LIFE-HISTORY STRATEGIES FOR ENERGY GAIN AND PREDATOR AVOIDANCE UNDER TIME CONSTRAINTS

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Clear empirical evidence shows that short-term foraging behavior is influenced by the risk of predation (reviews in Milinski 1986; Dill 1987; Sih 1987). Organisms typically reduce time spent foraging or alter foraging habitats when predation risk increases (Stein and Magnuson 1976; Milinski and Heller 1978; Sih 1980; Lima 1985; Gilliam and Fraser 1987). Such behavioral changes often are influenced by body weight and/or hunger (Cheverton et al. 1985; Stephens and Krebs 1986). Similar trade-offs between growth and predation risk may be implicated in onto-genetic niche shifts (Werner and Gilliam 1984; Werner 1986). Since ontogenetic niche or habitat shifts are an important component of life histories, factors influencing such shifts should be integrated into life-history theory (Werner and Gilliam 1984).

Few models of optimal trade-offs between maximizing energy gain and minimizing predation risk have considered habitat or patch choice over the whole or a large part of an organism's life history (Gilliam 1982; Werner and Gilliam 1984; Werner 1986). The work of Gilliam and Werner has led to the conclusion that fitness (net reproductive output) is maximized in pre-reproductive organisms if individuals choose habitats where their ratio of mortality rate (μ) to growth rate (g) is minimized. This "minimize μ/g" rule is attractive for its simplicity and intuitive insight. The derivation of the μ/g rule assumes that reproduction is continuous and extends over an indefinite time period (Gilliam 1982). However, well-separated pre-reproductive and reproductive periods are common, particularly in seasonal environments. Several authors have demonstrated that short-term behavioral decisions may depend on time in systems where certain states must be achieved by certain times (Caraco 1980; Stephens 1981; McNamara and Houston 1982, 1986; Houston and McNamara 1985; Lucas 1985). For example, small birds in winter may have to achieve certain minimal net energy intake during the day in order to survive the nonfeeding period from dusk to dawn. Under these

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conditions the achievement of this net intake becomes increasingly important relative to conflicting behaviors as dusk approaches (McNamara and Houston 1986).

Dynamic optimization models have recently been applied to a variety of behavioral problems (Macevicz and Oster 1976; Sibly and McFarland 1976; Iwasa et al. 1984; Ydenberg and Houston 1986), including trade-offs between energy gain and predation risk (Milinski and Heller 1978; Gilliam 1982; Mangel and Clark 1986; McNamara and Houston 1986; Clark and Levy 1988; Houston et al. 1988; Mangel and Clark 1988). These dynamic foraging models assume that behavioral decisions depend on the state or condition of the individual making the decision. They predict time courses of behavior, and they allow the costs and benefits of various behaviors to be expressed in a common currency (Mangel and Clark 1986; McNamara and Houston 1986).

The present work is concerned with habitat choice in the presence of the conflicting demands of energy gain and avoidance of predation. As did Gilliam (1982), we use a two-habitat model, and we consider ontogenetic shifts over an organism's life history. In contrast to Gilliam, we introduce a time constraint, by assuming a fixed pre-reproductive period. Given an objective of maximizing reproductive output at a fixed final time T, our results reveal the dependence of optimal foraging strategies both on the time remaining until T and on the current weight of an individual. A switching of habitat or behavior is predicted along a curve that is determined analytically in terms of the weight and habitat-dependent rates of growth and predation, as well as the functional dependence of reproductive output on the final weight. Our qualitative results extend those of Werner and Gilliam (1984), McNamara and Houston (1986, 1987), and Mangel and Clark (1986), although we use a single set of assumptions that differ in detail from all of those works. We present a deterministic theory, in contrast to the theories of Mangel and Clark and of McNamara and Houston. The theory generalizes in a straightforward way to more than two habitats.

ASSUMPTIONS AND PROBLEM FORMULATION

We consider behavioral decisions of pre-reproductive foragers that can choose between two habitats. Each habitat is characterized by weight-dependent rates of energy gain and predation risk. We assume that profitable habitats (with high rates of energy gain) are always riskier, since otherwise there would be no conflict to be considered. We also assume that the final time of reproduction, T, is fixed. The objective of an individual forager is to survive to time T with a high potential reproductive output. Reproductive output is assumed to increase with weight.

Although we confine our analysis to time periods that end with reproduction, our analysis and results apply to any fixed non-reproductive period in which future fitness (survival or reproductive success) increases with weight. Life-history traits that may be viewed from this perspective include the time until diapause in insects (Tauber et al. 1986) and pre-winter fattening in birds and mammals (Murie and Boag 1984; Lima 1986; Saur and Slade 1987). Similarly, we

may consider the aquatic stage of amphibians as a fixed time period in temporary-pond communities (Smith 1987; Wilbur 1987; Semlitsch et al. 1988). In these cases, future fitness typically increases with weight at the transition time.

In the following analysis, we demonstrate how the optimal habitat choice depends on the remaining time, in the time-constrained systems described above. The final reproductive output is denoted by R, and R is assumed to depend on the final body weight W. In the following development, weight may be replaced by some other index of size with no effect on the theory. Body weight at earlier times is denoted by w, and the rate of increase of w is denoted by $g_h(w)$, in order to indicate that the growth rate depends on the habitat and on w. The index h denotes the habitat; it may take the value 1 or 2. Growth is described by

$$dw/dt = g_h(w).$$ (1)

The mortality rate is also assumed to depend on w and h. Let $s(w,t)$ denote the probability of surviving to time T, starting at weight w at time t. If we follow the growth of a single individual, then w is determined as a function of t: $w = w(t)$. Since s depends on both t and w, the time derivative of s actually involves the variation of w, according to the chain rule of calculus. Thus, if $\mu_h(w)$ denotes the instantaneous mortality rate in habitat h, then

$$ds(w(t),t)/dt = \partial s/\partial t + g_h(w)\partial s/\partial w = \mu_h(w)s(w,t).$$ (2)

The expected reproductive output (fitness) starting at weight w at time t is denoted by $f(w,t)$. According to our assumptions, the fitness is given by the reproductive output R at time T (assuming that an individual survives to time T) multiplied by the probability of survival to time T. Therefore, we have

$$f(w,t) = s(w,t)R(W).$$ (3)

We use the notation $R(W)$ in order to indicate that the reproductive output depends on the final weight. The relationship (3) is of no direct use, since the habitat h must be chosen in order to specify which dynamics apply in equations (2). Thus, we must determine the optimal strategy (the choice of h that maximizes the expected fitness, $f(w,t)$) before or at the same time as we determine the fitness. It is apparent from equation (3) that the fitness depends on both w and t. Therefore, optimal strategies must also depend on both w and t: a stationary strategy (one that does not depend on time) cannot be optimal. In particular, strategies such as minimizing μ/g cannot be optimal under our assumptions, since such strategies do not depend on the time elapsed or the time to a final reproductive period.

We characterize the optimal strategy in terms of the dynamic programming equation. This equation can be derived by computing the expected fitness at weight w at time t in terms of the expected conditions at time $t + dt$. In the interval $(t, t + dt)$, an individual in habitat h may die, with probability $\mu_h(w)dt$, or may survive, with probability $1 - \mu_h(w)dt$. In the latter case, weight gain occurs at the rate $g_h(w)$. The fitness at time t equals the probability of survival to time

$t + dt$ multiplied by the fitness at $(w + dw, t + dt)$. Thus,

$$f(w,t) = [1 - \mu_h(w)dt]\, f(w + g_h(w)dt, t + dt). \qquad (4)$$

The optimal strategy at time t maximizes the right-hand side of equation (4).

The condition for maximization of the right-hand side of equation (4) can be simplified as follows: if dt (the time increment) is small enough, then the chain rule of multivariate calculus may be applied to the function $f(w + g_h(w)dt, t + dt)$. After substitution into equation (4), the result is

$$f(w,t) \approx f(w,t) + (\partial f/\partial t)dt + (\partial f/\partial w)g_h(w)dt - \mu_h(w)\, f(w,t)dt. \qquad (5)$$

After canceling $f(w,t)$ from each side, dividing by dt, and letting dt approach 0, the result is

$$\partial f/\partial t + g_h(w)\partial f/\partial w - \mu_h(w)\, f(w,t) = 0. \qquad (6)$$

This equation has exactly the same form as equation (2) since, according to equation (3), f is just a multiple of s. Equation (6) describes the fitness function corresponding to any strategy that chooses the habitat h as a function of time t and weight w. In order to obtain the optimal strategy, we must satisfy the maximization condition stated along with equation (4). The optimal h (denoted by h^*) must be chosen to maximize the part of the expression in equation (6) that depends on h; by definition,

$$n_h(w,t) = g_h(w)\partial f/\partial w - \mu_h(w)\, f(w,t). \qquad (7)$$

Thus, h^* must maximize equation (7). The latter expression is a sum of two terms. The first term accounts for weight gain and its effect on final fitness. The second term accounts for the possibility of predation and the consequent loss of expected reproductive output. Since $n_h(w,t)$ depends on both t and w, h^* has the same dependence.

Equation (6), together with the condition that h maximize equation (7), constitutes the *dynamic programming equation*. Its solution is the optimal expected reproductive output, as a function of time elapsed and the weight of an individual.

In Appendix A, the preceding analysis is extended to a somewhat more general situation in which individuals have the option of choosing the proportion of time spent in the respective habitats. The results obtained there show that the optimal strategy is to spend all available time in one or the other of the habitats.

The analytical solution of equations (6) and (7) is obtained in Appendix A. The remainder of this work is a description of that result and its implications. We can draw some important conclusions without going through the complete solution, by confining our attention to the period just before the final time, T. The values of w, h, and $n_h(w,t)$ at $t = T$ are denoted by W, H, and $N_h(W)$, respectively. At the final time, T, the fitness function is just the reproductive output: $f(W,T) = R(W)$. It then follows from the optimality condition (7) that the final habitat choice, H^*, must maximize

$$N_h(W) = g_h(W)(dR/dw)(W) - \mu_h(W)R(W). \qquad (8)$$

Here, dR/dw denotes the derivative of R with respect to W. The interpretation of equation (8) is analogous to the interpretation of equation (7), except that the foraging decision is to be made just before reproduction. We next define $\Delta N(W)$ by

$$\Delta N(W) = N_2(W) - N_1(W);\qquad(9a)$$

$$\Delta N(W) = [g_2(W) - g_1(W)]\, dR/dw - [\mu_2(W) - \mu_1(W)]R(W).\quad(9b)$$

For values of W for which $\Delta N(W) > 0$, habitat 2 is preferred according to equation (8); when $\Delta N(W) < 0$, habitat 1 is preferred. The boundary between these cases is a point, W^*, where

$$\Delta N(W^*) = 0.\qquad(10)$$

The implications of the existence of such a point are explained below.

Now we discuss conditions under which $\Delta N(W)$ should vanish at some value W^*. Our subject is interesting only if there is in fact a trade-off between foraging success and the avoidance of predation or other mortality factors. Therefore, without loss of generality, we confine ourselves to the case in which both the growth rate and the mortality rate are higher in one habitat than in the other; that is, $g_2(w) > g_1(w)$ and $\mu_2(w) > \mu_1(w)$. Under these assumptions, both terms in brackets in equation (9) are positive, as are dR/dw and R. If the final weight, W, is small, the marginal gain in reproductive output per unit of weight gained is relatively large compared with $R(W)$, since the reproductive output is small or nonexistent for small weights. However, if W is large, the marginal gain in reproductive output from increased weight is relatively small compared with $R(W)$, since the reproductive output is large and the marginal utility of increased weight eventually decreases for large weights. Therefore, we expect the growth term in equation (9b) to dominate if W is small, and hence, habitat 2 (which favors growth at the expense of predation risk) should be favored if W is small. However, the mortality term in equation (8) should dominate if W is large, and hence, habitat 1 should be favored, since large individuals have more to lose from predation than they can gain from additional weight gain. The preceding argument does not guarantee that $\Delta N(W)$ must always change sign at a plausible weight. For example, if μ_1 and μ_2 differ only slightly, then habitat 2 would always be favored. However, we confine our attention to cases in which ΔN does change sign.

If t is approaching T, then the optimal strategy is to choose habitat 2 if $\Delta N(W) < 0$, that is, if $W < W^*$, and to choose habitat 1 otherwise. It is clear that the switching point, W^*, cannot be determined simply from a knowledge of μ and g, since the quantities R and dR/dw also appear in equation (9b) and hence in equation (10). This provides a second argument against a strategy of minimization of μ/g, in addition to its disregard of the dependence of the strategy on elapsed time.

<center>DESCRIPTION OF THE OPTIMAL STRATEGY</center>

More-complete details of the following discussion are given in Appendix A. Here we outline the construction of the optimal strategy and interpret the corresponding phenomena.
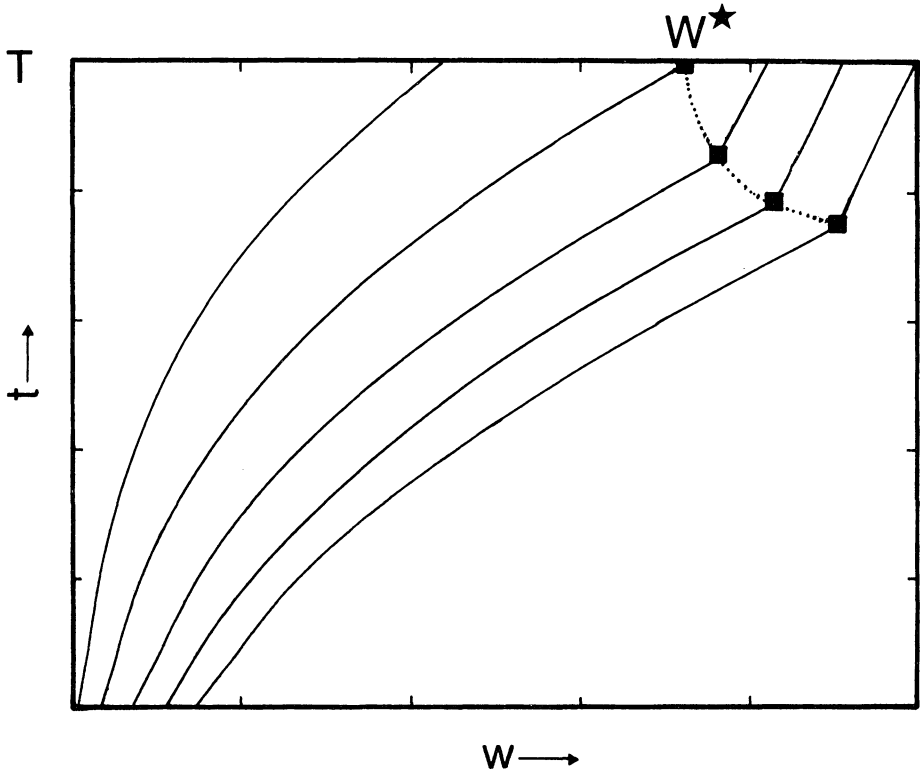
FIG. 1.—Optimal habitat choice for growth along five trajectories of time (t) versus weight (w). The ratio μ/g is lower in habitat 2 (fast growth) than in habitat 1. *Dotted curve,* The optimal switching curve, drawn in the w-t plane. The optimal strategy calls for foraging in habitat 2 (fast growth and high predation) when below the switching curve, and foraging in habitat 1 when above it. Note the abrupt change in growth rate as habitat switching takes place.

According to equation (7), the optimal strategy is to choose the habitat h that maximizes $n_h(w,t)$. This implies that an individual should switch habitat at a weight w and time t where $n_2(w,t) - n_1(w,t) = 0$. This difference is denoted by

$$\Delta n(w,t) = n_2(w,t) - n_1(w,t); \tag{11a}$$

$$\Delta n(w,t) = [g_2(w) - g_1(w)](\partial f/\partial w)(w,t) - [\mu_2(w) - \mu_1(w)] f(w,t). \tag{11b}$$

We have already considered the optimal strategy at the final time, T. Near equation (8), W^* was defined as the point on the line $t = T$ where $\Delta N = 0$. The optimal habitat, h^*, is obtained for earlier t by drawing trajectories backward from the final line where $t = T$, as in figure 1. The trajectories to the left of W^* have $h^* = h_2$, and those to the right of W^* have $h^* = h_1$, according to criterion (7). Along the trajectories to the right of W^*, $\Delta n(w,t)$ vanishes at some point w^*. The trajectories are continued below this point by switching from habitat 1 to habitat 2 as t decreases.

We call the dotted curve in figure 1 the *switching curve*, that is, the curve in the w-t plane where the net rates of change in fitness from foraging in the two habitats are equal: $\Delta n(w, t) = 0$. According to Appendix A, $\Delta n(w, t) = 0$, where

$$\frac{G_h}{G_2 - G_1} \frac{\Delta N}{R} + Q = q. \tag{12}$$

The quantities G_h, G_1, G_2, and Q refer to the values at $t = T$ and $w = W$ of g_h, g_1, g_2, and q, respectively. The quantity $q(w)$ is defined by

$$q(w) = \left[\frac{\mu_2(w)}{g_2(w)} - \frac{\mu_1(w)}{g_1(w)}\right] \bigg/ \left[\frac{1}{g_1(w)} - \frac{1}{g_2(w)}\right]. \tag{13}$$

Expressions (12) and (13) are complex, but they can be interpreted in terms of more-basic quantities. In order to facilitate such interpretation, we may multiply both numerator and denominator in expression (13) by a small weight change, dw. The quantity dw/g is the increment in weight multiplied by the rate of change of time with respect to weight gain, that is, the increment in time for a given weight gain. Therefore, after multiplication by dw, the denominator in expression (13) may be interpreted as the difference in time required for a given increment in weight in the two habitats. The ratio μ/g in the numerator may be interpreted as the ratio of mortality increment to weight increment. Therefore, after multiplication by dw, the numerator in expression (13) is the difference in mortality increment in the two habitats. Thus, $q(w)$ may be interpreted as the difference in the increments of mortality, divided by the difference in increments in time in the two habitats. Turning now to expression (12), the quantities Q and q may be interpreted according to the preceding. The first term consists of a weighting factor involving the ratio of the values of the growth rate G and the reproductive output R, multiplied by ΔN. The latter quantity changes sign at the switching point, W^*. Therefore, the first term in equation (12) is a weighted measure of the distance from the final point, W, to W^*. According to the criterion (12), one switches when the difference $q - Q$ equals this weighted measure of distance from W^*. One should expect to observe switching along trajectories finishing either to the right or to the left of W^* whenever q varies along a trajectory.

The optimal strategies fall into two major categories, as illustrated in figures 1 and 2. The distinction between them may be drawn quite generally in terms of the behavior of q defined above. The case depicted in figure 1 occurs if q increases as the weight w increases, and the case depicted in figure 2 occurs if q decreases as w increases. For simplicity, the interpretation of these conditions is given for a special case in which the growth rates and predation rates are proportional in the two habitats. We assume that

$$g_i(w) = \lambda_i \ell(w), \tag{14}$$

where λ_i are nonnegative constants that depend on the habitat, and $\ell(w)$ expresses the common dependence of the growth rates g_1 and g_2 on the weight w. We assume further that the mortality rates are proportional in the two habitats, that
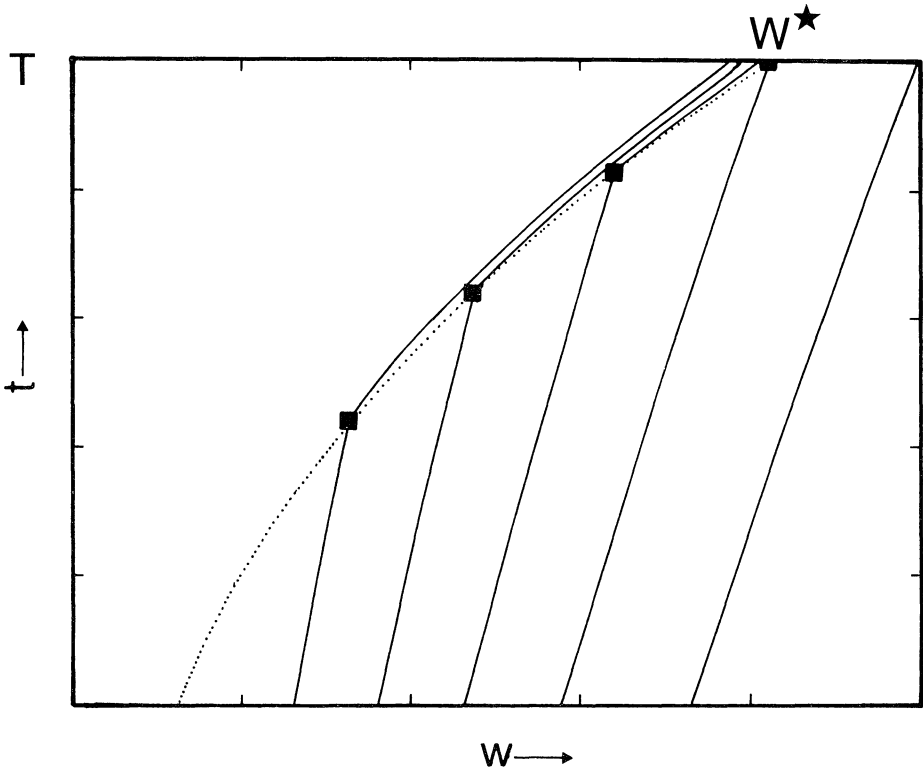
FIG. 2.—Optimal strategy and associated trajectories, where the ratio μ/g is lower in habitat 1 (slow growth) than in habitat 2. The final weights of individuals that switch are close together. However, the effect of early switching is to increase mortality rates greatly. Individuals starting out at small body weights are unlikely to reach the time of reproduction, but those that do will have high body weights.

is, that

$$\mu_i(w) = \gamma_i m(w),$$ (15)

where γ_i are nonnegative constants that depend on the habitat, and $m(w)$ expresses the common dependence of the mortality rates μ_1 and μ_2 on the weight w. In such a case, we have

$$\frac{\mu_2}{g_2} - \frac{\mu_1}{g_1} = \frac{m(w)}{\ell(w)}\left(\frac{\gamma_2}{\lambda_2} - \frac{\gamma_1}{\lambda_1}\right).$$ (16)

Thus, the difference in the ratios of μ/g is given by a factor that depends on the body weight times a second factor, which expresses the difference between the habitats.

Now we can show that under our assumptions (14) and (15), switching occurs if the mortality $m(w)$ actually varies with w, although there is no change in the sign of the difference in μ/g. The difference in μ/g cannot change sign as w changes

(according to our assumptions), since neither $\ell(w)$ nor $m(w)$ changes sign. However, according to equation (12), switching between habitats is determined by variation in $q(w)$. Substituting assumptions (14) and (15) into equation (13) yields

$$q(w) = m(w) \left(\frac{\gamma_2}{\lambda_2} - \frac{\gamma_1}{\lambda_1}\right) \bigg/ \left(\frac{1}{\lambda_1} - \frac{1}{\lambda_2}\right). \qquad (17)$$

Both quantities in large parentheses in equation (17) are independent of w. Therefore, q varies with w if $m(w)$ varies with w. As we have seen above, such variation implies habitat switching.

For the interpretation of the following two cases of ontogenetic habitat shifts, it is helpful to keep in mind that the ratio μ/g is a ratio of a death rate and a growth rate. Therefore, this ratio has the interpretation as a rate of death per unit of growth.

Case 1: μ/g Lower in Habitat 2 than in Habitat 1

In this case, habitat 2 offers a higher growth rate than habitat 1, and also a lower rate of increase in mortality per unit of weight gained (μ/g), for all body weights under consideration. According to a strategy of minimizing μ/g, habitat 2 would always be preferred. However, we have already seen that at the final time, T, there should be a switch of habitats at some weight W^*. The resolution of this conflict is depicted in figure 1. Most individuals start in habitat 2, except for those with exceptionally large body weights. Individuals that reach large body weights find it advantageous to switch to habitat 1, according to the same argument given above to explain the motivation for switching at W^*. It is at first sight surprising that the optimal strategy of some heavier individuals calls for overshooting the weight W^*. But if one recalls that predation risk decreases as weight increases, it becomes apparent that "excessive" weight gain may serve as a partial refuge from predation.

Case 2: μ/g Lower in Habitat 1 than in Habitat 2

In this case, habitat 2 offers a higher growth rate, but habitat 1 provides a lower rate of mortality increase per unit of weight gained. According to a strategy of minimizing μ/g, habitat 1 should be preferred. However, such a choice neglects the necessity of achieving a suitable weight for reproduction by the final time, T. The optimal strategy is depicted in figure 2. According to this strategy, individuals with low initial weights begin in habitat 1 and later switch to the riskier high-growth habitat. It is clear that a mixture of foraging in habitats 1 and 2 is necessary in order to achieve a weight suitable for reproduction, but it is perhaps not clear why individuals should start in habitat 1. Habitat 1 is preferred for the purpose of gaining weight safely because the ratio μ/g is lower in habitat 1 than in habitat 2. The higher weight thus achieved serves as a partial refuge against predation risk: if one must face high predation risk, it is better to postpone the time until a larger weight has been achieved.

One additional point requires further clarification. The weight W^* is not a universal optimal weight at T in either of the two scenarios described above. W^* is the origin of the switching curve or the optimal point of switching only when $w =$

W^* exactly at $t = T$. There is in fact a distribution of optimal weights at T that reflects the variation among individuals in their weights at times before T (figs. 1, 2). In our figures, there is a set of possible weights at a given time t, and according to the optimal strategy, each one of the corresponding individuals switches at a different weight and time, and each therefore reaches the final time at a different final weight. The result of switching from habitat 2 to habitat 1 in case 1 is a decrease in predation rates, but this also has the effect of lowering the final weight, W, for an individual. The reverse happens in case 2, in which the effect of switching is to increase both the predation rates and the final weight.

Although the strategy of minimizing μ/g differs from the present one, there are many similarities. It is apparent from figures 1 and 2 that, initially, individuals do best if they follow the rule of minimizing μ/g. However, at later stages, a switch in strategy may be advantageous. When the habitat with a high growth rate is initially favored, the switch is caused by diminishing returns from additional foraging, compared with increasing fitness losses from predation. When the habitat with a low growth rate is initially favored, the switch is caused by the necessity of achieving a body weight adequate for reproduction or metamorphosis by time T.

The rule of minimizing μ/g may be derived under a different set of conditions. If we consider the case of a metamorphosing amphibian and assume that metamorphosis occurs at a fixed weight and that the time required to reach that weight is of no consequence, then the optimal strategy is to reach the weight for metamorphosis while experiencing the least risk of predation. The ratio μ/g is interpreted as the rate of predation per unit of weight gain, and therefore, it is optimal to minimize μ/g, as was done by Werner (1986). Such a result is obtained from our theory if the condition that $f(T, W) = R(W)$ is omitted, and instead $(\partial f/\partial t)(w, t)$ is constrained to vanish.

Effect of Changes in Parameters on the Optimal Strategy

The optimal strategy as specified by the switching curve (eqs. 12, 13) alters if various parameters change. This feature allows the model to be tested experimentally. For example, if T or the perception of time remaining until reproduction is decreased experimentally, W^* is not altered, but the current position of an individual is moved forward in time. This is illustrated in figure 3, where μ/g is lower in habitat 1, but growth and predation rates are higher in habitat 2 (corresponding to case 2). By decreasing $T - t$, it can be seen that individuals that start out below the switching curve switch habitats at smaller sizes than they otherwise would. The smaller individual in figure 3 crosses the switching curve if the time remaining is shortened and hence should switch habitats according to the theory. The result for each of these organisms is a greater probability of predation and a smaller size by time T. Therefore, at the population level, we expect to see a greater fraction of individuals switching at an earlier age, with concomitant greater predation rates and smaller sizes at the final time. Alternatively, if T is increased, there is a point at which no members of the population switch, simply because time is no longer a constraint.

If predation risk or the perception of risk is increased in habitat 2, the position
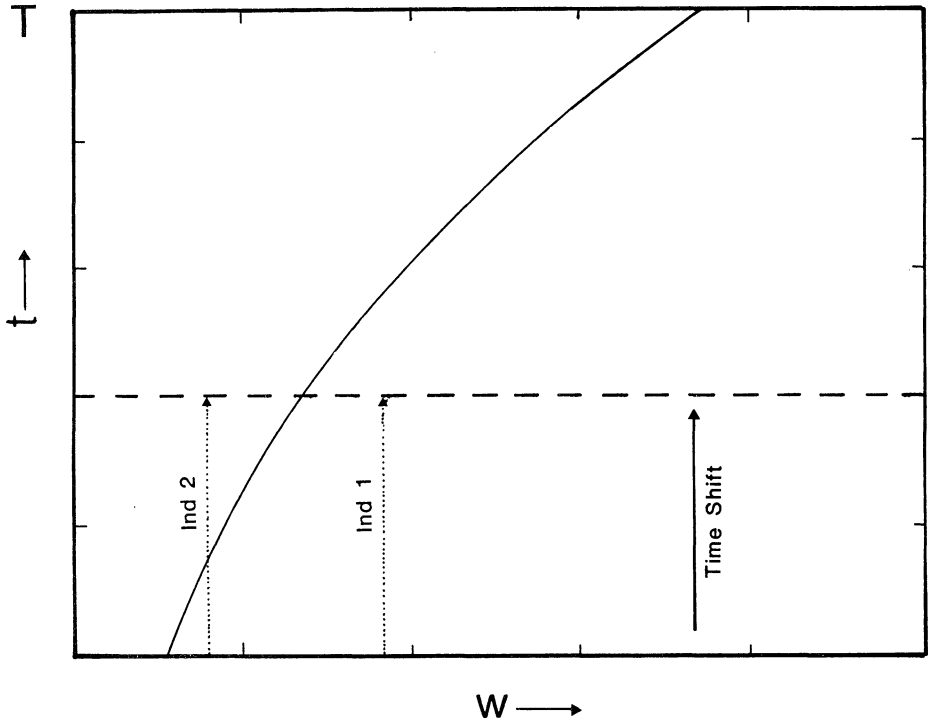
FIG. 3.—The effect on the optimal strategy of a shift in remaining time. *Solid curve*, The
optimal switching curve. *Dashed line* and the associated *dotted lines* illustrate the effect of a
change in the perceived time remaining until reproduction. If the corresponding dotted line
crosses the optimal switching curve, there is a habitat shift, according to the optimal strategy.
Individual 1 starts at a large weight and does not shift habitats, even under the time shift.
Individual 2 starts at a lower weight and makes a shift.

of W^* and the switching curve changes. The overall effect of an increase in
predation risk in habitat 2 is to delay the transition to that habitat for some
individuals and to prevent it entirely in others. This is illustrated in figure 4, where
the switching curve corresponding to figure 2 is shown as a dashed line, and the
new switching curve has a square plotted on it. Individuals marked 1 and 2 in
figure 4 would have switched at the points marked S_1 and S_2 on the dashed curve.
After the change in predation risk, individual 1 does not switch from habitat 1 and
consequently achieves a lower final body size than if switching had occurred.
Individual 2 switches, but at a later time than formerly; hence, individual 2 also
achieves a lower body size. Thus, one effect of an increased predation rate in the
second habitat is a lower mean body size in the population. The individuals that
switch experience higher predation rates. However, since fewer individuals
switch, overall predation rates in the population may increase or decrease depend-
ing on the starting sizes of individuals. The opposite effects may be expected if
predation were decreased in habitat 2.

Finally, if the growth rate is increased in habitat 1, then the position of the
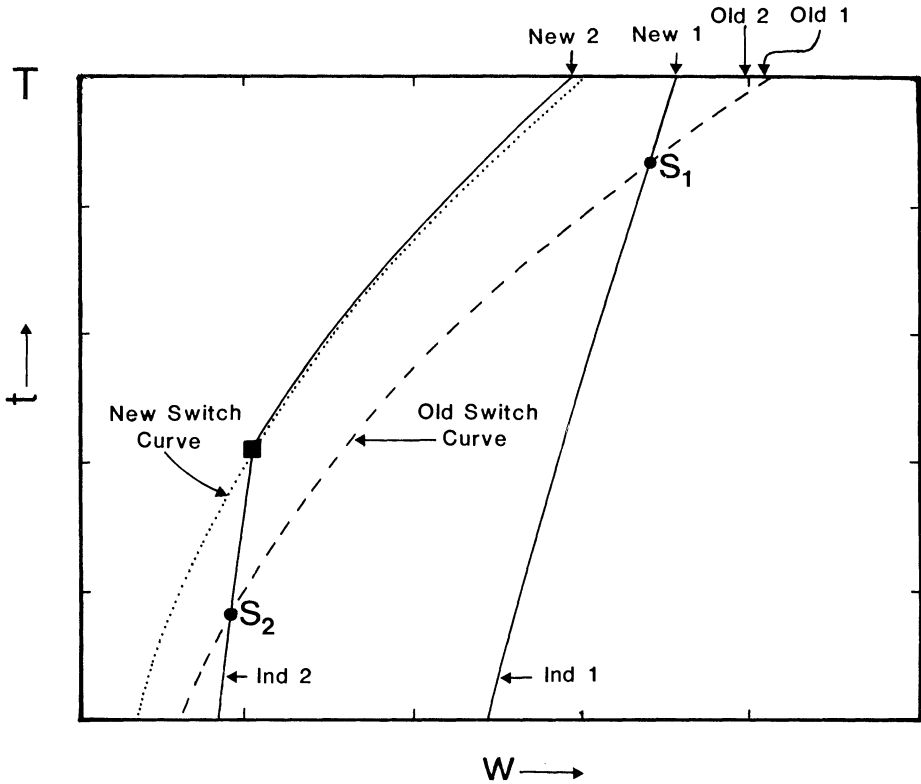
FIG. 4.—The effects on the optimal strategy of a change in mortality rate. *Dashed curve*, The old optimal switching curve, as in figure 2. *Dotted curve*, The new optimal switching curve if the mortality rate μ_2 is increased. The effect is to lower the weight intercept W^* on the line where $t = T$ and to shift the switching curve to the left. This corresponds to a switch to habitat 2 at a later time than in figure 2. The consequence of such a shift is a reduction in final body sizes. The trajectories for two individuals are shown. The points at which they would have switched habitats under the old conditions are denoted by S_1 and S_2, respectively. Individual 1 begins at a large weight and does not switch habitats after the increase in μ_2. Individual 2 begins at a smaller weight and switches later than if μ_2 were unchanged.

switching curve is changed as in figure 5. This results in a shifting of W^* and the switching curve to the left, since the value of remaining in habitat 1 has increased. Again, the result is to delay the time of switching for some individuals and to prevent it entirely for others. An individual starting with a high body weight (Ind. 1 in fig. 5) does not switch habitats in either case. Because the growth rate in habitat 1 is higher, that individual achieves a larger body size. An individual starting at a small size (Ind. 2) finishes near the new value of W^* if g_1 is increased. This results in a smaller body size than if switching had occurred earlier. Thus, the result of an increase in growth rate in the slow-growth habitat is not necessarily an increase in body weight, since the overall benefits of remaining in the slower but safer habitat are increased. Predation rates for the population as a whole decrease,
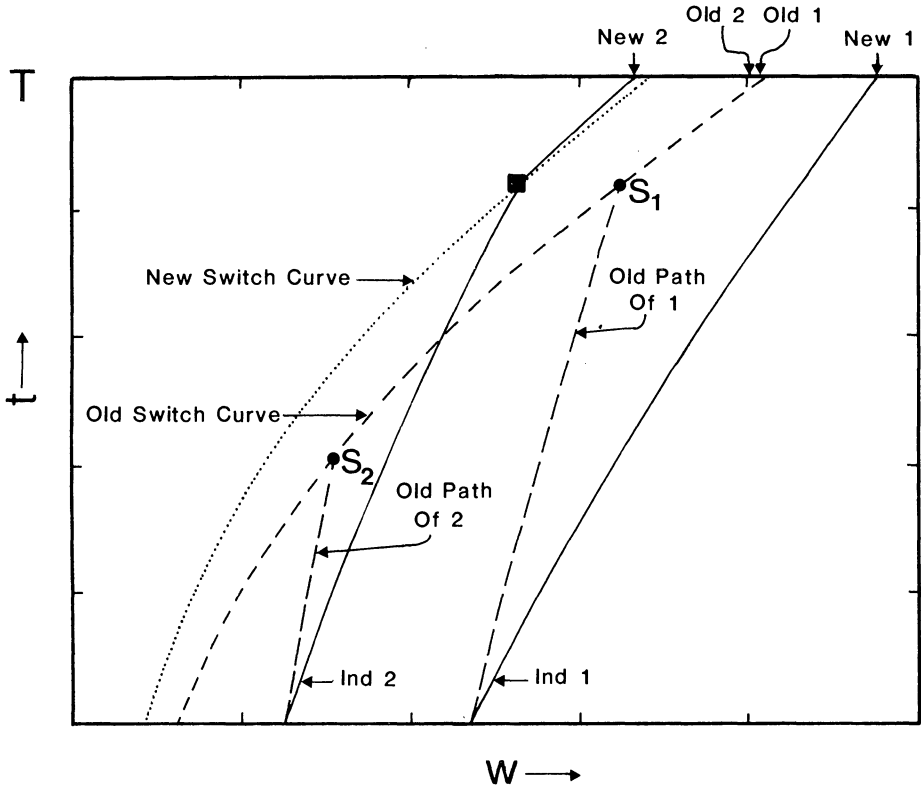
FIG. 5.—The effect on the optimal strategy of a change in growth rate. *Dashed curve*, The old switching curve, as in figure 2. *Dotted curve*, The new switching curve, after g_1 has been increased. The new switching curve is shifted to the left, as in figure 4. Individual 1 begins at a large weight and consequently does not shift habitats if g_1 is increased. Under the old set of conditions, this individual would have shifted habitats at point S_1 but would have reached a smaller body size than under the new regime. Individual 2 starts at a lower weight and switches habitats under both sets of conditions. However, the final weight for individual 2 is lower under the new set of circumstances.

and thus the overall fitness of the population increases, despite an overall decrease in body sizes at the time of reproduction.

DISCUSSION

The present work derives a number of important results concerning foraging and predator avoidance from a single set of assumptions. Some of these results were previously derived from a variety of differing assumptions by Gilliam (1982), Werner and Gilliam (1984), Mangel and Clark (1986), and McNamara and Houston (1986, 1987). The context of life-history strategies was emphasized by Gilliam and by Werner and Gilliam. The general dynamic programming approach with time constraints was advocated by Mangel and Clark and by McNamara and Houston.

It should be noted that none of these theories (including our own) allow for frequency-dependent decision making. In such a case, the problem would become a many-player game. The theory of such games is quite difficult, and it is beyond the scope of this work. One might attempt to approximate such results by considering decision making by a single individual that is part of a large group. Collective effects would be reflected in variations in foraging success and predation rates. The present formulation might suffice if individuals do not attempt to anticipate such collective effects.

Predictions

The feature that distinguishes our theory from previous theories of growth and predation-dependent ontogenetic niche shifts (Gilliam 1982; Werner and Gilliam 1984; Werner 1986) is our consideration of time constraints. We have introduced a time constraint by assuming that reproduction, or some other major event related to fitness, occurs at the end of a fixed time, T. We demonstrated that in a two-habitat model, with the objective of maximizing reproductive output (weight) at T, optimal strategies may involve habitat shifts along a curve in a weight-time plane. The position of the curve depends on weight and habitat-dependent growth and mortality rates as well as the relationship between final weight and reproductive output.

In their consideration of ontogenetic niche shift, Gilliam (1982) and Werner and Gilliam (1984) employed a rule that optimal strategies should minimize the ratio of μ (mortality) to g (growth) when choosing habitats. It is understood in their derivation that the strategies must depend not on time but only on the weight of an individual. Such an assumption is incompatible with our assumption of reproduction at a fixed time. We have shown that habitat shifts may emerge despite equal ratios of μ/g in the two potential habitats. This result agrees with intuition. Consider an organism with low growth rate near the time of reproduction occupying a habitat of low predation risk. If the organism is currently large enough to have a high reproductive value at the final time, T, then it should stay in the habitat. If it is small with a reproductive value near or at zero, then it should switch to a habitat of high growth despite higher predation rates.

A second major point of diversion between our theory and the μ/g model is our prediction that, within a single population, optimal weight and timing of habitat shifts may vary among individuals. This results from including a time constraint and allowing for some variation among weights of individuals at any given time. The μ/g theory predicts a single optimal weight for habitat shifts and makes no predictions about the timing of shifts. Our prediction is more closely aligned with empirical data concerning ontogenetic habitat shifts. For example, within amphibian populations, both the size and the timing of metamorphosis are variable. We expect systems without time constraints to experience variation in the timing of shifts but not variation in the weight at shifts. However, systems with time constraints are expected to experience variation in both.

Our approach and conclusions are similar to those of McNamara and Houston (1986) and Mangel and Clark (1986). These authors have used dynamic programming techniques to express behavioral decisions in some common currency of

fitness. This device makes it possible to relate the study of short-term behavior to long-term fitness. In both these works, foraging decisions are shown to depend on an individual's state and the time remaining in a period T. Our theory takes a more long-term dynamic view of this dynamic problem. We use a time period that incorporates ontogenetic change in body weight, and we allow growth and predation rates to depend on weight. We have chosen a deterministic formulation, in contrast to McNamara and Houston and to Mangel and Clark. The implications of this difference are explored in Appendix B.

The results corresponding to figures 4 and 5 illustrate an important point, which was derived under different assumptions by McNamara and Houston (1987). The effect of an increase in predation risk in one habitat is to decrease body sizes throughout the population but not necessarily to increase deaths from predation. The effect of an increase in growth rate in one habitat is to decrease predation mortality throughout the population but not necessarily to increase final body weights. Therefore, one must be exceedingly careful in assigning causes of mortality or changes in the condition of individuals in a population. One should be even more circumspect when attempting to ascribe population regulation to a single factor or to a restricted set of factors acting in isolation.

Testing the Theory

The major novel feature of our theory is the identification of time constraints as determinants of optimal timing and weights of ontogenetic niche shifts. Therefore, we concentrate on predictions concerning variation in the final time, T. Quantitative tests of the theory are limited by the extreme difficulty of quantifying parameters such as predation risk. However, the qualitative predictions of our theory are testable by both comparative and experimental methods, since the relationship between the state of an organism w and the time remaining in some period $(T - t)$ varies in nature and may be manipulated experimentally. In the following discussion, we consider two interesting life-history phenomena that may provide fruitful systems for application of this theory.

Diapause is a common feature in insect life histories; it appears to be an adaptation to permit survival under adverse environmental conditions such as extreme cold or drying. Individuals that do not enter diapause often die, and survival during and after diapause may depend on the condition of the individual at the onset (Tauber et al. 1986). Typically, diapause is induced by an environmental cue (such as the photoperiod), which is received long before the upcoming adverse environment. We may expect variation from year to year or from region to region in the relationship between physiological condition (e.g., weight) and the time remaining until the environment deteriorates. Our theory predicts that individuals in poor condition near the critical time will undertake more risky foraging than those in better condition. Therefore, in a comparison of two populations that differ in the time to the onset of adversity, we expect to see higher growth and mortality rates in the population experiencing the earlier onset. Within populations, individuals in poor condition late in the season are expected to take more risks than individuals in the same condition earlier in the season. A direct experi-

mental test could include manipulation of cues, such as photoperiod, that induce diapause.

Werner (1986) viewed size at metamorphosis in amphibians as a trade-off between growth and predation risk, where habitat 1 is an aquatic environment (larval stage) and habitat 2 is a terrestrial environment (adult stage). In these circumstances, our theory may be more suitably applied than a simple minimization of μ/g. The life histories of these amphibians are characterized by temporally discrete and often explosive breeding periods, with reproductive success a function of size at reproduction. Furthermore, the present theory makes predictions about both timing and size at metamorphosis, which typically vary within and between amphibian populations, as stated previously.

Our theory also applies when only the larval period is considered. Temporary-pond communities provide an excellent example of time constraints on foraging decisions. Ponds are subject to various drying regimes, larvae must metamorphose before drying or risk desiccation, and future reproductive success is an increasing function of size at metamorphosis (Smith 1987; Semlitsch et al. 1988). Therefore, larval stages of amphibians in temporary ponds provide a system in which discrete and variable time periods occur, and the payoff at the time of metamorphosis increases with body weight. Wilbur (1987) has manipulated drying regimes in experimental pond communities and demonstrated increased growth rate (and developmental rate) under rapid drying of at least one species, as our theory would predict. Under increased drying, *Bufo americanus* tadpoles metamorphosed earlier than, but at the same size as, those in ponds with stable water levels. This is not a direct test of our theory since uncontrolled factors associated with accelerated drying (such as increased temperature and food density) may account for the increased growth rate, rather than a switch to risky and more-rewarding foraging behavior. Nevertheless, this system appears to be suitable for the study of time constraints on foraging decisions.

SUMMARY

Short-term foraging behavior is typically influenced by the needs to obtain food at a high rate and to avoid predation. There is increasing evidence that the need to balance these conflicting demands plays a role in ontogenetic habitat shifts, including the spectacular shifts characteristic of complex life cycles. Previous theory has led to rules that are independent of time to predict the size at which habitat shifts take place. We develop a model that incorporates time constraints, by assuming that reproduction or some other major event, such as diapause or metamorphosis, must occur by a specified time or date. We incorporate recent formulations of dynamic programming that allow strategies to balance conflicting behaviors by expressing them in the common currency of future reproductive output. The resulting theory predicts optimal strategies for pre-reproductive habitat shifts that depend on both time and body weight. Our theory, although derived from a single set of assumptions, leads to a synthesis of insights gained from a diversity of previous dynamic optimization problems.

APPENDIX A

SOLUTION OF THE DYNAMIC PROGRAMMING EQUATION

This appendix contains a general formulation of the problem and its solution. We derive the dynamic programming equation for the case in which the forager is free to choose an arbitrary division of foraging time between two habitats. The result under this more general assumption is no different than if the forager were constrained to forage in only one habitat, except for a few switches. The main result of this appendix is an expression for the switching function along a trajectory. This is obtained by first calculating the time derivative of fitness along a trajectory. This result enables us to calculate the marginal value of weight gain, which in turn leads to an expression for the switching function.

The Dynamic Programming Equation

We change notation slightly from that of the text ("Assumptions and Problem Formulation") by defining

$$g(w, p) = g_1(w) + p[g_2(w) - g_1(w)] \tag{A1}$$

and

$$\mu(w, p) = \mu_1(w) + p[\mu_2(w) - \mu_1(w)]. \tag{A2}$$

Here, the variable p denotes the proportion of time spent in habitat 2. The dynamic programming equation can be derived as before by computing the expected fitness at weight w at time t in terms of the expected conditions at time $t + dt$. In the interval $(t, t + dt)$, the individual may be captured by a predator, with probability $\mu(w, p)dt$, or may escape predation, with probability $1 - \mu(w, p)dt$. In the latter case, weight gain occurs at the rate $g(w, p)$. Thus,

$$f(w, t) = [1 - \mu(w, p)dt] f(w + g(w, p)dt, t + dt). \tag{A3}$$

The expression on the right-hand side may be expanded to yield

$$f(w, t) = f(w, t) + \frac{\partial f}{\partial t} dt + \frac{\partial f}{\partial w} g(w, p)dt - \mu(w, p) f(w, t)dt. \tag{A4}$$

After canceling $f(w, t)$ from each side and dividing by dt, the result is

$$\partial f/\partial t + g(w, p) \partial f/\partial w - \mu(w, p) f(w, t) = 0. \tag{A5}$$

This equation describes the expected change in fitness, for any predetermined choice of p as a function of w and t. In order to maximize the left-hand side of equation (A5), p should be chosen to maximize the right-hand side of equation (A4). The optimal p^* maximizes

$$n(t, w, p) = g(w, p) \partial f/\partial w - \mu(w, p) f(w, t). \tag{A6}$$

This condition, together with equation (A5), constitutes the dynamic programming equation.

In our particular case, condition (A6) can be simplified. We write

$$n(t, w, p) = n(w, t, 0) + p\Delta n(w, t),$$ (A7)

where

$$\Delta n(w, t) = [g_2(w) - g_1(w)] \, \partial f/\partial w - [\mu_2(w) - \mu_1(w)] f(w, t).$$ (A8)

The optimal strategy must have $p^* = 1$ if $\Delta n(w, t) > 0$, and $p^* = 0$ if $\Delta n(w, t) < 0$. When $\Delta n(w, t) = 0$, we cannot determine p from this condition. The optimal strategy is exactly as determined in the text ("Assumptions and Problem Formulation"), although we started with a more general formulation.

A difficulty in solving equations (A5) and (A6) is that the control variable p must be determined along with the rest of the solution. This difficulty disappears if we know beforehand that p is constant. We have just shown that p^* is constant except when Δn changes sign. The following calculation is valid in a region where Δn does not change sign.

An Integral of the Dynamic Programming Equation

Equations (A5) and (A6) (or eqs. 6, 7) must be solved together. In order to compute p from equation (A6), f and $\partial f/\partial w$ must be known. We require an equation analogous to equation (A5) for $\partial f/\partial w$ (the marginal value of increased weight) in order to obtain p from equation (A6). The following method yields the required information about derivatives of f in the important case (assumed here) in which neither the growth rate nor the predation rate depends explicitly on the time.

The first step is to differentiate equation (A5) with respect to t to yield

$$\partial^2 f/\partial t^2 + g(w, p) \, \partial^2 f/\partial t \partial w - \mu(w, p) \, \partial f/\partial t = 0.$$ (A9)

The chain rule for a function of two variables implies that the total derivative along a trajectory is given by

$$\frac{d}{dt} \frac{\partial f}{\partial t} = \frac{\partial}{\partial t} \frac{\partial f}{\partial t} + g(w, p) \frac{\partial}{\partial w} \frac{\partial f}{\partial t}.$$ (A10)

Thus, equation (A9) may be rewritten as

$$\frac{d}{dt} \frac{\partial f}{\partial t} = \mu(w, p) \frac{\partial f}{\partial t},$$ (A11)

which is the required analogue of equation (A5). It now follows that

$$\frac{d}{dt} \left(\frac{1}{f} \frac{\partial f}{\partial t} \right) = 0.$$ (A12)

The proof consists in differentiating the quotient in equation (A12) and substituting equations (A5) and (A11). Therefore, the quotient in equation (A12) is constant along trajectories. Equation (A12) leads to the crucial information about $\partial f/\partial w$. If equation (A5) is substituted into equation (A12), the result is that

$$[g(w, p) \, \partial f/\partial w - \mu(w, p) f]/f(w, t) \text{ is constant along trajectories.}$$ (A13)

The relation (A13) constitutes a second integral of the dynamic programming equation.

Variation in the Switching Function along a Trajectory

The switching function is obtained from equation (A13) as follows. Equation (A8) may be solved for $\partial f/\partial w$ to yield

$$\frac{\partial f}{\partial w} = \frac{\Delta n + [\mu_2(w) - \mu_1(w)]f}{g_2(w) - g_1(w)}.$$ (A14)

When this result is substituted into equation (A13), the result is that

$$\frac{g(w, p)}{g_2(w) - g_1(w)} \frac{\Delta n}{f(w, t)} + q(w, t) \text{ is constant along trajectories}, \tag{A15}$$

where

$$q(w, p) = \frac{g(w, p)[\mu_2(w) - \mu_1(w)]}{g_2(w) - g_1(w)} - \mu(w, p). \tag{A16}$$

Moreover, it follows from some manipulations that, in fact, q is independent of p:

$$q(w) = \left[\frac{\mu_2(w)}{g_2(w)} - \frac{\mu_1(w)}{g_1(w)}\right] \bigg/ \left[\frac{1}{g_1(w)} - \frac{1}{g_2(w)}\right]. \tag{A17}$$

Another way of expressing condition (A15) is

$$\frac{g(w, p)}{g_2(w) - g_1(w)} \frac{\Delta n}{f(w, t)} + q(w) = \frac{G}{\Delta G} \frac{\Delta N}{F} + Q. \tag{A18}$$

The capitalized quantities in equation (A18) denote the values at the final point on the trajectory, where $t = T$ and $w = W$. Switching occurs if $\Delta n = 0$, that is, if

$$\frac{G}{\Delta G} \frac{\Delta N}{R} = q - Q. \tag{A19}$$

Equation (A19) determines the position of the switching point (if any) along a trajectory.

APPENDIX B
Methods: Deterministic versus Stochastic Theories

Our approach is derived from the calculus of variations. According to these ideas, one seeks to cover the state space with a family of (deterministic) optimal trajectories, analogous to filling a portion of space with light rays. These ideas carry over to control theory, and they are at the heart of the dynamic programming approach.

A deterministic approach might be interpreted as one in which an individual's behavior is determined quite early (perhaps at birth) and does not respond to changing conditions, since they are completely predictable if the world is truly deterministic. Although we consider a deterministic model, the strategy obtained can be applied in a stochastic setting. The optimal strategy obtained above expresses the optimal habitat choice in terms of an individual's weight and perception of the time remaining until reproduction, as well as growth and predation rates, each of which can vary in response to random influences.

The deterministic dynamic programming approach apparently has not been exploited as thoroughly as the stochastic theory in behavioral ecology. A notable exception is the work of Kozlowski and Wiegert (1986); a similar approach to life-history theory was taken by Schaffer (1983). They were concerned with the problem of the optimal allocation of energy to growth and reproduction. The situations that they considered are simpler than ours, since they assumed that the mortality rate is independent of body weight and time and that there is no growth after the switch to reproduction. Consequently, the theory required to construct their switching curves is simpler than ours. Their use of a deterministic model, and the conception of the optimal strategy as one that depends on the state of an individual and on the time remaining, is in complete agreement with our approach.

Recent work of McNamara and Houston (1986, 1987) and of Mangel and Clark (1986) has employed a dynamic programming approach, as in our work, but it has included random foraging success. Their work allows for the possibility of starvation, in contrast to the present work. The probability of starvation may be quite substantial in the case of small

birds in winter, as pointed out by McNamara and Houston. Random effects may also be important for amphibians that must metamorphose before a temporary pond dries up. We cannot give a complete theory for these cases here, but we attempt to indicate when stochastic effects may be neglected in the formulation of a strategy, with only slight consequences for the final payoff.

We first consider a stochastic strategy S_s, which is presumed to be optimal. A function that is maximized behaves like a quadratic near the maximizing argument. Thus, optimality of S_s implies that deviations of an alternative strategy S from S_s have an effect on the final payoff that is proportional to the square of the deviation of S from S_s. Therefore, a deterministic strategy must deviate substantially from S_s before the effect on the payoff is noticeable.

We now examine the circumstances under which a deterministic "optimal" strategy differs substantially from a stochastic one. In the simplest circumstances, a deterministic strategy corresponding to a stochastic one is obtained by averaging the dynamic equations over whatever random variables are present. For example, when one neglects variations in foraging success (as we have done), one replaces the probability distribution of a single foraging bout by its mean. In the case of birds foraging in winter, such a procedure is probably satisfactory if a large number of foraging bouts (at least 5 to 10) occur within a time scale when starvation might be a threat. Thus, we do not expect to find substantial differences between deterministic and stochastic optimal strategies unless there are few foraging opportunities before possible starvation. As we indicated above, such differences must be substantial if the final payoff is to be affected very much.

A similar discussion may be given for foraging strategies in anticipation of metamorphosis, when the cutoff time (when the pond dries up) is random. A deterministic strategy could be obtained by averaging the time to drying up in computing the time remaining ($T - t$ in our analysis). Such an approximation may fail if the time to drying up has a widely dispersed distribution and if catastrophic early drying cannot be detected early enough to alter the foraging strategy and complete metamorphosis. Otherwise, a deterministic strategy may be quite satisfactory.

Such informal analyses may be supplemented by analogies with theories that have been completely worked out. One such analogy is with the theory of optimal harvesting (developed in Ludwig 1979; Ludwig and Varah 1979). For problems of fisheries management, stochastic effects were found generally to have only a slight effect on the optimal strategy, except near certain threshold population sizes. A second comparison is between classical geometrical optics (deterministic) and diffraction theory (stochastic). The geometrical theory is perfectly adequate for many purposes, and the diffraction results may often be interpreted as corrections to underlying geometrical models. On the basis of these analogies, one would expect the main qualitative features of the strategies and payoffs to be provided by a deterministic theory, but such results may require modification in situations in which such risks as starvation or unforeseen drying up are substantial.

If a stochastic formulation is adopted, explicit analytical solutions such as that given in Appendix A are difficult to obtain. Moreover, one cannot aid intuition by drawing optimal trajectories. A more natural setting is then a discrete-time approach, combined with a numerical solution of the dynamic programming equation, as advocated by Mangel and Clark (1986) and McNamara and Houston (1986, 1987). The analytical approach adopted here generally provides superior insight into the dependence of the qualitative features on the assumptions made. However, such theory may become excessively complicated as model assumptions are elaborated.

The numerical approach complements the analytical one. Numerical methods are often easier to apply to complicated situations, but such results should always be compared with simpler analytical solutions and with intuition in order to ensure that unexpected results are not artifacts of the method or approximation employed. Experience in fields such as continuum mechanics has shown that problem solving often requires both analytical and numerical methods.

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