

RECONSTRUCTING LONG-TERM FLOOD REGIMES WITH RAINFALL DATA: EFFECTS OF FLOOD TIMING ON CADDISFLY POPULATIONS

DAVID A. LYTLE*

Department of Entomology and Field of Ecology & Evolutionary Biology, Cornell University, Ithaca, NY 14853
Present Address: Department of Entomology, Oregon State University, 2046 Cordley Hall, Corvallis, OR 97331

*Correspondent: david.lytle@science.oregonstate.edu

ABSTRACT—Flash floods are a defining feature of desert streams, but flow records are not always available to characterize long-term flood dynamics. In this study, rainfall data spanning 100 years were used as a proxy to quantify long-term flood regimes for southeastern Arizona (USA) streams. The frequency and seasonal timing of severe floods (>50% substrate movement) were highly variable at short temporal scales (days to several years), but clear patterns emerged in the long-term (several years to a century). To explore the ecological effects of flood timing, populations of the caddisfly *Phylloicus aeneus* (Calamoceratidae) were monitored in 2 streams over 3 years. The timing of individual floods relative to the long-term average strongly affected *P. aeneus* populations: early and timely floods had little effect on population size in the next year, but late floods significantly reduced population size in the next year. Thus, flood timing might play a role in regulating populations of desert stream organisms.

RESUMEN—Inundaciones repentinas son una característica distintiva de los arroyos de desierto, pero los datos hidrológicos no están siempre disponibles para caracterizar la dinámica de las inundaciones a largo plazo. En este estudio, datos de precipitación desde cien años atrás fueron utilizados como aproximación para cuantificar regímenes de inundación a largo plazo para arroyos del sudeste de Arizona, USA. La frecuencia y ocurrencia estacional de inundaciones severas (>50% movimiento de sustrato) fueron altamente variables a corto plazo (de días a varios años), pero modelos claros emergieron a largo plazo (varios años a un siglo). Para explorar los efectos ecológicos del patrón temporal de las inundaciones, las poblaciones de la tricóptera *Phylloicus aeneus* (Calamoceratidae) fueron monitoreadas en 2 arroyos durante 3 años. La ocurrencia temporal de inundaciones individuales en relación al promedio a largo plazo afectó fuertemente las poblaciones de *P. aeneus*: las inundaciones tempranas y oportunas tuvieron poco efecto en el tamaño poblacional del año siguiente, pero las inundaciones tardías redujeron significativamente el tamaño poblacional del año siguiente. De este modo, el patrón temporal de las inundaciones puede regular las poblaciones de organismos de arroyos de desierto.

Flash floods in desert streams inflict extraordinarily high mortality in populations of fishes (John, 1964; Meffe, 1984), invertebrates (Bruns and Minckley, 1980; Gray and Fisher, 1981; Molles, 1985; Lytle, 2000), and algae (Grimm and Fisher, 1989). In response to this strong ecological force, some organisms have evolved behaviors (Meffe, 1984; Lytle, 1999) or life-history strategies (Gray, 1981; Lytle, 2001, 2002) that impart resistance or resilience to floods, or allow floods to be avoided entirely. In some cases, these adaptations allow native species to survive flood events that reduce or eliminate populations of non-native species (Minckley and Meffe, 1987; Dudley and Mat-

ter, 1999). The frequency and seasonal timing of flood events are considered fundamental attributes of flood regimes (Poff, 1996; Richter et al., 1996). In desert streams, the timing of flood events is especially important, because flood timing affects the establishment of native riparian plants (Stromberg, 1997, 1998) and the reproductive timing of native fish (John, 1963). Although a characterization of the long-term flood regime would aid the understanding of these phenomena, historical flow data are not available for many desert streams. Instead, flood regimes must be characterized anecdotally or by using rainfall data as a proxy. The goal of this study was to characterize long-

term flash-flood regimes for montane Chihuahuan desert streams in southeastern Arizona by combining short-term flood data with long-term rainfall data. This characterization was then used to explore how flood timing regulates populations of a desert stream caddisfly.

Powerful convective thunderstorms occur seasonally in arid regions throughout the world. During the summer monsoon season (June through September) in the Sonoran and Chihuahuan deserts of North America, rainfall is generated almost entirely by convective thunderstorms (Fogel, 1981). These storm cells produce high-intensity, short-duration rains that are limited in aerial extent, in contrast to the gentle winter rains produced by large frontal systems. Storm cells typically bring runoff-producing rainfall to small areas (20 to 100 km²; Osborn and Lane, 1972). Because of the solitary nature of convective storm cells, they can be characterized as stochastic, sequentially-independent events with recurrence frequencies that follow a Poisson distribution (Fogel and Duckstein, 1969; Fogel, 1981). These statistical properties dictate the nature of floods as well; a stream can experience a severe flash flood where a storm happened to occur, while an adjacent stream experiences no flooding at all.

Only rainfall events exceeding a certain threshold magnitude cause flash floods (Osborn and Lane, 1972; Osborn et al., 1972). This threshold magnitude differs among streams because of physical differences, such as watershed area, channel roughness, stream gradient, and underlying geology (Gordon et al., 1992). Tracer particles can be used to find the threshold magnitude of rainfall for a particular drainage (Townsend et al., 1997). Tracers (usually painted substrate particles) are chosen to represent the particle size composition of streams, and flood intensity (physical impact of the flood) is a function of the percentage of tracers that moved, their size, and the distance they moved. These measures allow long-term rainfall data to be translated into a long-term profile of flood frequency and timing.

METHODS AND MATERIALS—Flood frequency was characterized directly over a 5-year period in 2 streams in the Chiricahua Mountains of southeastern Arizona, USA (31.7°N, 109.2°W). The streams

(North Fork Cave Creek and East Turkey Creek) were situated at similar elevations (1,935 m and 1,925 m) and had small drainage areas (5.4 and 4.7 km²). Baseflow in both streams was near 1 L/min. Stream rocks with intermediate-axis diameters of 10 to 18 cm (10 per stream) and 5 to 10 cm (20 per stream) were painted and placed, unembedded, in the active stream channel of both streams from 1994 to 1998. Tracers were checked following all monsoon rainfall events and movement distances were recorded. After floods, tracers were returned to their original positions and lost particles were replaced. Flash floods that caused >50% of the particles to move more than 1 m were considered biologically significant disturbances, because this degree of bed movement causes high mortality in many invertebrate taxa (Lytle, 2000).

Monsoon rainfall regime (frequency, magnitude, and timing of rainfall events) was characterized in the Chiricahua Mountains using National Oceanic and Atmospheric Administration daily rainfall data from 4 gauging stations covering a 100-year period (National Climatic Data Center, 1992): Portal (1914 through 1955) and Portal 4SW (1965 through 1993), Chiricahua National Monument (1909 through 1993), and Rucker Canyon (1893 through 1993). The gauging stations were situated at comparable elevations: 1,524, 1,643, 1,615, and 1,637 m, respectively. Because of their proximity, the 2 Portal stations were treated as a single station. Only years with data for the entire monsoon season (May through October) were included in the analysis: 65 years for Portal, 53 years for Chiricahua, and 72 years for Rucker. To determine the degree to which the magnitude of daily rainfall events was correlated among the 3 stations, a Pearson correlation matrix was calculated using a 10-year subset of the data (1983 through 1993). Days with no rainfall were excluded from the analysis.

A profile of rainfall event frequency versus rainfall threshold magnitude was generated from the long-term data. Rainfall frequency was estimated for each station by calculating, over all years, the mean number of rainfall events per season (ϕ) that exceeded a threshold magnitude of rain (d). This calculation was repeated for values of d ranging from 20 to 50 mm in 1-mm increments, because rainfall events below 20 mm are unlikely to cause severe floods (Osborn and Lane, 1972; Osborn et al., 1972) and rainfall events exceeding 50 mm were too rare to reliably characterize with this data set (only 31 events >50 mm observed). To test whether rainfall frequency conformed to a Poisson distribution, Chi-square goodness-of-fit tests were performed on observed frequency distributions at each threshold magnitude.

A profile of rainfall event timing versus rainfall threshold magnitude was generated from the long-

TABLE 1—Monsoon flash-floods (1994 through 1998) and pre-flood caddisfly populations in 2 desert streams in the Chiricahua Mountains, Arizona, USA. Only floods that caused >50% bed movement are included.

Year	N. Fork Cave Creek	<i>P. aeneus</i> (larvae/site)	East Turkey Creek	<i>P. aeneus</i> (larvae/site)
1994	29 July	(no data)	(no data)	(no data)
1995	no flood	(no data)	25 August	(no data)
1996	29 June	480	15 July	10
1997	17 August	661	17 August	39
1998	5 July	182	no flood	0
ϕ	0.8		0.8	
f	201 (20 July)		221 (9 Aug)	
σ	19.6 d		17.7 d	

term data. Rainfall timing was calculated as the long-term mean date of all rainfall events occurring during the monsoon season (f) that exceeded d . To estimate the timing of the first (f_1) and last (f_2) above-threshold rainfall events per season, this procedure was repeated using only the first and last above-threshold events for each year. In years experiencing only 1 above-threshold occurrence, the event was counted as both the first and last event. The standard deviation about this mean was also calculated to give a measure of among-year variability.

An estimate of the long-term frequency and timing of floods was obtained by combining the directly observed flood data with the long-term rainfall analysis. Using the rainfall analysis, values for f , f_1 , and f_2 of flood events were obtained from values of ϕ measured directly in each stream. Chi-square goodness-of-fit tests were used to test whether the timing of flood events departed significantly from a normal distribution. For these tests, the data were partitioned into frequency classes of 20-d intervals.

To determine how flood timing affects populations of stream organisms, final instar larvae of the caddisfly *Phylloicus aeneus* (Calamoceratidae) were counted prior to the monsoon season in both streams from 1996 to 1998. *P. aeneus* requires about a year to complete 5 instars and a pupal stage (Wiggins, 1996), suggesting that all individuals encounter at least part of the monsoon season. Adults emerge from June through August, and females emerge with fully-chorionated eggs, suggesting that ovarian diapause does not occur (Lytle, 2002). Adult lifespan is not known with any precision, but adults can live at least 7 d and possess mouthparts capable of ingesting water or nectar for a maintenance diet (pers. observ.). Although *P. aeneus* ranges from the southwestern United States to Costa Rica, the Arizona populations used in this study might represent an undescribed species (Bowles and Flint, 1997). Larvae were counted in randomly selected stream quadrats (Lytle, 2002), and these abundances were ex-

pressed as a percentage of the maximum abundance of final instars in each stream during the 3-year period. These values were plotted against the timing of the flash flood during the previous year. When no flood occurred in the previous year, timing was assigned a value of zero.

RESULTS—Tracer Particles and Flood Frequency—Eight flash floods that caused >50% bed movement occurred during the study period (Table 1). Most of the floods were powerful; in several cases, tracers were recovered over 100 m downstream, and tracers often were buried beneath substrates. Only once did floods occur simultaneously on both drainages. Neither stream experienced more than 1 flood per year, and flood frequency in both North Fork Cave Creek and East Turkey Creek was calculated as $\phi = 0.8$ floods/year. The average flood date was 209 (July 28).

Spatial Correlation of Rainfall Events—Monsoon season daily rainfall from 1983 through 1993 was significantly correlated among the 3 gauging stations (Bartlett's $\chi^2 = 51.1$, $df = 3$, $P < 0.001$). Pairwise Pearson correlation coefficients were low, however, ranging from 0.224 to 0.380, suggesting that despite this correlation gauges often did not receive similar amounts of rainfall on any particular day.

Rainfall Frequency—The frequency of rainfall events declined curvilinearly as threshold magnitude increased (Fig. 1). The relationship was nearly identical at all 3 gauging stations. Events exceeding 20 mm occurred at a frequency of about 4 events/season, and events greater than about 35 mm occurred at a frequency of less than 1 event/season. Observed rainfall fre-

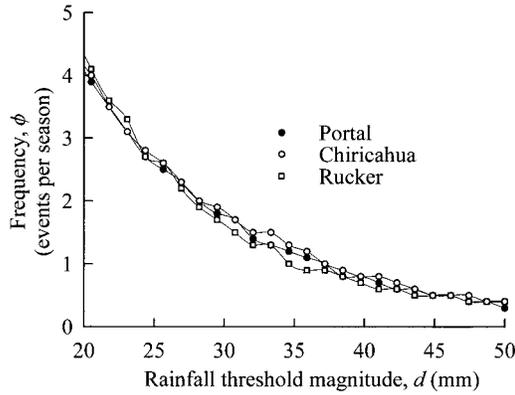


FIG. 1—Long-term rainfall frequency as a function of rainfall threshold magnitude at 3 rainfall gauging stations in the Chiricahua Mountains, Arizona, USA. Each point represents average number of events per season that equaled or exceeded rainfall threshold magnitude.

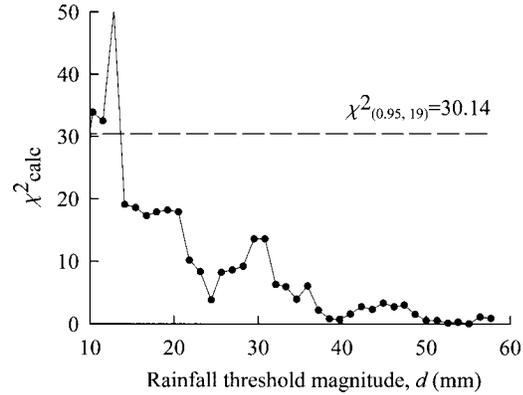


FIG. 2— χ^2 goodness-of-fit profile for rainfall frequency as a function of threshold magnitude. Points below critical 95% value (dashed line) were not significantly different from a Poisson distribution.

quencies did not depart significantly from the expected Poisson distribution except at the lowest threshold magnitudes, below approximately 15 mm (Fig. 2). Calculated χ^2 values generally became non-significant as threshold magnitude increased, indicating that larger, rare storms fit the Poisson assumption better than smaller, frequent ones. The relationship between ϕ and d was well-approximated by a second-order polynomial:

$$\phi = 13.75 - 0.58d + 0.0062d^2$$

If the value of d that causes flooding is known, or if flood frequency (ϕ) is known, this equation can be used to translate long-term rainfall regime into an estimate of long-term flood regime.

Rainfall Timing—The mean for all stations combined was $f = 225$ (August 13), and this value was constant at all values of d (non-significant slope coefficient; t -test, $\alpha = 0.05$, $df = 46$, $P > 0.50$), suggesting that rainfall timing did not vary systematically with d . Standard deviations around f ranged from 27 to 38 d, with an average value of 33.8 d.

The timing of the first and last rainfall events of the season changed substantially with rainfall threshold magnitude. At low values of d , f_1 occurred much earlier than f_2 (Fig. 3, bottom panel). At higher values of d (above approximately 40 mm) f_1 and f_2 occurred at sim-

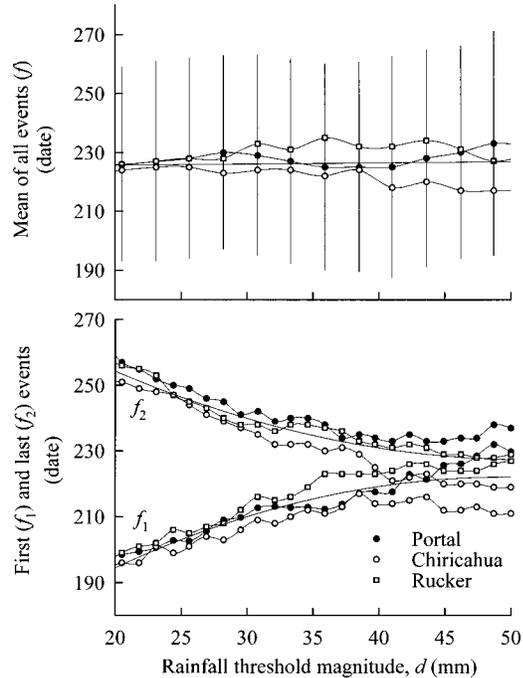


FIG. 3—Long-term rainfall timing as a function of rainfall threshold magnitude. Timing of all rainfall events (f , top panel) and timing of first (f_1) and last (f_2) rainfall events (bottom panel). Each point represents average occurrence date of all events that equaled or exceeded rainfall threshold magnitude. Error bars (SD) shown only for Portal data f because of space limitations on graph, but standard deviations were comparable at other sites. Regression lines (thin solid lines) are for the 3 stations combined.

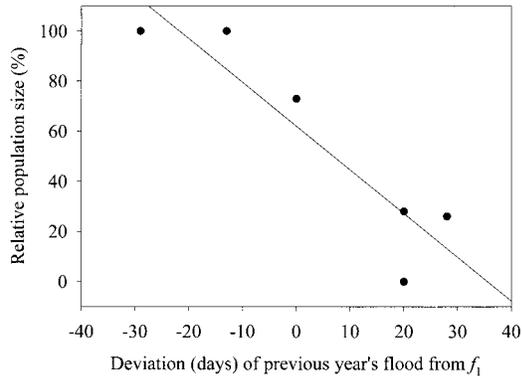


FIG. 4—Timing of flood during previous year affects *P. aeneus* population size in subsequent years. Populations were highest in years following early floods (relative to f_1); late floods reduced or eliminated populations.

ilar times. The following polynomial equations provided reasonable fits to the data:

$$f_1 = 144.5 + 3.13d - 0.0316d^2$$

$$f_2 = 299.5 - 2.81d + 0.0273d^2$$

Estimated Long-Term Flash Flood Timing—Using the value of $\phi = 0.8$ derived from direct observations of floods, inferences were made about the long-term timing of floods. From equation 1, $d = 37$ mm at $\phi = 0.8$ (the rainfall frequency measured in both streams), suggesting that rainfall events above this threshold magnitude produce floods that cause significant mortality in invertebrate populations. This results in estimated long-term mean dates of first and last flash floods of $f_1 = 217$ and $f_2 = 233$ for all 3 stations combined. Because f did not vary significantly as a function of d for the rainfall data (Fig. 3, top panel), $f = 225$ for all biologically significant floods combined. Chi-square tests demonstrated that at $\phi = 0.8$, none of the 3 measures of event timing departed significantly from a normal distribution (f , $\chi^2 = 9.38$; f_1 , $\chi^2 = 6.84$; f_2 , $\chi^2 = 7.63$; $df = 6$ and $P > 0.1$ for all tests).

Caddisfly Populations—Larval *P. aeneus* densities were consistently greater in North Fork Cave Creek than in East Turkey Creek in all years (Table 1). The timing of individual flood events had a significant effect on caddisfly population size in subsequent years (Fig. 4). Late floods in 1997 reduced the North Fork Cave Creek population by over 70% and locally

eliminated the East Turkey Creek population. Relative population sizes were highest following years with no floods or early floods, but populations were lowest following years with late floods (significant regression slope, $t = -4.621$, $df = 4$, $P < 0.01$).

DISCUSSION—A key result of this analysis is that while great temporal and spatial variation in rainfall exists in the short term (days to several years), analysis of long-term data (several years to centuries) revealed consistent patterns. Low correlation coefficients among rainfall gauging stations and the rarity of simultaneous floods observed with the tracer particle study suggest that conditions can be drastically different at a spatial scale of only several kilometers and a temporal scale measured in days. This heterogeneity results in part because rainfall is relatively uncommon in arid environments, and variability in rainfall increases as total rainfall decreases (Davidowitz, 2002). For this reason the probability of a rainfall or flood event occurring over a short time interval or within a small area is difficult to measure at these small scales. The congruence among all 3 gauging stations for long-term rainfall frequency and timing demonstrates that regional patterns do exist for these phenomena when data are examined at larger scales. The presence of consistent patterns might be important for determining the nature of ecological conditions and selective pressures experienced by organisms.

The patchiness of monsoon rainfall is well-known to those who have observed it; a storm can drench one valley while leaving a nearby valley dry, or one stream can experience a destructive flash flood while an adjacent tributary remains at base flow. Although the stochastic nature of monsoon storms is well-established from other studies, it should be cautioned that χ^2 is not a powerful test, and it is possible that distributions other than the Poisson might not be rejected either (Gordon et al., 1992). The assumption of sequentially-independent events might also break down in some arid regions, such as eastern New Mexico and Texas, where monsoon thunderstorms are often produced by large frontal systems rather than by isolated storm cells (Osborn and Lane, 1972).

The importance of the timing of individual floods relative to the long-term average is illus-

trated by the caddisfly data. Late floods had a stronger negative impact on populations than early floods. The presence of larger populations the following year suggests that streams experienced greater recolonization rates following early and timely floods. One explanation is that the phenology of *P. aeneus* is synchronized with the monsoon season so that the majority of individuals emerge into the aerial adult stage by early July, well in advance of the average first flood date of July 28 (Lytle, 2002). Emergence occurs from June until August, so it is likely that adults will be present to recolonize even after early floods. In contrast, most adults had likely returned to the stream to oviposit by the time the late floods occurred. Their offspring would have been killed or swept downstream by the floods, resulting in reduced populations the following year. While the regression between larval population size and flood timing was linear in this study, it is likely that the relationship is actually unimodal. Exceptionally early floods that occur prior to any caddisfly emergence should also depress populations, and this would produce a curve that rises to a maximum and then declines.

Analysis of flash-flood regimes over the short-term reveals trends that are relevant to the system from an ecological point of view. At this scale, it is easy to observe how the stochastic nature of flash floods drives large interannual variation in population sizes, and how a flooded stream can experience high mortality while a nearby stream is unaffected. Mortality of aquatic insects from flash floods exceeds 90% for most taxa, and some species are locally extirpated by floods (Lytle, 2000), so recolonization of flooded streams from adjacent, non-flooded drainages might also be important for maintaining species diversity in these systems. At longer times scales, however, the flood regime exhibits a more predictable pattern in terms of flood timing and frequency, suggesting that organisms might be able to evolve in synchrony with flash floods.

I thank B. Peckarsky, J. Dahl, C. Caudill, A. Encalada, and B. Taylor for comments on an early version of this manuscript. The Southwestern Research Station (American Museum of Natural History) provided research facilities for the caddisfly study. I also thank the ranchers, rangers, researchers, and others who collected the rainfall data over the decades.

This project was funded by grants from the American Museum of Natural History and the Cornell University Department of Entomology.

LITERATURE CITED

- BOWLES, D. E., AND O. S. FLINT, JR. 1997. The genus *Phylloicus* Müller (Trichoptera: Calamoceratidae) in the United States, with a redescription of *Phylloicus ornatus* (Banks). Eighth International Symposium on Trichoptera. W. Junk, Dordrecht, The Netherlands.
- BRUNS, D. A., AND W. L. MINCKLEY. 1980. Distribution and abundance of benthic invertebrates in a Sonoran Desert stream. *Journal of Arid Environments* 3:117–131.
- DAVIDOWITZ, G. 2002. Does precipitation variability increase from mesic to xeric biomes? *Global Ecology and Biogeography* 11:143–154.
- DUDLEY, R. K., AND W. J. MATTER. 1999. Effects of a record flood on fishes in Sabino Creek, Arizona. *Southwestern Naturalist* 44:218–221.
- FOGEL, M. M. 1981. Precipitation in the desert. In: Evans, D. D., and J. J. Thames, editors. *Water in desert ecosystems*. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania. Pp. 219–234.
- FOGEL, M. M., AND L. DUCKSTEIN. 1969. Point rainfall frequencies in convective storms. *Water Resources Research* 5:1229–1237.
- GORDON, N. D., T. A. MCMAHON, AND B. L. FINLAYSON. 1992. *Stream hydrology, an introduction for ecologists*. John Wiley and Sons, Chichester, United Kingdom.
- GRAY, L. J. 1981. Species composition and life histories of aquatic insects in a lowland Sonoran Desert stream. *American Midland Naturalist* 106:229–242.
- GRAY, L. J., AND S. G. FISHER. 1981. Postflood recolonization pathways of macroinvertebrates in a lowland Sonoran Desert stream. *American Midland Naturalist* 106:249–257.
- GRIMM, N. B., AND S. G. FISHER. 1989. Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of the North American Benthological Society* 8:293–307.
- JOHN, K. R. 1963. The effect of torrential rain on the reproductive cycle of *Rhinichthys osculus* in the Chiricahua Mountains, Arizona. *Copeia* 1963:286–291.
- JOHN, K. R. 1964. Survival of fish in intermittent streams of the Chiricahua Mountains, Arizona. *Ecology* 45:112–119.
- LYTLE, D. A. 1999. Use of rainfall cues by *Abedus herberti* (Hemiptera: Belostomatidae): a mechanism for avoiding flash floods. *Journal of Insect Behavior* 12:1–12.
- LYTLE, D. A. 2000. Biotic and abiotic effects of flash

- flooding in a montane desert stream. *Archiv für Hydrobiologie* 150:85–100.
- LYTLE, D. A. 2001. Disturbance regimes and life history evolution. *American Naturalist* 157:525–536.
- LYTLE, D. A. 2002. Flash floods and aquatic insect life history evolution: evaluation of multiple models. *Ecology* 83:370–385.
- 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. In: Matthews, W. J., and D. C. Heins, editors. *Community and evolutionary ecology of North American stream fishes*. University of Oklahoma Press, Norman. Pp. 93–104.
- MOLLES, M. C., JR. 1985. Recovery of a stream invertebrate community from a flash flood in Tesuque Creek, New Mexico. *Southwestern Naturalist* 30: 279–287.
- NATIONAL CLIMATIC DATA CENTER. 1992. NCDC summary of the day (CD-ROM). EarthInfo, Boulder, Colorado.
- OSBORN, H. B., AND L. J. LANE. 1972. Depth-area relationships for thunderstorm rainfall in southeastern Arizona. *Transactions of the American Society of Agricultural Engineers* 15:670–673.
- OSBORN, H. B., L. J. LANE, AND J. F. HUNDLEY. 1972. Optimum gaging of thunderstorm rainfall in southeastern Arizona. *Water Resources Research* 8:259–265.
- POFF, N. L. 1996. A hydrogeography of unregulated streams in the United States and an examination of scale-dependence in some hydrological descriptors. *Freshwater Biology* 36:71–91.
- 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.
- STROMBERG, J. C. 1997. Growth and survivorship of Fremont cottonwood, Goodding willow, and salt cedar seedlings after large floods in central Arizona. *Great Basin Naturalist* 57:198–208.
- STROMBERG, J. C. 1998. Dynamics of Fremont cottonwood (*Populus fremontii*) and saltcedar (*Tamarix chinensis*) populations along the San Pedro River, Arizona. *Journal of Arid Environments* 40:133–155.
- TOWNSEND, C. R., M. R. SCARSBROOK, AND S. DOLÉDEC. 1997. Quantifying disturbance in streams: alternative measures of disturbance in relation to macroinvertebrate species traits and species richness. *Journal of the North American Benthological Society* 16:531–544.
- WIGGINS, G. B. 1996. Larvae of the North American caddisfly genera (Trichoptera). University of Toronto Press, Toronto, Canada.

Submitted 9 April 2001. Accepted 7 May 2002.
Associate Editor was Steven Goldsmith.