Size and Timing of Metamorphosis in Complex Life Cycles: Time Constraints and Variation

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SIZE AND TIMING OF METAMORPHOSIS IN COMPLEX
LIFE CYCLES: TIME CONSTRAINTS AND VARIATION[1]

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Abstract. Complex life cycles are characterized by niche shifts at the time of metamorphosis. Current models predict optimal sizes for metamorphosis based on maximizing growth, minimizing mortality, or some balance of these goals. These models predict optimal sizes that are independent of the time of metamorphosis. Reproduction and other major events in the life history of organisms are often constrained to seasons, and the state (e.g., mass) of the organism at that time is related to fitness. Therefore, an organism's state as well as the time that that state is achieved are central variables in these time-constrained life histories.

We extend earlier theory to include explicit time constraints in three, hypothetical, complex life cycles. Dynamic optimization models are constructed to determine optimal time and mass trajectories for niche shifts. First, we consider the habitat shift at emergence in mayflies, where reproduction terminates a growth period in the first habitat and is constrained to a season. Second, we consider the habitat shift at metamorphosis in amphibians, where reproduction terminates a growth phase in the second habitat and reproduction is constrained to a single point in time. Third, we combine the first two effects to allow an extended period of reproduction in amphibians. Here optimal time and mass trajectories are determined for two niche shifts—the shift from aquatic to terrestrial habitat and the shift from a growth phase to a reproductive phase. We present analytical theory that allows both quantitative and qualitative predictions. Problem constructions and solutions are presented graphically to aid intuition in interpreting our results and extending the framework to other parameter values and other life-history examples.

The general conclusion is that time constraints on complex life histories lead to optimal sizes for niche shifts that vary with time. In time-constrained life histories, any variation in the state of individuals at some time prior to reproduction will be preserved to some degree at reproduction. Therefore, in time-constrained life histories, we expect optimal switches in habitat use or life history stage to depend not only on state but also on the time that state is achieved.

Key words: complex life cycles; dynamic programming; habitat shifts; metamorphosis; time-constrained life histories; time constraints.

INTRODUCTION

Complex life cycles, where individuals undergo abrupt ontogenetic transformation (metamorphosis), are ubiquitous in nature (Wilbur 1980, Werner and Gilliam 1984, Werner 1988). A discrete shift in habitat use often coincides with the transformation occurring at metamorphosis. Perhaps eighty percent of all animal species have life histories that include metamorphosis, and many of the remaining species undergo ontogenetic niche shifts without metamorphosis (Werner 1988). Despite the prevalence of ontogenetic niche shifts, their evolution and ecological implications have received relatively little theoretical attention (Istock 1967, Wilbur and Collins 1973, Lubchenco and Curbit 1980, Wilbur 1980, Caswell 1982, Werner and Gilliam 1984, Werner 1986, 1988, Ludwig and Rowe 1990).

Werner (1986) argues that the ecologically salient feature of metamorphosis is the associated shift in habitat use. Therefore, the evolution of such life cycles must be related to the ecological causes and consequences of ontogenetic niche shifts (Werner and Gilliam 1984, Werner 1986, 1988). Given that growth and mortality rates as well as fecundity vary with size, recent theory views ontogenetic niche shifts as strategies for achieving an optimal balance between growth benefits and mortality risks during ontogeny. When habitats vary in size-specific growth and mortality rates, optimal strategies often necessitate habitat shifts (Gilliam 1982, Werner and Gilliam 1984, Werner 1986, 1988). Gilliam (1982) concluded that fitness is maximized if individuals choose habitats where the ratio of mortality rate (μ) to growth rate (g) is minimized. Such a policy maximizes survival to each size in a time-invariant environment, since the individual accumulates each bit of mass at the lowest mortality cost. A

similar model has been used successfully to predict habitat shifts in pre-reproductive fish (Gilliam and Fraser 1987, Turner and Mittelbach 1990). Werner (1986) has suggested the use of Gilliam's model for predicting size at metamorphosis in amphibians.

The derivation of the "minimize μ/g" rule assumes that reproduction is continuous and extends over an infinite time horizon (Gilliam 1982). The corresponding switching rule predicts that all individuals will shift habitats at the same size. However, reproductive periods (the payoff) that are restricted to specific and short time periods are common: a case not considered by Gilliam. We refer to these as life histories with time constraints. Furthermore, temporal variation of switch sizes within populations is common to organisms with complex life cycles (e.g., Vannote and Sweeney 1980, Wilbur 1980, Ydenberg 1989), a feature that is not accommodated in the theory of Werner and Gilliam (1984), or of Werner (1986). For example, the size of emergent mayflies typically declines as the reproductive season progresses (e.g., Ide 1940, Sweeney and Vannote 1978, Vannote and Sweeney 1980).

Dynamic optimization models are well suited for this type of problem (Mangel and Clark 1986, 1988, McNamara and Houston 1986, Houston et al. 1988). These models assume that behavioral decisions depend on the state (e.g., mass) of the decision-maker; they predict time courses of behavior and allow the costs and benefits of short-term behaviors to be expressed in some common currency (e.g., fecundity at the payoff time). Incorporation of time constraints into theory for ontogenetic niche shifts demonstrates that costs and benefits of habitat shifts will vary with both an individual's state and the time remaining until the payoff (Ludwig and Rowe 1990). Under such conditions optimal sizes for habitat shifts vary with the time remaining to the payoff. Time constraints may then account in part for the observed temporal variability in size at some ontogenetic niche shifts.

The goal of the theory presented here is to explore the role of certain time constraints on optimal mass and time trajectories for habitat shifts in organisms with complex life cycles. We have considered three distinct examples of time effects: (1) A constrained period when habitat shifts are possible and the habitat shift occurs at reproduction. In this case growth is confined to the first habitat, as in mayflies. (2) A constrained period of reproduction that terminates a growth phase in the second habitat, as in amphibian metamorphosis. (3) A combination of the previous two effects to allow a variable time of reproduction. The life history then involves two decisions. The first decision concerns the time of metamorphosis or habitat shift, and the second decision concerns the timing of reproduction. The theory for the third case combines the theory of Ludwig and Rowe (1990) with the theory for the first case. It is noteworthy that our theory is analytical, and our constructions are graphical. The theory thus allows qualitative and quantitative predictions under a wide variety of assumptions.

MAYFLY EMERGENCE: AN EXAMPLE OF GROWTH IN A SINGLE HABITAT

Insects, like amphibians, have complex life cycles, where some transformation in both morphology and niche use occurs during ontogeny. Size attained during the larval growth period is directly related to adult reproductive success in most insects. Large females generally produce more or larger eggs, and large males often gain access to more females (Hinton 1981, Thornhill and Alcock 1983). While variation in size at metamorphosis occurs both within and between populations, most previous work concerned the latter (e.g., Roff 1981, 1983). Seasonal variation is pronounced in many groups (Vannote and Sweeney 1980, Forrest 1987). Proposed proximate causes for within-population variation include temperature (Sweeney and Vannote 1978, Vannote and Sweeney 1980), diet (Palmer 1984), and population density (Peters and Barbosa 1977).

Insects differ from amphibians since growth of somatic tissue is largely restricted to the larval or nymphal stage. While teneral mass gain may occur in some groups (e.g., Odonata, Hemiptera), others, such as Ephemeroptera and Megaloptera, and some Plecoptera, Trichoptera, Lepidoptera, and Diptera, have lost or reduced adult feeding structures (Borror et al. 1981). Werner and Gilliam (1984) suggested an extension of their model to insect size at metamorphosis. However, in those cases where no growth occurs in one of the habitats, a "minimize μ/g model" is clearly not applicable. Forrest (1987) provided a verbal explanation of within-season variance in size at metamorphosis in the mole cricket using a similar cost–benefit approach. Forrest recognized that the costs and benefits associated with size at metamorphosis varied within the reproductive season. Here we will present an explicit model, using an approach similar to both Werner and Gilliam and to Forrest, to explore some possible roles of time constraints on temporal size at emergence in insects.

For this exercise we will consider mayfly size at metamorphosis, as a simple example for the illustration of some central points. A general life history of mayflies is: eggs deposited in water hatch, grow, and develop as larvae; undergo partial metamorphosis and emerge to aerial subimagoes, then rapidly molt to adults (imagoes); mate, oviposit, and die (Brittain 1982). Adults lack feeding apparatus, so this stage is restricted to reproduction and in some cases to dispersal. In temperate regions, univoltine life cycles are common, with growth and mortality occurring throughout the year and emergence restricted to the warmer months (e.g., April through August). The total aerial reproductive phase of individuals may last only a few days, while the larval growth phase may last over a year. Size at metamorphosis is directly related to fecundity in fe-

males. Within mayfly populations, a great deal of variance in size at emergence occurs (e.g., Ide 1940, Sweeney and Vannote 1978, Vannote and Sweeney 1980). Early emergers are typically larger than later emergers.

There are costs and benefits in the decision to emerge. Delaying emergence carries with it the benefit of increasing size (fecundity), but also the cost of delaying reproduction. The former will generally encourage individuals to remain in the water and grow, while the latter will encourage emergence for early egg deposition. Some possible costs of delayed reproduction include priority effects, where early offspring have a competitive advantage due to low density or due to gaining a size advantage. We will represent this conflict as one between high fecundity associated with large size and high offspring quality associated with early eggs. Other benefits of large size and early emergence are possible; for example, in other insects large adults may have higher mating success, but early adults may gain access to higher quality mating territory.

At the beginning of an emergence season we assume some individual variation in body size, but allow all individuals to follow the same growth trajectory. Body size variation may occur due to variation in hatch date, due to variation in parental date of reproduction the previous season, or due to some stochastic variation in growth rates of larvae. We allow individuals to follow identical growth trajectories during the emergence season so that we may focus on the conflict between large size at emergence and early emergence, and to simplify the analysis.

Our objective is to formulate a model that offers one explanation for the observed seasonal decrease in size at emergence that is common to populations of mayflies and several other insect groups. The model incorporates two related themes that will be elaborated below and in further sections of this manuscript: (1) the benefits of incremental increases in some state variables (e.g., mass) vary with current state; and (2) the amount of time remaining affects the reproductive value of individuals. More specifically:

1) Incremental increases in mass have benefits from increased numbers of eggs and costs from increased time until emergence. However, relative increases in an individual's fitness with an increment of gain in mass vary with body size; one extra egg makes a greater percentage increase in fitness of individuals that could currently produce few eggs than of individuals that could currently produce many eggs. Such relative increases in fitness are the appropriate currency for comparing strategies when the effects of size and time are multiplicative, as we assume below. Therefore, selection on individuals to emerge early and forgo further growth will be stronger on larger individuals.

2) Smaller individuals late in the reproductive season have more to lose by remaining in the water to increase size at emergence than the same-size individuals have early in the season. Early in the season when the fitness

of eggs produced is relatively high, the relative cost of delaying oviposition of a fixed number of eggs is low. Later in the season when these eggs have little remaining fitness, the relative cost of a similar delay in oviposition is high.

Formulation of the model

We assume that net expected reproductive output depends upon both mass at emergence (W) and time of emergence (T). The effects of mass and time are assumed to act independently, so that the fitness F is a product of contributions from W and T. For example, the total number of eggs laid over a lifetime will depend upon mass at emergence. We assume that

$$\text{Total eggs} = E(W)$$
$$= \begin{cases} a(W - W_c)^\beta & \text{if } W > W_c, \\ 0 & \text{otherwise,} \end{cases} \quad (1)$$

where W_c is a critical lower mass for egg production, β is a parameter that determines the shape of the relationship, and a is a scale factor that adjusts for units of measurement. The expected contribution of each egg will depend upon time of emergence. We assume that

$$\text{Contribution} = C(T)$$
$$= \begin{cases} (T_c - T)^\alpha & \text{if } T < T_c, \\ 0 & \text{otherwise,} \end{cases} \quad (2)$$

where T_c is a critical upper limit for time of reproduction and α is a parameter that controls the shape of this dependence.

Growth.—We must also make an assumption about the rate of growth in mass, for example

$$\frac{dw}{dt} = g(w) = rw(1 - w/k). \quad (3)$$

Here the growth rate $g(w)$ has been assigned a logistic form, with growth proportional to both a rate constant r and mass w at small body sizes, and a maximum mass k. This equation may be integrated starting at an initial mass w_0 to obtain w as a function of t. The specific forms for $E(W)$, $C(T)$ and $g(w)$ given in Eqs. 1, 2, and 3 are for illustrative purposes only. The qualitative form of our conclusions holds quite generally.

Mortality.—We assume that prior to emergence, the mortality rate of an individual is $\mu(w)$. This imposes a cost to the delay of reproduction, in addition to the contribution effect $C(T)$.

We shall assume that the expected fitness of an individual that attains mass w at time t is given by

$$F(w, t, T) = E[W(T)]C(T)S(w, t, T), \quad (4)$$

where $W(T)$ is the mass achieved at time of reproduction T and $S(t, T)$ is the probability of survival from time t to time T. According to our definition of mortality,

$$S(w, t, T) = \exp\left\{-\int_t^T \mu[w(t')]dt'\right\}. \qquad (5)$$

In our example below, we choose $\mu(w)$ to be a constant independent of w.

Optimal time for emergence

We obtain the optimal emergence time by maximizing $F(w, t, T)$ as a function of T:

$$\frac{\partial F}{\partial T} = \frac{dC}{dT} E[W(T)]S(w, t, T)$$

$$+ C(t)S(w, t, T)\frac{dE[W(T)]}{dT}$$

$$- \mu[W(T)]E[W(T)]C(T)S(w, t, T)$$

$$= 0. \qquad (6)$$

This equation determines the optimal relationship between mass and time of emergence. After rearrangement, Eq. 6 becomes

$$\frac{-1}{C(T)}\frac{dC}{dT} = \frac{1}{E(W)}\frac{dE[W(T)]}{dT} - \mu[W(T)]. \qquad (7)$$

Each side of Eq. 7 can be interpreted separately.

The left-hand side of Eq. 7 will be denoted by L. It represents the relative loss in quality or value of eggs as a function of time at emergence (=time of oviposition). Since $C(T)$ eventually vanishes at high T, L increases sharply near a cutoff such as T_c. Under the assumption in Eq. 2

$$L = \frac{\alpha}{T_c - T}. \qquad (8)$$

The right-hand side of Eq. 7 will be denoted by R. It represents the relative gain in egg production per unit of time, minus mortality losses. According to the chain rule of calculus,

$$\frac{dE}{dT} = \frac{dE}{dW}\frac{dw}{dt} = \frac{dE}{dW}g(W). \qquad (9)$$

Therefore

$$R = \frac{g(W)}{E(W)}\frac{dE}{dW} - \mu(W). \qquad (10)$$

Under the assumption in Eq. 1

$$\frac{1}{E(W)}\frac{dE}{dW} = \begin{cases} \beta/(W - W_c) & \text{if } W > W_c, \\ 0 & \text{if } W < W_c. \end{cases} \qquad (11)$$

Thus we have

$$R = \frac{\beta g(W)}{W - W_c} - \mu(W) \quad \text{if } W > W_c. \qquad (12)$$

Note that R is infinite at $W = W_c$: R decreases sharply as W increases beyond W_c.

To summarize, the optimal relationship (Eq. 7) between mass and time of emergence implies that under the assumptions of Eqs. 1 and 2,

$$\frac{\alpha}{T_c - T} = \frac{\beta g(W)}{W - W_c} - \mu(W). \qquad (13)$$

In order to plot this relationship, it is simplest to solve for T:

$$T = T_c - \frac{\alpha(W - W_c)}{\beta g(W) - \mu(W)(W - W_c)}. \qquad (14)$$

The right-hand side of Eq. 14 vanishes at $W = W_c$, and it approaches $\alpha/\mu(W)$ if $g(W) \to 0$. Therefore $T = T_c$ where $W = W_c$, and T decreases as W increases. Fig. 1 shows this relationship for $T_c = 1$, $W_c = 0.1$, $k = 1$, $r = 0.1$, $\alpha = 0.1$, $\beta = 1$ and $\mu = 0.02$.

The preceding theory describes a common conflict within life histories; the benefits attained by reducing the time to reproductive maturity are offset to some degree by the costs of reduced pre-reproductive growth. In this particular example the payoff (maturity and reproduction) occurs at the time of habitat switching. The payoff period is constrained to a season. Within this season, payoffs depend upon both mass and time of habitat switching.

We have chosen to impose a univoltine life cycle, where all individuals must emerge within the current season. We believe this is a reasonable approximation for our focus on end-of-season phenomena. If we were to allow smaller individuals to delay reproduction until the following year, their time to reproduction would nearly double, as would their probability of mortality. If we were to allow a bivoltine life cycle, the advantage to early reproduction would increase dramatically since a second generation would now be possible for early reproducers. In fact, seasonal declines in size at emergence also occur in bivoltine mayfly populations (Vannote and Sweeney 1980).

We expect the qualitative conclusions of this theory to apply in many diverse life-history settings, when the following conditions are met. First, the opportunity to switch from one life history mode to another is confined to a season. Second, state (e.g., mass, fat reserves etc.) at the switch is related to future fitness. Third, early switches are associated with higher future fitness. Fourth, a delay in shift increases the state of that individual. The shift in life history mode need not include a shift in habitat use per se. Other life history switches may include those from a pre-reproductive to a reproductive phase, or from an active phase to an inactive phase such as hibernation or diapause. For example, consider an insect facing an upcoming winter, where overwinter survival requires diapause and is a function of fat reserves. Here, an early switch to diapause decreases the probability of winter arriving prior to diapause but decreases the level of an individual's stored fat. We would expect individuals entering diapause

early to have higher fat stores than those entering diapause late.

AMPHIBIAN METAMORPHOSIS: AN EXAMPLE OF GROWTH IN TWO HABITATS, WITH EXPLOSIVE BREEDING

The preceding theory suffices for life histories where significant growth does not occur in the second habitat. If significant growth does occur in the second habitat, optimal strategies must include a dependence on growth and mortality rates in the second habitat. Early discussions of amphibian life histories portrayed the larval aquatic stage as one devoted to growth, while the terrestrial stage included reproduction and dispersal (Wilbur and Collins 1973, Wassersug 1975, Wilbur 1980). If this were an accurate portrayal, then the arguments we have presented for mayflies would also be applicable to amphibians.

However, Werner (1986) presented data that show that significant (and in some species the majority of) growth occurs in the terrestrial stage. He has used Gilliam's (1982) theory to determine a size at metamorphosis that maximizes the "instantaneous population growth rate." This theory takes into account growth and mortality rates in the two habitats. However, it assumes reproduction over an infinite time horizon rather than a well-defined season.

Earlier we have assumed that the amphibian prereproductive period may be fixed (Ludwig and Rowe 1990). With such a time constraint we expect some variation in both size at and time of metamorphosis (Ludwig and Rowe 1990). Variation in both size at and time of metamorphosis is consistent with the amphibian literature (e.g., Wilbur and Collins 1973, Collins 1979, Smith 1987, Semlitsch 1988), but it is not accounted for in the theory of Gilliam and Werner. In this section we apply this time constraint to two examples taken from Werner (1986) to explore in more detail the effects of time constraints on the size at and timing of metamorphosis. We also present a case from Ludwig and Rowe (1990) for comparison with results in the following section. An additional example of growth and mortality curves is considered in Appendix A. Optimal strategies are determined by means of an analytical solution to this dynamic optimization problem. For clarity, solutions for each suite of conditions are presented in graphical form. The switch curves are described and the underlying processes discussed in the text, while the mathematical principles used are explained briefly here. Details of the solution are given in the Appendices.

Basic assumptions

We consider pre-reproductive foragers that can switch from one habitat to another. Individuals start in habitat 1 (aquatic) and reproduce in habitat 2 (terrestrial). Habitats are characterized by mass-dependent rates of energy gain and mortality. For our purposes we will
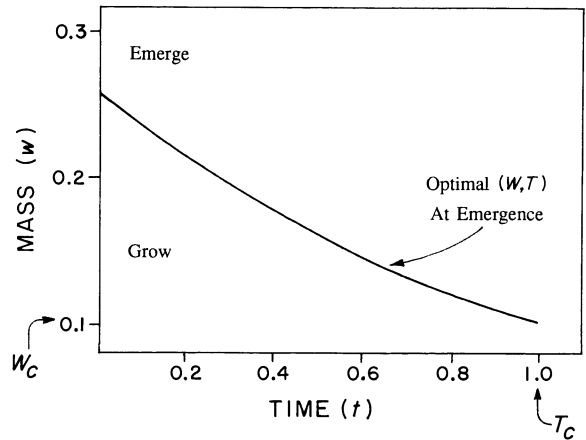

FIG. 1. Optimal size and time for mayfly emergence, where fitness is a positive function of mass and a negative function of time at emergence.

consider predation as the sole source of mortality. Time constraints are introduced by assuming that the pre-reproductive period is fixed (e.g., Ludwig and Rowe 1990): reproduction occurs at a fixed time T. This latter assumption differs from the assumptions of the mayfly emergence section (see *Mayfly emergence. . ..: Formulation of the model*, above). The discrepancy between these assumptions is removed in the second amphibian section (*Amphibian metamorphosis: . . . growth in two habitats, with prolonged breeding*, below). Potential reproductive success depends on mass at T, and there is a minimum mass below which no reproduction is possible. The objective of each forager is to survive until T with a high potential reproductive success.

We consider only a portion of the life history, where $T_0 < t < T$. At the start of our considerations ($t = T_0$) all individuals are still in habitat 1, but they have a range of sizes. This range in sizes may be the result of different birth dates (in which case larger individuals are older) or by random differences in growth rate early in the life history. Thus, individuals who switch habitats early in chronological time (with reference to T) may actually be older individuals.

Application of dynamic programming

If both growth and predation are higher in one habitat than the other, then possibly there is a tradeoff between growth and survival. Growth rate measures mass gain per unit time (in units of grams per day), while survival rate has units of individuals per individual per day. These two quantities cannot be compared directly, since their units are different. A "common currency" is the effect upon expected future reproductive output $f(w, t)$. Note that f depends upon current state w and the time t. Once a strategy of habitat shifting has been determined, $f(w, t)$ can be defined as

$$f(w, t) = R(W)S(w, t),$$

where W is the final mass achieved by an individual of mass w at time t, $R(W)$ is the reproductive output (number of viable offspring) produced by a female of mass W at time T, and $S(w, t)$ is the probability of survival to reproduce, for an individual of mass w at time t. S and W depend upon both w and t, since the optimal strategy depends upon these quantities.

The loss of expected fitness per unit time due to mortality is $\mu(w)f(w, t)$. The rate of gain of expected fitness due to growth is $g(w)\partial f/\partial w$. Therefore the net rate of expected fitness gain in a given habitat is $g(w)\partial f/\partial w - \mu(w)f$. The maximum principle of dynamic programming states that the quantity $f(w, t)$ will be maximized if the habitat is chosen to maximize the latter quantity. Notice that the units balance in this expression, since the ratio $(1/f)\partial f/\partial w$ has the same units as μ/g. We conclude that the switch point must satisfy

$$g_1(w)\frac{\partial f}{\partial w} - \mu_1(w)f = g_2(w)\frac{\partial f}{\partial w} - \mu_2(w)f, \quad (15)$$

or, by rearranging,

$$\frac{\mu_2(w) - \mu_1(w)}{g_2(w) - g_1(w)} = \frac{1}{f}\frac{\partial f}{\partial w}. \quad (16)$$

This is the main result of dynamic programming. Eq. 16 is more complicated than a simple rule of minimizing μ/g, but it is more generally applicable, at least if $f(t, w)$ can be determined. A thorough discussion of dynamic programming and its application to problems in behavioral ecology, e.g., habitat switching, is given in Mangel and Clark (1988).

The left-hand side of Eq. 16 depends only upon w, but the right-hand side is more complicated. The computation of f and $\partial f/\partial w$ leads to some mathematical theory, which is provided in Ludwig and Rowe (1990) and Appendix A. The result of that theory is that a certain quantity is constant (conserved) along a given individual's life history. The conserved quantity in the present case is

$$\mathcal{L}(w, t) = \frac{g_2(w)}{f}\frac{\partial f}{\partial w} - \mu_2(w). \quad (17)$$

This may be interpreted as the increment in relative fitness per unit time. Using the fact that $\mathcal{L}(w, t)$ is constant along life-history trajectories, we can solve for the right-hand side of Eq. 16 in terms of the final mass W and the corresponding reproductive output $R(W)$. The switching condition now takes the form

$$g_2(w)\frac{\mu_2(w) - \mu_1(w)}{g_2(w) - g_1(w)} - \mu_2(w)$$

$$= g_2(W)\frac{1}{R(W)}\frac{dR}{dW} - \mu_2(W), \quad (18)$$

as is shown in Appendix A. This consequence of Eqs. 16 and 17 relates the switching mass w to the mass at reproduction W. It can be solved graphically for specific assumed forms of the growth and mortality rates.

Two examples where the difference in μ/g changes sign

Werner (1986; see also Werner and Gilliam 1984, Werner 1988) suggests that size-specific growth rates (g) for the aquatic (habitat 1) and terrestrial (habitat 2) stages of amphibians may take the form of parabolas that cross (Fig. 2a). If predation rates (μ) are equal in both habitats, then the optimal strategy is to choose the habitat that provides the highest growth rate. If we define $\hat{w}$ as the size at which the two growth rates are equal, as in Fig. 2a, then we expect each individual to switch habitat when its mass reaches $\hat{w}$. This argument is valid whether time constraints are introduced or not.

If predation rates are relatively high in habitat 2 ($\mu_2 > \mu_1$), then we expect individuals to delay switching. Hence the optimal switch size will be greater than $\hat{w}$. Similarly, if $\mu_1 > \mu_2$, then the optimal switch size will be less than $\hat{w}$. In both cases individuals have forgone growth in order to reduce exposure to predation. If there are no time constraints, then all individuals switch at the same size, according to the theory.

Here we show that the introduction of time constraints leads to optimal switch sizes that vary. In general, the magnitude of deviation from $\hat{w}$ of the optimal switch masses will be some increasing function of size at T_0. A detailed theory appears in Appendices A and B. Here we describe the results of the analysis (Figs. 2 and 3) and the major processes that lead to the results.

Consider a case where $\mu_2 > \mu_1$ and growth rates cross at some size $\hat{w}$ (Fig. 2a and b). If there is a critical minimum mass W_c below which reproduction is impossible, then there is a critical initial mass w_c, such that individuals who start at w_c can just reach mass W_c by time T if they maximize growth by switching habitats at mass $\hat{w}$. Higher predation rates in habitat 2 discourage individuals from shifting to habitat 2. The smallest individuals (at mass w_c) do not have the opportunity to delay shifting, since any strategy that deviates from growth maximization will eliminate the possibility of reproduction. On the other hand, all individuals starting at masses greater than w_c could forgo some growth in order to delay exposure to predation in habitat 2; if individuals who start at large masses were to switch habitats when they reach mass $\hat{w}$, then they would spend an unacceptably long time in the more dangerous habitat 2. The switching size w_s will be an increasing function of mass at T_0 (Fig. 2b).

The preceding argument does not settle the issue of whether switching at size w_s actually leads to declining shift masses through the season. However, the argument in Appendix B shows that the time of switching, t_s, decreases as the initial mass increases in cases where growth curves cross and $\mu_2(w) - \mu_1(w)$ is small and positive. Alternatively, if $\mu_2(w) - \mu_1(w)$ is small and
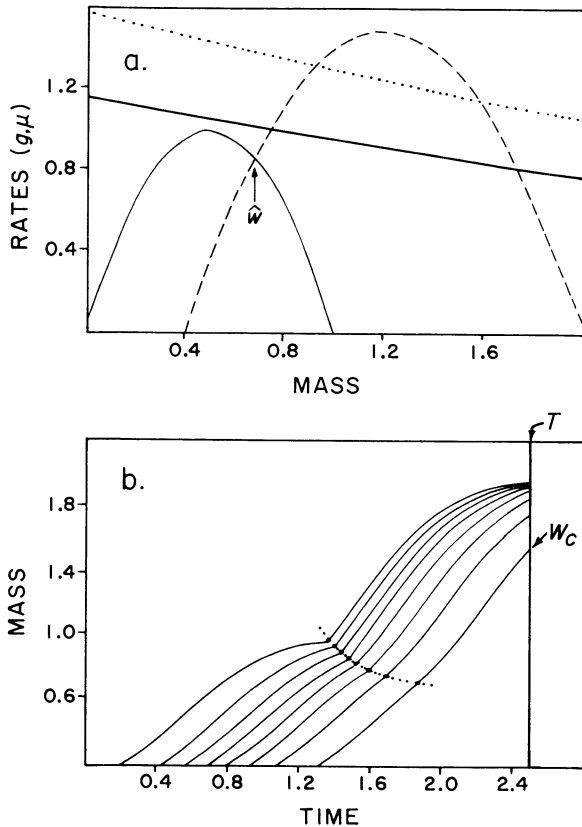
FIG. 2. (a) Growth (g) and mortality (μ) rates in the two-habitat model where growth rates cross and mortality in habitat 2 is greater than in habitat 1. Figure shows growth rates in habitat 1 (——) and habitat 2 (– – –), and mortality rates in habitat 1 (——) and habitat 2 ($\cdots$). $\hat{w}$ is the expected optimal habitat-switch size if mortality rates were equal in the two habitats. (b) Optimal time and size at metamorphosis ($\cdots$) for growth and mortality rates shown in Fig. 2a. Solid lines show individual growth trajectories in habitat 1 (below dotted line) and habitat 2 (above dotted line). T indicates the payoff time, where reproduction occurs. W_c shows the critical minimum mass at T for successful reproduction.

straints affect optimal shift sizes in life histories that include significant growth in both habitats. The underlying mechanism is that variation in mass among individuals at any time during the pre-reproductive period is preserved to some degree at the payoff time T. Therefore, variation in size at T_0 implies variation in fitness: small individuals do not catch up. On the other hand, in systems without time constraints catching up is not an issue.

As in the insect-emergence (mayfly) example, relatively large individuals at T_0 have relatively high fitness. Incremental gains in mass for these individuals have relatively little impact on fitness at the payoff time T. Given the relatively low benefits stemming from additional growth by large individuals, we expect larger individuals to trade growth in order to avoid predation to a greater degree than smaller individuals. These mechanisms lead to predictable variation in optimal shift masses that scale with time. It is interesting to note that the effect of these tradeoffs is to reduce the variation in body size from T_0 to T (Figs. 2 and 3). Larger individuals are more likely to survive to T, but have forgone potential growth in the process. Smaller individuals are less likely to survive to T, having placed a higher relative value upon growth in the face of predation.

This leads to two major points: (1) Initially large individuals are more likely to slow growth to avoid predation than initially small individuals. (2) The effect of switching at variable masses is to reduce the range of masses from the start of a period (T_0) to the final time (T), while increasing the variation in mortality among individuals who start at a variety of body masses. The decrease in size range and the increased variation in mortality rates independently affect point 1 above. By the final time, those that started off large have increased their probability of survival to the final
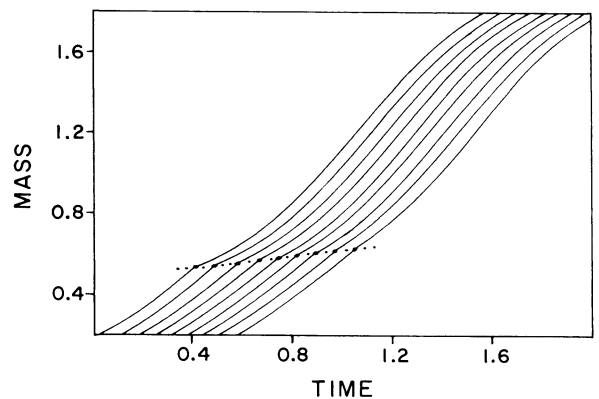
negative, then shift masses will increase through the season.

An example of this latter case where $\mu_1 > \mu_2$ is shown in Fig. 3. Growth rates are the same as those in Fig. 2a, but the predation rates have been reversed. In this case we expect the high predation rates of habitat 1 to encourage an early shift to habitat 2. The smallest individuals starting at w_c must simply maximize growth and shift at $\hat{w}$, or they will not make the minimum size for reproduction at T. Larger individuals at T_0 will shift early in time and at masses below $\hat{w}$. The deviation from $\hat{w}$ is again an increasing function of mass at T_0, for reasons stated above.

If $\mu_2(w) - \mu_1(w)$ is large, a more complicated theory is required. Such a theory is described in Appendices A and B. A variety of qualitative features is possible, but details will not be given here.

In summary, these examples illustrate how time con-

FIG. 3. Optimal size and time at metamorphosis ($\cdots$) for growth rates identical to and mortality rates reversed from Fig. 2a. Solid lines show individual growth trajectories in habitat 1 (below dotted line) and habitat 2 (above dotted line). The payoff time T does not appear in this figure—it is off to the right.
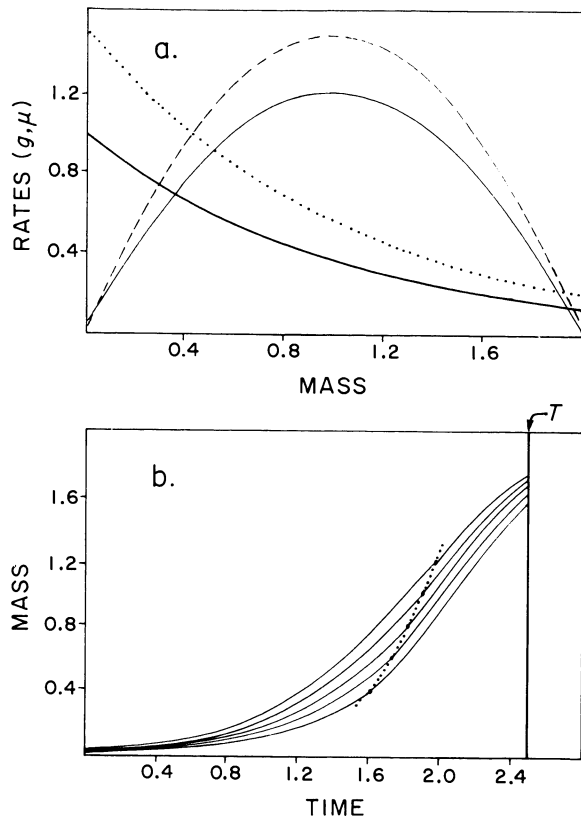
FIG. 4. (a) Growth (g) and mortality (μ) rates where the ratio of μ to g does not vary with size, and both rates are greater in habitat 2. Figure shows growth rates in habitat 1 (——) and habitat 2 (– – –), and mortality rates in habitat 1 (——) and habitat 2 (·····). (b) Optimal time and size at metamorphosis (·····) for growth and mortality rates shown in Fig. 4a. Solid lines show individual growth trajectories in habitat 1 (below dotted line) and habitat 2 (above dotted line). T indicates the payoff time, where reproduction occurs.

time by avoiding predators at the cost of reduced growth, while the opposite is true for individuals who started off small.

An example where the difference in μ/g doesn't change sign

It may happen that growth is always higher in one habitat than the other. There is a possible tradeoff between growth and mortality if the mortality rate is always higher in the same habitat. In such a case, it may be optimal to spend the entire pre-reproductive period in one habitat or the other. The situation is more complicated if switching from one habitat to the other is optimal. We first consider the case where not all individuals find it optimal to switch habitats by the final time T. We consider only the subset consisting of individuals who actually switch to habitat 2. A case where $\mu_2 > \mu_1$ is depicted in Fig. 4. Here the growth and mortality rates in the two habitats are proportional (Fig. 4a). This example was used earlier (Ludwig and

Rowe 1990) to illustrate optimal habitat shifts in spite of μ/g ratios that do not vary with mass. The corresponding switching curve is shown in Fig. 4b. Individuals who start out heavier switch habitats at a larger size than those who are initially lighter. They also switch at a later time than lighter ones, to avoid predation risk in habitat 2.

AMPHIBIAN METAMORPHOSIS: AN EXAMPLE OF GROWTH IN TWO HABITATS, WITH PROLONGED BREEDING

In contrast to the assumption of explosive breeding presented above, some amphibians have relatively prolonged breeding periods (e.g., a few weeks or months). In these species it is reasonable to assume an advantage to early breeders. For example, early larvae may be exposed to less competition than later larvae (Alford and Wilbur 1986, Wilbur and Alford 1986). In this final case we incorporate a prolonged breeding period with priority effects into the theory presented in the first amphibian section, above. The exercise is analogous to combining our mayfly emergence example (Fig. 1) with the earlier amphibian model presented (Fig. 4).

The result of combining the assumptions of the previous two major sections is surprisingly simple. One calculates the optimal time for reproduction by the method of the mayfly section: the key equation is Eq. 7. Then one computes pairs of switching points w and final masses W by the method of the first amphibian section and Appendix A, using Eq. 18. Finally, one computes the time for switching from Eq. A.9, which in the present case assumes the form of Eq. C.9. Details are given in Appendix C. The effect of all this is to shift the switching curves in the first amphibian section backwards in time by an amount given by $T_c - T$, as determined from Eq. 14. This shift will be strongest in individuals that start large, for the same reasons as were given in the mayfly example. The result of this shift is to transform Fig. 4b into Fig. 5. A corresponding transformation can be carried out for any of the other figures of the first amphibian section or Appendix A.

The inclusion of an early reproductive advantage into this example leads to earlier time of and smaller size at metamorphosis in individuals that are large early in the season. High growth rates in habitat 2 now have the additional advantage of decreasing time to reproduction. Larger individuals are in the best position to take advantage of this, since smaller individuals already must take relatively high risks to gain mass prior to reproduction. If early reproduction leads to a substantial fitness advantage, we expect declining switch curves for reproduction, and, in the cases considered above, declining switch curves for metamorphosis.

DISCUSSION

The present theory demonstrates that a variety of time constraints in complex life cycles leads to optimal

habitat-shift sizes that vary with time. This conclusion holds whether reproduction occurs at the time of shift to a second habitat or follows a growth period in the second habitat. The common mechanism for this phenomenon is our assumption that the reproductive period is localized. Under this assumption, any variation in size between individuals at some time during the pre-reproductive period will be preserved to some degree at the payoff (reproduction) time. Therefore, variation in size at this time reflects variation in fitness. We expect individuals with high fitness to take less risks for an incremental gain in mass.

We have represented the risks of gaining mass in two general forms. In the first case, organisms grow in one habitat and then switch to a second habitat at maturity to reproduce. Fitness depends on both mass at and time of maturity. Here, remaining in the first habitat to gain mass will delay maturity. In the second case, growth occurs in both habitats and the reproductive period is fixed to some brief period following growth in the second habitat. Fitness depends only on mass at the time of reproduction, but gaining mass carries a risk of mortality due to predation. In the third case the earlier two cases are combined.

In this section we discuss: (1) the implications of these models for the interpretation of seasonal variation in size and timing of metamorphosis, (2) the contrasting predictions of this theory with previous theory, and (3) the generality of time constraints in the life histories of organisms in seasonal environments.

INSECTS

Variation in size at metamorphosis over the reproductive season of insects is common (e.g., Ide 1935, Clifford and Boerger 1974, Sweeney and Vannote 1978, Vannote and Sweeney 1980, Forrest 1987). Mayflies are a convenient group for studying this problem, since metamorphosis to adult includes a habitat shift from aquatic to terrestrial and reproduction occurs in a single bout within hours or days of emergence. Therefore, the size at and time of emergence is equivalent to size and age at maturity and reproduction. Phenotypic plasticity in size at emergence has been studied primarily as a phenomenological problem. For example, temperature changes often affect growth and development rates differently, so that size at maturity must change (Sweeney and Vannote 1978, Vannote and Sweeney 1980). In mayflies which emerge in summer, the warmer temperatures of late summer may increase development rate relative to growth rate, resulting in declining size at emergence. Implicit in these arguments is the assumption that the single factor that scales with fitness is size. Therefore, late small emergers are victims of a fixed effect of temperature on development and growth rates.

We suggest that declining size at emergence is an adaptive response to the conflict between size and age at maturity (emergence). Individual larvae of relatively
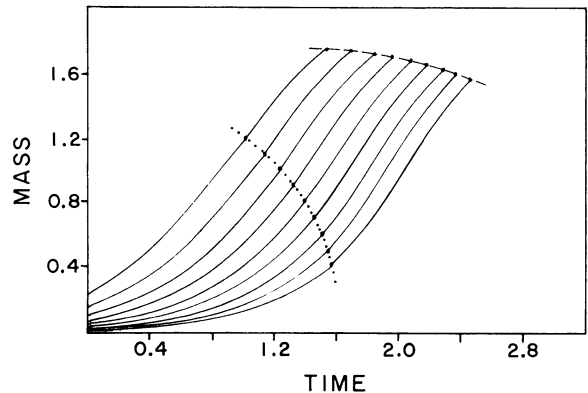

FIG. 5. Optimal time and size at metamorphosis (·····) and reproduction (– – –) for growth and mortality rates shown in Fig. 4a. Solid lines show individual growth trajectories in habitat 1 (below dotted line) and habitat 2 (above dotted line). This case differs from Fig. 4b only in our assumption of an advantage to early reproduction rather than a fixed payoff time (T).

large size will tend toward emerging early since the relative benefits of gaining mass decrease with present mass, while smaller larvae early in the season have much to gain by increasing mass. Later in the season smaller larvae will emerge, since the relative cost of delaying maturity increases as the season progresses. Our argument does not compete with the phenomenological view. In fact, the differential response of development and growth rates to temperature may have evolved in response to selection for optimizing size at and time of emergence (Forrest 1987).

Proposed proximate causes for seasonal variation in size at maturity in insects includes seasonal variation in resource levels or quality (e.g., Palmer 1984, Forrest 1987). Decreases in resource level at some time in the season will also lead to decreased size at emergence in the model we have presented. Lowered growth rates decrease the benefit (growth) of delaying maturity, without changing the costs of delaying maturity. Similarly, increased predation rates in the larval habitat will lead to smaller size at emergence for the same reason.

AMPHIBIANS

Background.—Traditional explanations for the evolution of amphibian life histories have focused on the larval growth phase, with little consideration of growth in the second habitat (Wilbur and Collins 1973, Wassersug 1975, Wilbur 1980). In this view, larvae have evolved to take advantage of the rapid growth opportunities of the aquatic habitat, while the function of the terrestrial phase is dispersal and growth. Wilbur and Collins (1973) introduced a model for predicting size at and time of metamorphs based on this view. The Wilbur-Collins model predicts that larvae assess recent growth history and set development rates based

on recent growth. Under high growth rates, larvae slow development relative to growth, leading to increased size at emergence. In low-growth conditions the alternative occurs. There is strong evidence that larval anurans do adjust development rates based on recent growth history (Alford and Harris 1988). Based on evidence of significant growth of amphibians in the terrestrial habitat, Werner (1986) introduced a model that placed greater emphasis on growth in the terrestrial phase. Werner's model also incorporates the idea of tradeoffs between growth and mortality, where increasing mass carries a mortality risk due to predation. His prediction was that larvae will metamorphose at a size where increments of growth in the terrestrial habitat come with less risk of mortality than those in the aquatic habitat. Individuals choose habitats where the ratio of mortality rate (μ) to growth rate (g) is minimized (Gilliam 1982, Werner and Gilliam 1984). This model also predicts increased size at metamorphosis when growth rates are increased in the aquatic habitat. It contrasts with the Wilbur-Collins model in predicting increased size of metamorphs if growth rates are reduced in the terrestrial habitat or if mortality rates are decreased in the aquatic habitat.

Time constraints. — Theory presented in the two major amphibian sections shares Werner's consideration of growth and mortality in both aquatic and terrestrial habitats, but contrasts with Werner's by our inclusion of time constraints. By assuming continuous reproduction over an infinite time horizon, the Werner model leads to optimal sizes at metamorphosis that do not vary with time. Therefore, individuals of given size metamorphosing or reproducing early are of equal fitness to later individuals. In contrast, we introduced a dependence of individual fitness on both mass and the time within a season that that mass is achieved. In this case, optimal size at metamorphosis and reproduction within a population can vary with time.

We have considered two effects of time constraints. In the first amphibian section (also in Ludwig and Rowe 1990) we introduced a reproductive period that is fixed in time, and in the second amphibian section we included an advantage to early breeders that is independent of size. In both cases growth and mortality rates depend on size, and reproductive output is an increasing function of mass. The first case is analogous to an explosive breeder. Here the optimal strategy must balance survival until the reproductive period and mass gain. The second case is analogous to a prolonged breeder, where eggs produced early have some advantage over later eggs (Alford and Wilbur 1986, Wilbur and Alford 1986). Here, the optimal strategy includes determination of the age at reproduction. Under both sets of assumptions optimal size at metamorphosis varies with time, and in the second case size at first reproduction also varies with time.

In both cases the ascending or descending character of optimal time and mass trajectories (switch curves)

for metamorphosis depends upon growth and predation rates in the two habitats. The prediction of this inclination requires a detailed knowledge of these rates, although some generalities emerge.

For amphibians, growth rates in the two habitats are expected to cross as shown in Fig. 2a (Werner 1986; see also Werner and Gilliam 1984, Werner 1988). Under this assumption and the assumption of no advantage to early breeders (see the first amphibian section), prediction of the inclination of the switch curves is straightforward. If mortality rates are higher in the terrestrial habitat, then we expect descending switch curves; otherwise ascending switch curves will result. For taxa where growth curves do not cross (e.g., Figs. 4a and A1a) more details about growth and mortality are required, and predictions of inclination are more complex.

Our distinction between ascending and descending switch curves will be altered if the time of reproduction is not fixed. If there are substantial increases in fitness for early breeders, then we generally expect to find descending switch curves for both metamorphosis and reproduction.

Predictions. — The basic predictions of this theory conform to the data on amphibian life cycles. First: size at metamorphosis varies in a systematic fashion throughout the season (Wilbur and Collins 1973, Collins 1979, Smith 1987, Semlitsch et al. 1988). Second: early reproducers are typically larger than later reproducers (e.g., Smith 1987, Semlitsch et al. 1988). In contrast to earlier theory (Wilbur and Collins 1973, Werner 1986), we suggest that this variation may reflect an adaptive response to time constraints. In these earlier theories, systematic seasonal variation in size at metamorphosis is accommodated only if a systematic seasonal variation in larval growth or mortality occurs. Seasonal variation in size at reproduction is not considered in these theories.

Our models of amphibian life histories share some qualitative predictions with the Werner model concerning variation between populations in size at metamorphosis. For example, a low growth rate or high predation rate within the aquatic habitat will favor a small size at metamorphosis (also predicted by the Wilbur-Collins model). We have shown this graphically in an earlier paper (Ludwig and Rowe 1990), and the same arguments apply here. There is evidence that amphibians do respond in such a manner. In experimental populations, when high densities of larvae lead to low growth rates, metamorphs are small (e.g., Wilbur 1977). High predation rates on Bufo americanus, by either the dragonfly Anax junius or the newt Notophthalmus viridescens dorsalis, result in early and small metamorphs (Wilbur 1988).

We have not explicitly considered changes in size-specific growth rates or predation rates during a season. Such changes probably occur in some amphibian populations. Decreases in population density late in the

season, due to metamorphosis of some portion of the population or due to predation, will lead to increased growth rates of the remaining larvae released from competition (Collins 1979, Alford and Harris 1988). Alternatively, resource levels may decline with season independently of larval density (Wassersug 1975, Wilbur 1980, Alford and Harris 1988). The effects of this within-season variation in growth rates (or predation rates) on size at metamorphosis can be predicted with our models (with similar results) by considering the first metamorphs under one growth rate and the remaining metamorphs under a second growth rate.

Our predictions about the effects of changes in growth rates within the season, however, cannot be distinguished from those of the Wilbur-Collins model or Werner's model. For example, all three models predict that a gradual decrease in larval growth rate will tend to decrease size at metamorphosis of the remaining larvae. In contrast to the Wilbur-Collins model, Werner's and ours predict variation in metamorph size due to variation in predation rates on larvae. Wilbur's (1988) experiments with *Bufo* (see above) support this assertion. Predictions from our theory contrast with Werner's in two important ways; first, we predict habitat shifts in some cases when the ratio μ/g does not differ between habitats (see also Ludwig and Rowe 1990), and second, we expect intrapopulation variation in size at metamorphosis even when larval growth and mortality rates are stable throughout a season. An appropriate test would be to compare temporal phenotypic variation in size at metamorphosis in individuals following stable growth and mortality schedules. Alternatively, potential cues to time, such as photoperiod, must be manipulated. We would expect to find riskier behavior of individuals that perceive a reduced time until reproduction. We are not aware of any such tests.

SUMMARY

Major events in the life history of organisms are often constrained to seasons. Some examples include seasonal reproduction in amphibians, fish, and birds, and emergence and diapause in insects. In these examples the state (e.g., mass or nutritional status) of individuals approaching these events may be related to fitness. Furthermore, seasonality of a life-history event implies that there is a good time and a bad time to undertake that event. In short, an organism's state as well as the time that that state is achieved are the important variables in seasonal life histories. Dynamic models provide an excellent and under-utilized tool to explore the optimal solutions to these state and time problems in life histories.

Both numerical and analytical approaches to dynamic programming can be illuminating. The numerical approach is simpler than our analytical methods, and can be applied to a wide variety of problems (Mangel and Clark 1988). Nevertheless we believe that superior insight sometimes may be gained from an analytical approach. For example, our Fig. 4 enables one to connect various qualitative features in the life-history trajectories to assumptions about the growth and mortality curves. Our solution method extends to many other problems where time t does not appear explicitly in the coefficients of the dynamic-programming equation. A theory such as ours for a two-stage decision process has not appeared previously in the ecological literature, as far as we are aware. The classical theory of the calculus of variations and of optimal control is a great source of ideas, methods, and solutions. We have tapped only a tiny portion of it.

LITERATURE CITED

Alford, R. A., and R. N. Harris. 1988. The effect of larval growth history on anuran metamorphosis. American Naturalist **131**:91–106.

Alford, R. A., and H. M. Wilbur. 1985. Priority effects in experimental communities: competition between *Bufo* and *Rana*. Ecology **66**:1097–1105.

Borror, D. J., D. M. DeLong, and C. A.Triplehorn. 1981. An introduction to the study of insects. Fifth edition. Saunders College Publishing, Philadelphia, Pennsylvania, USA.

Brittain, J. E. 1982. The biology of mayflies. Annual Review of Entomology **27**:119–147.

Butler, M. G. 1984. The life history of aquatic insects. Pages 24–55 *in* V. H. Rush and D. M. Rosenberg, editors. The ecology of aquatic insects. Praeger, New York, New York, USA.

Caswell, H. 1982. Stable structure and reproductive value for populations with complex life cycles. Ecology **63**:1223–1231.

Clifford, H. F., and H. Boerger. 1974. Fecundity of mayflies (Ephemeroptera), with special reference to mayflies of a brown-water stream of Alberta, Canada. Canadian Entomologist **106**:1111–1119.

Collins, J. P. 1979. Intrapopulation variation in the body size at metamorphosis and timing of metamorphosis in the bullfrog, *Rana catesbeiana*. Ecology **60**:738–749.

Forrest, T. G. 1987. Insect size tactics and developmental strategies. Oecologia (Berlin) **73**:178–184.

Gilliam, J. F. 1982. Habitat use and competitive bottlenecks in size-structured fish populations. Dissertation. Michigan State University, East Lansing, Michigan, USA.

Gilliam, J. F., and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. Ecology **68**:1856–1862.

Hinton, H. E. 1981. Biology of insect eggs. Pergamon, Oxford, England.

Houston, A., C. Clark, J. M. McNamara, and M. Mangel. 1988. Dynamic models in behavioral and evolutionary ecology. Nature **332**:29–34.

Ide, F. P. 1935. The effect of temperature on the distribution of mayfly fauna of a stream. University of Toronto Studies, Biological Studies **39**:1–76.

Istock, C. A. 1967. The evolution of complex life histories: an evolutionary perspective. Evolution **21**:592–605.

Lubchenco, J., and K. Curbit. 1980. Heteromorphic life histories for certain marine algae as adaptations to variations in herbivory. Ecology **61**:676–687.

Ludwig, D., and L. Rowe. 1990. Life history strategies for

energy gain and predator avoidance under time constraints. American Naturalist **135**:686–707.

Mangel, M., and C. Clark. 1986. Towards a unified foraging theory. Ecology **67**:1127–1138.

Mangel, M., and C. Clark. 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton, New Jersey, USA.

McNamara, J. M., and A. Houston. 1986. The common currency for behavioral decisions. American Naturalist **127**: 358–378.

McNamara, J. M., and A. Houston. 1987. Starvation and predation as factors limiting population size. Ecology **68**: 1515–1519.

Palmer, J. O. 1984. Environmental determinants of seasonal body size variation in the milkweed leaf beetle. Annals of the Entomological Society of America **77**:188–192.

Peters, T. M., and P. Barbosa. 1977. Influence of population density on size, fecundity and development rate of insects in culture. Annual Review of Entomology **22**:431–450.

Roff, D. 1983. Phenological adaptation in a seasonal environment: a theoretical perspective. Pages 251–270 *in* V. K. Brown and I. Hodek, editors. Diapause and life cycle strategies in insects. Dr. W. Junk, The Hague, The Netherlands.

———. 1981. On being the right size. American Naturalist **118**:405–422.

Semlitsch, R. D., D. E. Scott, and J. H. K. Pechmann. 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. Ecology **69**:184–192.

Shaffer, W. M. 1983. The application of optimal control theory to the general life history problem. American Naturalist **110**:601–617.

Sih, A. 1987. Predator and prey lifestyles: an evolutionary and ecological overview. Pages 203–224 *in* W. C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire, USA.

Smith, D. C. 1987. Adult recruitment in chorus frogs: effect of size and date at metamorphosis. Ecology **68**:344–350.

Stearns, S. C., and J. C. Koella. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. Evolution **40**: 893–913.

Sweeney, B. W., and R. L. Vannote. 1978. Size variation and the distribution of hemimetabolous insects: two thermal equilibrium hypotheses. Science **200**:444–446.

Thornhill, R., and J. Alcock. 1983. The evolution of insect mating systems. Harvard University Press, Cambridge, Massachusetts, USA.

Turner, A. M., and G. G. Mittelbach. 1990. Predator avoidance and community structure: interactions among piscivores, planktivores, and plankton. Ecology **71**:2241–2254.

Vannote, R. L., and B. W. Sweeney. 1980. Geographic analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. American Naturalist **115**:667–695.

Wassersug, R. J. 1975. The adaptive significance of the tadpole stage with comments on the maintenance of complex life cycles in anurans. American Zoologist **15**:405–417.

Werner, E. E. 1986. Amphibian metamorphosis: growth rate, predation risk and the optimal size at transformation. American Naturalist **128**:319–341.

———. 1989. Size, scaling and the evolution of complex life cycles. Pages 60–81 *in* B. Ebenman and L. Persson, editors. Size-structured populations. Springer-Verlag, Berlin, Germany.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size structured populations. Annual Review of Ecology and Systematics **15**:393–425.

Wilbur, H. M. 1977. Density-dependent aspects of growth and metamorphosis in *Bufo americanus*. Ecology **58**:196–200.

———. 1980. Complex life cycles. Annual Review Ecology and Systematics **11**:67–93.

———. 1987. Regulation of structure in complex systems: experimental temporary pond communities. Ecology **68**: 1437–1452.

———. 1989. Interactions between growing predators and growing prey. Pages 157–172 *in* B. Ebenman and L. Persson, editors. Size-structured populations. Springer-Verlag, Berlin, Germany.

Wilbur, H. M., and R. A. Alford. 1985. Priority effects in experimental communities: response of *Hyla* to *Bufo* and *Rana*. Ecology **66**:1106–1114.

Wilbur, H. M., and J. P. Collins. 1973. Ecological aspects of amphibian metamorphosis. Science **182**:1305–1314.

Ydenberg, R. C. 1989. Growth–mortality trade-offs, parent-offspring conflict, and the evolution of juvenile life histories in the avian family, Alcidae. Ecology **70**:1494–1506.

APPENDIX A

DYNAMIC PROGRAMMING AND SWITCHING CURVES

In this Appendix we set out our assumptions and the derivation of our conclusions in detail. The theory is an extension of that presented in Ludwig and Rowe (1990), but the present assumptions are slightly more special. The present treatment relies upon graphical representations of the growth and mortality rates and the associated switching condition in order to obtain qualitative results concerning the switching curve and associated trajectories.

Assumptions about growth and mortality

We assume that growth in the ith habitat is given by

$$\frac{dw}{dt} = g_i(w), \qquad i = 1, 2. \tag{A.1}$$

Typical growth functions are shown in Fig. 2a. The mortality rates are $\mu_i(w)$, as stated in the main text (see *Mayfly emergence: . . . growth in a single habitat: . . . Mortality*).

Assumptions about final fitness

We assume that the fitness (final reproductive output) of an individual is determined by her mass at the final time T as follows:

$$E(W) = a(W - W_c)^\beta, \tag{A.2}$$

where β is a shape constant and the constant a is a scale factor as in Eq. 1. We shall consider reproduction at a fixed time T in the present treatment, in contrast to the mayfly emergence section of the text. The extension to the more general case is given in Appendix C.

Dynamic programming equation

The dynamic programming equation for the fitness function $f(t, w)$ corresponding to these assumptions was derived in Ludwig and Rowe (1990). In the ith habitat it is

$$\frac{\partial f}{\partial t} + g_i(w) \frac{\partial f}{\partial w} - \mu_i(w)f = 0. \tag{A.3}$$

The switch between the habitats is predicted along a curve in the (w, t) plane where

$$[g_2(w) - g_1(w)] \frac{\partial f}{\partial w} - [\mu_2(w) - \mu_1(w)]f = 0. \tag{A.4}$$

In the following, w and t will denote the solution of Eqs. A.3 and A.4, i.e., (w, t) is the switching point for the trajectory on which it lies. We shall consider only the case where switching is from habitat 1 (aquatic) to habitat 2 (terrestrial).

Equation of the switching curve

It was shown in Ludwig and Rowe (1990) that the quantity $\ell(w)$ given by

$$\ell(w) = \frac{g_2(w)}{f(w)} \frac{\partial f}{\partial w} - \mu_2(w), \tag{A.5}$$

is constant along solutions of Eq. A.1. We use the subscript corresponding to the second habitat in Eq. A.5 and the following equations, since we are considering only trajectories that terminate in habitat 2 at time T. At the final time T it follows from Eq. A.2 (using R instead of ℓ, and otherwise using capital letters to denote quantities at time T) that

$$R(W) = G_2(W) \frac{E'(W)}{E(W)} - \mu_2(W)$$

$$= g_2(W) \frac{\beta}{W - W_c} - \mu_2(W). \tag{A.6}$$

Note that this quantity is the same as was defined in Eq. 12. On the other hand, the ratio involving f in Eq. A.5 can be determined from Eq. A.4 at the switching point. After substitution from Eq. A.4, Eq. A.5 becomes

$$\ell(w) = g_2(w) \frac{\mu_2(w) - \mu_1(w)}{g_2(w) - g_1(w)} - \mu_2(w). \tag{A.7}$$

Since $\ell(w)$ is constant along solutions of (A.1), we must have
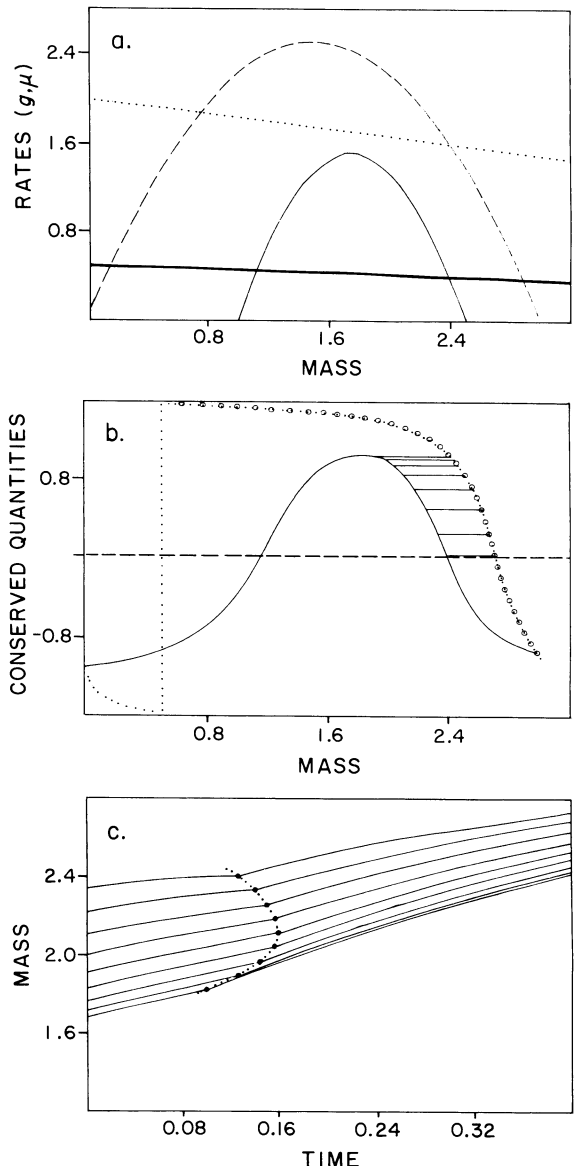
$$\ell(w) = R(W), \tag{A.8}$$

FIG. A1. Figs. A1a and A1c show assumptions about growth and mortality rates and about optimal fledging size and time (respectively) analogous to Ydenberg (1989). Fig. A1b shows data used to compute A1c from A1a. The details are given in Appendix A.

where w is the mass at which switching occurs, and W is the final mass attained.

Construction of the life-history trajectories

Life-history trajectories may be constructed as follows. First one must determine which portion of the boundary where $t = T$ corresponds to habitats 1 and 2. This may be done by examining the sign of Eq. A.4 at the boundary. Details are given below. The second step is to find pairs of values (w, W) that satisfy the switching condition (Eq. A.8). This may be done graphically, as is shown below. Having found such a pair, one may construct a trajectory that finishes in habitat 2, and that connects (W, T) with (w, t). The switching time, t, is determined by solving

$$T - t = \int_w^W \frac{1}{g_2(w')} \, dw', \tag{A.9}$$

which follows from Eq. A.1. Having found (w, t), one may then continue backwards in time to find the trajectory originating in habitat 1 that switches at (w, t). These steps will now be explained in more detail.

Optimal habitat at the final time

Eq. A.4 may be evaluated using Eq. A.2 to decide which habitat is optimal at the final time T. It becomes

$$S(W) = [g_2(W) - g_1(W)]\beta(W - W_c)^{\beta - 1}$$
$$- [\mu_2(W) - \mu_1(W)](W - W_c)^\beta. \tag{A.10}$$

If $S(W) > 0$ then habitat 2 is optimal; otherwise habitat 1 is preferred. For our purposes, we wish to check this condition while solving Eq. A.8. If $g_2(W) - g_1(W) > 0$, then $S(W) > 0$ implies that

$$\frac{\beta}{W - W_c} > \frac{\mu_2(W) - \mu_1(W)}{g_2(W) - g_1(W)}, \tag{A.11}$$

which in turn implies that $R(W) > \ell(W)$. Therefore if $R(W) > \ell(w)$ and $g_2(W) > g_1(W)$, then habitat 2 is preferred on the corresponding portion of the line $t = T$. Otherwise habitat 1 is preferred. On the other hand, if $g_2(W) < g_1(W)$, then habitat 2 is preferred where $R(w) < \ell(W)$. These conditions are used below.

Construction of pairs (w, W)

In order to solve Eq. A.8, the graphs of the two sides $\ell(w)$ and $R(w)$ may be plotted on the same axes (e.g., Fig. A1b). The arctangents of each side are plotted, since either side may be infinite at special points. The graph of $\ell(w)$ is drawn with a solid line, and the graph of R is dotted. In Fig. A1b, the dotted curve has a vertical asymptote at $W = W_c$, since the denominator of Eq. A.6 vanishes there. The solid curve has a local maximum, which is caused by a local minimum of the ratio $g_2(w)/g_1(w)$, which may be discerned from Fig. A1a. This local minimum in effect creates a "window" of masses for which habitat 1 is superior in view of the higher mortality rate in habitat 2. This "window" is analogous to a region where the ratio μ_1/g_1 is lower than μ_2/g_2, although our switching criterion (Eq. A.8) is different from a minimization of μ/g. Points on the dotted curve where habitat 2 is preferred according to the criteria derived above are drawn with circles (Fig. A1b), to distinguish them from the others. In the case of Fig. A1b, habitat 2 is preferred along almost the entire W axis, as is clear from Fig. A1a. Horizontal lines that connect the solid and the dotted curves from left to right correspond to feasible pairs (w, W), i.e., pairs where $W > w$ and habitat 2 is preferred at W. Note that the solid curve has a maximum, and hence the corresponding values of W have a minimum. The horizontal segments could be extended back to the leftmost branch of the solid curve, but they would not correspond to optimal trajectories. The corresponding features appear in Fig. A1c. The precise shape of the switching curve is difficult to discern from Fig. A1a; it depends upon the result of the integration in Eq. A.9. Graphs such as Fig. A1 may be used to understand and predict the effects of modifying assumptions, e.g., about growth and mortality rates.

APPENDIX B

DETERMINATION OF THE SWITCHING CURVE WHEN GROWTH CURVES CROSS

The theory of Appendix A has special implications near a point $\hat{w}$, where the growth curves cross. We wish to determine the slope of the switching curve near the critical point W_c.

We begin with Eq. A.8, which can be rewritten in the form

$$\frac{W - W_c}{\beta G_2(W) - \mu(W)(W - W_c)}$$
$$= \frac{g_2(w) - g_1(w)}{g(w)[\mu_2(w) - \mu_1(w)] - \mu(w)[g_2(w) - g_1(w)]}. \tag{B.1}$$

At $W = W_c$ the numerator of the left-hand side of Eq. B.1 vanishes. Therefore the numerator of the right-hand side must also vanish. Thus we see that $W = W_c$ corresponds to $w = \hat{w}$, as was pointed out in the first amphibian section of the text. In order to determine the slope of the switching curve at this point, we require the derivatives of W and $T - t$ as w varies near $\hat{w}$. If we regard W as a function of w as determined by Eq. B.1, and differentiate Eq. B.1 with respect to w at $\hat{w}$, the result is

$$\frac{1}{\beta G_2(W_c)} \frac{dW}{dw} = \frac{1}{g_2(\hat{w})} \frac{g_2'(\hat{w}) - g_1'(\hat{w})}{\mu_2(\hat{w}) - \mu_1(\hat{w})}. \tag{B.2}$$

If we perform a similar differentiation of Eq. A.9, the result is

$$\frac{d(T - t)}{dw} = \frac{1}{G_2(W)} \frac{dW}{dw} - \frac{1}{g_2(w)}. \tag{B.3}$$

If Eq. B.2 is substituted into Eq. B.3, the result is

$$\frac{d(T - t)}{dw} = \frac{1}{g_2(\hat{w})} \left[\beta \frac{g_2'(\hat{w}) - g_1'(\hat{w})}{\mu_2(w) - \mu_1(w)} - 1 \right]. \tag{B.4}$$

The sign of $d(T - t)/dw$ is determined by the sign of the quantity in brackets. In general, it can take on either sign, but note that $g_2' - g_1' > 0$ at $w = \hat{w}$, since the difference $g_2(w) - g_1(w)$ increases at $\hat{w}$. Therefore if $\mu_2(w) - \mu_1(w)$ is small, then the quantity in brackets will be positive. We conclude that $T - t$ increases as w increases, and hence t decreases as w increases. This situation is depicted in Fig. 2. It is possible for the switching curve to bend back if w becomes sufficiently large.

Construction of the switching curve in case $\mu_2 < \mu_1$

If the sign of $\mu_2(w) - \mu_1(w)$ is negative, a similar theory applies. We must have $w < \hat{w}$ in order for $W > W_c$. The quantity in brackets in Eq. B.4 is always negative in this case. Therefore $T - t$ increases as w decreases, and hence t decreases as w decreases. The corresponding result is depicted in Fig. 3.

APPENDIX C

VARIABLE TIME OF REPRODUCTION

We can combine the effects of time-dependent value of reproductive output and habitat switching. A typical life history begins in the aquatic habitat, switches to the terrestrial one at mass w and time t, and then reproduces at mass W at time T. The time T is not assumed to be fixed, as in the first amphibian section of the text, but is determined as in the mayfly emergence section. Thus $T = T(W)$, from the solution of Eq. 6 or Eq. 13. Are the derivations of Appendix A still valid?

Let the final reproductive value be

$$F(W) = C[T(W)]E(W). \tag{C.1}$$

The final condition on $f(w, t)$ is now

$$f[W, T(W)] = F(W). \tag{C.2}$$

It follows from differentiating Eq. C.2 that

$$T'(W)\frac{\partial f}{\partial t} + \frac{\partial f}{\partial w} = F'(W). \tag{C.3}$$

It follows likewise from differentiating Eq. C.1 that

$$F'(W) = T'(W)C'[T(W)]E(W) + C[T(W)]E'(W). \tag{C.3}$$

By substitution of Eq. 6, we obtain

$$F'(W) = [1 - g_2(W)T'(W)]CE' + T'CE\mu_2(W) \tag{C.4}$$

When this result is substituted in turn into Eq. C.3, the result is

$$T'(W)\frac{\partial f}{\partial t} + \frac{\partial f}{\partial w} = T'CE\mu_2 + (1 - g_2T')CE'. \tag{C.5}$$

On the other hand, Eq. A.3 states that

$$\frac{\partial f}{\partial t} + g_2\frac{\partial f}{\partial w} = \mu_2 f = \mu_2 CE. \tag{C.6}$$

If $\partial f/\partial w$ is eliminated between Eqs. C.5 and C.6, the result is

$$\frac{\partial f}{\partial t} = CE\mu_2 - g_2CE'. \tag{C.7}$$

We conclude that

$$\frac{-1}{f}\frac{\partial f}{\partial t} = g_2\frac{E'}{E} - \mu_2. \tag{C.8}$$

In view of Eq. C.6, this is exactly the same result as Eq. A.8. Therefore Eq. A.8 carries over to the more general case where time of reproduction varies with body mass, as long as the time is determined from the optimality condition (Eq. 7).

Since T depends upon W, the switching time t in Eq. A.9 is now given by

$$T(W) - t = \int_w^W \frac{1}{g_2(w')} \, dw'. \tag{C.9}$$

The effect of this change is to shift the switching curve back by a variable amount. This has the effect of converting the trajectories from those of Fig. 4 to Fig. A2.