
Effect of Introduced Crayfish and Mosquitofish on California Newts

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Abstract: *One goal of conservation biology is to explain population declines. We present field survey data and experimental evidence that implicate introduced predators as a possible cause of decline in the California newt (*Taricha torosa*). In 1994 and 1995 we surveyed 10 streams in the Santa Monica Mountains of southern California for amphibians. These streams contained California newts when surveyed between 1981 and 1986. Of the 10 streams surveyed in 1994, three contained introduced mosquitofish (*Gambusia affinis*) and/or crayfish (*Procambarus clarkii*). These three streams contained no California newt eggs, larvae, or adults. The seven streams without introduced predators contained California newts. We conducted laboratory and field experiments to determine if California newt larvae and egg masses are susceptible to predation by mosquitofish and crayfish. Results from these experiments indicate that crayfish consume California newt egg masses and that both mosquitofish and crayfish consume larval newts. In 24-hour field experiments, no newt larvae survived in crayfish enclosures, and only 13% of the larvae survived with mosquitofish. Newt larvae are known to have antipredator adaptations for native predators. Apparently, these adaptations are not adequate for coexistence with introduced crayfish or mosquitofish. Heavy rains in 1995 removed introduced crayfish from one stream. We found newt egg masses, larvae, and adults in that stream the following spring. This same stream showed no evidence of California newts when crayfish were present in matched-date surveys in 1994. These experiments and surveys present evidence that predation by mosquitofish and crayfish may cause localized decline of newts in mountain streams of southern California. Understanding the effects of nonnative species is an important step in preventing detrimental introductions in the future.*

Efecto de la introducción del cangrejo de río y del "mosquitofish" al tritón de California

Resumen: *Reportes recientes sobre la declinación a nivel mundial de anfibios han apresurado investigaciones sobre causas posibles. A pesar de esta atención, permanecen evidencias limitadas que explican esta declinación. En este documento, proecemos tanto recopilación de datos y evidencia experimental que implica depredadores introducidos como causas posible del declinamiento del tritón de California. En 1994, repetimos recopilaciones de datos para los anfibios en 10 arroyos que anteriormente fueron recopilados entre 1981-1986. De los diez arroyos analizados, tres contenían "mosquitofish" introducidas (*Gambusia affinis*) y/o cangrejo de río (*Procambarus clarkii*). Estos tres arroyos no contenían huevos, larva, o adultos de tritón de California (*Taricha torosa*). Los siete arroyos sin depredadores introducidos contenían tritón de California. Experimentos de campo y de laboratorio indican que el cangrejo de río consume masas de huevo del tritón de California. Experimentos similares indican que tanto el "mosquitofish" y el cangrejo de río consumen la larva de tritón. En experimentos de campo de 24 horas ninguna larva de tritón sobrevivió en recintos de cangrejo de río y solo 13% de la larva sobrevivió con el "mosquitofish." Hoy conocimiento que la larva de tritón ha tenido adaptaciones antidepredadores por depredadores nativos. Aparéntemente, estas adaptaciones no son adecuadas para la coexistencias con el cangrejo de río o el "mosquitofish." Aguaceros recios de 1995 removieron cangrejo de río introducidos de un arroyo. Encontramos masa de huevo, larva y adultos de tritón en ese arroyo esta primavera. El mismo arroyo no mostró evidencia de tritones de California cuando el cangrejo de río estaba presente en las mismas fechas de 1994. Estos experimentos y estudios presentan evidencias que de "mosquitofish" y cangrejo de río podrían producir declinamiento localizado de tritones en arroyos en las montañas de Santa Monica. Concluimos por hipótesis que los tritones adultos no pueden reproducir con éxito en arroyos con estos depredadores.*

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Introduction

Concern has increased recently about declines in amphibian populations worldwide (Barinaga 1990; Phillips 1990; Wake 1991; Blaustein et al. 1994a, 1994b; Cohn 1994; Pechmann & Wilbur 1994; Pounds & Crump 1994; Blaustein & Wake 1995). Despite studies designed to determine the origins of decline, few definitive answers have been presented. Because amphibians have permeable skin and unshelled eggs, and because they inhabit both water and land, amphibian populations may serve as indicators of environmental quality. Therefore, determining causes of amphibian decline could be an important step toward understanding the ongoing degradation of ecological resources.

Blaustein and Wake (1995) implicated habitat destruction as a primary contributor to amphibian decline. Destruction of habitat can be effected in many ways, including pollution, ultraviolet radiation, and alteration of wetlands. Introduced species are a separate stressor that may also contribute to amphibian decline (Hayes & Jennings 1986; Corn 1994). The direct and indirect effects of introduced species on the ecology of an organism have been documented in many studies (for review see Diamond & Case 1986). Several studies have documented the detrimental effect of fish introductions on native frogs (Cory 1963; Bradford 1991; Bradford et al. 1993; Brönmark & Edenhorn 1994). Hayes and Jennings (1986) implicated introduced bullfrogs as the primary cause of the decline of ranid species in western North America; they concluded that eradication of frogs in the Sierra Nevada were due to predation on tadpoles by introduced fishes. As convincing as these studies are, they are based primarily on survey data; few experiments have addressed the role of introduced predators in amphibian decline. Little is known about the impact of introduced species on native salamanders. In the Santa Monica Mountains of southern California, predation by introduced species may affect the distribution of California newts (*Taricha torosa*).

California newts are widely distributed in the Coast Range extending from northwestern to extreme southwestern California (Stebbins 1972). Adult California newts spend most of the year on land and return to streams to breed during winter rains (Stebbins 1972). After courtship and mating female newts oviposit in pools on undersides of rocks and on sticks. Adult newts leave the stream soon after breeding or remain in the water 3-6 weeks after egg masses hatch in May and June (Elliott et al. 1993). Reimer (1958) reported that larval newts begin metamorphosis in early September.

Aquatic predators are particularly detrimental to the egg and larval stages of most amphibians because these stages are restricted to water until metamorphosis. We studied two predators, mosquitofish (*Gambusia affinis*) and crayfish (*Procambarus clarkii*), both not native to

southern California. Virtually nothing is known about the effects of these predators on salamanders. Although California newt adults are known to be highly toxic to predators (Buchwald et al. 1964; Mosher et al. 1964), newt egg masses and larvae may be more vulnerable. Newt egg masses and larvae are known to have anti-predator defenses that facilitate coexistence with native predators. Egg masses contain a neurotoxin (Buchwald et al. 1964; Mosher et al. 1964), and larvae use chemical cues to hide from predators (Elliott et al. 1993; Kats et al. 1994). Because California newts have little or no evolutionary history with either introduced predator, anti-predator mechanisms for native predators may not be sufficient to allow coexistence with introduced species. We used field surveys to determine if California newts are sympatric with introduced predators. Laboratory and field predation trials tested hypotheses that introduced crayfish and mosquitofish adversely affect newt larvae and egg masses.

Methods

Field Surveys

We surveyed 10 streams in the Santa Monica Mountains (Los Angeles County) for amphibians (Fig. 1). Cold creek was divided into two distinct regions because a drainage culvert creates a barrier to most aquatic organisms between the two sections of stream. Ten streams were surveyed between 1981 and 1986, and all contained California newts (De Lisle et al. 1987). Unfortunately, De Lisle et al. (1987) did not note whether streams contained introduced predators. We surveyed the streams once between 15 May and 15 June 1994 and again between 15 May and 15 June 1995, which is during the breeding season when newts and their egg masses are normally found in streams (Stebbins 1972). We visually surveyed pools, runs, and riffles for both introduced predators and California newts for at least 350 m per stream. We

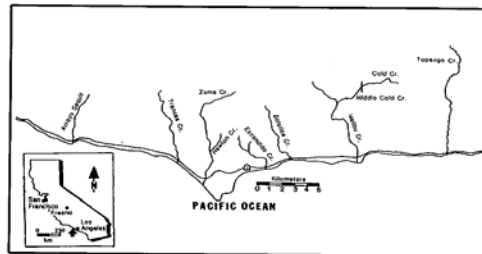


Figure 1. Study area location in southern California. The 10 streams surveyed are labeled.

used dive masks to examine pools because California newts prefer deeper, slow-moving water. Submerged rocks and vegetation were searched with an aquatic periscope or by hand for newt egg masses. Adult newts, egg masses, larvae, and introduced predators are relatively easy to count. In each stretch of stream we recorded the number of newts, and newt larvae, and egg masses, and the presence or absence of crayfish and mosquitofish. The particular stretches of Santa Monica Mountains streams (Los Angeles County) that we examined are perennial and contain no native fish.

Laboratory Predation Trials

Crayfish used in laboratory experiments were collected on 7 June 1994 from a local stream containing introduced crayfish. Crayfish (mass: mean = 20.4 g, SD = 3.9, $n = 12$; carapace length: mean = 4.5 cm, SD = 0.3, $n = 12$) were fed three pellets of rabbit food each per day. Mosquitofish (standard length: mean = 4.3 cm, SD = 0.2, $n = 12$) were collected from local streams or were obtained from the Los Angeles County Mosquito Abatement District in early June. They were maintained on a diet of Tetra-min fish food. *T. torosa* egg masses (mass: mean = 4.1 g, SD = 0.4, $n = 18$; number of embryos: mean = 18.7, SD = 4.7, $n = 18$) were collected between 10 May 94 and 12 June 94 from local streams free of crayfish and mosquitofish. Newt larvae were raised in the laboratory raised from egg masses collected between 10 May 94 and 12 June 94 from local streams free of crayfish and mosquitofish. Newt larvae (total length: mean = 14.1 mm, SD = 1.0, $n = 24$) were approximately 2 weeks old and were maintained on *Daphnia* ad libitum and/or freeze-dried bloodworms (Wardley Corporation).

All test organisms were maintained in aerated tubs (39 × 46.5 × 13 cm) in a cold room at 11°C on a 12-hour light-dark cycle. The tubs were filled to a depth of 6 cm with dechlorinated tap water.

Egg mass palatability trials began at 1500 hours on 8 June 1994. Crayfish were put in individual plastic tubs and fed three rabbit food pellets each on 7 June 1994. After feeding, the tub water was changed and the crayfish were deprived of food for 24 hours to standardize hunger. Each mosquitofish was fed two flakes of Tetra-min at 1500 on 7 June, after which the water in the tubs was changed. The fish were then deprived of food for 24 hours to standardize hunger. Egg masses were removed from the cold room 4 hours prior to the experiment at 1100 hours on 8 June to prevent temperature shock. At 1500 hours on 8 June, one egg mass was introduced into each of 18 tubs (39 × 46.5 × 13 cm). The temperature of the air and water was 22°C. The experiment was conducted on a 12-hour light/dark cycle. The three treatments, one egg mass with one crayfish, one egg mass with one mosquitofish, and one egg mass

alone were replicated six times simultaneously in a random spatial arrangement. The tubs were checked periodically to monitor predation or attempted predation. Embryo survivorship was checked at 24 and 48 hours, after which the experiment was concluded. Percent survival data were arcsin-square-root-transformed for data analysis. We used a one-way analysis of variance to compare groups; Fisher's protected least significant difference was used for pairwise comparisons.

Newt larvae palatability trials were conducted with identical methods as egg mass trials except that tubs contained refuge plates consisting of 10 cm × 10 cm × 5.5 mm black, opaque, plexiglas plates raised 1 cm from the bottom of the tub. One refuge plate was placed at the midpoint of the ends of each tub. The experiment consisted of three treatments: four larvae with one crayfish, four larvae with one mosquitofish, and four larvae alone. Four larvae were introduced into the center of each tub at 1500 hours on 22 June 94 after the predators had been deprived of food for 24 hours. Each tub was monitored for 1 minute every hour until 2200 hours and again from 700 to 1500 hours on the following day. During that minute we recorded larval movement, predator movement, number of larvae in refuge, and number of larvae consumed. Larval movement consisted of the total number of moves made by larvae. One body length of movement constituted a move. Predator movement consisted of total number of predator moves per minute. Movement of one body length constituted a move. Number in refuge was obtained by counting the number of larvae that were in refuge during the minute. Great care was taken not to disturb the organisms while observing them. The experiment lasted 24 hours and was conducted on a 12-hour light-dark cycle. Each treatment was replicated six times simultaneously in a random spatial arrangement. Percent survival data were arcsin-square-root-transformed for data analysis. A one-way analysis of variance was used to compare groups; Fisher's protected least significant difference was used for pairwise comparisons.

Field Predation Trials

Field predation experiments were conducted at a local stream that contained introduced crayfish. Each trial was conducted in a 72 × 45 × 21 cm plastic box with the bottom cut out to provide a natural substrate. Bottoms of boxes were sunk 5 cm in the rock and sand stream bottom in slow-moving areas of the stream. Depth of water in the boxes varied from 6 cm to 12 cm. The control treatment consisted of a box containing one newt egg mass. The experimental treatment consisted of a box containing one crayfish and one newt egg mass (mass: mean = 3.8 g, SD = 1.0, $n = 12$; embryo count: mean = 17.0, SD = 6.2, $n = 12$). Control and experimental treatments were paired side by side in the stream. Mosqui-

tofish were not included in field egg-mass predation experiments because they did not consume egg masses in laboratory trials. Crayfish (mass: mean = 21.4 g, SD = 2.4, $n = 6$; carapace length: mean = 4.7 cm, SD = 0.2, $n = 6$) were collected on the day of the experiment from pools in the stream. We conducted six replicates of each treatment; three replicates of each treatment were conducted on both 14 June and 16 June 1994. Crayfish were placed in the boxes at 1400 hours and allowed to acclimate until 1500 hours. At 1500 hours one egg mass was placed at the end of each box. We recorded embryo survivorship after 24 hours. All boxes in control and experimental replicates were covered with screening because crayfish can escape from captivity in the laboratory. Water temperature varied from 16.9 to 17.8°C. Air temperature varied from 18 to 22°C. Percent embryo survival data were arcsine-square-root-transformed for data analysis. We used a two-tailed t test to compare control and crayfish data.

Field predation experiments involving newt larvae were conducted with methods similar to egg mass experiments. Newt larvae averaged 13.8 mm total length (SD = 0.9, $n = 12$). Three treatments were performed: four newt larvae with three mosquitofish (standard length: mean = 3.9 cm, SD = 0.4, $n = 12$), four newt larvae with one crayfish (carapace length: mean = 4.9 cm, SD = 0.1, $n = 6$; mass: mean = 20.4 g, SD = 1.8, $n = 6$), and four newt larvae alone (control). The substrate of each box closely resembled a natural stream bottom, so natural rock and leaf refuge was available. Predators were placed in the tubs at 0700 hours and allowed to acclimate until 0730 hours. At this time the newt larvae were placed in the tubs. Each replicate lasted 24 hours. Larval survivorship was assessed the following morning at 0730 hours. Each treatment was replicated six times. Control and experimental treatments were placed side by side in the stream. Three replicates of each treatment were conducted on both 24 June and 25 June 1994. Percent survival data were arcsine-square-root-transformed for data analysis. A one-way analysis of variance was

used to compare groups; Fisher's protected least significant difference was used for pairwise comparisons.

Results

Distribution of *Taricha torosa* and Introduced Predators

All 10 streams surveyed contained newts 10 years ago (De Lisle et al. 1987); seven streams contained newts in 1994 (Table 1). The three streams without newts contained introduced predators. One contained crayfish, one contained mosquitofish, and one contained both. The seven streams with breeding newt populations in 1994 did not contain either of these introduced predators. Distributions of California newts and introduced predators were not random with respect to each other (Fisher's exact test, $p < 0.05$).

Eight of the 10 streams contained newts in 1995. The two streams without newts still contained introduced predators. Newts were found at one site, Trancas Creek, where they were absent in 1994. In 20 trips to this stream in June and July of 1994, no newt adults, larvae, or egg masses were found. In six pools that seemed ideal newt habitat, 126 crayfish (*P. clarkii*) were observed on 31 May 1994. On 7 June 1994, 117 crayfish were observed in the same six pools. In 1995 we did not find crayfish in these pools (Table 2). In 14 surveys of these six pools from February through July of 1995, no crayfish were observed, but we did observe California newts. On 3 May 1995, 51 newt adults were observed and 141 newt egg masses were counted in these six pools. Matched date surveys from 1994 and 1995 show this change in community composition at Trancas Creek (Table 2).

Predation Experiments

Introduced crayfish (*Procambarus clarkii*) consumed California newt egg masses in the laboratory. The sur-

Table 1. Distribution of California newts and introduced predators in 10 streams of the Santa Monica Mountains in 1994–1995.

Stream	<i>P. clarkii</i> (crayfish)	<i>G. affinis</i> (mosquitofish)	<i>T. torosa</i> (California newt)	Distance (m)
Cold Creek	Absent	Absent	Present	1500
Middle Cold Creek	Absent	Absent	Present	500
Newton Creek	Absent	Absent	Present	350
Arroyo Sequit	Absent	Absent	Present	500
Topanga Creek	Absent	Present	Absent	510
Malibu Creek	Present	Present	Absent	900
Solstice Creek	Absent	Absent	Present	400
Zuma Creek	Absent	Absent	Present	1150
Escondido Creek	Absent	Absent	Present	530
Trancas Creek (1994)	Present	Absent	Absent	711
Trancas Creek (1995)	Absent	Absent	Present	711

Table 2. Density of California newts and introduced crayfish in six pools in Trancas Creek in 1994–1995.

31 May 1994					
Pool	Crayfish (number)	Crayfish/m ²	Newt larvae/m ²	Newt egg masses	Newt adults
1	1	0.32	0	0	0
2	22	0.46	0	0	0
3	9	0.83	0	0	0
4	50	0.59	0	0	0
5	20	0.39	0	0	0
6	24	0.88	0	0	0
Total	126				
Mean density		0.58 ± 0.1 SE	0	0	0
2 June 1995					
Pool	Crayfish (number)	Crayfish/m ²	Newt larvae/m ²	Newt egg masses	Newt adults
1	0	0	10	12	2
2	0	0	0	2	2
3	0	0	15	11	1
4	0	0	24	26	8
5	0	0	0	6	0
6	0	0	0	10	1
Total	0				
Mean density		0	8.2 ± 4.1 SE	67	14

vival rate of newt embryos in crayfish tubs was 13% (Fig. 2). Five of six crayfish tested consumed more than 90% of the newt embryos enclosed in the egg mass gelatin. The other crayfish consumed 45% of the embryos in the egg mass. Crayfish scraped at the gelatin with their maxillipeds then consumed the embryos. Mosquitofish did not consume a significant number of embryos; predation was observed in only one tub, and overall 96% of the embryos survived. All embryos in control treatments survived. Crayfish predation on newt egg masses was significantly higher than in control and mosquitofish treatments (one-way ANOVA; $F = 68.2$, $df = 2, 15$, $p < 0.001$).

In the field, crayfish again consumed a significant number of embryos (two-tailed t test; $t = 3.6$, $p = 0.007$; Fig. 3). Two experimental replicates were lost because the crayfish in the experimental tubs escaped by burrowing. The crayfish had eaten all embryos contained in the egg masses before their escape, but we did not include these replicates in our analysis. In three of the four other crayfish replicates the crayfish consumed 85% or more of the embryos in the egg masses. In control treatments, 95% of embryos survived. The crayfish were again observed scraping through the gelatin coating to expose embryos.

In the laboratory both mosquitofish and crayfish consumed a significant number of newt larvae (one-way ANOVA; $F = 8.6$, $df = 2, 15$, $p = 0.002$; Fig. 2). In crayfish treatments 17% of larvae survived. In mosquitofish

treatments 46% of newt larvae survived. In control replicates 96% of larvae survived. There was no significant difference between treatments in predator movement, movement of larvae, or refuge use of larvae.

In field experiments survivorship was low for newt larvae with predators present. In crayfish treatments no larvae survived. In mosquitofish treatments 13% of larvae survived. In control treatments 88% of larvae survived and were recovered. Both crayfish and mosquitofish consumed a significant number of larvae (one-way ANOVA; $F = 31.5$, $df = 2, 15$, $p < 0.001$).

Discussion

One goal in ecology is to understand the importance of predators in determining community structure (Kats et al. 1988). The effects of predation on population dynamics have been well documented (Murdoch & Oaten 1975; Hassel 1978; Petranka 1983; Taylor 1984), as have the effects of predators on community structure (Paine 1966; Connell 1975; Diamond 1975; Macan 1977; Zaret 1980; Sih et al. 1985, 1992; Sih 1987; Alford 1989). Because predators have both direct predatory effects as well as indirect consequences on prey behavior, anti-predator adaptations are under strong selection pressures (Sih 1987). While coevolving with native predators prey organisms often evolve antipredator behaviors (for

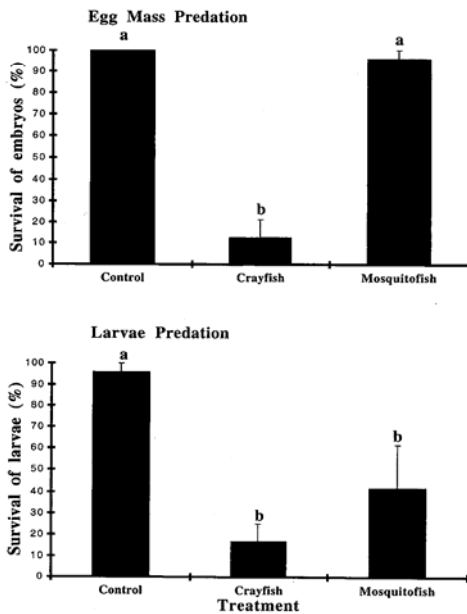


Figure 2. Mean percent survival (± 1 SE) of newt embryos and larvae in laboratory predation experiments ($n = 6$). Different alphabetic superscripts indicate means that differ significantly (Fisher's PLSD post-hoc test, $p < 0.05$).

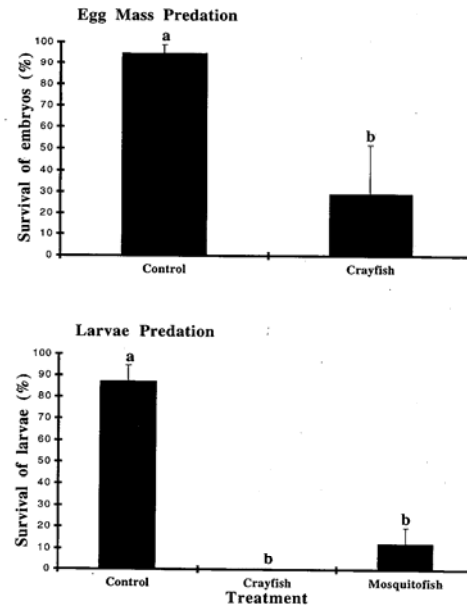


Figure 3. Mean percent survival (± 1 SE) of newt embryos and larvae in field predation experiments ($n = 6$). Different alphabetic superscripts indicate means that differ significantly (Fisher's PLSD post-hoc test, $p < 0.05$).

review see Dill 1987; Lima & Dill 1990). When nonnative predators are introduced, native prey organisms are exposed to new selection pressures. California newts that breed in streams of the Santa Monica Mountain do not appear to have adaptations that permit co-occurrence with introduced mosquitofish and crayfish.

Previously, California newt egg masses were thought to be well protected from predators. The embryos are enclosed in a mucopolysaccharide capsule that serves as an antipredator device (Ward & Sexton 1981; Kats et al. 1992). California newt eggs also contain a potent neurotoxin (Buchwald et al. 1964; Mosher et al. 1964). These predator-deterrent mechanisms appear effective against native predators, as most native stream predators avoid preying on California newt egg masses (personal observation). Three studies have examined predation on California newt egg masses (Kaplan & Sherman 1980; Marshall et al. 1990; Kats et al. 1992). These studies examined only intraspecific predation by cannibalistic adult newts. Introduced crayfish are not deterred by the gelatin capsule or embryo toxicity. Crayfish seem to be

pre-adapted for preying on California newt eggs. They have traits that make predation on newt eggs very likely: constant foraging in areas where newt eggs are likely to be found (e.g., in submerged vegetation, under rocks), apparent resistance to newt toxin, and an ability to tear through protective gelatin that normally shields developing embryos. The introduction of a predator that could consume newt eggs would be disastrous to a newt population because natural egg mass predation is minimal in streams free of nonnative predators.

Predation on newt larvae by crayfish and mosquitofish was observed in both laboratory and field experiments. Mosquitofish are capable of dramatically altering aquatic community structure (Hurlbert et al. 1972), as are crayfish (Feminella & Resh 1989; Olsen et al. 1991; Lodge et al. 1994). California newts were absent from both creeks that contained introduced mosquitofish. Crayfish are benthic feeders, and observations of newt larval behavior indicated poor defense mechanisms against crayfish. Newt larvae did not show significant use of refuge plates when exposed to chemical cues from introduced

predators in flow-through experiments (unpublished data); when exposed to actual predators, newt larvae still did not hide significantly. The lack of antipredator behavior in response to mosquitofish and crayfish likely leads to the high mortality observed in both the laboratory and the field.

The situation at Trancas Creek provided a natural experiment. In 1994 crayfish were abundant at Trancas Creek. In 1995 crayfish were not present. Heavy rainfall in the winter of 1994–1995 (Los Angeles 10-year mean rainfall = 32.7 cm; winter of 1994–1995 rainfall = 49.2 cm) may have washed the crayfish out of the creek. The adult newt population at Trancas Creek returned to the stream in the spring of 1995 and reproduced successfully. We know that crayfish have inhabited Trancas Creek for a minimum of 5 years (personal observation). Adult California newts are relatively long-lived (10–15 years; Twitty 1942). Adult newts have apparently been able to “outlast” crayfish and have resumed breeding at Trancas Creek. One other study has documented a similar return of amphibian adults after removal of introduced predators. After fish were removed from a pond with introduced fish, tree frogs returned the following spring to breed successfully (Brönmark & Edenhamn 1994). Introduction or colonization of fish into previously fishless waters have also affected amphibian populations in other systems (Macan 1966; Sexton & Phillips 1986; Semlitsch 1988; Ross 1991; Bradford et al. 1993; Semlitsch 1993). To our knowledge ours is the first study to examine the effects of an introduced invertebrate on amphibians.

We hypothesize that introduced crayfish and mosquitofish have the ability to inhibit reproductive success of California newts by direct predation on egg masses and larvae. Further, alteration of adult newt breeding behavior by introduced predators may prevent successful mating and oviposition. Oviposition site selection by other stream-breeding salamanders is influenced by predator presence (Kats & Sih 1992). In laboratory experiments (unpublished) we have observed crayfish attacking adult newts and forcing newts to leave the water. Toxic adult newts are presumably not susceptible to predation, but the effects of introduced predators on newt behavior might further inhibit successful breeding.

Our study indicates that introduced predators are detrimental to native amphibians. Determining the severity of this impact is essential for taking suitable measures to prevent further introductions and to preserve amphibian habitat. In southern California, nonnative crayfish are available as bait, and mosquitofish are distributed freely by county mosquito-control personnel. Thus, these predators are apparently introduced accidentally or deliberately into Santa Monica Mountain streams. Further introductions are probable. We conclude that habitats free of nonnative predators must be protected from these introductions to conserve the amphibian communities in the Santa Monica Mountains.

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