

## Population Declines of Yosemite Toads in the Eastern Sierra Nevada of California

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**ABSTRACT.**— This paper documents changes in the size of a breeding population of Yosemite toads, *Bufo canorus*, over 20 years at Tioga Pass, California. Surveys of *B. canorus* numbers in breeding aggregations were made yearly from 1971 to 1982, and less systematic observations were made from 1983 to 1991. Six other populations in the eastern Sierra Nevada were surveyed occasionally from 1973 to 1990. The total number of marked males entering the largest breeding pools at Tioga Pass declined nine-fold from 1974 to 1982. The mean number of toads found in daily searches during breeding also dropped over the 20 year study. Similar declines occurred at smaller breeding sites throughout Tioga Pass Meadow and at the six other populations. In 1990 we found evidence for continued reproduction by *B. canorus* at all but one location (Sylvester Meadow), although reproduction was minimal at Tioga Pass. No single source of mortality was responsible for all the declines. We interpret the decline in our study populations as caused primarily by drought, disease, and predation. Spring snow depths in 1976, 1977 and 1987-1991 were below the 62 year average, resulting in low tadpole survival. The death of adults from disease at Tioga Pass, and from predation at another site (Mildred Lake) also contributed to the declines. Although habitat destruction and localized human activities were not major factors, some natural variables responsible for the declines may have had anthropogenic components.

In February 1990, the National Research Council's Board on Biology sponsored a workshop to examine the evidence for a recent widespread decline in amphibian populations (Barinaga, 1990; Blaustein and Wake, 1990; Wake and Morowitz, 1990). Although the participants concluded that many populations are declining, they found little evidence for a single global cause. Possible reasons for the declines included habitat destruction, land use changes, introduction of exotic species, pesticide pollution, pathogens, acid rain, and predation by humans. These local factors may have acted synergistically with global effects, such as increased ultraviolet radiation exposure or changes in climate, to cause population declines (Blaustein and Wake, 1990). The workshop concluded that long-term studies are needed to separate natural population fluctuations from declines caused by human activities. They recommended that amphibian biologists reexamine their data from work done in the 1970s and 1980s (e.g., Bradford, 1991; Pechmann et al., 1991), and return to former study sites to evaluate current population sizes (e.g., Schuierer and Anderson, 1990).

Recent publications support several of the workshop's findings. First, mass mortality of adults and/or larvae, resulting in population size fluctuations, has been documented in various amphibians (Bradford, 1983, 1991; Pechmann et al., 1991; Olson, *in press*). However, yearly fluctuations did not always correlate with

an overall decline in numbers, reemphasizing the need for long-term studies to detect directional changes (Pechmann et al., 1991; Wissinger and Whiteman, 1992). Second, many of the declines apparently had multiple causes, which sometimes varied between populations of a species (Beebee, 1977; Beebee et al., 1990; Carey, *in press*; Olson, *in press*). Both natural and man-made factors were implicated. In some cases the declines were localized (Corn and Fogleman, 1984; Harte and Hoffman, 1989; Bradford, 1991; Wissinger and Whiteman, 1992) and in others they were widespread (Bradford, 1983). Several investigators suggested that apparently natural causes of decline may have had underlying anthropogenic components (Carey, *in press*; Olson, *in press*). For example, Carey (*in press*) hypothesized that acid precipitation or some other environmental factor had stressed populations of *B. boreas* in Colorado, resulting in immunosuppression and an outbreak of disease.

Anecdotal information suggests that the Yosemite toad, *Bufo canorus*, is one of the species which has declined (Blaustein and Wake, 1990). We studied the behavior and physiology of *B. canorus* intensively from 1971 to 1982 (Morton and Sokolski, 1978; Kagarise Sherman, 1980; Morton, 1981, 1982). Incidental to our main studies, we gathered information about the size of breeding populations at Tioga Pass, California. Six other populations within 53 km of our main study area were also surveyed during this period. In light of the current interest in am-

phibian numbers, and because our research spanned the period during which other populations declined, we reexamined our demographic data and resurveyed our study populations in 1990. This paper presents the trends in population abundance over a 20 yr period and identifies naturally-occurring factors contributing to losses in several populations. Our results provide a database for future studies of *B. canorus*, and comparative data for the analysis of amphibian population trends.

Yosemite toads inhabit an area of 240 km × 60 km in the central Sierra Nevada at elevations of 1950–3444 m (Karlstrom, 1962). They are sexually dichromatic (Karlstrom, 1962), diurnal (Mullally, 1953; Mullally and Cunningham, 1956; Karlstrom, 1962), and active above ground for only about four months each year (Karlstrom, 1962; Morton, 1981). Kagarise Sherman (1980) found that at Tioga Pass Meadow, adults emerge from hibernation in May or June and breed for 2–4 wk in May–July, depending on the depth of spring snowpack and time of its melt; most females spawn during a 2–3 d peak each year. Oviposition sites are the shallow edges (≤5 cm deep) of pools or slow moving runoff streams (Mullally, 1953; Karlstrom, 1962; Kagarise Sherman, 1980). Tadpoles transform in 50–63 d; some breeding sites are ephemeral and dry up before tadpoles metamorphose (Karlstrom, 1962; Cunningham, 1963; Kagarise Sherman, 1980).

#### METHODS

**Study Areas and Techniques.**—Our study area was Tioga Pass Meadow (TPM), a 0.5 × 1.0 km subalpine meadow near Tioga Pass, Mono County, California (119°E, 38°N, elevation 3030 m, Fig. 1). We made most of our observations within the main study pools, a 60 × 75 m area near Tioga Lake (#1 in Fig. 1, elevation 2950 m), where pairs spawned in four small tarns and several grassy depressions filled by melting snow. Breeding aggregations also formed at nine other sites in TPM.

Morton and his assistants studied *B. canorus* from June to August 1971–1976. Kagarise Sherman and 1–4 assistants gathered data during: 8 May–30 August 1976, 21 April–7 August 1977, 12 May–17 August 1978, 8 June–27 June 1979, 13 May–18 July 1981, and 12 June–29 July 1982. In 1983–1991 Morton was at TPM nearly daily from May or June through August, and he made unsystematic observations of *B. canorus*. In 1990 we resurveyed all breeding sites in TPM on 8 and 12 June, when, based on the snowmelt, toads should have been breeding. Morton searched for toads or signs of breeding again on 10 and 20 July 1990.

Beginning in 1973–1977, six other *B. canorus*

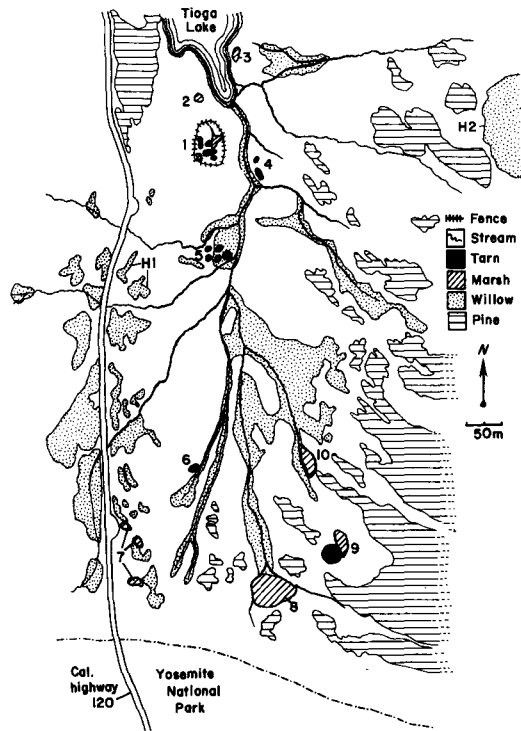


FIG. 1. Tioga Pass Meadow, California, showing location of main study pools (#1), small breeding sites (#2–10), and one hibernation site (H1). The edge of ca. 100 × 300 m willow thicket (H2) used by non-breeding females and immatures for hibernation and summer habitat is indicated. Tarns were small, steep-banked pools; details of the meadow's vegetation in Karlstrom (1962).

populations located between 1.6 km and 53.1 km from TPM (Fig. 2) were canvassed around breeding areas from June to early September. From 9 to 11 June 1990 we rechecked these six populations; Morton resurveyed three of the populations (Saddlebag Lake NW, Frog Lakes, and Hoover Lake) on 7–8 July 1990.

We marked Yosemite toads using a modified version of Martof's (1953) system. Each toad was given an identifying number by clipping off no more than one toe per forefoot and two toes per hindfoot; after 1976 we did not remove males' thumbs to avoid affecting their abilities to amplex females. We returned each toad to its capture location after marking. From 1971 to 1982 we toe-clipped males, females, and immatures (probably 2–3 yr old) throughout TPM, and in 1974, 1976–1979, 1981 and 1982, we marked all adult toads found breeding at the main study pools. Toads were also marked at Saddlebag Lake NW in 1976–1981, and at Sylvester Meadow in 1975 and 1976.

Unless otherwise indicated, the descriptive

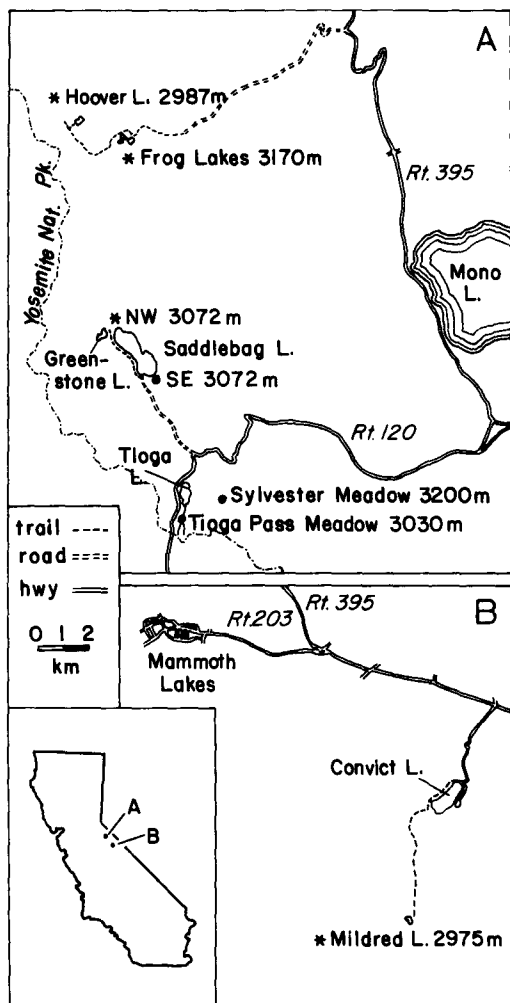


FIG. 2. Location of *Bufo canorus* populations surveyed in eastern Sierra Nevada, Mono Co., California. Sites indicated with an asterisk are located near permanent lakes.

statistics given are mean values  $\pm$  one standard deviation.

**Variation in Survey Procedures.**—We determined toad population sizes by five methods involving direct enumeration. We did not use mark-recapture models (e.g., Jolly-Seber) because several critical assumptions of these models were violated by our survey techniques.

First, we counted the total number of marked adults that gathered at the main study pools during breeding in a given year by: a) making repeated searches of the entire area, catching all toads seen, marking any unmarked animals, and recording toe-clip numbers (in 1974, 1979–1982); and b) encircling the pools with a 0.6 m high wire mesh fence with pairs of pitfall traps

sunk in the ground at approximately 12 m intervals (in 1976–1978). Toads were not able to get over or under the fence; buckets and the fence's perimeter were checked 3–6 times daily. These methods enabled us to make a nearly complete count of the *B. canorus* that entered the pools during a breeding season.

Second, we calculated the mean number of toads ( $\pm$  standard error) found per survey in the main study pools during breeding in 1971–1975, 1977–1982, and 1990. We systematically walked throughout all of the main study pools and recorded the number of males, females, unsexable immatures, and 1 yr olds captured or seen. (Toads were marked with visible tags in 1976–1982 and did not have to be recaptured to be identified; Kagarise Sherman, 1980.) Surveys were made around midday at the height of breeding activity. In 1977 and 1978 surveys were made throughout the breeding period. However, because surveys in earlier years were biased toward days of peak activity, to achieve equivalence in the 1977 and 1978 means we used surveys from the day on which the largest number of females spawned,  $\pm$  four days.

Third, in 1976 we did not conduct daily surveys of the main study pools. Instead, we computed the mean number of males and females found per survey by modifying 1976 fence data with a conversion factor based on the 1978 surveys. This was necessary because although we knew how many toads were inside the fence each day (Kagarise Sherman, 1980), some may have remained in their nighttime retreats in burrows or under objects (Karlstrom, 1962; Kagarise Sherman, 1980), and would not have been seen. The conversion factor was the mean percentage of males and females inside the fence that were actually found during the nine 1978 surveys described above. For example, on 1 July 1978, 135 males and 26 females were inside the fence (fence data), but only 40 males (30%) and 6 females (23%) were found during our survey that day. The conversion factors were thus  $32 \pm 11\%$  for males and  $26 \pm 24\%$  for females; these factors were multiplied by the 1976 fence data from nine days around the peak of female spawning. The adjusted values were then used to determine the mean number of males and females found per survey in 1976 at the main pools.

We feel justified in using 1978 data to generate the conversion factors for the 1976 data for two reasons. First, the amount of cover in the main study pools did not change between years, suggesting that the visibility of toads did not change. Second, we checked the procedure on the 1977 data. We compared the mean number of males and females found per survey to mean values computed from the fence data us-

ing 1978 conversion factors. The differences were not significant for either sex (male mean for survey data =  $20.0 \pm 11.6$ , modified fence data =  $21.6 \pm 11.3$ ; female mean for survey data =  $2.6 \pm 1.8$ , modified fence data =  $2.2 \pm 2.9$ ; Mann Whitney U,  $P > 0.05$ ,  $n = 9$ ).

Fourth, we made less systematic checks of the main study pools each spring when *B. canorus* should have been breeding in 1983–1989 and 1991. We walked through breeding habitat, looked for toads, eggs, and tadpoles, and listened for calling males. Numbers of breeding females cannot be accurately determined by counting clutches because eggs are often laid in communal masses. In addition, beginning in 1971 we monitored other sites in TPM (Fig. 1) for breeding activity. Breeding toads were occasionally counted to determine if similar changes in numbers were occurring at these sites. We also periodically searched for toads in non-breeding habitat and known hibernation sites (e.g., H1 and H2, Fig. 1).

Fifth, systematic surveys were infrequently made at *B. canorus* populations outside of TPM (Fig. 2) during breeding, and afterwards in the surrounding habitat. We recorded the number of adult, immature (2–3 yr old, and 1 yr old), and newly-transformed toads found during each survey. The level of effort varied among surveys, so we compared relative abundance (number of toads found/person hour of searching). Surveys were not made often enough to permit an analysis of differences in male and female numbers; therefore we combined adult males, adult females, and immatures ( $\geq 2$  yr old) to calculate yearly means.

Adverse weather may cause a decrease in *B. canorus* breeding activity (Kagarise Sherman, 1980). However, we did not note the weather conditions during each survey we made, but assumed that the variation introduced into our results by differences in weather was random with respect to year.

#### RESULTS AND DISCUSSION

*Numbers of B. canorus Marked.*—From 1971 to 1982 we individually marked 2270 *B. canorus* at TPM: 1259 males, 779 females, and 232 unsexable immatures (2–3 yr old). Smaller numbers of toads were marked at Saddlebag Lake NW (101 males, 76 females, 27 immatures in 1976–1981) and at Sylvester Meadow (two males, five females, eight immatures in 1975–1976).

*Population Declines in TPM.*—From 1974 to 1978 the total number of marked males entering the main study pools each year varied between 162 and 342 (Fig. 3). However, only 75 males appeared in 1979 and by 1982 the number of males had fallen to 28, a nine-fold decline from the 1974–1978 mean ( $257.5 \pm 83.1$ ). The drop in the

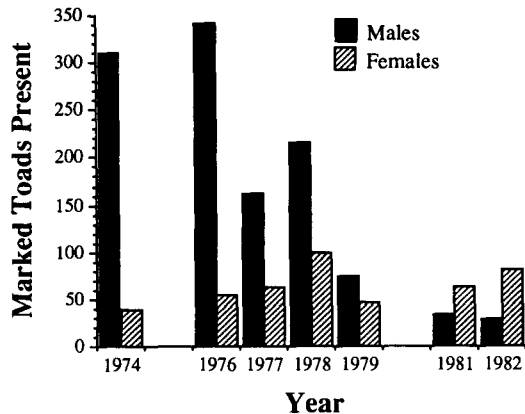


FIG. 3. Total number of marked *B. canorus* males and females present in main study pools at TPM each year. In 1974 and 1979–1982 toads were found in pools; in 1976–1978 toads were captured at fence encircling pools. Total numbers not determined in 1975 and 1980.

number of males cannot be attributed to movements to other breeding sites; only 1.5% (8/522) of the males that were seen at the main study pools in 1976–1979 were ever found breeding in nearby pools (#2–5 in Fig. 1; Kagarise Sherman, 1980). In contrast to males, the total number of marked females entering the main pools varied between 45 and 100, but showed no obvious decline from 1974 to 1982 (Fig. 3).

The mean number of males found per survey at the main study pools declined during 1979–1982; the mean number of females varied but did not decline until after 1982 (Fig. 4). Periodic checks of the main study pools in May–August 1983–1991 suggested that male numbers continued to decline, female numbers also fell, and breeding activity became sporadic. From 1983 to 1986 we heard or saw only 2–4 toads on any given day at the pools. Several males were heard calling in 1987–1988; two males were found in 1988. No calling males were heard in 1989. We found clutches in the main pools during 1983–1986, but did not find any females or eggs in 1987–1989. During two thorough searches of the pools in 1990 we found one female, two calling males and 4–6 egg masses. In 1991 we found only two egg masses and heard a single male calling on only two days.

At other breeding areas in TPM during 1973–1979 (#2–10 in Fig. 1), we regularly saw calling males, amplexed pairs, egg masses, tadpoles, new metamorphs, and 1 yr old toads. Around 1980 the maximum number of males counted during a single day began to decline, and by 1990 we did not find any toads or hear males calling, and located only one egg mass (at Area #10). The drop in male numbers from 1973 to 1990

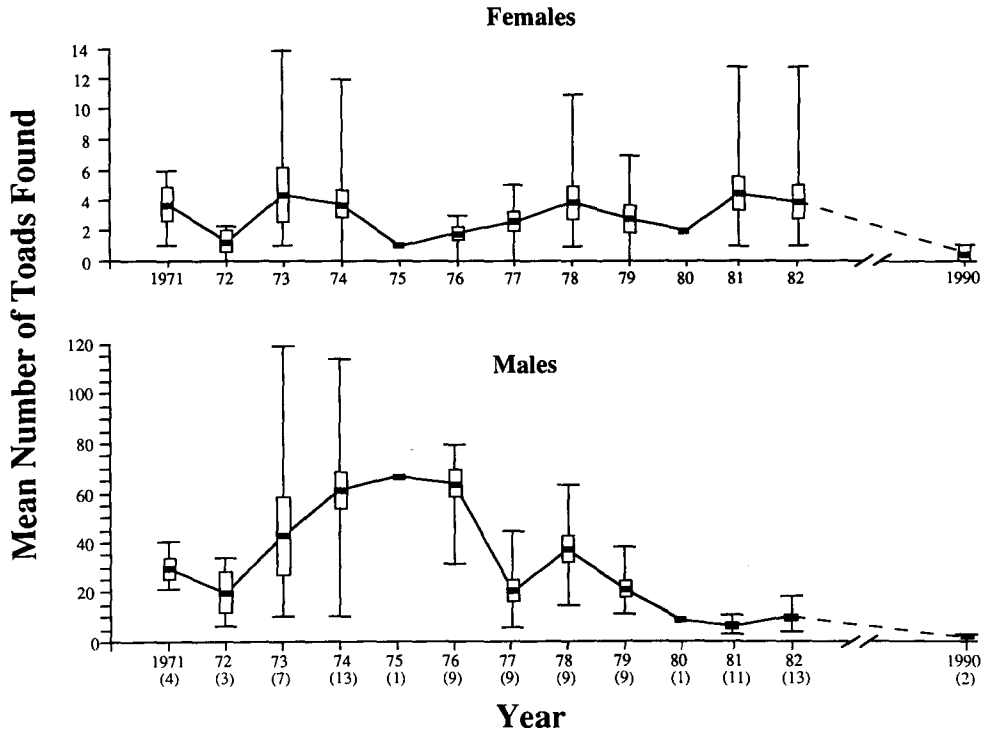


FIG. 4. Mean number of *B. canorus* males (lower) and females (upper) found during surveys of main study pools at TPM. Standard error (open box) and range (bar) shown; number of surveys indicated in parentheses below year. Data from 1976 are adjusted fence data (see text).

was significant at three of four areas where counts were made most frequently (Table 1). In contrast, the maximum number of females seen in these areas, while low, did not decline until sometime after 1982 (Table 1). We found no signs that *B. canorus* bred in any of these sites in 1991.

On 23 June 1991 E. L. Karlstrom visited his study area of 1954–1958 just south of TPM, within Yosemite National Park. He reported (pers. comm.) that there were no toads or signs of breeding in his former study area. The toads may have stopped breeding at his study site before our research began in 1971, because we never heard toads calling beyond the southern edge of TPM, or found signs of breeding in that area.

The number of *B. canorus* captured in non-breeding habitat in TPM also declined from 1971 to 1991. In the 1970s toads were abundant around willows and on hillsides. For example, on 10 July 1977, two people searching for three hours found 15 *B. canorus*. In contrast, Kagarise Sherman saw no toads in two hours of searching on 8 June and one hour on 12 June 1990. In June and July 1991, Morton found only two toads (one adult female and one 2–3 yr old immature)

in non-breeding habitat despite frequent searches.

The number of *B. canorus* found during systematic surveys of a large 100 × 300 m willow thicket east of TPM (H2 in Fig. 1) also declined during the study. In 1976 the mean number of toads ( $\geq 2$  yr old) caught/person h was  $5.3 \pm 3.2$  ( $n = 11$ , range = 3–48); 1977 results were  $8.0 \pm 3.0$  toads/person h ( $n = 10$ , range = 3–23). However, three surveys in 1990 produced a mean of only  $0.5 \pm 0.5$  toads/person h (range = 0–1).

*Population Declines Elsewhere.*—The six other populations we monitored differed in size when we began our work (Table 2). For example, a maximum of 18 toads were found in the tarns at Saddlebag Lake SE, compared to a maximum of 216 toads captured at Mildred Lake during one search in 1976. However, nearly all of these populations apparently decreased in size sometime between 1978 and 1981 (Table 2). Only the Saddlebag Lake NW population apparently remained steady from 1973 to 1982. Our surveys in 1990 suggest that this population may have also declined since 1982. Yet, with the exception of Sylvester Meadow, *B. canorus* continues to breed in all these locations. In 1990 we found

TABLE 1. Yearly maximum number of males and females seen at any one time at four small breeding areas in TPM. n = number of times area was checked during breeding. Spearman's rank correlations for males,  $P < 0.01$  at Area 4 ( $r_s = -0.854$ ), Area 5 ( $r_s = -0.964$ ) and Area 8 ( $r_s = -0.804$ );  $P > 0.05$  at Area 10 ( $r_s = -0.545$ ). For females in all areas,  $P > 0.05$ .

	1973	1974	1976	1977	1978	1979	1980	1981	1982	1990
Area 4										
n		(1)	(3)	(5)	(1)	(3)	(1)	(7)	(5)	(2)
Males	10	9	9	4	4	2	5	3	1	0
Females		2	3	1	0	2	2	1	2	0
Area 5										
n			(2)	(4)	(5)	(3)		(9)	(4)	(1)
Males			12	15	8	6		5	3	0
Females			1	1	3	0		1	3	0
Area 8										
n	(1)	(1)	(2)	(3)	(2)	(1)		(5)	(2)	(2)
Males	11	17	2	6	8	2		3	1	0
Females	0	1	1	4	1	2		2	0	0
Area 10										
n			(3)	(3)	(4)	(1)		(3)	(4)	(2)
Males			3	3	9	2		2	3	0
Females			1	1	3	2		2	2	0

the following numbers of egg masses at each location: Sylvester Meadow—0; Saddlebag Lake NW—14; Saddlebag Lake SE—20; Frog Lakes—2; Hoover Lake—3; Mildred Lake—45. Success-

ful reproduction in 1989 was indicated by the number of 1 yr old toads we found in 1990 at: Saddlebag Lake NW—6; Frog Lakes—25; Hoover Lake—2; Mildred Lake—2. Finally, E. L.

TABLE 2. Mean number  $\pm$  SD of *B. canorus* ( $\geq 2$  yr old) caught/person h during surveys at six populations in eastern Sierra Nevada, California, from 1973 to 1990. n = number of surveys; Range = actual number of toads caught/survey.

	1973	1976	1977	1981	1982	1990
Sylvester Meadow						
n		(2)	(3)	(1)		(1)
$\bar{x} \pm$ SD		12.0 $\pm$ 11.3	4.6 $\pm$ 3.9	2 $\pm$ -		0 $\pm$ -
Range		(2-20)	(2-9)	(2-)		(0-)
Saddlebag Lake NW						
n	(4)	(8)	(2)	(3)	(2)	(2)
$\bar{x} \pm$ SD	9.0 $\pm$ 4.8	6.4 $\pm$ 5.1	9.7 $\pm$ 6.2	6.8 $\pm$ 1.2	11.0 $\pm$ 4.2	2.9 $\pm$ 0.8
Range	(8-31)	(5-38)	(28-33)	(15-32)	(4-14)	(6-7)
Saddlebag Lake SE						
n			(1)			(1)
$\bar{x} \pm$ SD			9 $\pm$ -			1 $\pm$ -
Range			(18-)			(1-)
Frog Lakes						
n		(6)	(2)	(1)	(1)	(2)
$\bar{x} \pm$ SD		6.7 $\pm$ 4.0	11.5 $\pm$ 4.0	1 $\pm$ -	0 $\pm$ -	1.8 $\pm$ 2.5
Range		(4-67)	(43-143)	(5-)	(0-)	(0-7)
Hoover Lake						
n		(2)	(2)	(1)		(2)
$\bar{x} \pm$ SD		9.5 $\pm$ 4.6	10.2 $\pm$ 6.9	2.8 $\pm$ -		2.3 $\pm$ 1.0
Range		(25-85)	(16-60)	(21-)		(4-6)
Mildred Lake						
n		(5)	(3)			(1)
$\bar{x} \pm$ SD		20.4 $\pm$ 20.7	17.3 $\pm$ 7.6			1.7 $\pm$ -
Range		(13-216)	(37-97)			(10-)

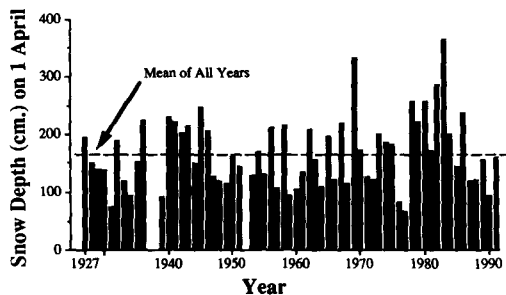


FIG. 5. Snow depth, in cm, on 1 April at Tioga Pass. Mean  $\pm$  SD of all years ( $n = 62$ ) was  $169.4 \pm 64.9$  cm. Source: State of California, Department of Water Resources, Bulletin 120.

Karlstrom and D. Martin reported (pers. comm.) that on 23 June 1991 they found considerable breeding activity at the Saddlebag Lake SE population, including 6–8 amplexed pairs, and numerous adults and egg masses at the Saddlebag Lake NW population.

The number of *B. canorus* found at a breeding site on a given day varied considerably (Fig. 4, Table 2), reinforcing the need for repeated censuses over many years to detect directional changes in population size. Daily survey results are affected by factors such as the time of day, experience of the searchers, weather conditions that day, and stage in the breeding season.

Nevertheless, in general our observations indicate that numbers of breeding *B. canorus* have declined at TPM and other locations in the eastern Sierra Nevada. Although we did not directly determine total population sizes because we did not census adults that skipped breeding, and did not count immatures in TPM or immatures 1 yr old or less at other populations, our measures are probably indicative of total population size. Yearly counts of the number of adults breeding are likely to vary more than total population counts (Pechmann et al., 1991; Crump et al., 1992; Wissinger and Whiteman, 1992; Olson, *in press*).

*Effects of Weather.*—The spring snow depth at TPM was highly variable (Fig. 5). Snow depths ranged from a low of 62.7 cm in 1977 to a high of 375.7 cm in 1983. In low snow years few tadpoles had transformed when all water in the main study pools evaporated. For example, the 1976 spring snow depth was one of the three lowest on record, and only 20–30 tadpoles out of ca. 56,800 eggs laid (#clutches  $\times$  mean clutch size) transformed before the pools dried up on 12 July (Kagarise Sherman, 1980). Snow depths have been below average at TPM since 1987 (Fig. 5), reflecting a widespread drought in California. Any tadpoles in the main study pools in 1987–1991 were probably unable to complete

their development, since all the snow in TPM usually melted by the end of June and the pools in the main study area dried up sometime in July. All embryos in egg masses found in the main study pools in 1990 and 1991 were killed by desiccation.

Deeper snows resulted in greater numbers of tadpoles transforming but delayed breeding (Kagarise Sherman, 1980). In 1976 the first males entered the main study pools on 14 May, while in 1978 breeding onset was delayed until 15 June by deep snow (Fig. 5). Many new metamorphs were found on 15 August 1978 near the pools, which contained water until at least mid-September. However, the later-maturing tadpoles may not have completed their development before cold fall weather set in.

The effects of spring snow depths on the success of reproduction may also be indicated by the maximum number of 1 yr old immatures found in surveys of the main study pools, since some metamorphs hibernated near the breeding site during their first winter (Kagarise Sherman, 1980). In 1972 the snow depth was below average (Fig. 5), and in 1973 the greatest number of such immatures found in a single survey was one. Similarly, after the record low snows of 1976 and 1977, a single 1 yr old was located in 1977, and none were found in 1978. By contrast, 21 of the immatures were found in a 1974 survey, 2 in 1975, 6 in 1976, and ca. 10–15 in 1979 following years of above average snow depths (1973, 1974, 1975 and 1978, respectively, Fig. 5). In recent years we have found no 1 yr old or newly transformed toads at the main study pools, suggesting that little successful reproduction has occurred.

A spring storm in 1977 allowed us to document the combined effects of drought and weather during breeding. After the lowest spring snow depth on record (Fig. 5), the main study pools were snow-free and some toads had emerged from hibernation in late April. Then a 27 d storm deposited 60 cm of snow on TPM and delayed breeding until 30 May. Despite the additional snowfall, only a few tadpoles had transformed by 1 August when the pools dried up. Adult toads were also affected by spring storms. In 1977 males that emerged from hibernation before the April storm lost more weight, were less likely to breed, and were less likely to be recaptured than males that emerged from hibernation after the storm (Kagarise Sherman, 1980).

These results suggest that several weather variables interact to affect *B. canorus* hatching success and survival to metamorphosis at TPM. The depth and water content of the spring snowpack determine how much water will be available to fill the pools. The amount of snow

covering the pools and hibernacula affects when breeding begins. Spring snow storms interrupt breeding and may kill eggs and tadpoles by freezing, but also add water to the pools, thereby increasing the number of tadpoles that transform. Rain or snow storms after breeding may also increase tadpole survival by adding water to pools. Warm temperatures after spawning may speed tadpole development (e.g., Waldman, 1982), but cause faster evaporation of the pools.

The effects of weather on the outcome of *B. canorus* breeding were illustrated by Morton's additional observations in 1992. After a low winter snowfall (108.2 cm) and warm April, all snow had melted in TPM by 5 June; the toads bred sometime in May. However, four major storms in June and July replenished the main study pools, and some tadpoles likely transformed before the pools dried up on 2 August.

Populations of *B. canorus* may be less affected by spring snow depths if their breeding areas are partially filled by water from nearby lakes. At Saddlebag Lake NW, Frog Lakes, Hoover Lake, and Mildred Lake, toads breed in shallow marshes and pools adjacent to lakes, but whether water from these lakes flows into breeding habitat is unknown. The breeding area at Saddlebag Lake NW, located between two lakes (Fig. 2), seems most likely to be partially filled by lake water. Interestingly, the Saddlebag NW population seems to have declined less than the others we surveyed (Table 2). In addition, despite very low snowfall in 1976 we found new metamorphs at Frog Lakes, Hoover Lake and Mildred Lake (maximum in a single survey = 12 at Frog Lakes, 1 at Hoover Lake, and 12 at Mildred Lake), suggesting that these populations were less affected by spring snow depths than those breeding in exclusively snow-melted pools.

Among years, the variability in spring snow depths may have contributed to breeding population fluctuations at TPM. For example, a large number of tadpoles likely survived to transform in 1969, a year of unusually deep snow (Fig. 5). When the 1969 cohort of toads became sexually mature and began breeding 3–6 yr later (Kagaris Sherman, 1980) they probably comprised the large numbers of toads found at the main study pools in 1973–1975 (Figs. 3, 4). By contrast, below average snow depths in 1976, 1977, and 1987–1991, resulting in nearly total reproductive failure likely contributed to the decline in breeding toad numbers 3–6 yr later in 1979–1982 and 1990 (Figs. 3, 4). Drought may have also contributed to population declines at our other study sites.

The complete failure of reproduction and loss of a year-class in some years, with excellent

tadpole survival and recruitment in other years, is characteristic of amphibians dependent on ephemeral water for breeding and may contribute to variation in adult numbers (e.g., Bragg, 1960; Pechmann et al., 1991; Crump et al., 1992; Wissinger and Whiteman, 1992; Olson, *in press*). Drought has been implicated in the decline of other amphibian populations (Corn and Fogelman, 1984; Pounds, 1991; Crump et al., 1992). Interestingly, drought-related declines in *Rana pipiens* in Colorado occurred in 1976 and 1977 (Corn and Fogelman, 1984), coincident with two years of record low snows in the Sierra Nevada.

Weather conditions before and during breeding may also affect how many adults attempt to breed (Pechmann et al., 1991; Wissinger and Whiteman, 1992; Crump et al., 1992). The combination of low winter snow depths and the spring storm at TPM may have caused the reduced numbers of *B. canorus* males entering the main study pools in 1977 (Fig. 3). Crump et al. (1992) suggested that the failure of *B. perigrinus* to breed in recent years may be explained either by catastrophic mortality, or by adults remaining underground because weather conditions are inappropriate for breeding.

*Mortality Unrelated to Predation.*—During 1971–1975 we sometimes caught adult *B. canorus* with missing or deformed extremities, and in 1974 we found four toads with discolored growths on their bodies. All these toads appeared healthy when recaptured in later years. We did not find toads with other signs of illness. Except for an occasional toad that had been killed on California Highway 120, or a dead female in the breeding pools, we did not find dead *B. canorus* in TPM.

In contrast, from 1976 to 1982 we found 36 dead toads in the main study pools and throughout TPM during and after breeding. Three of the dead males and five of the females were weak, sluggish and bloated before dying, or were found dead with reddened ventral surfaces and toe membranes; 21 others (16 males, 5 females) were found with similar symptoms. Six of the affected males and two of the females recovered and were recaptured in subsequent years; the remainder were never seen again.

The deaths of other individuals during 1976–1982 may have also been related to illness. Four males and two females died while crossing a large snowdrift near the main study pools, perhaps because they were weakened by illness. One of three females that died after being amplexed by several males had sores on her dorsal and ventral sides. If she were ill she may have been less able to avoid being amplexed by multiple males. An additional 19 *B. canorus* were found dead, without any obvious signs of illness.



We found the majority of the dead or ill toads in 1977 (10/36 = 27.8% dead; 7/21 = 33.3% ill) and 1978 (13/36 = 36.1% dead; 8/21 = 38.1% ill), just before the population began to decline (Figs. 3, 4). Similar numbers of males (17/36 = 47.2%) and females (18/36 = 50%) were found dead (1/36 of unknown sex = 2.8%), but more apparently sick males than females were seen (16/21 = 76.2% vs. 5/21 = 23.8%).

Probably illness in 1977 and 1978 caused extensive adult mortality and contributed to the population decline at TPM. Similar disease-related mortality of adults and/or larvae in wild populations has been reported in salamanders (Hunsaker and Potter, 1960; Nyman, 1986; Worthylake and Hovingh, 1989; Pfennig et al., 1991), frogs (Hunsaker and Potter, 1960; Glorioso et al., 1974; Nyman, 1986; Bradford, 1991; Carey, *in press*), and toads (Dusi, 1949; Carey, *in press*). The bacteria *Acinetobacter* was implicated in the die-off of one salamander (*A. tigrinum*; Worthylake and Hovingh, 1989), *Aeromonas hydrophila* and two *Enterobacter* species were cultured from two dead *R. muscosa* (Bradford, 1991), and *A. hydrophila* was implicated in the other cases. The symptoms we observed in *B. canorus* were suggestive of the anuran septicemia "red-leg," caused by *A. hydrophila* (Reichenbach-Klinke and Elkan, 1965; Shotts, 1984; Hayes and Jennings, 1986; Bradford, 1991). However, because the symptoms of several infections are similar and multiple bacteria may be present in sick animals (Glorioso et al., 1974; Shotts, 1984; Worthylake and Hovingh, 1989), identifying the causative agent is not possible without bacteriological analyses (Hayes and Jennings, 1986).

*Aeromonas hydrophila* is ubiquitous in fresh water and has been isolated from healthy adult and larval *R. pipiens* (Hird et al., 1981). The bacteria may become pathogenic when animals are stressed in some way (Glorioso et al., 1974; Shotts 1984; Hird et al., 1981; Nyman, 1986; Carey, *in press*). Several possible stressors may have made the toads at TPM more vulnerable to pathogens.

First, low temperatures favor the growth of *A. hydrophila* and other potentially pathogenic bacteria in captive frogs (Carr et al., 1976), and reduce the ability of ectothermic animals to respond to infections (Carey, *in press*). Amphibians may be especially susceptible while hibernating and in the spring after emerging (Hird et al., 1981; Carey, *in press*). At TPM the 27 d spring storm in 1977 and the unusually deep snow and long hibernation period in 1978 may have contributed to the disease outbreak we observed in 1977 and 1978. Second, Carey (*in press*) described physiological evidence suggesting that even brief handling causes stress in ectotherms. Our capture, measurement, and toe-clipping techniques may have made the

toads more vulnerable to disease. However, except for the use of the fence and pitfall traps in 1976–1978, we did not change our techniques during the study. Toe-clipping began in 1971, and we walked around the pools daily each year, either capturing or visually locating toads. We attempted to minimize negative effects of the fence by checking the traps frequently and covering the pitfall traps at night. However, we may have inadvertently contributed to the spread of pathogens between toads and breeding sites by using the same marking and measuring equipment throughout the season.

*Avian Predation.*—On five occasions in 1976 and 1977 we saw American robins (*Turdus migratorius*) eating tadpoles from the main study pools when they were nearly dry. Insects also occasionally killed tadpoles (Kagarise Sherman, 1980; Morton, unpubl.). Robin predation on stranded tadpoles occurred at other breeding sites in TPM (K. Uemura, pers. comm.), and was reported for larval *B. boreas halophilus* in Yosemite National Park (Karlstrom, 1954). Brewer's blackbirds (*Euphagus cyanocephalus*) ate all transforming *R. muscosa* tadpoles in 1979 at Ridge Lake in King's Canyon National Park (Bradford, 1991). During the same summer this population also suffered mass mortality of adults due to disease, and was extinct when rechecked in 1989. However, our observations indicate that avian predation on *B. canorus* tadpoles probably does not greatly affect the population size, because only tadpoles in pools that were nearly dry were taken.

Karlstrom (1962) suggested that California gulls (*Larus californicus*) and Clark's nutcrackers (*Nucifraga columbiana*) might prey on adult *B. canorus*. From 1976 to 1982 we observed both species attacking the toads 22 times (Table 3), as they crossed a snowdrift near the main study pools (12 times), while in the breeding area (7 times), and near hibernacula (3 times). Of the 22 attacks, 9 were on males, 3 on females, and 10 on toads of unknown sex, suggesting that males were attacked more often. Observations of predation varied between years but did not increase during the study (Table 3).

We found considerable evidence of avian predation when we canvassed the *B. canorus* population at Mildred Lake on 11 June 1990. Twelve female and 10 male carcasses were discovered in the breeding area. Female remains consisted of the bones and skin of the head and back, eggs and oviducts, and occasionally a hind leg; male carcasses usually included only the bones and skin from the upper half of the head and back. We saw two common ravens (*Corvus corax*) foraging along the edges of the pools and marshes but did not see them attack any toads. Observations of ravens preying on other toad species and leaving similar remains (Kagarise

TABLE 3. Frequency of predation by Clark's nutcrackers and California gulls on *B. canorus* at TPM. During unsuccessful attacks (U), toads were left uninjured; during "successful" attacks (S), toads were carried off, or killed and left by the bird. \* = includes 1 female found eviscerated in main study pools, attributed to Clark's nutcracker predation; n = number of observations.

n	1976	1977	1978	1979	1981	1982
	(2)	(6)	(2)	(6)	(4)	(2)
Clark's nutcracker						
#U	2	1	0	2	1	0
#S	0	5	1	4	3*	0
California gull						
#U	0	0	1	0	0	1
#S	0	0	0	0	0	1
Percent of total observations	9.1%	27.3%	9.1%	27.3%	18.2%	9.1%

Sherman, 1980; Olson, 1989) implicate ravens in the deaths of toads at Mildred Lake.

Sightings of common ravens have increased in the Sierra Nevada at a rate of 9.5%/yr over the 24 yr period from 1966 to 1989; during 1980-1989 the rate was an even greater 19.6%/yr (USFW Breeding Bird Survey, unpubl. data). The increase in raven numbers may be related to increasing human activities, since ravens appear to be commensal with humans (see also Olson, *in press*). We occasionally saw ravens at TPM but never observed them hunting in toad breeding sites. However, ravens may have contributed to *B. canorus* population declines at Mildred Lake and elsewhere in the Sierra Nevada.

Predation on adult toads in breeding aggregations has been reported for four species: *B. americanus* (Schaaf and Garton, 1970; Groves, 1980), *B. boreas* (Olson, 1989, *in press*), *B. canorus* (Mulder et al., 1978; Kagarise Sherman, 1980), and *B. exsul* (Kagarise Sherman, 1980). Despite the irritating, toxic secretions of toads' skin glands (e.g., Low, 1972; Hayes, 1989), some predators are able to consume unprotected body parts while avoiding glandular areas. Raccoons (*Procyon lotor*) and striped skunks (*Mephitis mephitis*) were suggested as likely predators of *B. americanus* (Schaaf and Garton, 1970; Groves, 1980). Corvids were responsible for most predation in the other three species. Clark's nutcrackers were responsible for nearly all the attacks on *B. canorus* we witnessed. Black-billed magpies (*Pica pica*) killed many of the 96 *B. exsul* whose carcasses were found during a two year study at Deep Springs, California (Kagarise Sherman, 1980). Common ravens were also seen killing several *B. exsul* and may have left the piles of dismembered toads found at Deep Springs (Kagarise Sherman, 1980). Olson (1989) also reported raven predation in three of 15 *B. boreas* breeding aggregations in Oregon. Be-

tween 7 and 59 carcasses were found at each aggregation, and between 1.7 and 23.6% of the aggregated toads were killed.

Despite the presence of potential mammalian predators (see Karlstom, 1962) we never saw any attack *B. canorus*, and we found only one western garter snake (*Thamnophis elegans*) in 20 yr.

*Effects of Adult Mortality.*—Our data indicate that *B. canorus* is a late maturing, long-lived species. Male toads first entered breeding aggregations when they were 3-5 yr old, while females first bred at 4-6 yr (Kagarise Sherman, 1980). Reported ages at sexual maturity are similar in *B. boreas* (Carey, 1976; Olson, *in press*). Recaptures of marked *B. canorus* in 1981 and 1982 indicate that individuals may live a long time. Two females were first marked as adults ( $\geq 4$  yr old) in 1971, making them at least 15 yr old; eight other marked females were at least 9-13 yr old when last recaptured. Assuming that breeding males were at least 3 yr old when first captured, five males were a minimum of 10-12 yr old when last recaptured. Recapture or phalangeal growth ring data revealed similar maximum ages in other toads (Hemelaar and van Gelder, 1980; Gittins et al., 1982; Olson, *in press*).

Crump et al. (1992) suggested that long life spans may be selected in species like *B. perigrinus* that inhabit unpredictable environments and experience variable recruitment success, and that after periods of low recruitment or poor breeding conditions, populations will become biased toward aging adults and may be unable to recover. Mass mortality of adults due to disease or predation may also have a serious impact on long-lived anurans that mature slowly (see also Olson, *in press*). When many breeding adults die in these species, there may be years in which no breeding occurs because none of the younger toads are mature enough to breed. When

combined with episodic juvenile recruitment, such populations may continue to decline.

*Timing of Decline in Male and Female Numbers.*—Male numbers dropped before female numbers in the main study pools (Figs. 3, 4) and probably at other breeding sites in TPM (Table 1). This sexual asymmetry in the timing of the decline is likely related to three differences in behavior between males and females. First, males spent more time in the breeding pools than females each year. The mean number of days spent in the main study pools was 2.1, 1.5, and 1.8 times greater for males than females in 1976, 1977 and 1978, respectively (Kagarise Sherman, 1980). Second, males attempted to breed more often than females. Of 522 marked males that entered the pools from 1976 to 1979, 66% were present once, while 34% were present in 2, 3 or 4 yr. Of 197 marked females, 86% were present once, compared to 14% that were present in 2, 3, or 4 yr (Kagarise Sherman, 1980). The dimorphism in breeding frequency was also reflected in the larger percentage of previously unmarked females, compared to males, that entered the main pools each year (1976 = 81.8% vs. 58.2%; 1977 = 65.1% vs. 30.9%; 1978 = 65% vs. 17.1%; 1979 = 54.3% vs. 13.3%; 1981 = 46% vs. 30.3%; 1982 = 48.1% vs. 21.4%). Third, males and females tended to inhabit different areas in TPM when not breeding (Morton, unpubl. data). Males stayed in the central meadow after breeding and hibernated there, whereas many females (and immatures) spent the years between breeding in the large willow thicket east of TPM (H2 in Fig. 1).

Such differences may expose males more to pathogens or predators, thereby causing a more rapid decline in male numbers. Males were probably more exposed to aquatic pathogens like *A. hydrophila* because they spent more time in the pools and returned to breed each year. By remaining in the willows at the periphery of TPM, non-breeding females and immatures may have reduced their exposure to diseased conspecifics. Breeding males may also have been more vulnerable to predation, because they spent more time in breeding aggregations and vocalized, which might have attracted predators. We observed more avian attacks on males than females during our studies (but found similar numbers of male and female carcasses at Mildred Lake).

A similar sexually dimorphic pattern of breeding attendance and population decline was reported for *B. boreas* (Olson, *in press*). Interestingly, the decline at one *B. boreas* population in 1991 was caused by a drop in male numbers while female numbers "... were not unusual" (Olson, *in press*). Olson suggested that female *B. boreas* might be less affected, at least initially,

by mass predation on adults during breeding because most females do not breed every year.

*Habitat Changes and Human Disturbance.*—Habitat destruction has been frequently implicated in amphibian population declines (e.g., Barinaga, 1990; Blaustein and Wake, 1990). However, habitat changes in all areas we surveyed in the eastern Sierra Nevada have been minimal in the last 20 yr. Only minor natural changes in the breeding habitat of *B. canorus* in TPM have occurred since 1971, including the silting in of one tarn at Area #5 (Fig. 1), and the increased growth of willows on the western side of the main study pools. No livestock grazing, logging, road construction or other major disturbances have occurred; our study populations are all in national forest or wilderness areas.

Known local human influences have been limited to the effects of backpackers, tourists, and fishermen. The potential for human disturbance may vary with the ease of access to each breeding area. The main study pools are less than 200 m from Highway 120 and beside Tioga Lake, which is a popular fishing spot. Similarly, Saddlebag Lake is used by many fishermen. The SE tarns are 0.4 km from a road and campground; the NW breeding habitat is 2.4 km from the road but accessible by boat and level hiking trail. The other populations we surveyed are farther from roads and can be reached only by steep hiking trails (Sylvester Meadow—1.6 km to nearest road, Frog Lakes—2 km, Hoover Lake—4 km, Mildred Lake—5.6 km). The lack of relationship between the distance from the nearest road and the declines in our study populations suggests that localized human activities were not the main cause of the decreases.

In summary, there was a decline in the numbers of breeding *B. canorus* at Tioga Pass Meadow and elsewhere in the eastern Sierra Nevada from 1971 to 1991. The combined effects of drought-induced reproductive failure in at least seven years since 1971 and the death of many breeding adults due to disease probably caused the decrease in toad numbers at TPM. Drought may have also affected the other populations we surveyed, and raven predation likely added to the decline in the population at Mildred Lake. Our data suggest that a widespread factor like drought can interact with more localized effects, perhaps differing between populations, to cause population declines. In addition, all three contributors to the declines (drought, disease, and predation) may have had anthropogenic components, including global climate changes and an increase in numbers of common ravens. Unfortunately, our research techniques may have made toads more susceptible to disease, or increased the transmission of pathogens be-

tween sites in TPM. We hope to continue our study for the next decade to check these conclusions.

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