta)$, enter appropriate expressions for θ_c and θ_k ($\theta_c = 1$, $\theta_k = \theta$ for $k = a$ and $k = a'$ otherwise $= 1$) in equation (2) and substitute for V_{i+1} in equation (5):

$$f(b_i, \theta) = \frac{\lambda^{i+1}}{L_{i+1}} \left(\sum_{i+1}^a \beta_j + \theta \sum_{a+1}^{a'} \beta_j + \theta^2 \sum_{a+1}^m \beta_j \right). \quad (\text{A18})$$

Differentiating with respect to θ gives

$$\begin{aligned} \frac{df}{d\theta} = & - \frac{\lambda^i}{L_{i+1}} \frac{d\lambda}{d\theta} \left[\sum_{i+1}^a (j-i)\beta_j + \theta \sum_{a+1}^{a'} (j-i)\beta_j + \theta^2 \sum_{a+1}^m (j-i)\beta_j \right] \\ & + \frac{\lambda^{i+1}}{L_{i+1}} \left(\sum_{a+1}^{a'} \beta_j + 2\theta \sum_{a+1}^m \beta_j \right). \end{aligned} \quad (\text{A19})$$

Substitute for $d\lambda/d\theta$ using equation (A15):

$$\frac{df}{d\theta} = \frac{\lambda^{i+1}}{L_{i+1}} \left(\sum_{a+1}^{a'} \beta_j + 2\theta \sum_{a+1}^m \beta_j \right) \frac{\sum_0^i (j+1)\beta_j + (i+1) \left(\sum_{i+1}^a \beta_j + \theta \sum_{a+1}^{a'} \beta_j + \theta^2 \sum_{a+1}^m \beta_j \right)}{\sum_0^a (j+1)\beta_j + \theta \sum_{a+1}^{a'} (j+1)\beta_j + \theta^2 \sum_{a+1}^m (j+1)\beta_j}. \quad (\text{A20})$$

iv) $i < a < a' = m$.—This is equivalent to a pattern of predation involving removal of a single age class a (see eq. [17]).

v) $0 < a < i < a' < m$.—To find $f(b_i, \theta)$, enter appropriate expressions for θ_c and θ_k ($\theta_c = 1$, $\theta_k = \theta$ for $k = a$ and $k = a'$ otherwise $= 1$) in equation (2), and substitute for V_{i+1} in equation (5):

$$f(b_i, \theta) = \frac{\lambda^{i+1}}{L_{i+1}} \left(\sum_{i+1}^{a'} \beta_j + \theta \sum_{a+1}^m \beta_j \right). \quad (\text{A21})$$

Differentiating with respect to θ gives

$$\frac{df}{d\theta} = - \left(\lambda^i L_{i+1}^{-1} \frac{d\lambda}{d\theta} \right) \left[\sum_{i+1}^{a'} (j-i)\beta_j + \theta \sum_{a'+1}^m (j-i)\beta_j \right] + (\lambda^{i+1} L_{i+1}^{-1}) \sum_{a'+1}^m \beta_j. \quad (\text{A22})$$

Substitute for $d\lambda/d\theta$ using equation (A15):

$$\frac{df}{d\theta} = \frac{\lambda^{i+1}}{L_{i+1}} \left[\sum_{a'+1}^m \beta_j - \frac{\left(\sum_{a'+1}^{a'} \beta_j + 2\theta \sum_{a'+1}^m \beta_j \right) \left(\sum_{i+1}^{a'} (j-i)\beta_j + \theta \sum_{a'+1}^m (j-i)\beta_j \right)}{\sum_0^a (j+1)\beta_j + \theta \sum_{a'+1}^{a'} (j+1)\beta_j + \theta^2 \sum_{a'+1}^m (j+1)\beta_j} \right]. \quad (\text{A23})$$

vi) $0 \leq a < i < a' = m$.—This is equivalent to a pattern of predation involving removal of a single age class a (see eq. [11]).

vii) $a = i < a' < m$.—

$$\frac{df}{d\theta} = \frac{\lambda^{i+1}}{L_{i+1}} \left(\sum_{i+1}^{a'} \beta_j + 2\theta \sum_{a'+1}^m \beta_j \right) \frac{\sum_0^i (j+1)\beta_j + (i+1) \left(\theta \sum_{i+1}^{a'} \beta_j + \theta^2 \sum_{a'+1}^m \beta_j \right)}{\sum_0^i (j+1)\beta_j + \theta \sum_{i+1}^{a'} (j+1)\beta_j + \theta^2 \sum_{a'+1}^m (j+1)\beta_j}. \quad (\text{A24})$$

viii) $c = a < i < a' < m$.—

$$\frac{df}{d\theta} = \frac{\lambda^{i+1}}{L_{i+1}} \left\{ \sum_{a'+1}^m \beta_j - \frac{\left(\sum_0^{a'} \beta_j + 2\theta \sum_{a'+1}^m \beta_j \right) \left[\sum_{i+1}^{a'} (j-i)\beta_j + \theta \sum_{a'+1}^m (j-i)\beta_j \right]}{\theta \sum_0^{a'} (j+1)\beta_j + \theta^2 \sum_{a'+1}^m (j+1)\beta_j} \right\}. \quad (\text{A25})$$

ix) $0 \leq a < i = a'$.—

$$\frac{df}{d\theta} = \frac{\lambda^{i+1}}{L_{i+1}} \left\{ \sum_{i+1}^m \beta_j - \frac{\left(\sum_{a'+1}^i \beta_j + 2\theta \sum_{i+1}^m \beta_j \right) \left[\theta \sum_{i+1}^m (j-i)\beta_j \right]}{\sum_0^i (j+1)\beta_j + \theta \sum_{i+1}^i (j+1)\beta_j + \theta^2 \sum_{i+1}^m (j+1)\beta_j} \right\}. \quad (\text{A26})$$

Predation on All Age Classes

Note that in this pattern newborn uncensused offspring, as well as individuals of all other ages, are liable to predation. V_{i+1} is found from equation (2), putting in appropriate values for θ_c and θ_k ($\theta_c = \theta$, $\theta_k = \theta$ for all k). Substituting for V_{i+1} in equation (5) gives

$$f(b_i, \theta) = \frac{\lambda^{i+1}}{L_{i+1}} \sum_{i+1}^m \theta^{j-i} \beta_j. \quad (\text{A27})$$

Differentiating with respect to θ ,

$$\frac{df}{d\theta} = - \frac{\lambda^i}{L_{i+1}} \frac{d\lambda}{d\theta} \left[\sum_{i+1}^m (j-i)\theta^{j-i} \beta_j \right] + \frac{\lambda^{i+1}}{L_{i+1}} \frac{1}{\theta} \left[\sum_{i+1}^m (j-i)\theta^{j-i} \beta_j \right]. \quad (\text{A28})$$

Again, with appropriate values for θ_c and θ_k , $d\lambda/d\theta$ is found from equation (1):

$$\frac{d\lambda}{d\theta} = \frac{\lambda}{\theta}. \quad (\text{A29})$$

Substituting for $d\lambda/d\theta$ in equation (A28) gives

$$\frac{df}{d\theta} = 0. \quad (\text{A30})$$

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