
Effects of Urbanization on the Distribution and Abundance of Amphibians and Invasive Species in Southern California Streams

SETH P. D. RILEY,* ‡‡ GARY T. BUSTEED,* LEE B. KATS,† THOMAS L. VANDERGON,†
LENA F. S. LEE,* ROSI G. DAGIT,‡ JACOB L. KERBY,* ††† ROBERT N. FISHER,§
AND RAYMOND M. SAUVAJOT*

*Santa Monica Mountains National Recreation Area, National Park Service, 401 W. Hillcrest Drive, Thousand Oaks, CA 91360, U.S.A.

†Department of Biology, Pepperdine University, 24255 Pacific Coast Highway, Malibu, CA 90263, U.S.A.

‡Resource Conservation District of the Santa Monica Mountains, 122 N. Topanga Canyon Blvd, Topanga, CA 90290, U.S.A.

§U.S. Geological Survey, San Diego Field Station, 5745 Kearny Villa Drive, Suite M, San Diego, CA 92123, U.S.A.

Abstract: *Urbanization negatively affects natural ecosystems in many ways, and aquatic systems in particular. Urbanization is also cited as one of the potential contributors to recent dramatic declines in amphibian populations. From 2000 to 2002 we determined the distribution and abundance of native amphibians and exotic predators and characterized stream habitat and invertebrate communities in 35 streams in an urbanized landscape north of Los Angeles (U.S.A.). We measured watershed development as the percentage of area within each watershed occupied by urban land uses. Streams in more developed watersheds often had exotic crayfish (*Procambarus clarkii*) and fish, and had fewer native species such as California newts (*Taricha torosa*) and California treefrogs (*Hyla cadaverina*). These effects seemed particularly evident above 8% development, a result coincident with other urban stream studies that show negative impacts beginning at 10–15% urbanization. For Pacific treefrogs (*H. regilla*), the most widespread native amphibian, abundance was lower in the presence of exotic crayfish, although direct urbanization effects were not found. Benthic macroinvertebrate communities were also less diverse in urban streams, especially for sensitive species. Faunal community changes in urban streams may be related to changes in physical stream habitat, such as fewer pool and more run habitats and increased water depth and flow, leading to more permanent streams. Variation in stream permanence was particularly evident in 2002, a dry year when many natural streams were dry but urban streams were relatively unchanged. Urbanization has significantly altered stream habitat in this region and may enhance invasion by exotic species and negatively affect diversity and abundance of native amphibians.*

Key Words: amphibian declines, California newts, California treefrogs, crayfish, exotic species, Pacific treefrogs, urban streams

Efectos de la Urbanización sobre la Distribución y Abundancia de Anfibios y Especies Invasoras en Arroyos del Sur de California

Resumen: *La urbanización afecta de muchas formas negativas a los ecosistemas naturales, particularmente a los sistemas acuáticos. La urbanización también está reconocida como uno de los potenciales causantes de las dramáticas declinaciones recientes en las poblaciones de anfibios. Entre 2000 y 2002 determinamos la distribución y abundancia de anfibios nativos y depredadores exóticos y caracterizamos el hábitat y las comunidades de invertebrados en 35 arroyos en un paisaje urbanizado al norte de Los Ángeles. Medimos el desarrollo de la cuenca como el porcentaje de la superficie ocupada por usos urbanos en cada cuenca.*

‡‡email seth_riley@nps.gov

††Current address: Environmental Science and Policy, 1 Shields Avenue, University of California, Davis, CA 95616, U.S.A.

Paper received May 27, 2004; revised manuscript accepted February 7, 2005.

Los arroyos en cuencas más desarrolladas a menudo tenían cangrejos de río exóticos (*Procambarus clarkii*) y peces, y tenían menos especies nativas, como tritones (*Taricha torosa*) y ranas arborícolas (*Hyla cadaverina*). Estos efectos parecieron particularmente evidentes arriba de 8% de desarrollo, un resultado que coincide con otros estudios de arroyos urbanos que muestran impactos negativos a partir de 10-15% de urbanización. La abundancia de *H. regilla*, el anfibio nativo con mayor distribución, fue menor en presencia de cangrejos de río exóticos, aunque no encontramos efectos directos de la urbanización. Las comunidades de macroinvertebrados bentónicos también fueron menos diversas en los arroyos urbanos, especialmente las especies sensibles. Los cambios en la comunidad de la fauna en arroyos urbanos se pueden relacionar con cambios en el hábitat físico del arroyo, tales como menos hábitat con pozas y más hábitat con corriente y una mayor profundidad y flujo de agua, lo que produce arroyos más permanentes. La variación en la permanencia de los arroyos fue particularmente evidente en 2002, año en el que muchos arroyos naturales se secaron y los arroyos urbanos permanecieron relativamente sin cambios. La urbanización ha alterado significativamente a los hábitats de arroyos en esta región y puede incrementar la invasión de especies exóticas e incidir negativamente en la diversidad y abundancia de anfibios nativos.

Palabras Clave: arroyos urbanos, cangrejos de río, declinaciones de anfibios, especies exóticas, *Hyla cadaverina*, *Hyla regilla*, *Taricha torosa*

Introduction

Freshwater ecosystems are particularly susceptible to disturbance and have become degraded throughout the world (Ricciardi & Rasmussen 1999; Baron et al. 2002). The severe disturbance of urbanization is a significant threat to freshwater systems such as streams (Paul & Meyer 2001). The increased area of impervious surfaces in urban areas produces increased runoff, leading to significant changes in hydrology and consequently in stream habitat, increased inputs of nutrients or pollutants, and, in the end, often radically altered ecological communities. Significant changes have been documented in the abundance and diversity of everything from algae to invertebrates to fishes in urban streams (reviewed in Paul & Meyer 2001). These changes can occur even at fairly low levels of urbanization, frequently beginning when 10–15% of the watershed has become urbanized or converted to impervious surface cover (Paul & Meyer 2001; e.g., Limburg & Schmidt 1990; Booth & Jackson 1997). Amphibian communities, however, have received little attention in urban streams, despite the fact that they may be particularly susceptible to urban impacts.

For more than a decade considerable attention has been paid to declines of amphibian populations worldwide (Blaustein & Wake 1990; Alford & Richards 1999). A range of causes of these declines has been identified, from disease to pollution to exotic species introductions. Many amphibian declines are also related to the loss, degradation, and fragmentation of remaining natural habitat (e.g., Lehtinen et al. 1999; Guerry & Hunter 2002), but perhaps because these threats are generally acknowledged for all taxa, they are less often implicated as a cause of amphibian declines. The sensitivity of amphibians to environmental change, however, renders them particularly susceptible to changes associated with habitat loss and disturbance. Most amphibians require some standing wa-

ter, at least for breeding. The high rate of loss and degradation of wetlands, therefore, may particularly affect amphibian communities.

The impact of urbanization on amphibian communities has received some attention in the conservation literature, particularly at broad spatial scales. Davidson et al. (2001, 2002) evaluated causes for amphibian declines throughout California and found that the absence of four sensitive species from historical locations was significantly correlated with the amount of surrounding urbanization. Similarly, Knutson et al. (1999) found that urbanization was the strongest (negative) factor in multivariate models of the abundance and distribution of anurans in Iowa and Wisconsin. Although these broad-scale studies are important, there has been little published research at finer scales or on stream-dwelling species. More specific and intensive studies (e.g., Delis et al. 1996) are necessary to determine more local patterns and to evaluate the potential mechanisms of negative impacts. As Knutson et al. (1999) acknowledge, their broad-scale models explain relatively little of the variation in amphibian distribution. Landscape-level studies of multiple streams that also include information about relevant local factors may be particularly useful (Lowe & Bolger 2002). For instance, Orser and Shure (1972) found that dusky salamander (*Desmognathus fuscus*) abundance was inversely related to urbanization in six Georgia streams because of increased erosion and decreased bank soil stability and vegetative cover.

There are many specific ways that amphibians can be adversely affected by urbanization. Of particular concern for many aquatic taxa, including amphibians, is flow regime (Poff et al. 1997; Baron et al. 2002) because the timing and volume of water inputs can be dramatically altered in urban areas. Reduced or altered flow can affect native fish species and communities (e.g., Marchetti & Moyle 2001), but increases in water input can also

threaten native aquatic biota, particularly in Mediterranean ecosystems, where native animals are adapted to a seasonal flow regime (Gasith & Resh 1999). In arid systems, more plentiful and permanent water can allow the invasion and persistence of exotic species, which may then eat (Knapp & Matthews 2000), compete with (Kiesecker et al. 2001) or hybridize with (Riley et al. 2003) native species (reviewed in Kats & Ferrer 2003). Significant disturbance of the streambed and surrounding habitats, such as the channelization and bank stabilization that is common in developed areas, most likely also negatively affects amphibian communities. Erosion and sedimentation of streams can increase in urban areas because of deliberate activities such as road construction (Welsh & Ollivier 1998), and as an indirect result of other factors such as increased fire frequency (Kerby & Kats 1998). Finally, collection by humans and predation by domestic cats and dogs may also affect urban amphibian populations.

We examined amphibian distribution, abundance, and reproduction across a range of natural and urban streams in a rapidly urbanizing landscape in southern California. Our goals were to evaluate the degree of urbanization in these watersheds; determine how the distribution and abundance of amphibians, introduced aquatic taxa, and benthic macroinvertebrates vary relative to urbanization; and measure how stream morphology and permanence are affected by urbanization. In the face of increasing urbanization, a better understanding of the threats to amphibians in urban areas will allow more effective conservation of amphibians and other aquatic species.

Methods

Study Area

The 76-km Santa Monica Mountains are bounded on the south by the Pacific Ocean, on the east by the city of Los Angeles, on the west by agricultural areas, and on the north by an eight-lane highway (Highway 101) and the Simi Hills (Fig. 1). The city of Malibu and parts of other incorporated areas are entirely within the mountains, and although much of the area remains undeveloped, new developments sprout up continually throughout the region. Many of the watersheds of the Santa Monica Mountains extend across Highway 101 into the Simi Hills (Fig. 1). Although much of the Simi Hills is protected open space, there is also considerable development within them, especially along streams and near the Highway 101 corridor. California is one of five locations in the world with a Mediterranean climate—cool, wet winters and hot, dry summers. Southern California is particularly arid, annually receiving 44 cm of rain, usually between October and April. Overall, the study area consists of a large expanse of typical Mediterranean climate habitat interspersed with pockets of urbanization and so provides an ideal landscape for investigating urban impacts.

Aquatic amphibian species in the region include California newts (*Taricha torosa*), Pacific treefrogs (*Hyla regilla*), California treefrogs (*H. cadaverina*), western toads (*Bufo boreas*), spadefoot toads (*Scaphiopus hammondi*), and red-legged frogs (*Rana aurora*). Red-legged frogs, formerly common in a number of streams in the

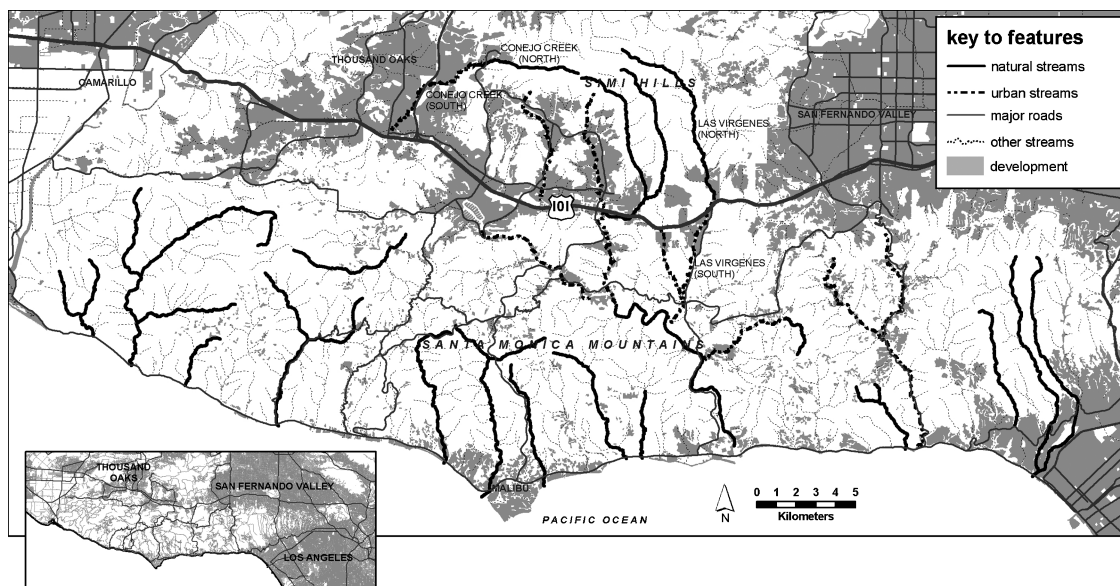


Figure 1. Streams surveyed for amphibians and introduced aquatic species in the Santa Monica Mountains and Simi Hills of southern California.

region (De Lisle et al. 1986), now occur only in one small population in the Simi Hills. Exotic stream species include red swamp crayfish (*Procambarus clarkii*) from the southeastern United States, bullfrogs (*R. catesbeiana*), and a number of fish species, including bass (*Micropterus* spp.), bluegill (*Lepomis macrochirus*), and mosquitofish (*Gambusia affinis*).

Reach Selection

Because our goal was a comprehensive survey of stream amphibian communities in the area, we attempted to survey all the major streams rather than selecting particular study streams. We surveyed a section of at least 500 m where possible. Along some longer streams there were major barriers such as freeways or significant changes in the degree of urbanization. For these streams we surveyed the stream above and below the barrier or change and treated each reach as a separate stream (e.g., north and south Las Virgenes, north and south Conejo Creek, Fig. 1). These reaches are not entirely independent because the upstream reach is contained within the watershed of the downstream reach. We believe, however, that the differences between the reaches were potentially significant in terms of the attributes we were examining. We surveyed 30 streams in 2000, 33 in 2001 (5 were new streams with 2 of the 2000 streams not sampled), and 35 in 2002. Streams were all first or second order except for two third-order streams, so they were generally small streams and of a similar size across the study area.

Stream Surveys

At each stream we selected a starting point based on accessibility and the likelihood of having water during the spring survey period (April–June). Most amphibians breed between February and June in this area, and many streams dry up by July or August. Starting points were recorded with a global positioning system to within 2–5 m. On first reaching the stream, we measured dissolved oxygen, salinity, air temperature, water temperature, pH, conductivity, water flow, and nitrate and phosphate levels.

Moving upstream, we determined whether each habitat segment was a run, riffle, or pool and measured its length, width, and depth; we also measured the length of dry stretches. We visually searched for larval and adult amphibians and exotic species in each segment, examining the water column and stream bottom. The relatively low density of aquatic vegetation in these streams increased the effectiveness of visual surveys. In segments with dense aquatic vegetation or algal blooms, we also used dipnets to capture and count animals. Counts were recorded for each species in each segment. If it was not feasible to count each individual, we used abundance categories of >20, >50, >100, >500, and >1000 (although the latter two categories were rarely used). We surveyed

for adult and metamorphic amphibians along the stream edge. We also measured reproductive effort by counting egg masses. For egg masses of California newts and Pacific treefrogs, we searched under rocks and on submerged branches and vegetation. We used a diving mask to count newt egg masses in deep pools. California treefrogs lay eggs singly, which makes counting them impracticable, and we found egg strings from western toads in only one stream. To standardize efforts, our method was reviewed each year and senior personnel conducted survey-team training each spring before surveys and monitored the work periodically throughout the survey period.

In 2001 we also collected benthic macroinvertebrate samples at each stream. Aquatic invertebrates are important components of stream biota that can be sensitive to changes in stream habitat and water quality (Karr & Chu 1999). They are also important prey for aquatic amphibians (Kerby & Kats 1998). For invertebrate sampling, we followed Environmental Protection Agency and California Aquatic Bioassessment protocols (Harrington & Born 2000), modified as appropriate for these small Mediterranean streams. We collected three invertebrate samples at each stream in a random selection of three of the first five riffle habitats. We used kick-net sampling in the middle of the stream and at each edge. Samples were preserved in 70% ethanol and sent to Sustainable Land Stewardship International Institute (Sacramento, California) for identification to family, genus, and, where possible, species.

Analysis

WATERSHED URBANIZATION, STREAM GRADIENT, AND WATER QUALITY

We measured the degree of urbanization within the watershed by calculating the percentage of area upstream from the starting point that consisted of urban land uses. Although impervious surface cover has often been used to measure urban stream impacts and is particularly useful with respect to hydrology (Scheuler 1994; e.g., Finkbine et al. 2000), the amount of urban land use in the watershed gives a more complete picture of the effects of urbanization. Morley and Karr (2002) found that percent urban cover was more highly correlated with their index of biological integrity for benthic invertebrates than impervious surface area.

We used geographic information systems (GIS) to generate land-use and stream-gradient information. Specifically, we used the grid module of Arc/Info 8.3 software (ESRI, Redlands, California) to calculate the watershed extent above the starting point from 10-m digital elevation models (DEMs) obtained from the U.S. Geological Survey. Land-use cover data provided by the Southern California Association of Governments were intersected with the watershed coverage to create a merged data set. The amount of urban area (industrial, commercial, residential, transportation, floodways) was then summarized for

each watershed. Stream gradient was calculated by measuring the difference in elevation (based on the DEMs) over the surveyed stream reach and dividing by the surveyed length. We analyzed conductivity and flow data (from 2001) because we believed these parameters were the most reliably measured and often reflect impacts from urbanization (Paul & Meyer 2001; e.g., Willson & Dorcas 2003).

SPECIES DISTRIBUTION AND ABUNDANCE, BENTHIC MACROINVERTEBRATES, HABITAT CHARACTERISTICS, AND PERMANENCE

We were interested in how biological and physical stream characteristics changed relative to urbanization and whether those changes were continuous or related to a certain threshold of development. Many urban stream studies cite a threshold of development or impervious surface area when effects begin to appear, often about 10–15% (Paul & Meyer 2001). To examine differences between urban and natural streams on average, we classified streams in watersheds with > 8% development as urban and those with < 8% development as natural. Eight percent was the lowest level at which decreases in vertebrate diversity, specifically fishes, have been seen (Yoder et al. 1999; reviewed in Paul & Meyer 2001), and it is the level at which exotic species began to appear in the streams in our study area.

Because we attempted to survey all the major streams in the Santa Monica Mountains and Simi Hills, we realized other important factors would also vary among streams. Stream gradient, in particular, varied from 0.6% to 12.8% and was also correlated with urbanization: urban streams generally had lower gradients (Pearson correlation coefficient = -0.486). Therefore we also included stream gradient as a variable in our analyses. For categorical analyses, we classified streams below the median gradient of 3.5% as low gradient and streams above 3.5% as high gradient. We used two-way analysis of variance (ANOVA) to test for differences between urban and natural and high- and low-gradient streams. Then, to test for continuous relationships and further investigate the nature of potential changes around the threshold of 8% urbanization, we used multiple piece-wise regression analysis (Singer & Willet 2003), including gradient as a second continuous variable. Using piece-wise regression, we were able to test whether the dependent variables were significantly related to urbanization and gradient, whether the slope of the relationship with urbanization changed above and below the 8% threshold, and whether there was a significant jump effect at this threshold as measured by a significant change in the intercept of each regression line with the 8% level of urbanization (see Fig. 2 for examples).

We tested for a relationship between species presence and urbanization with 2×2 contingency tables and used Fisher's exact tests when too many cell frequencies were < 5. We tested for relationships between urbanization and stream permanence with 2×2 contingency tables

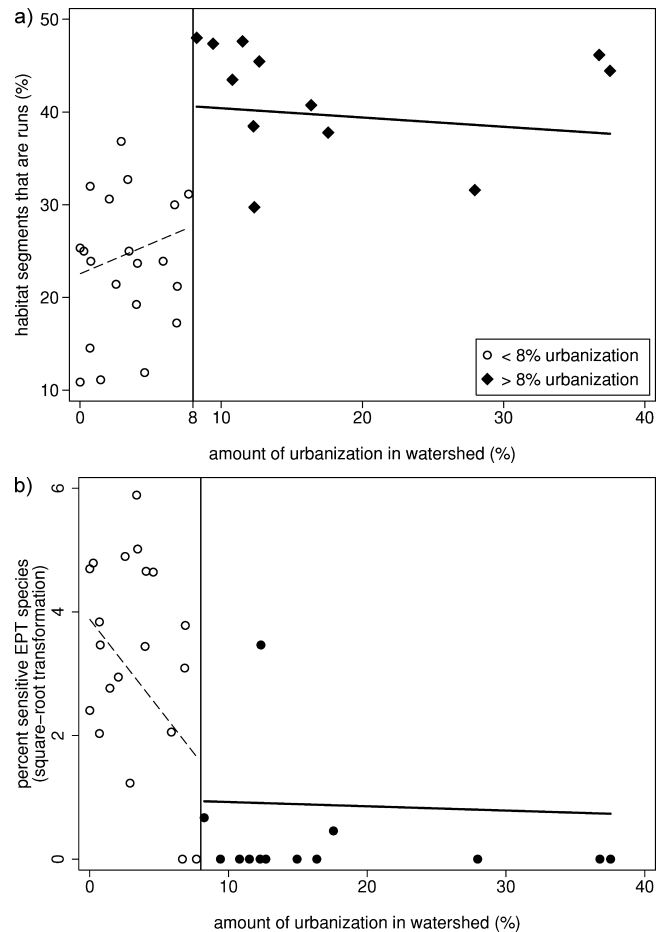


Figure 2. Piece-wise regression analyses of the percentage of watershed urbanization and (a) habitat segments that were runs in 2001 and (b) percent sensitive species (Ephemeroptera, Plecoptera, Trichoptera [EPT]), showing a significant difference in intercept but not slope in (a) and a significant difference in slope but not intercept in (b). The vertical line at 8% urbanization represents the cutoff between streams classified as urban or natural. Urban streams are filled circles (urban = 1) and natural streams are open circles (urban = 0). In (a) neither regression line is significantly different from zero, and the slopes of the lines are not significantly different from each other, but the intercepts where each line intersects the 8%-urbanization line are significantly different. In (b) the regression line for natural streams (< 8% urbanization) is significantly negative, whereas the line for urban streams is not different from zero. There is no significant difference in the intercepts with the line at 8% urbanization, but the slopes are significantly different from each other.

(percentage of streams with dry stretches) and Mann-Whitney tests (length of dry streambed). For stream flow, stream habitat characteristics, and invertebrate community indices, we used multiple piece-wise regression and

two-way ANOVA to test for relationships with urbanization and stream gradient. We tested for multicollinearity in the piece-wise regression analyses, and tolerances were always > 0.177 . Stream habitat characteristics included the average length of pools, riffles, runs, and of all habitat segments, average depth for runs, riffles, and pools, and the proportion of each stream that consisted of each habitat type, both the proportion of the length and the proportion of the segments.

Dependent variables for the invertebrate communities were species richness; diversity; the richness and percentage of insects from the Ephemeroptera, Plecoptera, and Trichoptera (EPT) orders; the percentage of insects from sensitive EPT taxa (tolerance values 0–2); the percentage of individuals from the most dominant taxon; the percentage of insects from intolerant taxa (tolerance values 0–3); and the percentage of insects from tolerant taxa (tolerance values 8–10). Mayflies (Ephemeroptera), stoneflies (Plecoptera), and caddisflies (Trichoptera) are orders of stream invertebrates that can be particularly susceptible to changes in stream habitat complexity and water quality. Because some families in these orders are less sensitive, we also evaluated EPT taxa and overall taxa that are particularly sensitive or insensitive to disturbance, based on tolerance values. Tolerance values represent the relative sensitivity of different invertebrate families within an order to aquatic disturbance and pollution generally but are not specific to the type of stressor (Harrington & Born 2000).

For Pacific treefrogs, we examined larval and egg mass density at the scale of the stream and the scale of the habitat segment within streams. For abundance classes, we used the minimum number of individuals as a conservative estimate of abundance (e.g., for class $x > 50$, we used 50). We used t tests and Mann-Whitney tests to test for relationships between treefrog density and both urbanization and crayfish presence. We report statistical results with a p value of 0.10 or less because of the high variability inherent in these data, the low power of the nonparametric tests used for most of the abundance data, and most importantly to increase our power to detect biologically important effects. Statistical tests were performed with SYSTAT and SPSS (for the piece-wise regressions) software (SPSS, Chicago, Illinois).

Results

Watershed Characteristics, Stream Flow, and Conductivity

The percentage of urbanization in the watersheds varied from 0.0 to 37.5%, with a mean of $8.4 \pm 9.5\%$ and a median of 5.9%. Stream gradient varied from 0.6% to 12.8%, with a mean of $4.6 \pm 3.4\%$ and a median of 3.5%.

Stream flow was not significantly related to gradient but was positively related to urbanization in the ANOVA (urban/natural $F_{1,29} = 5.33, p = 0.028$) and showed a significant jump effect in the piece-wise regression analysis

(intercept difference: $t = 1.98, p = 0.057$). The interaction between gradient and urbanization was also significant in the ANOVA ($F_{1,29} = 5.33, p = 0.028$). For low-gradient streams, flow was significantly higher in urban streams (mean of $1.27 \text{ m}^3/\text{second}$) than in natural streams (mean of $0.11 \text{ m}^3/\text{second}$), but there was no significant difference in high-gradient streams. Conductivity in urban streams (1643.3 microsiemens), was significantly higher than in natural streams (903.8 microsiemens) (Mann-Whitney $U = 49, p = 0.005$). The conductivity data could not be transformed for the ANOVA or piece-wise regression analyses with gradient.

Species Distribution

In more urban watersheds, some native amphibians such as California newts and California treefrogs were conspicuously absent from streams, whereas exotic aquatic species such as crayfish and introduced fish species were often present (Table 1). In natural streams, species presence was significantly more likely for California newts and California treefrogs and significantly less likely for exotic crayfish and fishes (newts $\chi^2 = 6.37, p = 0.012$; California treefrogs $\chi^2 = 5.22, p = 0.022$; Fisher exact tests: crayfish $p = 0.000$, exotic fish $p = 0.000$). Western toads exhibited variability in distribution between years. In 2000, but not in 2001, toads were detected significantly more often in urban streams (Fisher exact tests: 2000 $p = 0.034$, 2001 $p = 0.130$). Bullfrogs were present in only one stream, and Pacific treefrogs were found in every stream surveyed. The small overall sample size and skewed nature of the presence/absence data rendered logistic regression models (incorporating both urbanization and stream gradient) inappropriate.

Abundance

Because Pacific treefrogs were present in every stream surveyed, we examined the abundance of larvae and egg masses relative to both urbanization and the presence of crayfish. At the stream scale, larval treefrog density was not related to crayfish presence (2000 Mann-Whitney $U = 74, p = 0.521$; 2001 $U = 84, p = 0.873$) or to urbanization in 2000 ($U = 96, p = 0.693$), although in 2001 larval density was marginally higher in urban streams (1.21 tadpoles/m vs. 0.82 tadpoles/m in natural streams; $t = -1.704$ df = 30, $p = 0.10$). Egg mass density was significantly lower in urban streams in 2001 ($U = 183, p = 0.014$), when there were 0.254 egg masses/m in urban streams and 0.395 egg masses/m in natural streams, but was not related to urbanization in 2000 ($U = 103, p = 0.453$). Egg mass density was also significantly lower in streams with crayfish both in 2000, with 0.081 egg masses/m in streams without crayfish versus 0.004 egg masses/m in streams with crayfish ($U = 95.5, p = 0.055$), and in 2001, with 0.244 egg masses/m in streams without crayfish and 0.050 egg masses/m in streams with crayfish ($U = 142, p = 0.013$).

Table 1. Distribution of native amphibians and introduced aquatic species in streams in the Santa Monica Mountains and Simi Hills, California.

Stream	Area developed (%) ^a	Native species ^b				Introduced species ^b		
		TATO	HYCA	BUBO	HYRE	CRAY	RACA	exotic fishes
Lang Ranch, north	0.00	X			X			
Palo Comado Canyon	0.00			X	X			
Temescal Canyon	0.01	X			X			
Sullivan Canyon	0.17				X			
Big Sycamore Canyon	0.26	X	X		X			
Las Virgenes, north	0.70				X			
Wood Canyon	0.71				X			
La Jolla Canyon	0.75				X			
Rustic Canyon	1.45	X			X			
Solstice Canyon	2.07	X	X		X			
Cold Creek, upper	2.55	X	X		X			
Corral Canyon	2.91			X	X			
Arroyo Sequit	3.38	X	X		X			
Ramirez Canyon	3.46	X	X		X			
Serrano Canyon	3.99		X		X			
Trancas Canyon	4.06	X	X		X	X		
Deer Creek	4.58		X		X			
Carlisle Canyon	5.88	X	X	X	X			
Zuma Canyon	6.69	X	X		X			
Newton Canyon	6.84	X	X		X			
Tuna Canyon	6.89	X	X		X			
Cheeseboro Canyon	7.68			X	X			
Triunfo Canyon	8.26			X	X	X	X	X
Old Topanga Canyon	9.42			X	X			X
Lang Ranch, south	10.79			X	X			
Topanga Canyon, Upper	11.51			X	X	X		
Las Virgenes, south	12.28			X	X	X		X
Cold Creek, Lower	12.34	X	X		X			
Topanga Canyon, Lower	12.69	X	X	X	X			
Lower Malibu Creek	14.95				X	X		X
Erbes	16.37				X	X		X
Liberty Canyon	17.57				X			
Medea Creek, north	27.96			X	X	X		X
Lindero Canyon	36.77				X	X		X
Medea Creek, South	37.54			X	X	X		X

^aDevelopment includes industrial, commercial, residential, transportation, and floodway areas. Streams in watersheds with >8% development are classified as urban.

^bAbbreviations: TATO, *Taricha torosa*; HYCA, *Hyla cadaverina*; HYRE, *Hyla regilla*; BUBO, *Bufo boreas*; CRAY, *crayfish*, *Procambarus clarkii*; RACA, *Rana catesbeiana*.

In streams that had both crayfish and Pacific treefrogs, at the scale of the stream habitat segment larval treefrog density was significantly higher in segments without crayfish than in those with them, both in 2000 (0.730 tadpoles/m without crayfish and 0.293 tadpoles/m with them, $U = 2367$, $p < 0.001$) and in 2001 (2.820 tadpoles/m without crayfish and 0.820 tadpoles/m with them, Mann-Whitney $U = 3720$, $p < 0.001$).

Stream Habitats

Stream habitat was affected by urbanization (Table 2) and in some cases by gradient (Table 3). There was variation between years, but some effects were also consistent in both years, specifically the tendency for habitat segments, particularly runs, to be longer and for runs and pools to be deeper in urban streams. Overall, the effects of de-

velopment were particularly strong in 2001, when urban streams had longer pools, riffles, and runs, a higher percentage of the stream length in runs, and a lower percentage of the habitat segments as pools but a higher percentage of them as runs (Table 2, Fig. 3). When gradient was also an important factor, some effects were difficult to test for in high-gradient streams because we had only two high-gradient urban streams. In a number of cases, however, particularly in 2000, urban low-gradient streams ($n = 10$) were significantly different from natural low-gradient streams ($n = 6$) (e.g., for average stream segment length in 2000; Tables 2 & 3).

Based on the piece-wise regression analyses, the habitat changes relative to urbanization were related more to a jump effect (i.e., a large change at about 8% watershed urbanization) than to a change in the slope of the relationship. There was never a significant difference in the slopes

Table 2. Stream habitat characteristics in urban and natural streams in the Santa Monica Mountains and Simi Hills, California.

Stream characteristic	2000		2001	
	urban	natural	urban	natural
Average stream segment length (m)	21.08 ^a	9.46	17.65 ^b	8.81
Average pool length (m)	12.16	6.99	13.93 ^b	5.79
Average riffle length (m)	20.10 ^a	11.37	16.40 ^b	10.59
Average run length (m)	25.52 ^c	10.43	19.25 ^b	8.12
Stream length consisting of pools (%)	23.34	34.91	11.52	22.30
Stream length consisting of riffles (%)	43.85	47.75	41.82 ^a	55.35
Stream length consisting of runs (%)	32.81 ^a	17.34	46.35 ^b	22.35
Segments that are pools (%)	29.96	45.02	13.63 ^d	31.30
Segments that are riffles (%)	42.10	38.00	44.42	45.32
Segments that are runs (%)	27.93 ^a	16.98	41.73 ^b	23.38
Average pool depth (cm)	54.88 ^c	39.04	81.09 ^c	47.54
Average riffle depth (cm)	24.43 ^b	14.25	17.96	16.53
Average run depth (cm)	40.65 ^b	21.10	39.43 ^c	26.39

^aSignificant difference between urban and rural, low-gradient streams, Bonferroni comparisons based on overall $p = 0.05$.

^bSignificant difference between urban and rural streams at $p < 0.01$.

^cSignificant difference between urban and rural streams at $p < 0.10$.

^dSignificant difference between urban and rural streams at $p < 0.05$.

above and below 8%, but there was a statistically significant intercept change in 2001 for average pool length, percentage of segments that were pools, and percentage of segments that were runs (Fig. 2a). Also, for the habitat variables that showed a significant effect of urbanization in the ANOVA (significant F test), in 11 of 13 cases (3 of 4 in 2000 and 8 of 9 in 2001) the intercept difference was greater than the slope difference based on inspecting the t and p values (Table 3). In fact, there was little statistical evidence of continuous effects of urbanization on habitat; only 1 of 52 regression coefficients (26 variables \times 2 years \times 2 coefficients, urban and rural) computed for habitat variables were significantly different from 0 (average pool length in 2000; $t = 2.634$, $p = 0.015$).

Stream Permanence

Although there was annual variation, urban streams consistently had less dry streambed than natural streams (Table 4). Urban streams were not significantly wetter than natural streams in 2000, which was an El Niño year (streams with any dry: $\chi^2 = 0.785$, $p = 0.376$; percent stream length dry: Mann-Whitney $U = 118$, $p = 0.278$), but in 2001 and 2002 more natural streams had dry streambed and a greater percentage of the surveyed reaches were dry (2001—streams with any dry: Fisher exact test $p = 0.035$; percent stream length dry: $U = 156$, $p = 0.040$; 2002—streams with any dry: $\chi^2 = 6.65$, $p = 0.010$; percent stream length dry: $U = 224$, $p = 0.003$). In 2002, a very dry year, most or all of the surveyed reach of some of the natural streams was dry.

Invertebrates

Invertebrate communities also varied between streams and were related strongly to urbanization and stream gradient. Urban streams had lower invertebrate diversity,

greater dominance by the most common taxon and by more-tolerant taxa, and decreased percentages of more sensitive or intolerant taxa overall and within the EPT orders specifically. Within low-gradient streams, overall and EPT richness were also significantly lower in urban streams (Table 5). The piece-wise regression analyses for invertebrates were different from those for habitat variables, in that urbanization effects seemed to be more related to a change in slope than in intercept. Although there was a significant intercept difference for species richness, there was a significant slope difference for EPT taxa and for sensitive EPT taxa (Fig. 2b), and for four of the five variables where there was a significant urbanization effect in the ANOVA, the slope difference was greater than the intercept difference (t and p values, Table 3). The slopes of the relationship between urbanization and invertebrate indices were also significantly different from zero in three cases for natural streams (richness, $t = -2.43$, $p = 0.022$; EPT taxa, $t = -2.56$, $p = 0.016$; and sensitive EPT taxa, $t = -2.47$, $p = 0.020$) and in one case for urban streams (richness, $t = -2.31$, $p = 0.029$). For every variable, the slope of the relationship with urbanization was greater for natural streams than for urban streams.

The effect of stream gradient on invertebrates was consistently significant for five of the eight variables in both the categorical (ANOVA) and the continuous (piece-wise regression) analyses (Table 3). The proportion of EPT insects (EPT index) was not significantly related to urbanization, although it was related to gradient in both analyses.

Discussion

Habitat Changes, Distribution, and Abundance

In urban streams the absence of some native amphibians and the presence of exotic species such as crayfish and

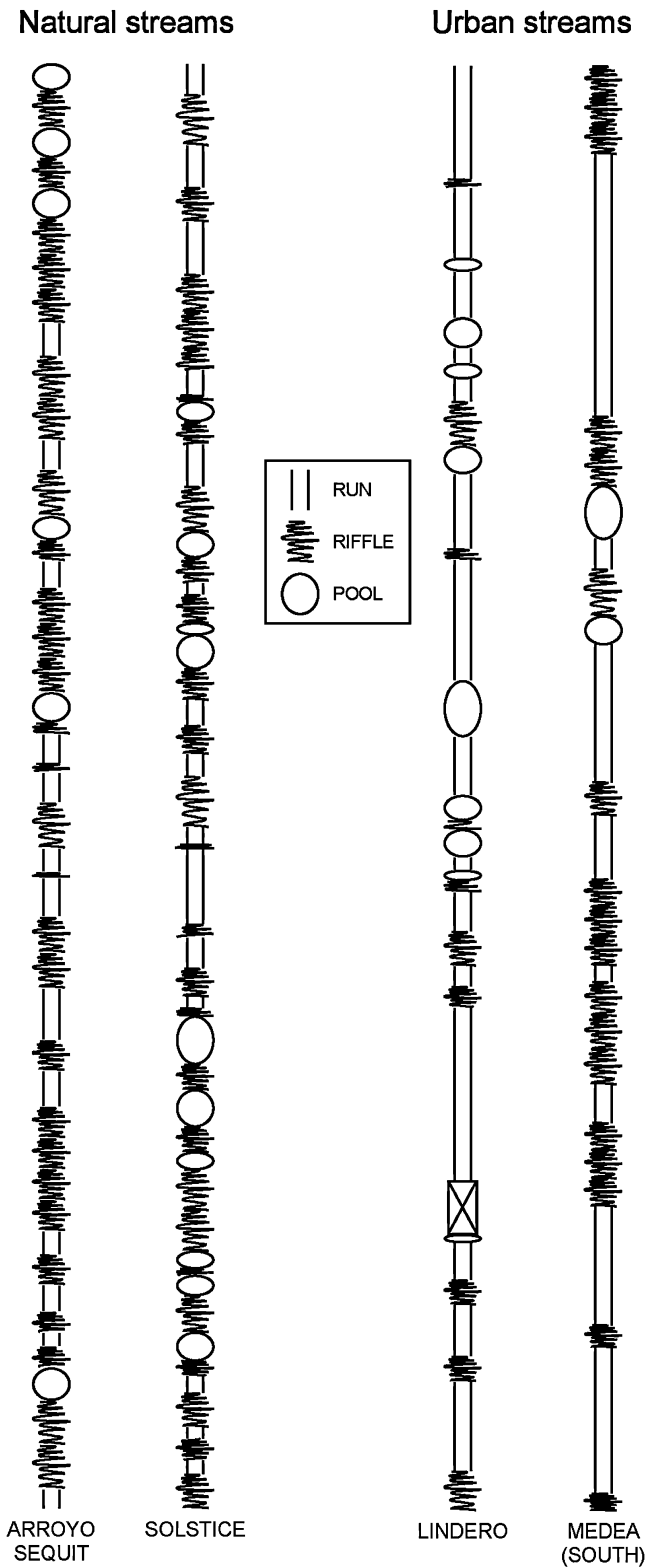


Figure 3. Schematic representation of habitat diversity (runs, riffles, and pools) in two urban and two natural streams in the Santa Monica Mountains and Simi Hills of southern California. The rectangle with an X on Lindero Creek represents a culvert.

Table 4. Stream permanence in urban and natural streams in the Santa Monica Mountains and Simi Hills, California.

Year and stream type	Length of dry stream (%)	Streams with dry bed (%)
2000		
urban	0.57	16.7 (2/12)
natural	8.22	33.3 (6/18)
2001		
urban	0.00	0 (0/12)
natural	5.79	30 (6/20)
2002		
urban	4.41	23.1 (3/13)
natural	38.11	68.2 (15/22)

introduced fishes are striking. Exotic crayfish also affect the abundance of Pacific treefrogs, the most widely distributed native amphibian. Macroinvertebrate communities were also less diverse and weighted toward tolerant species in urban streams. These faunal changes are most likely related to the significant differences in habitat structure, water quantity, and stream permanence associated with urban streams. The larger quantity of water in more urban streams is not surprising given increased water inputs in urban areas from, for example, watering lawns and gardens and washing cars and especially from increased runoff from impervious surfaces. These increased amounts of water most likely contribute to the changes in stream habitat structure that we saw, and both these factors have profound implications for populations of native and exotic species. In urban streams, habitat segments are longer and a greater percentage of the stream

Table 5. Macroinvertebrate community indices in urban and natural streams in the Santa Monica Mountains and Simi Hills, California.

	2001	
	urban (n = 13)	natural (n = 20)
Taxonomic richness	23.15 ^a	29.40
EPT ^b taxa	5.08 ^a	9.40
Percent EPT invertebrates	23.26	32.98
Percent sensitive EPT (TV ^c = 0-2)	0.97 ^d	13.33
Percent intolerant (TV = 0-3) organisms	1.03 ^e	10.65
Percent tolerant (TV = 8-10) organisms	13.34 ^f	9.90
Percent most dominant taxon	45.91 ^e	33.69
Shannon diversity	1.65 ^d	2.23

^aSignificant difference between urban and rural, low-gradient streams, bonferroni comparisons based on overall $p = 0.05$.
^bAquatic insect orders Ephemeroptera, Plecoptera, and Trichoptera.
^cTolerance values, a measure of sensitivity to disturbance and pollution with 0 being most sensitive and 10 most tolerant.
^dSignificant difference between urban and rural streams at $p < 0.01$
^eSignificant difference between urban and rural streams at $p < 0.05$.
^fSignificant difference between urban and rural streams at $p < 0.10$.

consists of runs. Overall, the result is fewer pools and a general decrease in habitat complexity (Fig. 3).

Determining the precise mechanisms behind the species distributions in these streams will require more detailed study, but there is already information about some of the important interactions in this system. For example, crayfish can negatively affect populations of native amphibians such as newts and treefrogs (Gamradt & Kats 1996; Goodsell & Kats 1999). For native species, a critical question is whether they would be present in the "urban" streams without the influences of development and exotic species. In the case of the California newt, it seems likely that they would be. In the Santa Monica Mountains and Simi Hills newts prefer pools for egg laying, and lower-gradient streams may have less pool habitat, but newts also lay eggs in slow-moving runs (Gamradt & Kats 1997). California newts breed in "ponds, reservoirs and slow-flowing streams" (Stebbins 1985), and in some parts of their range, newts will breed in cattle ponds and other bodies of water that are not particularly pristine (P. C. Trenham, personal communication).

At least three factors are detrimental to newt populations in urban streams. The increased quantity and flow of water and the concomitant increase in run habitat, decrease in pools, and decrease in habitat diversity reduce high-quality newt breeding habitat and negatively affect invertebrate prey communities. More permanent water in urban streams also allows increased presence and abundance of exotic predators, specifically crayfish. Although crayfish presence does not exclude newts, dense crayfish populations can reduce and even eliminate newt reproduction (Gamradt & Kats 1996). Finally, newts are highly visible, slow-moving animals that are easily collected by people. It is perhaps not surprising then that newts have been eliminated from virtually all urban streams in this area. At least 15 years ago, newts were present in two streams (Triunfo Canyon and Lower Malibu Creek), where we did not detect them (De Lisle et al. 1986). These streams were classified as urban in our study and now contain crayfish, introduced fishes, and in one case, bullfrogs.

The distribution of California treefrogs may be more strongly related to specific habitats, but urbanization may still play a role. Of the 14 streams with California treefrogs, the average gradient was 6.7%. All 14 had a gradient greater than the 3.5% median, and the two urban streams had gradients of 4.8% and 4.9%. California treefrogs prefer streams with large boulders and significant rock pool habitat (Cunningham 1964; Dole 1974; Harris 1975), both of which were typical of many of the higher-gradient streams. Nonetheless, the stream habitat alteration that appears to frequently accompany development, specifically an increase in run habitat and a decrease in pools, would be likely to negatively affect this species. California treefrogs are also very closely associated with stream habitat, in one study never moving more than 10 m from the stream, and only 5 m during the active season (Harris

1975); significant alteration of the streambed could reduce or eliminate populations. As with newts, we did not detect California treefrogs in the highly modified streams of Triunfo Canyon and Lower Malibu Creek, where they were found before 1985 (De Lisle et al. 1986).

Pacific treefrogs were present in every stream we surveyed, even those with the highest percentage of development in the watershed. Pacific treefrog density was also high in some of the most urban streams. It is not surprising that this species was the most prevalent amphibian in our surveys because it is a very widespread and adaptable frog that has not suffered the significant declines of other amphibians in California (e.g., Fisher & Shaffer 1996). Even Pacific treefrogs, however, were affected in this area: larval and egg mass densities were significantly lower in the presence of crayfish, and these exotic predators were more common in urban streams. Matthews et al. (2001) found that exotic trout species significantly restricted the distribution and reduced the abundance of Pacific treefrogs in the Sierra Nevada. Goodsell and Kats (1999) found Pacific treefrog tadpoles in 65% of the stomachs of exotic mosquitofish, and the presence of exotic fishes can reduce Pacific treefrog survival to near zero (Adams 2000). In the Washington studies, pond permanence by itself also reduced the survival and presence of native anurans (Adams 1999, 2000), a factor that could be leading to detrimental effects on this species in more permanent urban streams.

Our stream surveys were probably not the most effective tool for measuring the distribution and abundance of western toads. Toads often breed in ponds or small pools, and although we detected them in some of our streams, often we found them in only a few places or in a side pool, or we detected few individuals. Toads were most likely breeding in other pools and possibly human-made ponds (e.g., on golf courses) that we did not survey. Toads also can breed and develop quickly, so multiple visits within a year would be more effective for detection. Their association with urban streams, at least in 2001, may be related to an association with lower-gradient streams, where ephemeral pools may be more likely to form. Overall, stream gradient was significantly lower in streams with toads (0.025 with toads vs. 0.056 without toads, $t = 3.33$, $df = 32.8$, $p = 0.002$). Because of their more terrestrial habits, fast development time, and ability to breed in other, often ephemeral bodies of water, toads may be less affected than other native amphibians by the habitat and flow changes and introduced aquatic predators associated with urban streams. However, other effects of urbanization such as terrestrial habitat loss and fragmentation and the loss of ephemeral pools could negatively affect toads.

The presence of introduced species such as crayfish, exotic fishes, and bullfrogs generates two important questions: How did they get into a stream? Why do they persist? Most likely these species were dropped off by people

using them as fish bait or releasing pets. Bait-bucket introductions are a common potential mechanism of introduction for many aquatic animals, but they are difficult to document. Although the cause of the introduction is important in terms of preventing future instances, the more critical issue is why these animals persist. Permanent water is almost certainly the most important factor in exotic persistence. The climate in southern California is characterized by a long, dry summer, and many of the natural streams in the area are ephemeral. The increased likelihood of permanent water in urban streams (Table 4) coupled with the increased likelihood of introductions because of the higher human density could explain why so many of the urban streams have exotic species. Trancas Creek, the one natural stream with crayfish, is the exception that proves the rule. At the top of Trancas Creek is the Malibu golf club. The golf club ponds have crayfish populations that provide a recurring source of propagules, and golf-course maintenance generates perennial water availability.

Benthic macroinvertebrate communities were also significantly altered in urban streams, where they were less diverse and consisted more of disturbance-tolerant species and less of sensitive EPT taxa. Although more intensive monitoring would be necessary to reliably measure water-quality differences and their potential effects on invertebrates, the habitat changes, specifically the decrease in stream habitat diversity, associated with urban streams would definitely adversely affect invertebrate communities.

Stream Gradient and Urbanization Threshold Effects

Stream gradient can be an important determinant of stream ecological characteristics, and this was true for macroinvertebrate communities in particular in streams in the Santa Monica Mountains (Table 3). For habitat variables, gradient was rarely significant, although lower-gradient streams generally had more runs and longer pools and runs in 2000.

A confounding problem in our study, and possibly in other studies of development and stream ecology, is that stream gradient and urbanization are strongly negatively correlated (see also Morley & Karr 2002). Because our goal was to survey the entire region, we did not select only the most comparable streams. Therefore it is difficult for us to conclude as much about the effects of urbanization on high-gradient streams because we had only two streams in this category. The strong negative correlation between urbanization and gradient is not surprising, given that it is much easier to build on ground with gradual slopes and people like to live and work near water. This trend is especially dangerous for organisms like amphibians that require intact aquatic systems.

The effects of urbanization on amphibian distribution, stream habitat, and macroinvertebrate communities appeared to be related to a threshold level of development

within the watershed more than to the absolute level of development. Differences between urban and natural streams were often significant, but coefficients in the piecewise regression analyses were generally not. In other words, below about 8% watershed development, the effects of development may not yet be visible, but once this level of development was reached significant changes occurred and further effects were not as great as the jump across the threshold. Interestingly, the type of threshold effects may be different for macroinvertebrate communities than for habitat. For habitat the change around 8% urbanization seemed to be related more to a jump in the value of the variable rather than to a change in the slope or strength of the relationship. For invertebrates, the change in slope was generally more important than a jump effect. Two facts, that for a number of invertebrate indices the slope for natural streams was significantly different from zero, and that the natural slopes were always greater than the urban slopes, suggest that urban impacts on invertebrate communities may actually start below the 8% threshold apparent for habitat changes and amphibian and invasive species distributions.

The threshold effect of urbanization has been detected in other studies of urban streams (Paul & Meyer 2001), although in Santa Monica Mountain streams the threshold level appears to be at the low end of the 10–15% seen elsewhere. Stream communities in arid areas such as deserts or Mediterranean ecosystems may be particularly susceptible to urban impacts because the increased regularity of water flow increases stream permanence beyond that of natural conditions. In North Carolina the abundance of two plethodontid salamanders decreased with increasing watershed disturbance (including both agricultural and urban development), and for one species, the southern two-lined salamander (*Eurycea cirrigera*), there was a strong threshold effect at 20% disturbance (Willson & Dorcas 2003).

Conservation Management Implications

Land managers in urban areas should be aware that urban development can have profound implications for aquatic communities and that these effects may be manifested before they are expected. A relatively low level of development, as little as 10% or even 8%, as in our study, may be enough to significantly affect the system. Given the threshold nature of the effects, arresting watershed development just after the threshold is reached may be too late. Also, development does not have to be next to the riparian area itself, or even directly upstream, to have an effect; development within the watershed overall is the most significant factor. Directly addressing this issue for amphibians in the Southeast, Willson and Dorcas (2003) found that development within three different buffer zones regularly used in land-use planning had no effect on amphibian populations, whereas overall watershed development had a strong impact. Morley and Karr

(2002) also found that, while local effects can also be important, watershed development was a better predictor of stream changes than local development.

Those concerned with amphibian conservation must similarly be aware of the effects of urbanization on stream-dwelling species. Urban impacts on stream communities in general and on amphibian communities in particular may be especially severe and occur especially easily in arid environments, where the extra inputs of water in urban areas represent a great departure from the natural hydrological regime. Flow and permanence changes can then greatly facilitate the establishment of exotic species with the accompanying damage to native communities (e.g., Eby et al. 2003).

Our results indicate that monitoring for amphibians and exotics should be included as a regular component of stream-monitoring protocols. Although physical and chemical measures of stream conditions are clearly important, whenever possible it is desirable to measure biological conditions directly (Morley & Karr 2002). Frequently, biological conditions are evaluated by integrating multiple measures into an index of biological integrity, including measures of taxa such as algae, fish, and aquatic invertebrates. Both the evaluation of overall stream health and amphibian conservation would benefit greatly from including amphibians in the biological assessment of streams in general and of urban streams in particular.

Acknowledgments

We thank the many volunteers, interns, students, and National Park Service (NPS) biologists who helped collect the stream data for this project, including K. Asmus, E. Becerra, C. Bromley, M. Chang, J. Chraft, G. Gonzalez, H. Johnson, K. McCurdy, G. Pasrich, P. Roby, C. Schoonmaker, J. Sikich, J. Spring, J. Suing, F. Villalba, B. Westhouse, S. Williams, and the Topanga Canyon Stream team. We thank the NPS, California Department of Parks and Recreation, Mountains Recreation and Conservation Authority, Rancho Simi Recreation and Park District, Conejo Open Space and Conservation Agency, and Ahmanson Land Company for research access and permits. We thank A. Blaustein and two anonymous reviewers for comments on an earlier version of the manuscript. We particularly thank M. Mitchell and C. Wells for extensive and invaluable assistance with piece-wise regression.

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