FLASH FLOODS AND AQUATIC INSECT LIFE-HISTORY EVOLUTION: EVALUATION OF MULTIPLE MODELS

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Abstract. In disturbance ecology there is a tension between ecological and evolutionary viewpoints, because while disturbances often cause mortality in populations (an ecological effect), populations may also evolve mechanisms that ameliorate mortality risk (an evolutionary effect). Flash floods cause high mortality in the juvenile aquatic stage of desert stream insects, but these ecological effects may be mitigated by the evolution of life-history strategies that allow the terrestrial adult stage to avoid floods. Life-history theory predicts that, to balance trade-offs between juvenile growth and mortality risk from floods, (1) most individuals should emerge before the peak of the flood season, (2) optimal body size at emergence should decline as flood probability increases, and (3) a second decline in body size at emergence should occur as the reproductive season ends. These predictions were tested with data on body mass at and timing of emergence of the caddisfly *Phylloicus aeneus* measured in three montane Chihuahuan Desert (Arizona, USA) streams over two years. *P. aeneus* that had not reached the adult stage were eliminated from site-years that experienced flash floods, suggesting that timing of emergence is an important fitness component. On average 86% of emergence occurred before the long-term (~100 yr) mean arrival date of the first seasonal flood, supporting prediction 1. The presence of two consecutive declines in body mass at emergence in most site-years was congruent with predictions 2 and 3. To test whether the two declines were associated with increasing flood probability and end of the reproductive season, respectively, maximum-likelihood methods were used to compare five body-size models: a null model that contains no parameters related to flood regime or reproductive season, a seasonal model that incorporates a reproductive time constraint, and three disturbance models that incorporate both reproductive time constraints and flood dynamics. The disturbance models outperformed the other models, suggesting that at least some of the body-mass pattern was influenced by flood dynamics. The timing of the first flood of the season was the most important determinant of observed emergence patterns. Overall, this study demonstrates that aquatic insects can compensate for flash floods by using state-dependent emergence strategies that are synchronized with long-term flood dynamics.

Key words: Akaike's information criterion; body size; Chihuahuan Desert (USA) stream insects; disturbance; flash flooding; life-history evolution; maximum likelihood; model evaluation; phenotypic plasticity; Phylloicus aeneus; state-dependent strategy.

INTRODUCTION

A recurring problem in ecology is understanding how species diversity and abundance are maintained, or even enhanced, in systems where organisms experience high mortality from disturbances (MacArthur and Levins 1967, Connell 1978, Pickett and White 1985, Collins 2000). Ecologically, disturbance regimes affect diversity and abundance patterns through local exclusion of taxa (Meffe 1984), mediation of competitor species (Hemphill and Cooper 1983, Denslow 1985, Airoldi 2000), alteration of trophic structure (Wootton et al. 1996, Wootton 1998), and exclusion of taxa from regional species pools (Diamond 1975, Drake 1991,

McPeek and Brown 2000). Evolutionarily, disturbance regimes alter the organisms themselves by changing population gene frequencies (Vrijenhoek 1985, Vrijenhoek et al. 1985) and by influencing the evolution of life-history strategies (Bradford and Roff 1993, 1997, Philippi 1993*a, b*), behaviors (Meffe 1984, Lytle 1999), and morphologies (Gill 1981, Christensen 1985). There is a tension between ecological and evolutionary viewpoints because while disturbances certainly produce measurable ecological effects, such as mortality within populations, adaptive evolution in response to disturbance regimes is expected to ameliorate or even eliminate some of these effects (Cohen 1966, Iwasa and Levin 1995, Lytle 2001). However, because the timing (date of occurrence within a season), predictability (variance in timing), frequency (expected number of disturbances per season), and severity (expected mortality) of disturbances may vary from year to year it is not surprising that even organisms with adaptations for

surviving some disturbances experience mortality from events that occur outside normally observed parameter values (Poff 1992, Turner et al. 1997, 1998). For this reason the magnitude of disturbance-regime parameters may determine when disturbances control species diversity and abundance through ecological mechanisms, and when disturbances drive the evolution of features that allow taxa to persist in disturbance-prone systems.

The interplay between mortality from disturbances and adaptation to disturbances is exemplified by seasonal flash floods in desert streams. While flash floods can cause >90% mortality in the juvenile stages of aquatic insects (Gray 1981, Molles 1985, Grimm and Fisher 1989, Lytle 2000a), scoured stream reaches are rapidly recolonized by individuals in their aerial adult stage (Williams and Hynes 1976, Gray and Fisher 1981, Fisher et al. 1982, Boulton et al. 1992). Because the timing of emergence into the adult stage relative to the timing of flash floods largely determines the probability of surviving to recolonize (Gray 1981, Lytle 2001), timing of emergence may play a critical role in allowing many insect taxa to persist in flood-prone streams. Thus, life-history events such as timing of emergence may be an important target of natural selection in flood-prone systems.

Models have been developed to investigate how environmental variability affects the evolution of life-history traits such as bet-hedging strategies (Cohen 1966, Venable and Lawlor 1980, Sasaki and Ellner 1995), diapause timing (Cohen 1970, Hairston and Munns 1984), and size at and timing of maturation (Cohen 1971, King and Roughgarden 1982, Kozłowski and Weigert 1987, Ludwig and Rowe 1990, Rowe and Ludwig 1991). The ''seasonal time constraint'' theory developed by Rowe and colleagues is particularly useful for understanding aquatic-insect emergence strategies because it shows how individuals maximize fitness by maturing according to a state-dependent mechanism. The switch from growth to reproductive stage depends on both current body size and the amount of time remaining in the season for reproduction, which is determined by the onset of winter or other unfavorable environmental conditions. Adding parameters that specify disturbance timing, predictability, frequency, and severity to the seasonal time-constraint model produces several novel predictions (Lytle 2001). First, when disturbance regimes are sufficiently predictable, frequent, and severe, most individuals should emerge from the disturbance-prone habitat before the height of the disturbance season. For taxa that do not grow significantly during the adult stage (many aquatic insects in the Ephemeroptera, Trichoptera, and Diptera), individuals will benefit by using this stage as a refuge from disturbances, but they pay an opportunity cost by not feeding. Second, because these costs and benefits are influenced by body size, larger juveniles are expected to emerge early and avoid mortality from floods while smaller juveniles are expected to risk more of

the flood season in order to continue growing. Thus, when there is variation in juvenile body size within a population, body size at emergence should decline during the season as disturbance probability increases. Third, with some disturbance regimes there is a finite probability that a disturbance might not occur during a given year. In this case the optimal strategy for smaller individuals is to risk the entire disturbance season in order to continue growing and then emerge towards the end of the reproductive season—a risky strategy with a high payoff. In years with no disturbances, this strategy will produce a second decline in body size at emergence associated with the end of the reproductive season, similar to that predicted by seasonal time-constraint models. In years when disturbances do occur these individuals will suffer high mortality.

Is it reasonable to expect optimal emergence strategies to evolve?

In order to maximize fitness using these optimal emergence strategies, organisms must be able to assess both the time of the season and their own state (body size, in most models). Furthermore, for strategies to evolve to optima there must be (or have been) heritable variation in the traits governing these sensory mechanisms. For insects, many life-history changes such as pupation or diapause are under hormonal control and are initiated when a sensory threshold, such as critical day length or body size, is exceeded (Nijhout 1994). Most insects use photoperiod to mark seasonal progression (Saunders 1981, Danks 1994, Nylin and Gotthard 1998), and some taxa are sensitive to small differences in day length (Nijhout 1994). The critical day length used to initiate life-history changes can vary widely both among and within populations, and these differences are heritable as quantitative characters in some taxa (Danilevskii 1965, Nylin et al. 1994, Tammaru et al. 1999). Insects are also capable of assessing body size via specialized stretch receptors or other means (Nijhout 1994), and some possess sharply defined critical body sizes for molting, pupation, or diapause (Nijhout 1981). Like critical day length, critical body size can also be heritable (e.g., body size at diapause in cricket populations along a cline in season length [Mousseau and Roff 1989]). Critical day length and critical body size are not fixed within individuals, however, and often vary in response to environmental cues (such as food availability) or to each other (Nijhout 1981, Tauber et al. 1986). These interactions among genetically determined threshold traits and environmental conditions can produce state-dependent life-history strategies, which in turn produce the phenotypic plasticity in body size and timing of maturation so commonly observed in insects (Nylin and Gotthard 1998). Thus, the emergence strategies predicted by state-dependent optimization models may occur in nature as the expression of quantitatively heritable traits mediated by environmental conditions.

Multiple competing models

This study compared five competing models (sensu Hilborn and Mangel 1997) that make different assumptions about how seasonal time constraints and disturbance regimes affect body size at emergence. The results were used to address three questions concerning the importance of these ecological factors: (1) Do seasonal time constraints on reproduction significantly affect patterns of body size at emergence? (2) Do flash-flood regimes affect patterns of body size at emergence? (3) If flash-flood regimes play a significant role in generating body size at emergence patterns, which components of the flood regime are the most important?

STUDY SYSTEM

Study sites

Streams in the arid southwestern United States and northern Mexico experience disturbances from flash floods generated by highly localized convective thunderstorms, and it is common for one drainage to experience flash flooding while adjacent drainages remain at base flow (Molles 1985, Lytle 2000b). Flash floods occur suddenly, and they scour the stream substrate as well as cause mortality in excess of 90% for most invertebrate taxa (Gray 1981, Molles 1985, Grimm and Fisher 1989, Lytle 2000a). Study sites were located in three montane Chihuahuan Desert streams (in the Chiricahua Mountains of southeastern Arizona, USA: North Fork Cave Creek [NFC], East Turkey Creek [ETC], West Turkey Creek [WTC]), were at similar elevations (1935 m, 1925 m, and 1900 m, respectively), and had small drainage areas (5.4, 4.7, and 9.1 km², respectively). Flash-flood timing and predictability were characterized using long-term rainfall data (~100-yr period from three gauging stations), and flood frequency was measured directly in the study streams using five years of tracer particle data (Table 2; analysis described in Lytle 2000b).

Study organism

Phylloicus aeneus (Banks) is a case-building caddisfly in the neotropical family Calamoceratidae. Populations in Arizona, USA, require approximately a year to mature (Wiggins 1996) suggesting that all individuals encounter at least part of the monsoon flood season. Deciduous leaf litter serves both as a primary food source and as a case-building material (Wiggins 1996). Populations are restricted to stream reaches below ~2200 m in elevation by the availability of deciduous leaf litter, and above ~1500 m by stream permanence. After completing five larval instars, individuals pupate for 15 ± 1.3 d in stream margins (Lytle 2000b). Females, which are approximately twice as large as males, emerge with 100–800 fully chorionated eggs (Lytle 2000b), suggesting ovarian diapause does not occur. Eggs are oviposited in a single gelatinous mass (*personal observation*). Maximum adult lifespan is at least 7 d, and adults have mouthparts capable of ingesting water or nectar (*personal observation*). Although *P. aeneus* is reported to range from the southwestern United States down to Costa Rica, the Arizona populations used in this study may represent an undescribed species (Bowles and Flint 1997).

Observed emergence patterns: methods.—Body mass at emergence and timing of emergence of *Phylloicus aeneus* were measured in all three sites in 1997 and 1998. The site-years were considered spatially independent because the drainages are unconnected, and temporally independent because winter runoff and spring leaf abscission changed the distribution of detritus between years (John 1964, also see *Results*). At each site pupae were collected from four pools >2 m in length at 3-d intervals (1997) or at 7-d intervals (1998) for the duration of the emergence season (June–August) and kept in tanks (aerated stream water) until emergence. Adults were fixed in 95% ethanol and frozen (1997) or preserved directly in 95% ethanol (1998), and emergence date was recorded. To measure body mass, adults were dried for 24 h at 60°C and weighed.

Because the availability of deciduous detritus affects *P. aeneus* growth rates (Lytle 2000b), per capita resource abundance (square centimeters deciduous detritus per larva) was measured in all site-years. At the beginning of the emergence season, each of the four pools per study stream was divided into 0.125-m² quadrats, and a point estimate of detritus type (deciduous, coniferous, woody debris, or fine organic) was made within each quadrat. Total numbers of final-instar larvae per pool were estimated in 1996–1998 by subsampling (0.013-m², which is 1/10 of a quadrat) 8–40 of the deciduous-containing quadrats per pool.

Observed emergence patterns: results.—*Timing of emergence.*—A total of 683 pupae were collected from five site-years and eclosed into adults (ETC-1998 had no *P. aeneus*). Of these, 42% were females and 58% were males, indicating a male-biased sex ratio. Congruent with disturbance-model prediction 1, most individuals emerged prior to the long-term mean date of the first monsoon flood: 97% in NFC-1997 and ETC-1997, 89% in WTC-1997, 65% in WTC-1998, and 86% overall (NFC-1998 experienced a flood before this date) (N = four site-years, t = 4.112, P = 0.0261). In most site-years two consecutive emergence groups were observed (Fig. 1).

Larval populations and flash floods.—Numbers of final-instar larvae present at each site-year were highest at the beginning of the emergence season in early June and declined as the season progressed, presumably due to emergence (Fig. 2). Abundances of earlier instars (quantified in 1997 only) declined over the course of the season, a pattern consistent with a univoltine life history. Significant flash floods (>50% bed movement) occurred in most site-years (Fig. 2). These flash floods removed nearly 100% of any larvae that remained in

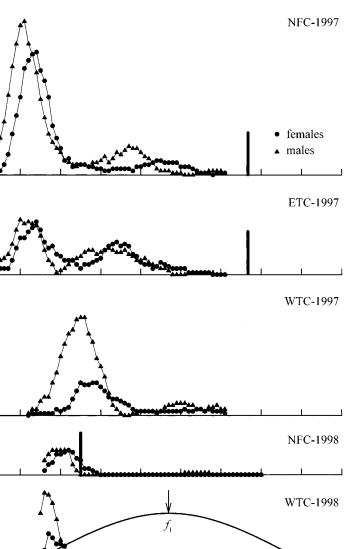FIG. 1. Patterns of *Phylloicus aeneus* emergence at the five site-years. Data are from 1997 and 1998 at sites in three montane Chihuahuan Desert streams (Arizona, USA): NFC = North Fork Cave Creek, ETC = East Turkey Creek, and WTC = West Turkey Creek. Solid bars denote occurrences of flash floods causing >50% movement of substrates. The solid line (bottom panel) gives the probability of f_1, the first monsoon-season flood (not shown to scale); T_c marks the critical time for reproduction.

the stream. Late floods (occurring after f_1, the first monsoon-season flash flood of the year) occurred on 17 August in NFC-1997 and ETC-1997 and on 25 August in ETC-1996, but few final-instar larvae remained in the streams by this time.

The occurrence of flash floods as well as their timing appeared to affect numbers of final-instar larvae in sub-sequent years. Initial numbers of final-instar larvae were relatively high following years with no floods or floods that occurred prior to f_1, and numbers of final-instar larvae were relatively low following years with floods that occurred after f_1 (Fig. 2). Possibly due to the late 17 August flood in ETC-1997, no final-instar larvae were found the following year in ETC-1998.
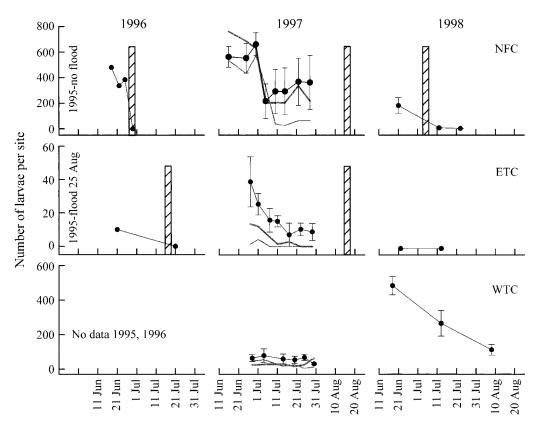
FIG. 2. Larval abundance at the three study sites, 1996–1998. Final instars (instar V, solid black lines) were counted in all years, other instars (IV, thick gray lines; III, thin gray lines; earlier instars not observed) were counted in 1997. Hatched bars denote flash floods causing >50% movement of substrates. Floods caused close to 100% loss of individuals. For explanation of study-site codes see Fig. 1.

Resource abundance.—Per capita resource abundance varied significantly among site-years (Fig. 3; ANOVA, $F = 35.7$, df = 5, 18, $P < 0.0001$). ETC-1998 contained no deciduous detritus or larvae at all and was excluded from further study. At all three sites, detritus abundance changed significantly between years (Tukey-Kramer multiple comparisons, $P < 0.01$), lending support to the assumption that sites are independent among years because of annual changes in detritus abundance.

Body mass at emergence.—Body mass at emergence was highly variable, ranging from 5 to 18 mg in males, and from 11 to 34 mg in females (Fig. 4). Controlling for differences in resource abundance among site-years, female mean body mass was significantly larger than male mean body mass (Fig. 5; ANCOVA, $F = 141.1$, df = 1, 7, $P < 0.0001$). Mean body mass was positively correlated with resource abundance for both males and females (Fig. 5; ANCOVA, $F = 23.79$, df = 1, 7, $P = 0.0018$, $R^2 = 0.96$), suggesting that growth rates were higher in site-years with more deciduous leaf litter. Two consecutive declines in body mass were visible in most site-years for males and females (Fig. 4), a result congruent with the predictions of the disturbance model. After dividing each season's data into

an early and a late-emergence group based on Fig. 2 (i.e., making a division midway between the two emergence peaks), simple linear regressions indicated significantly negative body-mass declines in the majority of emergence groups (Fig. 4, Table 1). Although these regressions suggest that declines in body mass were present, they provide no insight into the ecological mechanisms that might be generating declines. For this, the data were analyzed with five models that predict body size at emergence as a function of growth rate, fecundity, seasonal time constraints, and flash-flood regime.

MODELS OF OPTIMAL BODY SIZE AT METAMORPHOSIS

Five models that predict optimal body size (W) as a function of timing of metamorphosis (T) were compared using the observed patterns of *Phylloicus aeneus* body mass at emergence. The models varied in complexity from very simple (no biological parameters) to parameter-rich (growth, seasonal constraints, fecundity, and disturbance regime fully specified).

The five models were derived from a general disturbance model (Lytle 2001: Eq. 12, shown here as Eq. 1). The disturbance model is an extension of Rowe and
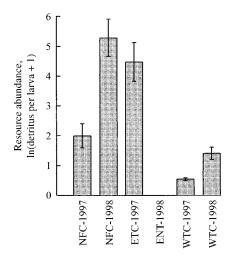
FIG. 3.   Per capita resource abundance (detritus, measured as square centimeters/larva) at the site-years used in this study. Resource abundance was significantly different among site-years. See Fig. 1 for explanation of study-site codes.

Ludwig's (1991) model that predicts how seasonal time constraints on reproduction affect optimal body size at and timing of maturity. See Lytle (2001) and Rowe and Ludwig (1991) for a full treatment of the model's assumptions and derivation. In the disturbance model, optimal body size at emergence (W) is a function of disturbance regime, fecundity, seasonal constraints, and growth rate:

$$
\lambda\phi\left\{\frac{1}{\sigma\sqrt{2\pi}}\exp\left[-\frac{(T_R(T) - f)^2}{2\sigma^2}\right]\right.
$$
$$
\left. - \frac{1}{\sigma\sqrt{2\pi}}\exp\left[-\frac{(T_E(T) - f)^2}{2\sigma^2}\right]\right\}
$$
$$
= \frac{\alpha}{T_c - T_R(T)} - \frac{\beta r W\left(1 - \dfrac{W}{k}\right)}{W - W_C}. \quad (1)
$$

The left side of Eq. 1 represents the relative fitness effects of the flood regime, where λ is flood severity, ϕ is flood frequency, $T_R(T)$ is time of reproduction, $T_E(T)$ is time of emergence from the stream, f is the mean date of flash-flood occurrence, and σ is the standard deviation around this mean. Emergence at time $T_E(T)$ occurs after individuals complete the larval growth stage at time T and go through pupation for a fixed period ρ, so that $T_E(T) = T + \rho$. Similarly, oviposition at time T_R occurs after the adult stage ξ is completed, so that $T_R(T) = T + \rho + \xi$. This form of the model implicitly assumes that mortality in the adult stage is negligible relative to mortality from disturbances in the larval and pupal stages. The first term on the right side of Eq. 1 represents the relative fitness effects of seasonal time constraints on reproduction, where T_c denotes the date the reproductive season ends and α is a rate parameter that influences how rapidly

T_c approaches. The second term on the right side of Eq. 1 represents the relative fitness effects of growth rate, where W is body size at emergence, k is maximum body size, W_c is minimum body size for reproduction, r is growth rate, and β is a parameter that scales the relationship between body size and fecundity. After substituting suitable parameter values (Table 2), Eq. 1 can be solved for W in terms of T to give optimal body size at metamorphosis as a function of time of metamorphosis.

Null model

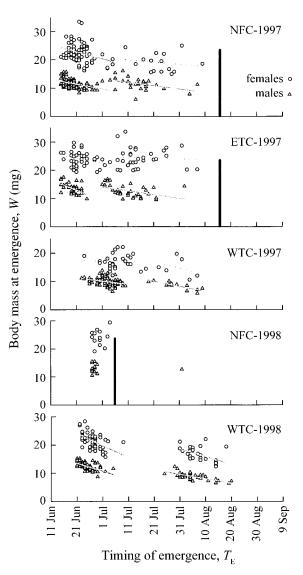The first model considered is the simplest because it contains no information about disturbance regime,

FIG. 4.   Body mass at emergence as a function of timing of emergence at the five site-years. Solid bars denote occurrences of flash floods. Solid lines denote significantly negative regression slopes; dotted lines were nonsignificant. See Table 1 for regression-analysis details.

TABLE 1. Statistics for linear regressions in Fig. 4; Slopes in bold are significant ($\alpha = 0.05$)

Site-year†	Emergence group	Sex	N‡	Slope	1 SE
NFC-1997	early	F	76	**−0.250**	0.089
		M	90	**−0.168**	0.040
	late	F	15	−0.078	0.122
		M	26	**−0.117**	0.052
ETC-1997	early	F	37	−0.151	0.092
		M	34	**−0.370**	0.107
	late	F	31	−0.031	0.080
		M	33	**−0.133**	0.048
WTC-1997	early	F	28	−0.054	0.083
		M	75	**−0.113**	0.041
	late	F	6	−0.228	0.288
		M	13	**−0.176**	0.034
WTC-1998	early	F	52	**−0.420**	0.101
		M	71	**−0.285**	0.050
	late	F	30	**−0.277**	0.080
		M	37	**−0.153**	0.026

† NFC = North Fork Cave Creek, ETC = East Turkey Creek, WTC = West Turkey Creek; all three sites are montane Chihuahuan Desert streams (Arizona, USA).
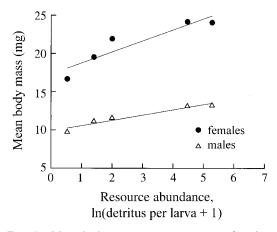
‡ Number of adults in the sample.

FIG. 5. Mean body mass at emergence as a function of resource abundance (detritus, measured in units of cm²/larva). For both males and females, body mass at emergence was significantly positively associated with resource abundance.

seasonal constraints, growth, or mortality. When $\lambda = 0$ the left side of Eq. 1 drops out, signifying that disturbances do not affect fitness. Similarly, when $\alpha = 0$ the first term on the right side drops out, signifying that seasonal time constraints do not affect fitness. Solving for W,

$$W = k. \qquad (2)$$

The null model assumes that the optimal emergence strategy is to always emerge at a constant maximum body size k (Fig. 6). A single body size may be favored for a variety of reasons, including size-selective pre-dation (Brooks and Dodson 1965), competition (Hutchinson and MacArthur 1959), physiological constraints on metabolic rates (Hamilton 1961), or tradeoffs between growth rate and other life-history parameters (Roff 1981). Under the assumption of normally distributed errors the maximum-likelihood estimate of k is the mean of W, and s (in Eq. 4) is the standard error about this mean (Edwards 1992). The null model does not incorporate any information about disturbance regime, seasonal time constraints on reproduction, growth rates, or other biological parameters. Because of this simplicity, the null model was used to test the null hypothesis that no seasonal decline in body size occurred.

TABLE 2. Summary of variables and parameters used in the models.

Variable	Definition (units)†	Parameter used and/or data source
W	Body mass at maturity (mg)	Measured directly (1997 and 1998 field data)
W_c	Minimum body mass necessary for maturation (mg)	11 mg (females), 5 mg (males); smallest adults recorded in 1997 and 1998 data
k	Maximum body mass (mg)	34 mg (females), 18 mg (males); largest adults recorded in 1997 and 1998 data
r	Larval growth rate	Estimated from models
T	Timing of metamorphosis (D)	$T_E - \rho$
T_E	Timing of emergence (D)	Measured directly (1997 and 1998 field data)
T_R	Timing of reproduction (D)	$T_E + \xi$
T_c	Critical time for reproduction (D)	246 (3 September); latest known capture date of an adult
f	Mean date of all monsoon floods (D)	225 (13 August); Lytle 2000*b*
f_1	Mean date of 1st monsoon flood (D)	209 (28 July); Lytle 2000*b*
f_2	Mean date of last monsoon flood (D)	241 (29 August); Lytle 2000*b*
σ	Standard deviation of f, f_1 and f_2 (d)	30 d; Lytle 2000*b*
ϕ	Flood frequency (no. floods/yr)	0.8; Lytle 2000*b*
λ	Flood severity (mortality rate)	0.95; Lytle 2000*a*
ρ	Length of pupal stage (d)	15 d; Lytle 2000*b*
ξ	Length of adult stage (d)	>7 d; also estimated from models
α	Parameter scaling T_c	0.1; chosen to produce a decreasing curve near T_c
β	Parameter that scales body mass − fecundity relationship	1.0; relationship is linear for females (Lytle 2000*b*), assumed to be linear for males
s	Standard deviation of residuals (mg)	Estimated from models

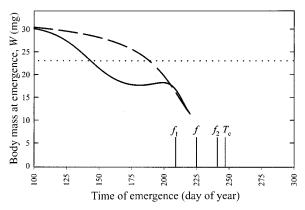† D = day number (in a year); equivalent to the Julian day.

FIG. 6. Summary of qualitative model predictions and major components of the disturbance regime. Parameters values from Table 2 (females), $\xi = 10$ d, and $r = 0.01$. The disturbance parameters f, f_1, and f_2 denote, respectively, the long-term mean dates of all monsoon-season floods, the first flood only, and the last flood only. The shaded area represents the probability distribution of f_1. T_c denotes the critical time for reproduction. The null model (dotted line) predicts a constant optimal body size at emergence, although the y-intercept may vary. The seasonal model (dashed line) predicts a steady decline in body size as T_c approaches, although the steepness of the curve may vary. The disturbance models (solid line) predict declines in body size associated with disturbance regime (f, f_1, or f_2 depending on the model; fixed first/last disturbance model shown here) and with T_c.

Seasonal model

Second, I constructed a model that incorporates larval growth rate, fecundity, and seasonal time constraints (but not disturbances). This model is similar to the single-habitat growth model proposed by Rowe and Ludwig (1991), and it generally predicts that body size at emergence should decline as the time constraint on reproduction, T_c, approaches (Fig. 6). The seasonal model was obtained from Eq. 1 by setting $\lambda = 0$, which removed all disturbance-related parameters from the model:

$$\frac{\alpha}{T_c - (T + \rho + \xi)} = \frac{\beta r W \left(1 - \dfrac{W}{k}\right)}{W - W_c}. \tag{3}$$

Solving for W and using the positive root gives W as a function of T, the optimal timing of metamorphosis. Three parameters (r, ξ, and s) were estimated for each data set using maximum likelihood. All other parameter values were obtained from field data or the literature (Table 2).

Mean disturbance model

Third, I developed a disturbance model by specifying the flood-related parameters in Eq. 1 in addition to the growth, fecundity, and seasonal time constraints present in the seasonal model. Flood timing was specified with the mean date of all flash floods ($f = 225$), rather than the dates of the first and last floods. The purpose

of this model was to test whether adding information about the overall flood regime could explain variation in the body size data that could not be explained by the seasonal model alone. Three parameters (r, ξ, and s) were estimated for each data set using maximum likelihood. All other parameter values were obtained from field data or the literature (Table 2).

Fixed first/last disturbance model (Fig. 6)

Fourth, I constructed a model by parameterizing Eq. 1 with the timings of the first and last floods of the monsoon season, rather than the mean date of all flood events combined. This was done by replacing the mean date of disturbance in Eq. 1 with the mean date of the first disturbance of the season (f_1, which replaced f in the T_E term) and the last disturbance of the season (f_2, which replaced f in the T_R term). This model assumes the first and last flash floods are more important than other floods (Lytle 2000b). There is evidence for this; the first flood of the season, in addition to removing 95% of *P. aeneus* larvae, removes almost all of the deciduous detritus that late-instar larvae use as a food and case-building material (Lytle 2000a). Similarly, the last flood of the season marks the time after which oviposited eggs face no flood mortality. In this model the disturbance-related parameters ($f_1, f_2, \phi, \lambda, \sigma$) were fixed at specific values (Table 2). All non-disturbance parameter values were the same as those used in the seasonal model. Thus, the fixed-disturbance model includes information about growth rate, seasonal time constraints, and fecundity, in addition to information about disturbance regime. Three parameters (r, ξ, and s) were estimated from the data using maximum likelihood.

Variable first/last disturbance model

Fifth, I developed a model that also allowed flood frequency (ϕ) to vary among site-years, rather than remaining fixed at the value estimated from long-term rainfall data. The purpose of this was to see if using a flexible, parameter-rich model where the disturbance regime is allowed to vary freely could provide a better fit to the data. Over-fitting of the model was a potential problem here, so the model's parameter estimates were tested using external data. The timing of the first and last floods covary characteristically with flood frequency, so f_1 and f_2 were allowed to vary as functions of ϕ (these functions were derived from Eqs. 1–3 in Lytle [2000b: chapter 2]). Because of these interrelationships, only ϕ needed to be estimated for each site-year using maximum likelihood. The variable first/last model was the most parameter-rich of the models, because four of them (ϕ, r, ξ, and s) were estimated for each data set.

MODEL COMPARISONS

Methods

Fit of models to data.—A normal-based likelihood function (Edwards 1992, Hilborn and Mangel 1997)

TABLE 3. Females: Maximum-likelihood parameter estimates (MLE), negative log-likelihood (*L*), and bias-corrected Akaike information criterion (AIC) model comparisons.

Model	Site-year‡	*N*§	r_{MLE}	ξ_{MLE} (d)	$\phi_{MLE}\|$ (yr^{-1})	$k_{MLE}\|$ (mg)	s_{MLE} (mg)
					Parameter estimates†		
Null	NFC-1997	91	⋯	⋯	⋯	21.93	3.549
	ETC-1997	68	⋯	⋯	⋯	24.16	3.003
	WTC-1997	34	⋯	⋯	⋯	16.67	2.767
	NFC-1998	13	⋯	⋯	⋯	24.06	2.704
	WTC-1998	82	⋯	⋯	⋯	19.53	3.597
Seasonal and mean disturbance	NFC-1997	91	0.0021	0	⋯	[34]	3.225
	ETC-1997	68	0.0032	0	⋯	[34]	3.512
	WTC-1997	34	0.0013	0	⋯	[34]	2.646
	NFC-1998	13	0.0028	0	⋯	[34]	2.771
	WTC-1998	82	0.0020	0	⋯	[34]	2.499
Fixed first/last disturbance	NFC-1997	91	0.0063	15	[0.8]	[34]	3.227
	ETC-1997	68	0.0097	12	[0.8]	[34]	3.176
	WTC-1997	34	0.0034	19	[0.8]	[34]	2.575
	NFC-1998	13	0.0088	16	[0.8]	[34]	2.759
	WTC-1998	82	0.0059	15	[0.8]	[34]	2.443
Variable first/last disturbance	NFC-1997	91	0.0042	0	0.61	[34]	3.170
	ETC-1997	68	0.0173	21	1.0	[34]	2.935
	WTC-1997	34	0.0051	24	0.92	[34]	2.548
	NFC-1998	13	0.0167	27	1.0	[34]	2.717
	WTC-1998	82	0.0039	9	0.66	[34]	2.375

† Model parameters: *r* = growth rate, ξ = adult life span, φ = flood frequency, *k* = maximum body mass, *s* = standard error of residuals. Variables that do not appear in a particular model are denoted by ellipses.

‡ NFC = North Fork Cave Creek, ETC = East Turkey Creek, WTC = West Turkey Creek; all three sites are montane Chihuahuan Desert streams (Arizona, USA).

§ *N* = no. of females in the site-year.

‖ Values in brackets were assigned rather than estimated with maximum likelihood.

¶ Negative log-likelihood of data given the model.

The bias-corrected Akaike information criterion, $AIC_C = 2L + 2p[N/(N - p - 1)]$, where *p* is the total number of estimated parameters; $\Delta_i = AIC_C$ scaled to smallest value for that data set; rank is from best (1) to worst (4); Δ_i represents the distance from the best-fit model.

was used to measure the quantitative fit of the models to the *Phylloicus aeneus* data. The assumption of normally distributed errors was confirmed by inspection of residual plots. Under each of the five models, negative log-likelihoods (*L*'s) were calculated for the 10 data sets (males and females from five site-years):

$$L\{W|\text{model}\}$$
$$= N\left[\log(s) + \frac{1}{2}\log(2\pi)\right] + \sum_{i=1}^{N} \frac{(W_i - W_{\text{pred}})^2}{2s^2} \quad (4)$$

where each W_i is one of *N* observed body sizes, W_{pred} is body size predicted under a given model, and *s* is the standard deviation of the residual errors. Because females are larger than males, sexes were analyzed separately. Parameters that were not specified a priori in the models were estimated using standard maximum-likelihood techniques (Hilborn and Mangel 1997). Because negative log-likelihoods of independent data sets can be combined additively (Edwards 1992), they were summed for the five site-years to test the overall performance of each model. Models were compared using the bias-corrected Akaike's information criterion (AIC_C), which evaluates models based on both the likelihood of the model given the data and the number of parameters estimated from the data. AIC_C was used

instead of *G* statistics and associated significance tests because some of the models were non-nested. AIC_C values were standardized to Δ_i units by subtracting the AIC_C value of each data set's best-fit model; Δ_i units represent the relative "distance" from the best-fitting model (Burnham and Anderson 1998). All other factors being equal, AIC_C and associated Δ_i units favor more parsimonious models over those with many estimated parameters.

Recovery of reasonable parameter estimates.— Aside from providing a close fit to the data, models must also estimate parameter values that make biological sense. Because resource abundance was measured in each site-year and not used in any of the models and because it is correlated with growth rate (Lytle 2000*b*), it served as an independent data set for the evaluation of the maximum-likelihood estimate (MLE) of *r* (growth rate) values, r_{MLE}. ANCOVA was used to test the hypothesis that r_{MLE} was positively associated with resource abundance (log + 1 transformed) for each model. Because it is known that the adult stage, ξ > 7 d, the ability of a model to consistently recover ξ_{MLE} > 7 served as a heuristic test of its performance. A test of the variable-disturbance model was to see that it recovered flood frequency values close to φ = 0.8 floods/yr.

TABLE 3. Extended.

	Model comparisons#							
	Per site-year				Site-years combined			
L¶	p	AIC_C	Δ_i	Rank	p	AIC_C	Δ_i	Rank
244.283	2	492.706	16.021	4	10	1522.974	74.668	4
171.261	2	346.705	0	1				
82.850	2	170.087	2.467	4				
31.378	2	67.960	0	1				
221.320	2	446.792	63.722	4				
235.671	3	477.616	0.931	2	15	1475.575	27.269	3
181.992	3	370.355	23.650	4				
81.108	3	169.020	1.400	2				
31.692	3	72.047	4.087	3				
191.444	3	389.198	6.128	3				
235.774	3	477.826	1.141	3	15	1456.735	8.429	2
175.064	3	356.505	9.800	3				
80.408	3	167.620	0	1				
31.639	3	71.947	3.987	2				
189.602	3	385.508	2.438	2				
234.111	4	476.685	0	1	20	1448.306	0	1
169.705	4	348.045	1.340	2				
80.048	4	169.479	1.859	3				
31.439	4	75.880	7.920	4				
187.275	4	383.069	0	1				

Results

Null model.—For individual site-years, the null model typically performed either best (no. 1 rank) or worst (no. 4 rank) under AIC_C when compared to other models (Tables 3 and 4). Because it was the most parsimonious of the models, the null model was favored under AIC_C primarily when sample sizes were low (NFC-1998 females and males). Overall, however, the null model had the poorest fit to the data of all the models (rank = 4 for both females and males). The null model lagged behind the best-fit model (the variable first/last model) by 74.7 and 153.3 Δ_i units for females and males, respectively (Tables 3 and 4), indicating that it was not even reasonably close to the best-fit model (<10 units can be considered heuristically close; Burnham and Anderson 1998).

Seasonal model.—For most site-years the seasonal model performed better under AIC_C than the null model, suggesting that adding information about seasonal time constraints explained more of the variation in body size at emergence. It did not perform better than any of the disturbance models (rank = 3 for both females and males; Tables 3 and 4), and it was a distant 27.2 and 18.1 Δ_i units away from the best-fit model. ξ_{MLE} was estimated at 0 d for all site-years, suggesting that the model underestimated adult life-span. Values of r_{MLE} were significantly positively associated with resource abundance, indicating that the model did recover reasonable estimates of growth rate (Table 5, Fig. 7).

Mean disturbance model.—For all 10 data sets, the maximum-likelihood estimate of ξ under the mean disturbance model was 0 d, which made the parameter estimates for this model identical to those of the seasonal model. Because of this, values of r and s were identical to those produced by the seasonal model (Tables 3 and 4), and information about the overall mean date of disturbance did not explain any additional variation in body size relative to the seasonal model. For these reasons, the mean disturbance and seasonal models were treated as identical in further analyses.

Fixed first/last disturbance model.—The fixed first/last model performed consistently better under AIC_C than either the null or seasonal models and better than the variable first/last disturbance model in half the cases (Tables 3 and 4, Fig. 8), suggesting that adding information about the beginning of the flash-flood season explained more of the variation in the body-mass data. In no case did it receive the lowest ranking of the models. The fixed first/last model did not fit the data as well as the variable first/last model (rank = 2 for both females and males), but overall it was only 8.4 and 14.4 Δ_i units away from the variable first/last model, making it the closest contender for best-fit model. It was the best-fit model in 3 out of the 10 data sets. Estimates of ξ averaged 15 d for females and 12 d for male, indicating that the model recovered reasonable parameter estimates. As with the seasonal model, r_{MLE} was positively associated with resource abundance (Table 5, Fig. 7).

Analysis of a reduced version of the fixed first/last model, where seasonal time constraints were removed by setting $\alpha = 0$, showed that omitting seasonal time constraints resulted in a poor fit to the data. The model dropped to 272.9 (females) and 373.7 (males) Δ_i units

TABLE 4. Males: Maximum-likelihood parameter estimates (MLE), negative log-likelihood (*L*), and bias-corrected Akaike information criterion (AIC) model comparisons.

Model	Site-year‡	*N*§	r_{MLE}	ξ_{MLE} (d)	$\phi_{MLE}\|$ (yr^{-1})	k_{MLE} (mg)	s_{MLE} (mg)
					Parameter estimates†		
Null	NFC-1997	116	···	···	···	11.57	1.723
	ETC-1997	67	···	···	···	13.13	2.038
	WTC-1997	88	···	···	···	9.73	1.487
	NFC-1998	16	···	···	···	13.23	1.518
	WTC-1998	108	···	···	···	11.13	2.160
Seasonal and mean disturbance	NFC-1997	116	0.0023	0	···	[18]	1.789
	ETC-1997	67	0.036	0	···	[18]	1.924
	WTC-1997	88	0.0018	0	···	[18]	1.318
	NFC-1998	16	0.0037	0	···	[18]	1.631
	WTC-1998	108	0.0028	0	···	[18]	1.195
Fixed first/last disturbance	NFC-1997	116	0.0071	13	[0.8]	[18]	1.720
	ETC-1997	67	0.0134	0	[0.8]	[18]	1.902
	WTC-1997	88	0.0052	18	[0.8]	[18]	1.286
	NFC-1998	16	0.0119	12	[0.8]	[18]	1.516
	WTC-1998	108	0.0077	17	[0.8]	[18]	1.273
Variable first/last disturbance	NFC-1997	116	0.0130	21	0.98	[18]	1.672
	ETC-1997	67	0.0098	2	0.71	[18]	1.901
	WTC-1997	88	0.0052	18	0.80	[18]	1.286
	NFC-1998	16	0.0010	7	0.68	[18]	1.514
	WTC-1998	108	0.0043	8	0.59	[18]	1.166

† Model parameters: r = growth rate, ξ = adult life span, ϕ = flood frequency, k = maximum body mass, s = standard error of residuals. Variables that do not appear in a particular model are denoted by ellipses.

‡ NFC = North Fork Cave Creek, ETC = East Turkey Creek, WTC = West Turkey Creek; all three sites are montane Chihuahuan Desert streams (Arizona, USA).

§ *N* = no. of males in the site-year.

∥ Values in brackets were assigned rather than estimated with maximum likelihood.

¶ Negative log-likelihood of data given the model

The bias-corrected Akaike information criterion, $AIC_C = 2L + 2p[N/(N - p - 1)]$, where p is the total number of estimated parameters; $\Delta_I = AIC_C$ scaled to smallest value for that data set; rank is from best (1) to worst (4); Δ_i represents the distance from the best-fit model.

away from the best-fit model, demonstrating that although adding disturbance regime to the seasonal model greatly improved model fit, seasonal time constraints on reproduction are still needed to account for patterns in the data.

Variable first/last disturbance model.—The parameter-rich variable disturbance model was the best-fit model overall ($\Delta_i = 0$ for both males and females) and for 4 of the 10 individual data sets (Tables 3 and 4). In two cases where sample sizes were very low, however (NFC-1998 females and males), the model actually received the highest negative log-likelihood making it the worst-fit model for those data sets. The large number of parameters estimated from the data (4) caused it to fare poorly in cases where negative log-likelihoods of all models were similar. Estimates of disturbance frequency (ϕ) were variable, ranging from 0.59 to 1.0 floods/yr. They were not consistent between males and females within site-years nor among years at the same site (Tables 3 and 4), suggesting the variable first/last model did not recover reasonable estimates. Estimates of the adult stage (ξ) were also variable, ranging from 0 to 27 d for females (Table 3) and from 2 to 21 d for males (Table 4). Furthermore, growth rate (r_{MLE}) values

were highly variable and not significantly associated with resource abundance (Table 5, Fig. 7).

DISCUSSION

Flash floods had severe ecological effects on *Phylloicus aeneus* by removing nearly 100% of juveniles from the study sites. However, this high removal is somewhat misleading from a population perspective because most individuals had already emerged into the adult stage prior to flooding. These adults would have been able to recolonize flooded streams or migrate to adjacent drainages. The timing of adult emergence relative to the timing of floods appeared to affect population sizes in subsequent years. Following seasons with no floods or floods near the average long-term date (f_1), numbers of final-instar larvae were high the following year. When floods occurred late in the season, populations in subsequent years were reduced or locally eliminated, presumably because most adults had already reproduced and their offspring were removed by floods. These patterns suggest that timing of emergence is an important fitness component in *P. aeneus*.

Body mass is another important fitness component for *P. aeneus* because it is tightly linked with both the

TABLE 4. Extended.

| | Model comparisons# | | | | | | | |
| | Per site-year | | | | Site-years combined | | | |
L¶	p	AIC_C	Δ_i	Rank	p	AIC_C	Δ_i	Rank
227.731	2	459.566	2.646	2	10	1612.763	153.337	4
142.778	2	289.748	7.097	4				
159.765	2	323.671	23.355	4				
29.384	2	63.693	0	1				
236.435	2	476.984	128.906	4				
232.026	3	470.264	13.344	4	15	1477.476	18.051	3
138.890	3	284.161	1.510	2				
149.118	3	304.526	4.210	3				
30.528	3	69.060	5.367	3				
172.545	3	351.321	3.242	2				
227.488	3	461.194	4.274	3	15	1473.786	14.361	2
138.133	3	282.651	0	1				
147.013	3	300.316	0	1				
29.356	3	66.710	3.017	2				
179.272	3	364.771	16.692	3				
224.282	4	456.920	0	1	20	1459.426	0	1
138.110	4	284.865	2.214	3				
147.010	4	302.502	2.186	2				
29.341	4	70.316	6.623	4				
169.846	4	348.078	0	1				

mass and number of eggs produced ($R^2 = 0.86$ and 0.92, respectively), and a doubling in body mass produces a doubling in number of eggs (Lytle 2000*b*). In this study body mass of adults varied two-fold within site-years and by an even greater amount among site-years, suggesting that many individuals emerged before reaching their maximum possible body mass. Because of this steep relationship between growth (which only occurs in juveniles) and egg production, there is a premium on remaining within the stream to feed even as the threat of flash floods increases. For *Phylloicus* females, body mass at emergence is positively correlated with fecundity (Lytle 2000*b*), and the fact that males grew larger where resources were more abundant (Fig. 5) suggests that this is also true for males. Juvenile growth may be less important for organisms where size at emergence is decoupled from fitness (e.g., odonates

that feed as adults, McPeek and Peckarsky 1998; but see Johansson and Rowe 1999).

The life-history predictions discussed in the *Introduction* were largely borne out by the data. First, most emergence occurred before the height of the flash-flood season suggesting that much of the caddisfly population was in the aerial adult stage when floods were most likely. Second, in most site-years body mass at emergence declined as the flood season progressed, reflecting changes in the optimal tradeoff between growth and mortality. Third, site-years for which there are data showed a second decline in body mass towards the end of the emergence season. According to theory, this second decline is produced by smaller individuals that risked the flood season in order to grow larger. This risky strategy worked well in WTC-1997 and WTC-1998 when no floods occurred, and in NFC-1997 and

TABLE 5. Summary of ANCOVA results for the effect of *Phylloicus aeneus* sex on maximum-likelihood estimates of growth rate (r_{MLE}, the response variable) at different per capita resource abundances (in square centimeters of deciduous detritus per larva, $\ln(x + 1)$ scale.

Model	R^2	Source of variation	df	$MS \times 10^6$	F	P
Seasonal and mean disturbance	0.88	sex	1	0.78	8.11	0.0248
		resource abundance	1	4.20	43.47	0.0003
		error	7	0.10		
Fixed first/last disturbance	0.88	sex	1	12.54	8.92	0.0203
		resource abundance	1	62.68	44.59	0.0003
		error	7	1.41		
Variable first/last disturbance	0.27	sex	1	19.32	0.62	0.4574
		resource abundance	1	62.56	2.00	0.2000
		error	7	31.24		

Notes: Separate ANCOVAs were used to test each model. For the seasonal and fixed first/last disturbance models only, growth rate was positively correlated with resource abundance, and males had higher growth rates than females.
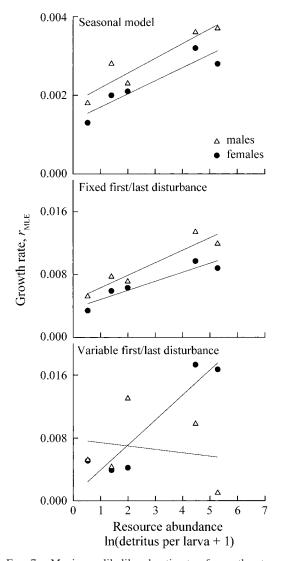
FIG. 7. Maximum-likelihood estimate of growth rate as a function of resource abundance. Resource abundance (in units of cm²/larva) was correlated with growth rates from the seasonal and fixed first/last disturbance models (significant ANCOVAs, Table 5), but not with growth rates from the variable first/last disturbance model (nonsignificant ANCOVA, Table 5).

ETC-1997 when late floods occurred. It failed in NFC-1998 when an early flood occurred.

Do seasonal time constraints affect body size at emergence?

The seasonal time-constraint model fit the data better under AIC_C (bias-corrected Akaike's information criterion) than did the null model, except when sample sizes were very low (NFC-1998), suggesting that significant body-mass declines occurred and could be partly explained by a model incorporating seasonal time constraints. This result provides further evidence (in addition to the regressions in Fig. 4) for rejecting the

null hypothesis that there were no declines in body mass present in the data. Seasonal time constraints have been shown experimentally to affect body size at emergence in aquatic insects; Johansson and Rowe (1999) found that artificially shortened photoperiod caused damselflies to increase development rate and mature at smaller body sizes.

Do flash-flood regimes affect body size at emergence?

All of the disturbance models performed as well as or better than the seasonal model, suggesting that adding information about disturbance regimes explained
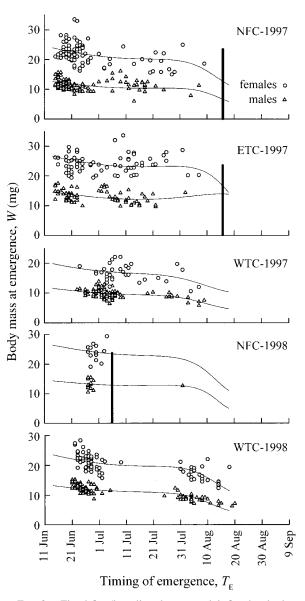

FIG. 8. Fixed first/last disturbance model, fitted to body-mass data, for the three montane stream study sites in 1997 and 1998. Solid vertical bars denote occurrences of flash floods. For site codes, see Fig. 1.

patterns in the data that the seasonal model could not. Disturbance and seasonal time constraints play complementary roles in shaping emergence strategies, however. Without a seasonal time constraint on reproduction *no* emergence is expected after the peak of the disturbance season (except for individuals reaching their maximum body mass), which explains why the first/last disturbance model performed so poorly when seasonal time constraints were omitted.

Which components of the flood regime are the most important?

Of the three disturbance models, the variable first/ last model provided the best fit to the data under AIC_C. However, this model failed to recover realistic parameter estimates. Unlike with the other models, growth-rate estimates were uncorrelated with resource abundance. Estimates of flood frequency also differed for males and females in the same site-years, suggesting that the variable first/last model overfitted the data at the expense of biological realism. The mean disturbance model had the opposite problem because it failed to explain the data any better than the seasonal model. This may have occurred because the mean date of all monsoon floods was close to the end of the season date (day 225 vs. 246), and so disturbances in this model did little more than reinforce the body-mass decline associated with the seasonal time constraint. The mean disturbance model also estimated a maximum adult life-span of 0 d, although this is known to be at least 7 d. The fixed first/last model, on the other hand, fit the data fairly well (it was within 8.4 and 14.4 Δ_i units of the variable first/last model) and recovered reasonable estimates of adult life-span (14 d on average, although it estimated 0 d in one instance) and growth rate (significantly correlated with resource abundance).

The comparison of multiple competing models suggests that the first flood of the monsoon season is the most critical disturbance event for *P. aeneus* life histories. There are several possible reasons for this. First, the first flood of the season causes nearly 100% removal of remaining larvae (Lytle 2000*a*; Fig. 2). This high removal rate suggests the first flood of the season is the primary selective force driving emergence patterns, although subsequent floods may be important for oviposition timing. Second, the first flood of the season removes almost all deciduous detritus from streams, and this resource is not completely replaced until leaf abscission occurs the following spring (Lytle 2000*a*). This reduces or eliminates any prospects for further growth in late-instar larvae that manage to survive. Interestingly, because only fine (<2 mm) particulate organic matter remains in streams after flash floods, post-flood conditions may be ideal for early instar *P. aeneus,* which feed on and build cases from this size class of detritus (Lytle 2000*a*). Third, if a second flood does occur (this should happen in 19 out of 100 years) it tends to occur near T_c, the end of the season. Because

emergence, mating, and oviposition must be completed before this time, the models suggest there is no life-history strategy that individuals can use to avoid these late floods. This is supported by the observation that larval populations were lowest in years following late floods.

The disturbance models predict two periods of emergence during a season, and this was observed in most site-years (Fig. 1). The lines fitted to the body-mass data by the first/last disturbance model, however, only slightly suggest two declines in body mass (Fig. 8). In terms of model dynamics, this occurred because growth rates would have to have been very high to produce two distinct declines in body mass separated by such a small amount of time (only 10 d in the case of ETC-1997 males). This suggests that other factors not included in the model could be important, such as growth rates that vary during the season. Indeed, physical processes such as seasonal temperature increases have been suggested as a potential cause of seasonal body-size declines (Vannote and Sweeney 1980), but this mechanism can only account for a single seasonal decline and not the two declines that were observed. In general, models that allow flexible growth rates would need to optimize both body size and growth rate simultaneously (e.g., Abrams et al. 1996). This model dynamic may also explain why estimated growth rates were higher for males than females. Males exhibited larger seasonal size changes relative to their maximum body mass than did females, and the model accounts for this by estimating higher per capita growth rates.

An alternative explanation for the two emergence periods is that they were produced by either multivoltinism or multiple developmental pathways within populations. Vannote and Sweeney (1980) observed two consecutive seasonal declines in body size in seven temperate aquatic-insect taxa and attributed the pattern to multivoltinism (i.e., the first generation emerged in spring to produce a second generation in fall). In each case body size of the second group was at least 50% smaller than that of the first. In the mayfly *Baetis,* multivoltinism also produced two emergence periods during a single season, but a decline in body size was only associated with the first period (Peckarsky et al. 1993, 2001). In spring some individuals (possibly ones that experienced exceptional growth over the winter) could gain in fitness by producing an extra generation over the summer, so long as an early flood does not occur that year. In *P. aeneus,* however, the larval population structure does not suggest that a multivoltine life history occurs (Fig. 2; Wiggins 1996).

In consecutive years with no flash floods, a semivoltine strategy is possible for *P. aeneus.* For example, Moreira and Peckarsky (1994) observed two emergence periods during a single season in a semivoltine stonefly, and attributed the pattern to multiple developmental pathways; depending on whether an individual was oviposited early or late in the season, devel-

opment to maturity would take either two or three years. Flash floods certainly do not favor this strategy in *P. aeneus* because it requires two consecutive years without floods to be successful. In the first year a flood would remove any remaining larvae, and in the following year an early flood remove their progeny. The observation of two emergence periods in NFC-1997 and ETC-1997 following years where floods removed most remaining larvae is also evidence against this strategy. Because flash floods occur most years in this system, they should be expected to select against life-history strategies such as semivoltinism.

In general, rapid life cycles and continuous emergence throughout the disturbance season are observed in taxa inhabiting streams prone to flash floods (Gray 1981). Other life-history strategies, however, such as state-dependent declines in body size at emergence, allow longer-lived organisms to maximize fitness in these disturbance regimes. Even though the timing of individual flash floods is difficult to predict with any certainty, theory shows that, in evolutionary time, life-history strategies that are synchronized with long-term patterns of flood occurrence may be favored. Although flash floods have the potential to cause very high mortality, state-dependent emergence strategies allow populations to persist and even thrive in these habitats.

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