what lakes?

Trends Sierra Nevada Lakes 98.[illegible]-15

E. M. 1984. Recognition of individual s... cies odours by salamanders of the *Plethodon* ... *us–P. jordani* complex. Anim. Behav. 32:353...

986. Behavioral isolating mechanisms in ... ic terrestrial salamanders. Herpetologica 42... 4.

.987. Species discrimination between ... ig and nonhybridizing terrestrial salaman... opeia 1987:924–931.

A., C. A. SIMON, G. A. MIDDENDORF AND ... ANO. 1977. Iguanid substrate licking ... to novel situations in *Sceloporus jarrovi* ...)6–709.

E. 1983. Integrating the ecology and ph... of plethodontid salamanders. Herpetolog... –310.

.. A., AND R. G. JAEGER. 1988. Territorial ... iones of female red-backed salamanders ... gy 78:143–152.

.. G., AND W. F. GERGITS. 1979. Intra- and ... ecific communication in salamanders through ... al signals on the substrate. Anim. Behav. ... 6.

M. GOY, M. TARVER AND C. E. MAROU... Salamander territoriality: pheromonal ... s as advertisement by males. Ibid. 34:8...

A. 1984. Neontological inferences of ... ry pattern and process in the salaman... Plethodontidae, p. 119–217. *In*: Evolution... logy. Vol. 17. M. K. Hecht, B. Wallace ... rance (eds.). Plenum Press, New York, N...

ND R. HIGHTON. 1978. Geographic ... on and divergence in the salamanders of ... *m welleri* group (Amphibia: Plethodonti... ool. 27:431–448.

). B. WAKE AND K. P. YANEV. 198... gene flow among populations having ... f genetic fragmentation. Genetics ...

, D. M. 1975. Intraspecific odor pref... n salamanders of the same sex: dep... on and proximity of residence. Can. J. ... 6–1361.

977. Chemical communication in ... d reptiles, p. 135–168. *In*: Chemical ... ebrates. D. Muller-Schwarze and M. M... .). Plenum Press, New York, New Y...

A, V. C. 1976. Size and environment ... lity for salamanders. Ecology 50:69...

1977. Observations of salamanders ... Urodela, Plethodontidae) dying in ... etol. 11:1–5.

K. 1987. Social behavior of the west... salamander, *Plethodon vehiculum* ... lissert. University of Victoria, Vic... umbia.

, R. L., AND R. A. NUSSBAUM. 197... biology and population structu...

western red-backed salamander, *Plethodon vehiculum* (Cooper). J. Herpetol. 7:215–224.

SEVER, D. M. 1978a. Female cloacal anatomy of *Plethodon cinereus* and *Plethodon dorsalis* (Amphibia, Urodela, Plethodontidae). J. Herpetol. 12:397–406.

———. 1978b. Male cloacal glands of *Plethodon cinereus* and *Plethodon dorsalis* (Amphibia, Urodela, Plethodontidae). Herpetologica 34:1–20.

SIMON, G., AND D. M. MADISON. 1984. Individual recognition in salamanders: cloacal odours. Anim. Behav. 32:1017–1020.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. W. H. Freeman & Co., San Francisco, California.

SPSSX USER'S GUIDE. 1985. SPSS Inc. McGraw-Hill Book Co., Inc., New York, New York.

STOREY, R. M., AND E. D. BRODIE, JR. 1970. *Plethodon vehiculum*. Catalogue of American Amphibians and Reptiles 83:1–83.

TRISTRAM, D. A. 1977. Intraspecific olfactory communication in the terrestrial salamander *Plethodon cinereus*. Copeia 1977:597–600.

WAKE, D. B., G. ROTH AND M. H. WAKE. 1983. On the problem of stasis in organismal evolution. J. Theor. Biol. 101:211–224.

KRISTINA OVASKA, *The Bellairs Research Institute, McGill University, St. James, Barbados, W.I.*

Accepted 7 Nov. 1988.

Copeia, 1989(3), pp. 775–778

ALLOTOPIC DISTRIBUTION OF NATIVE FROGS AND INTRODUCED FISHES IN HIGH SIERRA NEVADA LAKES OF CALIFORNIA: IMPLICATION OF THE NEGATIVE EFFECT OF FISH INTRODUCTIONS.—In high elevation (>2500 m) lakes of the Sierra Nevada of California, the distribution of a native ranid frog (*Rana muscosa*) and introduced trout (*Salmo* spp.) and charr (*Salvelinus* spp.) appear to be allotopic, i.e., populations of frogs and fish appear not to co-occur in the same lake (e.g., Grinnell and Storer, 1924; ..., 1963; Zardus et al., 1977). Although quantification of this relationship is poor, the pattern is substantiated by the occurrence of conspicuously large numbers of *R. muscosa* in lakes that lack fish. Prior to the stocking of Sierra Nevada lakes with salmonid fishes, which began over a century ago, fish were naturally absent from most of this region (Hubbs and Wallis, 1948; Christenson, 1977). Today, hundreds of high Sierra Nevada lakes are populated with trout and charr (Christenson, 1977).

The apparent allotopic distribution of frogs and fish has been interpreted as a case of elimination of native frog populations due to predation by introduced fishes (Grinnell and Storer, 1924; Walker, 1946; Hayes and Jennings, 1986). The hundreds of high Sierra Nevada lakes that now contain trout and charr may have previously supported substantial populations of frogs. Hayes and Jennings (1986) argued that predation by introduced fishes is the most compelling hypothesis explaining the apparent declines that have occurred among most of the native ranid frogs in western North America.

The present study tests the hypothesis that populations of two native frogs, *R. muscosa* and *Pseudacris* (=*Hyla*) *regilla*, and introduced fishes do not co-occur in high Sierra Nevada lakes. The study also assesses the importance of lake depth in determining the occurrence of these animals.

Methods.—Data were obtained for 67 lakes in the Tablelands and Ansel/Blossom lakes areas of Sequoia National Park and Kings Canyon National Park, both in California. These two areas were selected because both frogs and fishes occur in each area, numerous lakes occur in each area, and both areas lie within a 1 d hike from a road. The two areas, which together are approx. 18 km² in total area, lie 23 km apart in the watersheds of the Kings and Kaweah rivers. Forty-nine of the lakes surveyed appear on U.S. Geological Survey 15 min quadrangles (Mineral King, Triple-Divide Peak); the remainder are small and, in some cases, ephemeral. The precise locations and other data for all lakes are on file at Headquarters, Sequoia and Kings Canyon National Parks, Three Rivers, California.

Surveyed lakes ranged from approx. 2910–3430 m in elevation, from approx. 0.004–7 ha in area, and from 0.3–37 m in maximum depth. Rooted vegetation was generally sparse and restricted to water shallower than 0.5 m deep. Shorelines were typically rocky, surrounded by subalpine forest or alpine fell-fields plant communities of Munz and Keck (1965). Fingerling rainbow trout (*Salmo gairdneri*), brook charr (*Salvelinus fontinalis*), and possibly golden trout (*Salmo aguabonita*) have been introduced to several lakes in each area at various times since about 1930, and possibly earlier (Meyer, 1965; Christenson, 1977; Zardus et al., 1977). Anuran amphibians observed in each area were the mountain yellow-legged frog (*R. muscosa*) and the Pacific treefrog (*P.* [=*Hyla*] *regilla*). *Bufo bo-*

OCCURRENCE OF FISH AND TADPOLES IN ... ATER THAN 1.5 M DEEP. Values represent ... lakes. The data from Zardus et al. (1977) ... ır lakes that were included in the present ... data for tadpoles from Zardus et al. (1977) ... ıpoles or frogs visible in large numbers in ..." The distributions of fish and tadpoles ... lakes did not overlap in the present study ... < 0.001), nor in Zardus et al. (1977) (G-test, $P < 0.01$).

Present study			Zardus et al. (1977)		
Fish present	Fish absent	Total	Fish present	Fish absent	Total
0	30	30	0	2	[illegible]
7	3	10	116	15	131
7	33	40	116	17	133

ximum depth of the lakes was mea... ılumb line from a small boat in 81 ... .es that were deeper than 1.0 m. In ... ıder of lakes deeper than 1.0 m, the ... ıint in the lake was visible from shore ... epth at this point was estimated ... e depth of lakes shallower than 1.0 m ... ıted visually or by plumb line. Stat... are described in Sokal and Rohlf ...

Fish and tadpoles were allotopically ... ı among the lakes in the two stu... ı and tadpoles did not coexist in ... akes surveyed, yet 49 lakes cont... or tadpoles. To test the hypoth... stributions did not overlap, data ... for lakes deeper than 1.5 m ... selected because fish appeared to ... to such lakes (Fig. 1). In the 40 ... ın 1.5 m, fish and tadpoles sho... ly non-overlapping distribution ... : 0.001). This pattern was app... R. muscosa distribution (n = 40 ... h contained tadpoles; Fig. 1) and ... a distribution (n = 40 lakes ... tained tadpoles, Fig. 1). However ... ıs significant only for *R. musc*... 0.001). The analysis of the da... al. (1977) for 133 other lakes ...) showed that the populations of ... es do not coexist (Table 1; $P < 0.01$) ... ıilar analysis, the hypothesis of ...

TABLE 2. OCCURRENCE OF *Rana muscosa* TADPOLES AND *Pseudacris regilla* TADPOLES IN LAKES GREATER THAN 1.3 M DEEP. Lakes containing fish are excluded. Values represent number of lakes. The distributions of the two species among the lakes were not significantly different (G-test, $P \gg 0.05$).

	P. regilla tadpoles present	*P. regilla* tadpoles absent	Total
R. muscosa Tadpoles present	6	25	31
R. muscosa Tadpoles absent	3	3	6
Total	9	28	37

... overlapping distributions of *R. muscosa* tadpoles and *P. regilla* tadpoles was tested (Table 2). The minimum depth for analysis was 1.3 m, which is approximately the minimum lake depth for *R. muscosa* (Fig. 1). Among the 37 lakes greater than 1.3 m deep which did not contain fish, the distributions of *R. muscosa* and *P. regilla* populations did not differ significantly (Table 2; G-test, $P \gg 0.05$). Six lakes contained both *R. muscosa* and *P. regilla* tadpoles (Table 2).

Lake depth is an important factor determining the occurrence of fish and *R. muscosa* tadpoles: fish appear to be restricted to lakes with a maximum depth greater than approx. 1.5 m, and *R. muscosa* tadpoles to lakes with a maximum depth greater than 1.3 m (Fig. 1). In lakes with maximum depths greater than these values, the occurrence of fish and *R. muscosa* tadpoles was not significantly influenced by depth. This is shown by a comparison of the maximum depths of inhabited and uninhabited lakes for each of these two taxa (Fig. 1; Mann-Whitney U test, $P \gg 0.05$). In contrast, *P. regilla* tadpoles occurred in even the shallowest lakes (Fig. 1). *Pseudacris regilla* inhabited lakes with significantly shallower maximum depths than either *R. muscosa* or fish (Mann-Whitney U test, $P <$ 0.001 in both cases). The distribution of *P. regilla* tadpoles was not significantly influenced by lake depth above the minimum lake depth of 0.3 m (Mann-Whitney U test, $P \gg 0.05$).

Discussion.—The present study documents the observation that fish and viable frog populations do not coexist in high Sierra Nevada lakes (e.g., Grinnell and Storer, 1924; Cory, 1963; Zardus et al., 1977). The distribution of trout and charr in the study areas has been established by stocking, which has been repeated in hundreds of lakes in the Sierra Nevada for over at least four decades (Christenson, 1977; Zardus et al., 1977). The exclusion of frog populations from lakes containing introduced salmonids may be due to predation on tadpoles and frogs by the introduced fishes. *Salmo* spp. and *Salvelinus* spp. are almost exclusively insectivorous or carnivorous (Moyle, 1976) and will strike tadpoles of *R. muscosa* when they are placed in a lake (pers. obs.). Cory (1963) reported that larval and post-metamorphic *R. muscosa* show a distinctive escape behavior in waters containing fish but lack such behavior in waters devoid of fish. Tadpoles and frogs have few refuges from fishes in high Sierra Nevada lakes that are deep enough to support fish because during most of the year these lakes lack vegetative cover, and large tributary streams are lacking. Moreover, in the case of *R. muscosa*, tadpoles at high elevation always overwinter at least once, during which time they seek the warmer, deeper water beneath the ice cover (Bradford, 1984).

The impact of introduced salmonids on *R. muscosa* populations may have been substantial. Prior to stocking of high Sierra Nevada lakes and streams with trout and charr, virtually all high Sierran lakes were barren of fish (Hubbs and Wallis, 1948; Moyle, 1976; Christenson, 1977). Although several native salmonids inhabited the west slope of the Sierra Nevada, steep canyon gradients prevented colonization of high elevation lakes and streams as Pleistocene glaciers receded, except for much of the upper Kern River basin that was not subject to glaciation (Schreck and Behnke, 1971; Moyle, 1976; Christenson, 1977). Prior to stocking, however, populations of *R. muscosa* may have been present in most lakes and streams of the high Sierra Nevada. Evidence for this assertion is that the historic range of *R. muscosa* is primarily the Sierra Nevada at 1400–3700 m elevation (Zweifel, 1955) and *R. muscosa* populations currently occur in a large proportion of the lakes deeper than 1.5 m that lack fish (present study; pers. obs.). In many of these lakes, *R. muscosa* are exceedingly abundant (Grinnell and Storer, 1924; Bradford, 1983, 1984). In some cases hundreds of frogs and hundreds of tadpoles can be counted along a 100 m section of shoreline (Bradford, 1984). As a result of stocking with salmonids, about 60% of the approx. 3000 lakes in the Sierra Nevada are now inhabited by fish, primarily rainbow trout, gold-

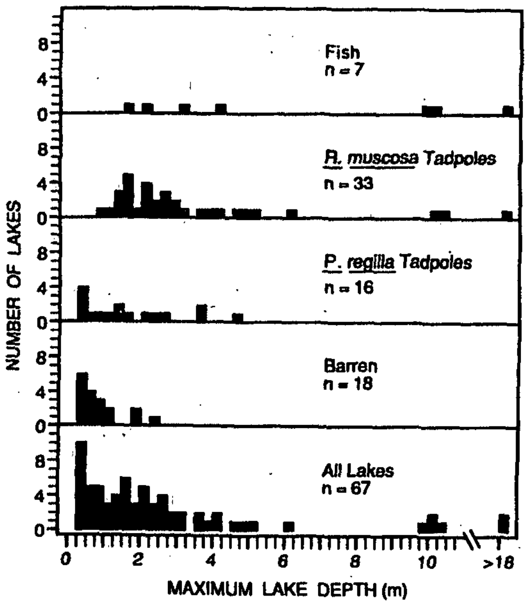

Fig. 1. Occurrence of introduced fishes (rainbow trout, *Salmo gairdneri*, or brook charr, *Salvelinus fontinalis*) and tadpoles of the mountain yellow-legged frog (*Rana muscosa*) and Pacific treefrog (*Pseudacris* [=*Hyla*] *regilla*), as a function of maximum depth in 67 high Sierra Nevada lakes. Tadpoles did not coexist with trout or charr in any lakes, whereas *R. muscosa* and *P. regilla* tadpoles coexisted with each other in seven lakes.

reas may be present but was not observed during the lake survey or other visits.

Each lake was examined at least once for the presence of fish and tadpoles during the summers of 1978 or 1979. The occurrence of fish was determined by visual observation from shore or boat of individual fish or signs of surface feeding. These determinations were corroborated by data in recent National Park Service surveys (Zardus et al., 1977), general knowledge of backcountry rangers, and/or the presence or absence of signs of fishermen. The presence of tadpoles was assumed to represent the existence of a reproductively viable population of frogs in a lake. During the summer, tadpoles of both *R. muscosa* and *P. regilla* occur almost entirely in shallow water near shore (Bradford, 1984) and are easily detected by searching the shoreline, even in the deepest lakes. The entire shoreline was searched in all but the largest lakes, in which case at least one-third of the shoreline was searched.

Table 1. Occurrence of Fish and Ta[dpoles in] Lakes Greater than 1.5 m Deep. Valu[es are] number of lakes. The data from Zardus et [al. (1977)] exclude four lakes that were included in th[e present] study. The data for tadpoles from Zardus e[t al.] are for "tadpoles or frogs visible in large nu[mbers in] open water." The distributions of fish and [tadpoles] among the lakes did not overlap in the prese[nt study] (G-test, $P < 0.001$), nor in Zardus et al. (19[77]) ([G-]test, $P < 0.01$).

	Present study			Zardus et al. (1977)		
	Fish present	Fish absent	Total	Fish present	Fish absent	[illegible]
Tadpoles present	0	30	30	0	[illegible]	[illegible]
Tadpoles absent	7	3	10	116	16	[illegible]
Total	7	33	40	116	17	[illegible]

The maximum depth of the lakes was m[ea]sured by plumb line from a small boat in 3[illegible] the 47 lakes that were deeper than 1.0 m [illegible] the remainder of lakes deeper than 1.0 m, [the] deepest point in the lake was visible from sho[re] and the depth at this point was estimated [vi]sually. The depth of lakes shallower than 1.0 [m] was estimated visually or by plumb line. Stati[s]tical tests are described in Sokal and Rohlf (1981).

Results.—Fish and tadpoles were allotopically distributed among the lakes in the two stud[y] areas. Fish and tadpoles did not coexist in any of the 67 lakes surveyed, yet 49 lakes contained either fish or tadpoles. To test the hypothesis that the distributions did not overlap, data were compared for lakes deeper than 1.5 m. This depth was selected because fish appeared to be restricted to such lakes (Fig. 1). In the 40 lakes deeper than 1.5 m, fish and tadpoles showed significantly non-overlapping distributions (Table 1; $P < 0.001$). This pattern was apparent for fish vs *R. muscosa* distribution (n = 40 lakes, 28 of which contained tadpoles, Fig. 1) and fish vs *P. regilla* distribution (n = 40 lakes, seven of which contained tadpoles, Fig. 1). However, the pattern was significant only for *R. muscosa* (G-test, $P < 0.001$). The analysis of the data in Zardus et al. (1977) for 133 other lakes in the region also showed that the populations of fish and tadpoles do not coexist (Table 1; $P < 0.01$).

In a similar analysis, the hypothesis of non[-]

[Table 2.] Occurrence of *Rana muscosa* Ta[dpoles and *Pseudacris*] *regilla* Tadpoles in Lakes G[reater than] 1.3 m Deep. Lakes containing fish are ex[cluded. Values re]present number of lakes. The distr[ibutions of the two s]pecies among the lakes were no[t significa]ntly different (G-test, $P \gg 0.05$).

	P. regilla tadpoles present	*P. regilla* tadpoles absent
R. muscosa tadpoles present	6	25
R. muscosa tadpoles absent	3	3
Total	9	28

[overla]pping distributions of *R. muscosa* [and] *P. regilla* tadpoles was tested (Tabl[e] [The mi]nimum depth for analysis was 1.3 [m, ap]proximately the minimum lake [depth for *R.*] *muscosa* (Fig. 1). Among the 37 lak[es] [greater tha]n 1.3 m deep which did not contai[n fish, the dist]ributions of *R. muscosa* and *P. reg*[*illa*] [distribu]tions did not differ significantly [(G-test], $P \gg 0.05$). Six lakes containe[d *R. mus*]*cosa* and *P. regilla* tadpoles (Tabl[e] [La]ke depth is an important factor [influenc]ing the occurrence of fish and *R. m*[*uscosa*]. [Ty]pically fish appear to be restricted to [lakes with] maximum depth greater than app[roximately] [1.5 m a]nd *R. muscosa* tadpoles to lakes w[ith maxi]mum depth greater than 1.3 m (Fig. [In lakes] with maximum depths greater tha[n] [these depths], the occurrence of fish and *R.* [*muscosa* tad]poles was not significantly influence[d by depth.] This is shown by a comparison of th[e maximum] depths of inhabited and uninhabit[ed lakes for] each of these two taxa (Fig. 1; Ma[nn-Whitney] U test, $P \gg 0.05$). In contrast, *P. reg*[*illa*] occurred in even the shallowest la[kes.] *Pseudacris regilla* inhabited lakes [with signifi]cantly shallower maximum depth[s than] *R. muscosa* or fish (Mann-Whitney [U test, $P <$] 0.01 in both cases). The distributio[n of *P. regilla*] tadpoles was not significantly influ[enced by] depth above the minimum lake d[epth] (Mann-Whitney U test, $P \gg 0.05$

Discussion.—The present study c[onfirms the] assertion that fish and viable fr[og populations] do not coexist in high Sierra Nev[ada lakes] (Grinnell and Storer, 1924; Cory [...] et al., 1977). The distribution of t[...]

en trout, and brook charr (Meyer, 1965; Christenson, 1977), and may be devoid of *R. muscosa*.

The impact of fish introduction was probably much less significant for populations of *P. regilla* and the other two aquatic breeding anurans that occur at high elevation in some parts of the Sierra Nevada, *B. boreas* and *B. canorus*. These species metamorphose within one season (Karlstrom, 1962) and thus are not restricted to permanent or deep water. In the present study, *P. regilla* inhabited significantly shallower lakes than fish; more than one-half of the lakes inhabited by *P. regilla* were shallower than any lake inhabited by fish (Fig. 1).

Lake depth appears to be a significant factor determining the occurrence of fish and *R. muscosa*, largely because both fish and *R. muscosa* tadpoles are restricted to permanent water. *Rana muscosa* tadpoles require two (and sometimes three) summers to develop through metamorphosis (Zweifel, 1955; pers. obs.). Moreover, overwintering fish and frogs (but not tadpoles) are susceptible to winterkill due to oxygen depletion in shallow lakes (Bradford, 1983). Consequently, both fish and *R. muscosa* occur primarily in lakes greater than about 1.3 m deep. In contrast, *P. regilla* tadpoles at high elevations undergo metamorphosis within one season and inhabit many lakes that are shallow and dry up during late summer (pers. obs.). *Pseudacris regilla* may select shallow lakes for breeding because water temperature is generally higher than in deeper lakes (unpubl.). Metamorphosed *P. regilla* overwinter on land.

Acknowledgments.—Research was supported in part by National Science Foundation grant DEB 81-03513, administered by G. A. Bartholomew, and National Institute of Health training grant GM 07191. I am grateful for assistance from G. A. Bartholomew, L. Cory, S. Oates, D. Riska, B. Smith, and the National Park Service.

Literature Cited

Bradford, D. F. 1983. Winterkill, oxygen relations, and energy metabolism of a submerged dormant amphibian, *Rana muscosa*. Ecology 64:1171–1183.

———. 1984. Temperature modulation in a high-elevation amphibian, *Rana muscosa*. Copeia 1984: 966–976.

Christenson, D. P. 1977. History of trout introductions in California high mountain lakes, p. 9–16. *In:* Proceedings of a symposium on the management of high mountain lakes in California's national parks. A. Hall and R. May (eds.). 1976, California Trout, Inc. and Amer[illegible] eries Society, Fresno, California.

Cory, L. 1963. Effects of introduced [illegible] evolution of native frogs in the high Sierra [illegible] mountains, vol. 2, p. 172. *In:* Proc. XVI [illegible] Congr. Zool. J. A. Moore (ed.). 20–27 A[illegible] Washington, D.C., published by XVI In[illegible] Congress of Zoology, Washington, D.C.

Grinnell, J., and T. I. Storer. 1924. A[illegible] in the Yosemite. University of Californ[illegible] Berkeley, California.

Hayes, M. P., and M. R. Jennings. 1986. D[illegible] ranid frog species in western North Am[illegible] bullfrogs (*Rana catesbeiana*) responsible? [illegible] tol. 20:490–509.

Hubbs, C. L., and O. L. Wallis. 1948. Th[illegible] fish fauna of Yosemite National Park and [illegible] ervation. Yosemite Nature Notes 27:131–1[illegible]

Karlstrom, E. L. 1962. The toad genus *Bu*[illegible] Sierra Nevada of California; ecological and sy[illegible] atic relationships. Univ. Calif. Publ. Zool. [illegible] 104.

Meyer, F. A. 1965. Golden trout waters of Cali[illegible] nia. California Department of Fish and Gam[illegible] land Fish. Admin. Rept. No. 65-1.

Moyle, P. B. 1976. Inland fishes of California. [illegible] versity of California Press, Berkeley, Californ[illegible]

Munz, P. A., and D. D. Keck. 1965. A Califo[illegible] flora. University of California Press, Berkeley, [illegible] ifornia.

Schreck, C. B., and R. J. Behnke. 1971. Trou[illegible] the upper Kern River basin, California, with r[illegible] erence to systematics and evolution of western No[illegible] American *Salmo*. J. Fish. Res. Bd. Canada 28:98[illegible] 998.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. 2nd ed. W. H. Freeman & Co., San Francisco, Califo[illegible] nia.

Walker, M. V. 1946. Reptiles and amphibians [illegible] Yosemite National Park. Yosemite Nature No[illegible] 25:1–48.

Zardus, M., T. Blank and D. Schulz. 1977. Stat[illegible] of fishes in 137 lakes in Sequoia and Kings Cany[illegible] National Parks, California. U.S. Department of [illegible] Interior, National Park Service, Sequoia and King[illegible] Canyon National Parks, Three Rivers, Californ[illegible]

Zweifel, R. G. 1955. Ecology, distribution, and sy[illegible] tematics of frogs of the *Rana boylei* group. Univ. Calif. Publ. Zool. 54:207–292.

David F. Bradford, *Department of Biology, University of California, Los Angeles, Californ[illegible] 90024. Present address: Environmental Scien[illegible] and Engineering Program, School of Public Health, University of California, Los Angeles, Californ[illegible] 90024.* Accepted 23 Nov. 1988.