# Disturbance Regimes and Life-History Evolution

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ABSTRACT: Disturbance regimes are ecologically important, but many of their evolutionary consequences are poorly understood. A model is developed here that combines the within- and among-season dynamics of disturbances with evolutionary life-history theory. "Disturbance regime" is defined in terms of disturbance timing, frequency, predictability, and severity. The model predicts the optimal body size and time at which organisms should abandon a disturbance-prone growth habitat by maturing and moving to a disturbance-free, nongrowth habitat. The effects of both coarse-grained (those affecting the entire population synchronously) and fine-grained disturbances (those occurring in a patch dynamics setting) are explored. Several predictions are congruent with previous theory. Infrequent or temporally unpredictable disturbances should have little effect on the evolution of life-history strategies, even though they may cause high mortality. Similar to seasonal time constraints on reproduction, disturbance regimes can synchronize metamorphosis within a population, resulting in a seasonal decline in body size at maturity. Other model predictions are novel. When disturbances cause high mortality, coarse-grained disturbances have a much stronger effect on life-history strategies than fine-grained disturbances, suggesting that population structure (relative to the scale of disturbance) plays a critical evolutionary role when disturbances are severe. When within-population variance in juvenile body size is high, two consecutive seasonal declines in body size at maturity can occur, the first associated with disturbance regime and the second associated with seasonal time constraints.

*Keywords:* body size, timing of metamorphosis, patch dynamics, state-dependent strategy, geometric mean fitness, arithmetic mean fitness.

While the ecological effects of disturbances have been relatively well studied, the evolutionary consequences of disturbances are less understood. Ecologically, disturbances can mediate the coexistence of competitors (Hutchinson 1961; MacArthur and Levins 1967; Huston 1979; Chesson 1994; Lavorel and Chesson 1995), eliminate nonnative taxa (Meffe 1984; Minckley and Meffe 1987; Closs and Lake 1996), facilitate invasive taxa (McEvoy et al. 1993), and alter community food web structure (Wootton 1998). Although it seems reasonable that strong ecological forces acting within populations could influence the evolution of life-history strategies or morphologies, variation in disturbance timing, predictability, frequency, and severity can make it difficult to predict the sign and strength of selection. Several studies (Harper 1977; Lacey et al. 1983; Venable and Brown 1988; Turner et al. 1998) have suggested that the frequency of disturbances relative to an organism's life span may be evolutionarily important. While it is intuitive that organisms may not adapt to phenomena that are unlikely to occur during their life spans (e.g., volcanoes, large fires, big floods, or storms [Turner et al. 1998]), it is not clear how frequently disturbances must recur in order to elicit evolutionary responses.

From an evolutionary perspective, disturbances can be categorized as either fine-grained events that affect only a portion of the population at a time or coarse-grained events that affect the entire population simultaneously (Iwasa and Levin 1995). Fine-grained disturbances (the "patch dynamics" perspective of Pickett and White [1985]) include gap formation in forest canopies (Runkle 2000), flash floods (Lytle 2000a), and scouring of marine benthos (Airoldi 2000). Coarse-grained disturbances include interannual variability in growing season length or annual rainfall (Philippi 1993; Danforth 1999), as well as disturbances with large areal coverage, such as hurricanes (Turner et al. 1998). The spatial scale of a disturbance relative to the spatial distribution of the population is important because it determines how fitness should be estimated in models of life-history evolution. When disturbances occur synchronously over the entire population, as with coarse-grained disturbances, the geometric mean of reproductive success over multiple seasons is the correct measure of fitness (Cohen 1966; Gillespie 1977). If the population occurs across many habitat patches that experience disturbances at different times, as with fine-grained disturbances, and the breeding population consists of individuals pooled from these patches, the arithmetic mean is appro-

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priate. Thus, evolutionary models incorporating fine- and coarse-grained disturbances are inherently different. In practice, models can sometimes be modified to account for one case or the other (Iwasa and Levin 1995; see below).

Much of the theory concerning how disturbances affect life-history evolution has focused on coarse-grained disturbances. Building on the theory of Cohen (1966, 1970, 1971), models have been developed to explore how resources in plants are allotted to growth versus reproduction when the length of the growing season varies across years (King and Roughgarden 1982a, 1982b; Kozłowski and Weigert 1986, 1987). For organisms that produce diapausing seeds or eggs, bet-hedging models predict that among-year environmental variability may favor reproductive strategies where only a fraction of offspring germinate or hatch in a given season (Venable and Lawlor 1980; Ellner 1985a, 1985b; Bradford and Roff 1993, 1997; Sasaki and Ellner 1995). In each of these models, the "disturbance" is the occurrence of an unfavorable physical environment in a particular year, and the life-history strategy that maximizes the geometric mean of reproductive output over many years has the highest fitness. The disturbance does not need to be abiotic, however. Hairston and Munns (1984) used a similar approach to model how among-year variability in the onset of severe fish predation affected the optimal time for copepods to begin producing fish-resistant diapausing eggs.

Most of these coarse-grained models focus on environmental variability among years, but many disturbance dynamics occur within years. Relevant parameters include the frequency (expected number of disturbances per season), severity (expected mortality from a single disturbance), timing (when disturbances occur during a season), and predictability (variance in within-season timing) of disturbances (Pickett and White 1985; Richter et al. 1996). Although seasonal timing and predictability are implicit in many of the coarse-grained models, they assume that only one disturbance occurs per season (frequency = 1). Some types of disturbance, however, occur multiple times per season or not at all, for example, flash floods (John 1964; Grimm and Fisher 1989) and the drying and refilling of temporary ponds (Semlitsch and Wilber 1988; Newman 1989). Thus, a parameter that specifies within-season frequency is needed to adequately model these kinds of disturbances.

The goal of this article is to develop a general disturbance model that combines the timing, frequency, severity, and predictability of disturbances (both fine and coarse grained) with evolutionary life-history theory. This theoretical framework allows the investigation of several questions. How do disturbance regimes affect life-history attributes of organisms with complex life cycles, such as the size at and timing of maturity? How frequently and predictably must disturbances recur to affect the evolution of these traits? How does population structure influence the evolutionary response to disturbance? Used in this way, this disturbance model may be useful for determining when ecologically important disturbance regimes also have evolutionary consequences.

## Disturbance Model

The following model explores how among-season variability in disturbance regime (sensu Cohen 1966 and related papers) and within-season disturbance dynamics (based on Ludwig and Rowe 1990; Rowe and Ludwig 1991) affect life-history evolution. In this model, disturbances affect individual fitness directly via mortality and indirectly by causing mortality in offspring. The model is based on the following life cycle: juveniles grow in a particular habitat where they risk mortality from disturbances; at time $T$, juveniles stop growing and begin metamorphosis for a fixed time period; at time $T_E$, nongrowing adults move to a second habitat that is free from disturbance; at time $T_R$, adults reproduce by placing offspring back in the disturbed habitat. Thus, juveniles face a trade-off between growth and disturbance mortality. Because the risk of disturbance changes during the season, the model seeks the optimal body size, $W$, and time, $T$, at which juveniles should stop growing and mature into the reproductive stage.

### Disturbances and Survivorship

The disturbance regime consists of the timing, predictability, frequency, and severity of disturbances. Survivorship is a function of the time spent in this disturbance regime. The probability of an individual surviving $i$ disturbances before adulthood is $S_i = (1 - \lambda)^i$, where $\lambda$ is the probability of mortality from a single disturbance event (disturbance severity). Assuming that disturbance events occur independently according to a Poisson distribution, the probability of $i$ disturbances occurring from some time $t$ to adulthood at time $T_E$ is

$$P_i = \frac{u_1^i e^{-u_1}}{i!}, \tag{1}$$

where $u_1 = \int_t^{T_E} g(t)dt$, a time-inhomogeneous Poisson rate parameter. The frequency of disturbances, such as thunderstorms and flash floods, conforms to a Poisson distribution (Fogel and Duckstein 1969; Lytle 2000b). The function $g(t)$ describes the timing of disturbances throughout the season; it is assumed to have a single maximum. In the examples explored below, $g(t) = \phi Z(t)$, where $\phi$ is the average number of events per season (disturbance fre-

quency) and $Z(t)$ is a normal distribution with mean disturbance date $f$ (disturbance timing) and standard deviation $\sigma$ (disturbance predictability). The adult stage is assumed to occur after metamorphosis so that $T_E = T + \rho$, where $\rho$ is the duration of the metamorphic stage, a fixed quantity. Because $u_1$ is evaluated through $T_E$, metamorphosing individuals risk mortality from disturbances even though no growth occurs during this stage. Metamorphosis thus entails a fixed cost. For organisms that do not undergo metamorphosis, $\rho = 0$.

The probability of offspring surviving $j$ disturbances after reproduction is $O_j = (1 - \lambda)^j$. The probability of $j$ disturbances occurring from the time of reproduction to the end of the disturbance season is

$$P_j = \frac{u_2^j e^{-u_2}}{j!}, \tag{2}$$

where $u_2 = \int_{T_R}^{T_Z} g(t)dt$ and $T_Z$ is some date well beyond the end of the disturbance season ($g(t) \rightarrow 0$ at $T_Z$). Reproduction occurs after metamorphosis and the adult life stage ($\xi$, a fixed quantity) are completed, so that $T_R = T + \rho + \xi$.

### Growth and Reproduction

The growth rate of individuals is assumed to follow a logistic form:

$$\frac{dw}{dt} = rw\left(1 - \frac{w}{k}\right), \tag{3}$$

where $k$ is maximum body mass, $w$ is body mass, and $r$ is a growth rate constant. The number of offspring produced by an individual, $E$, is related to body mass:

$$E(W) = \begin{cases} a(W - W_C)^\beta & \text{if } W > W_C, \\ 0 & \text{otherwise,} \end{cases} \tag{4}$$

where $W$ is body mass at time of reproduction, $W_C$ denotes the minimum body size for offspring production, $\beta$ is a parameter that controls the shape of the relationship, and $a$ is a scale factor that adjusts for units of measurement.

### Seasonal Time Constraints

As in the Rowe and Ludwig model, seasonal time constraints on reproduction affect the expected value, or contribution, per offspring:

$$C(T_R) = \begin{cases} \left(\dfrac{T_C - T_R}{T_C}\right)^\alpha & \text{if } T_R < T_C, \\ 0 & \text{otherwise,} \end{cases} \tag{5}$$

where $T_C$ is the upper time limit for reproduction and $\alpha$ is a parameter that controls how rapidly this time constraint approaches. For $\alpha > 0$ $C(T_R)$ decreases as $T_C$ approaches (earlier offspring are more valuable than later ones), and adults are unable to reproduce after $T_C$.

### Arithmetic Mean Fitness

For an individual that matures at time $T$ in a season where $i$ disturbances occur before adulthood and $j$ disturbances occur after reproduction, fitness is $W_{ij}(T) = S_i \times O_j \times E(W(T)) \times C(T_R)$. When disturbances are fine grained and occur in a patch dynamic setting so that disturbances happen independently in each patch according to $g(t)$ and the progeny from all patches mix to form a single breeding population, the arithmetic mean is the appropriate way to calculate long-term fitness. Arithmetic mean (AM) fitness is estimated by summing fitness across all possible disturbance seasons weighted by their probability of occurring:

$$F_{AM}(T) = \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} P_i P_j W_{ij} \tag{6}$$

$$= \sum_{i=0}^{\infty} (1 - \lambda)^i \frac{u_1^i e^{-u_1}}{i!}$$

$$\times \sum_{j=0}^{\infty} (1 - \lambda)^j \frac{u_2^j e^{-u_2}}{j!} \tag{7}$$

$$\times E \times C$$

$$= e^{-\lambda u_1} \times e^{-\lambda u_2} \times E \times C. \tag{8}$$

Timing of reproduction is optimized by maximizing fitness as a function of $T$. This is done by taking the first derivative of $F_{AM}$ with respect to $T$ and setting it equal to 0. First, taking the natural log of both sides for convenience,

$$\ln[F_{AM}(T)] = -\lambda u_1 - \lambda u_2 + \ln(E) + \ln(C), \tag{9}$$

$$\frac{d\ln[F_{AM}(T)]}{dT} = -\lambda g(T_E)$$

$$+ \lambda g(T_R) + \frac{E'}{E} + \frac{C'}{C} = 0, \tag{10}$$

$$\lambda[g(T_R) - g(T_E)] + \frac{E'}{E} + \frac{C'}{C} = 0. \tag{11}$$

After incorporating the biological assumptions outlined above (see appendix), equation (11) becomes

$$\lambda\phi[Z(T_R) - Z(T_E)] = \frac{\alpha}{T_C - T_R} - \frac{\beta r W\left(1 - \frac{W}{k}\right)}{W - W_C}. \quad (12)$$

The left side of equation (12) represents the relative change in fitness due to disturbance regime. When $\phi$ or $\lambda \to 0$ or $T_E \to T_R$, this side approaches 0, and disturbances have no effect on optimal metamorphosis strategy. Additionally, when the left side of equation (12) is 0 and $\rho$ and $\xi \to$ 0, $T_R \to T$ and equation (12) collapses to that of Rowe and Ludwig (1991), where metamorphosis into the adult stage is driven primarily by seasonal time constraints (for cases where their $\mu(w) \to 0$). The Rowe and Ludwig (1991) single-habitat growth model is, therefore, nested within the more general case described here.

## Disturbance Model Results

### General Behavior

After substituting parameter values, equation (12) can be solved for $W$ in terms of $T$, yielding two roots. Figure 1 shows the optimal relationship between body size and timing of metamorphosis for the positive root and parameter values $\phi = 1$, $f = 150$, $\sigma = 25$, $\alpha = 0.1$, $\beta = 1$, $k = 10$, $W_C = 2$, $\xi = 10$, $\rho = 10$, $T_C = 250$, and $r = 0.01$. In the case where disturbances do not cause mortality ($\lambda = 0$ curve), $W$ declines solely as a function of the end of the season ($T_C$). Body mass, $W$, becomes progressively smaller as $T_C$ approaches, and all individuals larger than $W_C$ begin metamorphosing with sufficient time remaining to complete their metamorphic and adult stages before $T_C$. This is a state-dependent strategy because the decision to continue growing or begin metamorphosis is based on current body mass (Rowe and Ludwig 1991; Nylin and Gotthard 1998).

When disturbances cause mortality, this pattern is altered in several ways ($\lambda = 1$ curve). Although individuals attaining large body sizes early in the season may metamorphose at this time (period A), no metamorphosis occurs as disturbances become more likely (period B, where $W > k$, the maximum body size). This occurs because offspring produced at this time have low value since they would be placed in the disturbance-prone habitat at the height of the disturbance season. The largest individuals ($W$ near 10) begin metamorphosis during period C, with progressively smaller individuals metamorphosing as the disturbance season builds. Note that individuals metamorphosing at this time will escape the peak of the disturbance season by becoming adults, and their offspring
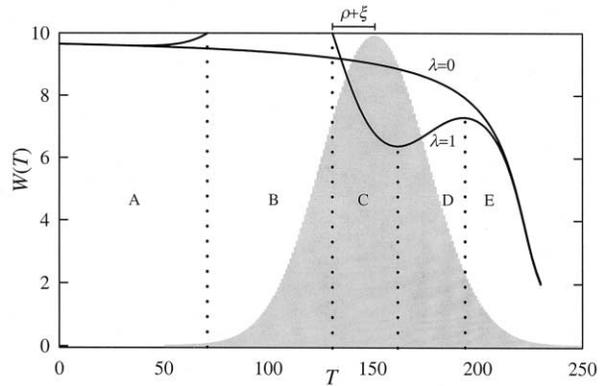


**Figure 1:** Optimal body size ($W$) versus optimal timing of metamorphosis ($T$) when disturbances cause high mortality ($\lambda = 1$) or none at all ($\lambda = 0$), under arithmetic mean assumptions. Shaded region represents disturbance timing $Z(T)$ with parameters $f = 150$ and $\sigma = 25$. Other parameter values: $\phi = 1$, $\alpha = 0.1$, $\beta = 1$, $k = 10$, $W_C = 2$, $\xi = 10$, $\rho = 10$, $T_C = 250$, and $r = 0.01$. Only individuals that have attained large body sizes (near $k = 10$) early in the season metamorphose during period A. For the $\lambda = 1$ curve, no metamorphosis occurs during period B because $W > k$, the maximum body size. Individuals metamorphose during period C because reproduction (at time $T + \rho + \xi$) will occur after the peak of the disturbance season. During period D, $W$ increases as the disturbance season wanes, then decreases during period E in response to $T_C$.

will be placed in the disturbance-prone habitat just as the probability of disturbance begins to decline. Very small individuals ($W < 6$ in this example) risk the worst of the disturbance season to continue juvenile growth. After the peak of the disturbance season has passed (period D), the marginal benefits of remaining in the juvenile stage begin to outweigh the risks, and smaller individuals that have survived thus far are expected to continue growing. Finally, during period E, the approach of $T_C$ causes any remaining individuals to begin metamorphosis at progressively smaller body sizes.

### Population Synchrony

In addition to influencing $W$, disturbances may also affect the synchrony of metamorphosis within a population. Figure 2 shows a series of juvenile growth trajectories. It is assumed that growth trajectories are offset because of variability early in the life cycle (different oviposition dates, different initial growth rates, etc.). Metamorphosis occurs where growth trajectories cross the $W(T)$ curve. Lack of metamorphosis during period B causes a relatively large number of trajectories to stack up; these trajectories intersect the steep $W(T)$ curve in period C, producing synchronous metamorphosis over a relatively short period of time. For smaller individuals, a similar delay (period D)
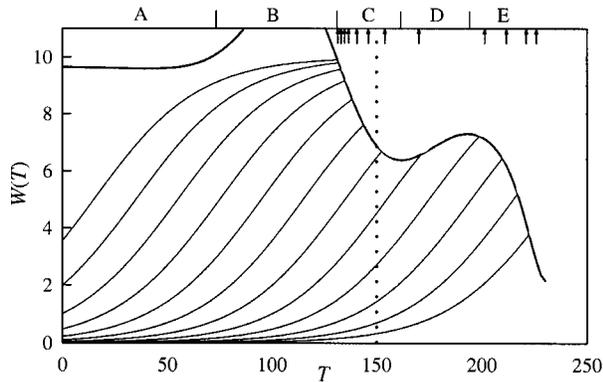
**Figure 2:** Effect of the $W(T)$ curve on hypothetical growth trajectories. Individuals metamorphose (denoted by *arrows*) when their growth trajectories intersect the curve. Dashed line is the mean disturbance date $f$. Parameter values same as those in figure 1; $\lambda = 1$ curve. Most metamorphosis occurs when the $W(T)$ curve declines steeply during periods C and E (see text).

and synchronous period of metamorphosis (period E) occur before $T_C$. These results suggest that disturbances can serve to synchronize the metamorphosis of individuals that are following different growth trajectories. Given a particular level of initial within-population size variability, disturbance regimes should favor greater temporal synchrony in metamorphosis while simultaneously increasing the observed variability in body size at metamorphosis.

### *Geometric Mean Fitness*

When disturbances are synchronized across patches or when the entire population experiences the same large-scale disturbances, the geometric mean is the appropriate measure of long-term fitness. Geometric mean (GM) fitness is calculated by summing the logarithm of fitness across all possible disturbance seasons:

$$F_{GM}(T) = \sum_{i=0}^{\infty} \sum_{j=0}^{\infty} P_i P_j \ln(W_{ij}) \qquad (13)$$

$$= \sum_{i=0}^{\infty} \ln\left[(1-\lambda)^i\right] \frac{u_1^i e^{-u_1}}{i!}$$

$$+ \sum_{j=0}^{\infty} \ln\left[(1-\lambda)^j\right] \frac{u_2^j e^{-u_2}}{j!} \qquad (14)$$

$$+ \ln(E) + \ln(C)$$

$$= \ln(1-\lambda)u_1 + \ln(1-\lambda)u_2$$

$$+ \ln(E) + \ln(C). \qquad (15)$$

Differentiating with respect to $T$ and setting this quantity equal to 0,

$$\ln(1-\lambda)g(T_E) - \ln(1-\lambda)g(T_R) + \frac{E'}{E} + \frac{C'}{C} = 0, \qquad (16)$$

$$\ln\left(\frac{1}{1-\lambda}\right)[g(T_R) - g(T_E)] + \frac{E'}{E} + \frac{C'}{C} = 0. \qquad (17)$$

Comparing equation (17) with equation (11) demonstrates that the optimality conditions for the geometric and arithmetic mean fitnesses differ by a single term: $\lambda$ in the arithmetic mean (AM) model becomes $\ln[1/(1-\lambda)]$ in the GM model. Thus, using the geometric rather than the arithmetic mean influences only how disturbance severity affects the optimal life-history strategy. Disturbance severity has a proportionately higher effect under GM assumptions because $\ln[1/(1-\lambda)] > \lambda$. For $\lambda$ near 0, both models will produce essentially the same results, but for $\lambda > 0.8$, $\ln[1/(1-\lambda)]$ is greater than twice $\lambda$. As $\lambda$ approaches its maximum at 1, $\ln[1/(1-\lambda)]$ approaches infinity. Figure 3 shows that, unlike the AM model, under
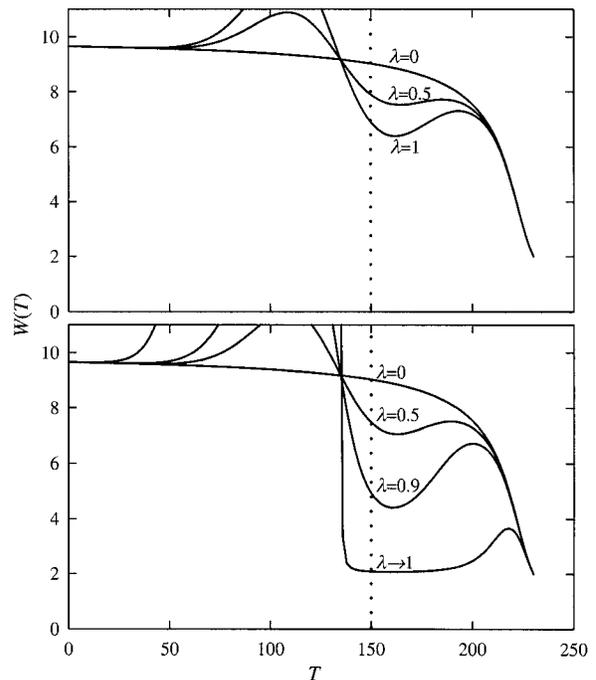


**Figure 3:** Effect of disturbance severity on optimal body size and optimal timing of metamorphosis, under arithmetic mean (*top panel*) and geometric mean (*bottom panel*) assumptions. Parameter values same as those in figure 1. For small $\lambda$, both models make similar predictions. Large $\lambda$ causes disturbances to have a much more pronounced effect under geometric mean assumptions.
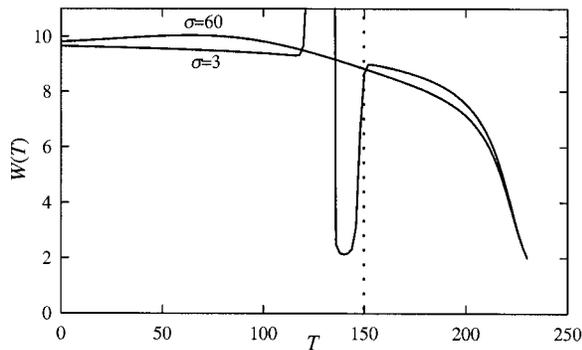
**Figure 4:** Effect of disturbance predictability ($\sigma$) on the $W(T)$ curve, under arithmetic mean assumptions. Dashed line is the mean disturbance date. Parameter values same as those in figure 1; $\lambda = 1$ curve. When disturbance regimes are predictable ($\sigma = 3$ curve), individuals emerge synchronously and at a wide range of body sizes. Unpredictable disturbance regimes produce no life-history response ($\sigma = 60$ curve, which is very similar to $\lambda = 0$ curve in fig. 1).

GM assumptions, disturbances drive nearly all the body size pattern when $\lambda$ is high.

### Disturbance Predictability

Variance in the mean date of disturbance ($\sigma$) also has an effect on optimal body size at metamorphosis. When disturbances always occur within a narrow time interval, the optimal strategy is to metamorphose immediately before the mean date of disturbance, irrespective of body size ($\sigma = 3$; fig. 4). This strategy causes body size at metamorphosis to decline sharply immediately before the mean date of disturbance, which produces highly synchronous metamorphosis into the adult stage at a wide range of body sizes. Conversely, when disturbances are unpredictable, individuals do not respond to the disturbance regime, even though disturbances can produce high mortality ($\sigma = 60$; fig. 4). In fact as $\sigma$ increases, the $W(T)$ curve becomes identical to the case where disturbances cause no mortality ($\lambda = 0$ curve; fig. 1). In this situation, there is simply no life-history strategy, in terms of age and size at metamorphosis, that can be used to avoid a highly unpredictable source of mortality. The sensitivity of this result to changes in $\sigma$ is explored below.

### Disturbance Frequency and Severity

The mean number of disturbances per season ($\phi$) and the expected mortality from a disturbance ($\lambda$) also influence size at and timing of metamorphosis. More frequent disturbances produce a greater decline in size at metamor-

phosis before the mean date of disturbance (fig. 5). A similar pattern occurs when frequency is constant but severity is allowed to vary. Under AM assumptions, the relationship between disturbance frequency and severity is multiplicative. For this reason, an increase in frequency can counteract a decrease in severity and vice versa, although severity is bounded between 0 and 1, while frequency can theoretically take on any positive value.

### Sensitivity Analysis

According to the model, how predictable must the timing of disturbances be to induce changes in an organism's life-history strategy? Similarly, how frequently must disturbances recur to produce a change in an organism's optimal maturation strategy? There are no universal answers to these questions because any answer depends on many initial parameter values. Qualitatively, however, the sensitivity of the disturbance model predictions to changes in only one or two parameters can be investigated. The difference between a "baseline" curve where no disturbances occur and a curve where disturbances do occur can be quantified as the sum of squared differences between the two curves. The sum of squares can be interpreted as a measure of disturbance regime selection strength because it describes the degree of difference in optimal phenotype attributable solely to disturbance regime. For individuals in disturbance-prone habitats, the greater the departure from this optimum the lower the expected fitness.

Figure 6 shows the relationship between selection strength (log +1 scale) and variation in disturbance predictability ($\sigma$) for organisms with different growth rates. If body size at maturity is assumed to be fixed, growth rate can be equated with life span; higher growth rates
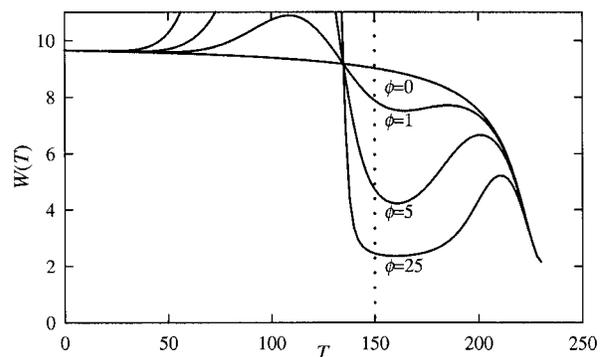


**Figure 5:** Effect of disturbance frequency ($\phi$) on the $W(T)$ curve, under arithmetic mean assumptions. Parameter values same as those in figure 1. Greater disturbance frequencies favor metamorphosis before the mean date of disturbance (*dashed line*), irrespective of body size.
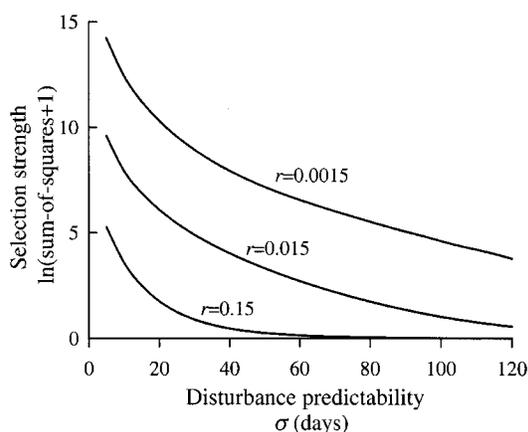
**Figure 6:** Selection strength versus disturbance predictability for organisms with different growth rates, under arithmetic mean assumptions. Selection strength measures the degree of difference between the no-disturbance curve ($\lambda = 0$ curve) and a curve where disturbance is a factor ($\lambda > 0$). Parameter values same as those in figure 1.

suggest a shorter life span, and slower growth rates suggest a longer life span. Sum of squares differences were calculated at daily intervals over the course of the entire season (from $t = 0$ to $T_C = 230$). In all cases, selection was strongest when disturbances were more predictable (low $\sigma$), but the relative magnitude of selection depended on the growth rate of the organism. Within the realm of more predictable disturbances ($\sigma < 40$ d in this example), selection strength roughly doubled with every order of magnitude increase in growth rate. As disturbances became unpredictable, selection strength approached 0 regardless of growth rate, but this happened at much lower values of $\sigma$ for faster growing organisms. For this reason, slower-growing organisms were more likely to show evolutionary responses to highly unpredictable disturbance regimes than faster-growing organisms.

Selection strength changed in response to disturbance frequency (shown in fig. 7 as return interval, the reciprocal of $\phi$) in a way qualitatively similar to predictability. In all cases, selection strength was highest for short return intervals, but as with disturbance predictability, selection strength was greatest for organisms with slow growth rates. Under GM assumptions, selection strength was proportionately higher at all return intervals, causing the curves in figures 6 and 7 to shift upward.

### Discussion

Combining disturbance ecology with a model of life-history evolution generated predictions that are congruent with well-known theory and data, as well as some novel

predictions. In general, the model showed that life-history strategies that mitigate the negative fitness effects of disturbances are possible, and these strategies are strongly influenced by disturbance timing, predictability, frequency, and severity.

### *Disturbance Regimes Can Produce Multiple Seasonal Declines in Body Size at Metamorphosis*

The disturbance model predicts that when disturbances are sufficiently predictable (i.e., $\sigma$ is low relative to the organism's life span) and when within-population variance in juvenile body size is large, a single population will metamorphose during two distinct periods. The first period is associated with the disturbance regime and the second with seasonal constraints. Multiple peaks of emergence during a single season have been observed in aquatic insect species (Vannote and Sweeney 1980; Peckarsky et al. 1993; Moreira and Peckarsky 1994; Taylor et al. 1998), but this pattern has been attributed to multi- or semivoltinism of populations (i.e., two distinct cohorts were thought to have been observed). Peckarsky et al. (2001) suggested that patterns of body size at emergence observed in a mayfly with two consecutive cohorts per season were in fact driven by a biotic disturbance regime, the onset of fish predation. Since multivoltinism alone can produce two consecutive emergence groups in the absence of disturbance, care must be taken in attributing this type of pattern entirely to a disturbance regime when interpreting field data. From a modeling perspective, however, the size structure of the population makes no difference in terms of predicting
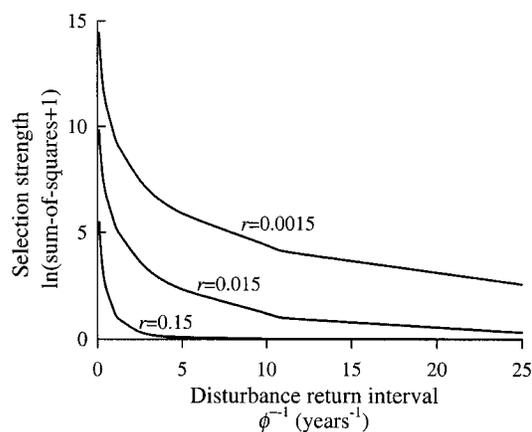


**Figure 7:** Selection strength versus disturbance return interval for organisms with different growth rates, under arithmetic mean assumptions. Selection strength measures the degree of difference between the no-disturbance curve and any curve where disturbance occurs. Parameter values same as those in figure 1.

patterns of body size at metamorphosis, and so the disturbance model should work just as well if multiple cohorts are present.

## Disturbance Regimes Can Increase Synchrony of Metamorphosis While Simultaneously Increasing Variation in Body Size at Metamorphosis

Previous theory (Ludwig and Rowe 1990; Rowe and Ludwig 1991; Rowe et al. 1994) has shown that time constraints can cause organisms to mature over a discrete period of time, producing a decline in body size at metamorphosis. Assuming initial variation in body size within a population and constant growth rates, time constraints produce an inverse relationship between variance in time of metamorphosis and variance in body size at metamorphosis (illustrated in fig. 2). Disturbance regimes generate a similar phenomenon. Disturbance regimes that are sufficiently predictable, cause sufficient mortality, and occur with sufficient frequency can cause variance in time of metamorphosis to decrease while variance in body size at metamorphosis increases. The degree of this inverse relationship depends on the steepness of the $W(T)$ curve and the amount of size variation initially present in the population.

While size variation within populations is common, constant growth rates during development are not always observed (Gotthard et al. 1999). The distinction between development rate and growth rate is important here. The disturbance model, like most other models of optimal size at and timing of metamorphosis, allows development rate to vary in response to disturbances or seasonal constraints, meaning individuals can accelerate ontogeny to mature earlier. Increasing growth rate involves the accelerated acquisition of resources, often by way of increased foraging rates (Lima and Dill 1990). Models that allow variable growth rates predict increased growth rates at the expense of increasingly risky foraging behavior (Houston et al. 1993; Werner and Anholt 1993; Abrams and Rowe 1996). Experimental manipulations on several insect taxa (referenced in Johansson and Rowe 1999) have shown that time constraints accelerate development, which causes individuals to mature earlier and at smaller body sizes. This observation suggests that flexibility in development rate is an important variable, although growth rates could also play a role. To model how disturbances affect life histories where the assumption of constant growth rates may be violated, as in some insects (Gotthard et al. 1999) and amphibians (Wilbur 1987; Semlitsch and Wilbur 1988), disturbance regimes need to be incorporated into more sophisticated models that simultaneously optimize timing

of metamorphosis and growth rate (e.g., Abrams et al. 1996).

## Coarse-Grained and Fine-Grained Disturbance Regimes Produce Similar Life Histories Except When Disturbances Are Severe

The modeling results show that, when disturbance severity is low or moderate, using either the geometric or arithmetic mean to estimate fitness results in nearly the same life history. This is true regardless of disturbance frequency, predictability, or timing. Thus, population structure, relative to the spatial scale of disturbances, does not influence life-history strategies when disturbances cause low or moderate mortality. Severe coarse-grained disturbances, however, have a much stronger effect on life-history strategies than do severe fine-grained disturbances. In fact, when disturbances are coarse-grained and severe, they can completely override the effects due to seasonal time constraints. In these cases, metamorphosis should coincide entirely with the disturbance regime, and only the smallest individuals (those below the minimum size for reproduction) should risk disturbances by remaining in the juvenile growth habitat.

## Slow-Growing Organisms Adapt to Disturbance Regimes More Readily than Fast-Growing Organisms

Life histories of organisms that have fast growth and mature quickly do not respond to disturbances as strongly as slow-growing, long-lived organisms. This finding is congruent with results from earlier studies, which suggest that disturbances must recur on a timescale comparable to the organism's life span to elicit an evolutionary response (Harper 1977; Lacey et al. 1983; Venable and Brown 1988; Turner et al. 1998). This occurs because when disturbance are unpredictable and organisms have rapid growth rates, the best strategy is always to continue the rapid growth, even if disturbances are frequent and cause high mortality. It makes sense that rare or benign disturbances should have few consequences for adaptive evolution, but there is no discrete threshold frequency or severity at which this occurs. Instead, selection strength drops off exponentially with increasing disturbance return interval, and this relationship depends strongly on the growth rate of the organism.

Several assumptions made in the model development may affect the generality of the results presented here. These include assumptions of logistic growth of individuals, mortality from disturbances only, and no size-dependent mortality. Equation (3) assumes a fixed upper limit to growth, and it is possible that nonasymptotic growth forms might produce different results. Although

the choice of growth curve can influence optimal strategies (Day and Taylor 1997; Czarnołęski and Kozłowski 1998), it is important to note that disturbance regimes cause metamorphosis even during the exponential phase of growth trajectories (fig. 2). Thus, although an unrestricted maximum body size could result in a larger size at metamorphosis for some individuals (and, thus, increase population-wide variance in body size at metamorphosis), disturbance should produce at least some decline in body size for even nonasymptotic growth functions. Disturbances in the juvenile growth habitat were assumed to be the only source of mortality in order to highlight their effects on life-history strategies. Mortality in the adult habitat would likely diminish the fitness benefits of maturing, resulting in larger final body sizes and flattening of the body size/timing of metamorphosis reaction norm (Rowe and Ludwig 1991; Werner and Anholt 1993). Thus, the effects of juvenile-habitat disturbance on patterns of body size at metamorphosis should be reduced as adult mortality increases. For organisms with size-specific mortality (e.g., John 1964), disturbance regimes should favor metamorphosis at smaller body sizes if mortality risk from disturbances increases with body size. This would occur because while survivorship for growing individuals decreases, survivorship for their small offspring would be relatively high. The reverse would be true if mortality risk from disturbances decreases with body size.

Following the example of previous models, the time constraint on reproduction was included in the disturbance model as a continuous function that decreases to 0 at $T_C$, the last day of the reproductive season. In fact, the end of the reproductive season could also be treated as a type of disturbance, with a characteristic frequency, timing, severity, and predictability. This approach would be particularly suitable for season-ending events, such as the first winter frost or the drying date of temporary rain pools, phenomena that are well described by probability distributions.

Although the disturbance model developed here treats a specific kind of evolution (evolution of optimal body size and timing of metamorphosis), some of the model's qualitative results may apply to other evolutionary and ecological scenarios. For example, the disturbance modeling approach could be used to locate the critical range of disturbance frequencies within which organisms are likely to adapt to particular disturbance regimes, such as plants adapting to fire regimes (Christensen 1985). Beyond this critical range, disturbances may actually exclude taxa from the system (an ecological effect) rather than drive evolutionary change of life-history attributes. Broadening this approach to include other aspects of disturbance (spatial extent, synergistic effects of multiple kinds of disturbance) and other evolutionary processes (behavioral, morphological) could clarify under which conditions disturbance regimes are important for ecology, evolution, or both.

## APPENDIX

### Incorporating Biological Assumptions

From equation (11), optimal body size at metamorphosis under the arithmetic mean assumptions is given by

$$\lambda[g(T_R) - g(T_E)] + \frac{dE(W(T))}{dT}\frac{1}{E(W(T))} + \frac{dC(T_R)}{dT}\frac{1}{C(T_R)} = 0. \tag{A1}$$

The $E'/E$ term represents the relative gain in fitness, as a function of $T$. By the chain rule of calculus and by substituting equation (3),

$$\frac{dE(W(T))}{dT} = \frac{dE}{dW}\frac{dw}{dt} = \frac{dE}{dW}rW\left(1 - \frac{W}{k}\right). \tag{A2}$$

Under the assumption in equation (4),

$$\frac{dE(W(T))}{dT}\frac{1}{E(W(T))} = \begin{cases} \dfrac{\beta rW\left(1 - \frac{W}{k}\right)}{W - W_C} & \text{when } W > W_C, \\ 0 & \text{otherwise.} \end{cases} \tag{A3}$$

The $C'/C$ term represents the relative change in offspring value due to seasonal time constraints on reproduction. Under the assumption in equation (5),

$$\frac{dC(T_R)}{dT} \times \frac{1}{C(T_R)} = -\frac{\alpha}{T_C - T_R}. \tag{A4}$$

Assuming that $g(t) = \phi Z(t)$, where $\phi$ is disturbance frequency and $Z(t)$ is a probability distribution describing the timing of disturbance events within a season (assumed later to be a normal distribution), equation (A1) becomes

$$\lambda \phi [Z(T_R) - Z(T_E)] = \frac{\alpha}{T_C - T_R} - \frac{\beta rW\left(1 - \frac{W}{k}\right)}{W - W_C}. \tag{A5}$$

The geometric mean form (eq. [17]) can be treated in the same way, and the result differs only in the $\lambda$ term.

## Literature Cited

Abrams, P. A., and L. Rowe. 1996. The effects of predation on the age and size of maturity of prey. Evolution 50: 1052–1061.

Abrams, P. A., O. Leimar, S. Nylin, and C. Wiklund. 1996. The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. American Naturalist 147:381–395.

Airoldi, L. 2000. Effects of disturbance, life histories, and overgrowth on coexistence of algal crusts and turfs. Ecology 81:798–814.

Bradford, M. J., and D. A. Roff. 1993. Bet hedging and the diapause strategies of the cricket *Allonemobius fasciatus.* Ecology 74:1129–1135.

———. 1997. An empirical model of diapause strategies of the cricket *Allonemobius socius.* Ecology 78:442–451.

Chesson, P. L. 1994. Multispecies competition in variable environments. Theoretical Population Biology 45: 227–276.

Christensen, N. L. 1985. Shrubland fire regimes and their evolutionary consequences. Pages 86–100 *in* S. T. A. Pickett and P. S. White, eds. The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Closs, G. P., and P. S. Lake. 1996. Drought, differential mortality and the coexistence of a native and an introduced fish species in south east Australian intermittent stream. Environmental Biology of Fishes 47:17–26.

Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. Journal of Theoretical Biology 12: 119–129.

———. 1970. A theoretical model for the optimal timing of diapause. American Naturalist 104:389–400.

———. 1971. Maximizing final yield when growth is limited by time or by limiting resources. Journal of Theoretical Biology 33:299–307.

Czarnołęski, M., and J. Kozłowski. 1998. Do Bertalanffy's growth curves result from optimal resource allocation? Ecology Letters 1:5–7.

Danforth, B. N. 1999. Emergence dynamics and bet hedging in a desert bee, *Perdita portalis.* Proceedings of the Royal Society of London B, Biological Sciences 266: 1985–1994.

Day, T., and P. D. Taylor. 1997. Von Bertalanffy's growth equation should not be used to model age and size at maturity. American Naturalist 149:381–393.

Ellner, S. P. 1985a. ESS germination strategies in randomly varying environments. I. Logistic-type models. Theoretical Population Biology 28:50–79.

———. 1985b. ESS germination strategies in randomly varying environments. II. Reciprocal yield-law models. Theoretical Population Biology 28:80–116.

Fogel, M. M., and L. Duckstein. 1969. Point rainfall frequencies in convective storms. Water Resources Research 5:1229–1237.

Gillespie, J. H. 1977. Natural selection for variances in offspring numbers: a new evolutionary principle. American Naturalist 111:1010–1013.

Gotthard, K., S. Nylin, and C. Wiklund. 1999. Seasonal plasticity in two satyrine butterflies: state-dependent decision making in relation to daylength. Oikos 84: 453–462.

Grimm, N. B., and S. G. Fisher. 1989. Stability of periph-

yton and macroinvertebrates to disturbance by flash floods in a desert stream. Journal of the North American Benthological Society 8:293–307.

Hairston, N. G., Jr., and W. R. Munns, Jr. 1984. The timing of copepod diapause as an evolutionarily stable strategy. American Naturalist 123:733–751.

Harper, J. L. 1977. Population biology of plants. Academic Press, New York.

Houston, A. I., J. M. McNamara, and J. M. C. Hutchinson. 1993. General results concerning the trade-off between gaining energy and avoiding predation. Philosophical Transactions of the Royal Society London B, Biological Sciences 341:375–397.

Huston, M. 1979. A general model of species diversity. American Naturalist 113:81–101.

Hutchinson, G. E. 1961. The paradox of the plankton. American Naturalist 95:137–145.

Iwasa, Y., and S. A. Levin. 1995. The timing of life history events. Journal of Theoretical Biology 172:33–42.

Johansson, F., and L. Rowe. 1999. Life history and behavioral responses to time constraints in a damselfly. Ecology 80:1242–1252.

John, K. R. 1964. Survival of fish in intermittent streams of the Chiricahua Mountains, Arizona. Ecology 45: 112–119.

King, D., and J. Roughgarden. 1982a. Graded allocation between vegetative and reproductive growth for annual plants in growing seasons of random length. Theoretical Population Biology 22:1–16.

———. 1982b. Multiple switches between vegetative and reproductive growth in annual plants. Theoretical Population Biology 21:194–204.

Kozłowski, J., and R. G. Weigert. 1986. Optimal allocation of energy to growth and reproduction. Theoretical Population Biology 29:16–37.

———. 1987. Optimal age and size at maturity in annuals and perennials with determinate growth. Evolutionary Ecology 1:231–244.

Lacey, E. P., L. Real, J. Antonovics, and D. G. Heckel. 1983. Variance models in the study of life histories. American Naturalist 122:114–131.

Lavorel, S., and P. L. Chesson. 1995. How species with different regeneration niches coexist in patchy habitats with local disturbances. Oikos 74:103–114.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Ludwig, D., and L. Rowe. 1990. Life-history strategies for energy gain and predator avoidance under time constraints. American Naturalist 135:686–707.

Lytle, D. A. 2000a. Biotic and abiotic effects of flash flooding in a montane desert stream. Archiv für Hydrobiologie 150:85–100.

———. 2000b. Disturbance regimes and life history evolution. Ph.D. diss. Cornell University, Ithaca, N.Y.

MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. American Naturalist 101:377–385.

McEvoy, P. B., N. T. Rudd, S. C. Cox, and M. Huso. 1993. Disturbance, competition, and herbivory effects on ragwort *Senecio jacobaea* populations. Ecological Monographs 63:55–75.

Meffe, G. K. 1984. Effects of abiotic disturbance on coexistence of predator-prey fish species. Ecology 65: 1525–1534.

Minckley, W. L., and G. K. Meffe. 1987. Differential selection by flooding in stream-fish communities of the arid American southwest. Pages 93–104 *in* W. J. Matthews and D. C. Heins, eds. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

Moreira, G. R. P., and B. L. Peckarsky. 1994. Multiple developmental pathways of *Agnetina capitata* (Plecoptera: Perlidae) in a temperate forest stream. Journal of the North American Benthological Society 13:19–29.

Newman, R. A. 1989. Developmental plasticity of *Scaphiopus couchii* tadpoles in an unpredictable environment. Ecology 70:1775–1787.

Nylin, S., and K. Gotthard. 1998. Plasticity in life-history traits. Annual Review of Entomology 43:63–83.

Peckarsky, B. L., C. A. Cowan, M. A. Penton, and C. Anderson. 1993. Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. Ecology 74:1836–1846.

Peckarsky, B. L., B. W. Taylor, A. R. McIntosh, M. A. McPeek, and D. A. Lytle. 2001. Variation in mayfly size at metamorphosis as a developmental response to risk of predation. Ecology 82:740–757.

Philippi, T. 1993. Bet-hedging germination of desert annuals: beyond the first year. American Naturalist 142: 474–487.

Pickett, S. T. A., and P. S. White. 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York.

Richter, B. D., J. V. Baumgartner, J. Powell, and D. P. Braun. 1996. A method for assessing hydrological alteration within ecosystems. Conservation Biology 10: 1163–1174.

Rowe, L., and D. Ludwig. 1991. Size and timing of metamorphosis in complex life cycles: time constraints and variation. Ecology 72:413–428.

Rowe, L., D. Ludwig, and D. Schluter. 1994. Time, condition, and the seasonal decline of avian clutch size. American Naturalist 143:698–722.

Runkle, J. R. 2000. Canopy tree turnover in old-growth

mesic forests of eastern North America. Ecology 81: 554–567.

Sasaki, A., and S. Ellner. 1995. The evolutionarily stable phenotype distribution in a random environment. Evolution 49:337–350.

Semlitsch, R. D., and H. M. Wilbur. 1988. Effect of pond drying time on metamorphosis and survival in the salamander *Ambystoma talpoideum*. Copeia 1988:978–983.

Taylor, B. W., C. R. Anderson, and B. L. Peckarsky. 1998. Effects of size at metamorphosis on stonefly fecundity, longevity, and reproductive success. Oecologia (Berlin) 114:494–502.

Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems 1:511–523.

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.

Venable, D. L., and J. S. Brown. 1988. The selective interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. American Naturalist 131:360–384.

Venable, D. L., and L. Lawlor. 1980. Delayed germination and dispersal in desert annuals: escape in time and space. Oecologia (Berlin) 46:272–282.

Werner, E. E., and B. R. Anholt. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. American Naturalist 142:242–272.

Wilbur, H. M. 1987. Regulation of structure in complex systems: experimental temporary pond communities. Ecology 68:1437–1452.

Wootton, J. T. 1998. Effects of disturbance on species diversity: a multitrophic perspective. American Naturalist 152:803–825.

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