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Mass Mortality and Extinction in a High-elevation Population of *Rana muscosa*

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ABSTRACT.—***Rana muscosa*** **is one of several high-elevation amphibians that have recently disappeared from seemingly pristine sites. The present study documents an event of mass mortality among larval and metamorphosed *R. muscosa* in a lake in Kings Canyon National Park, California, and the ultimate extinction of the population. In 1979 metamorphosed individuals declined from ca. 800 individuals in early summer to nearly zero in late summer. During this time many carcasses were collected, individuals showed symptoms of red-leg disease, and blood from an affected individual contained the bacterial pathogen characteristic of this disease, *Aeromonas hydrophila*. Also during the summer of 1979, nearly all of the approximately 1100 tadpoles began metamorphosis, but all metamorphosing individuals were consumed by Brewer's blackbirds (*Euphagus cyanocephalus*). This population of *R. muscosa* continued to exist until at least 1983, but was extinct by 1989. Recolonization of the site will probably never occur because streams connecting to extant populations of *R. muscosa* now contain introduced fishes.**

Recent, dramatic population declines have been reported for a number of amphibian species, particularly in montane environments (e.g., Barinaga, 1990). One species showing this pattern is *Rana muscosa*, the mountain yellow-legged frog, which has disappeared in many historic localities at high elevation in the Sierra Nevada of California (Phillips, 1990; L. Cory, pers. comm.; Bradford, pers. obs.). Unfortunately, virtually no information is available about the causes of these disappearances, nor whether they are natural or anthropogenic. Moreover, virtually no data are available for natural fluctuations in population size or population age/size structure for this species.

Natural population fluctuations of *R. muscosa* at high elevation may be severe. For example, climatic factors are often extreme, with winterkill apparently occurring in some years (Bradford, 1983), and both tadpoles and adults often occur at high densities (e.g., 2.5 frogs/m of shoreline; Grinnell and Storer, 1924; Bradford, 1984). The present study documents an event of mass mortality among metamorphosed and larval *R. muscosa* due to disease and predation by Brewer's blackbirds (*Euphagus cyanocephalus*), and the eventual extinction of the population. Both factors may be natural, but the possibility exists that an anthropogenic component is involved.

MATERIALS AND METHODS

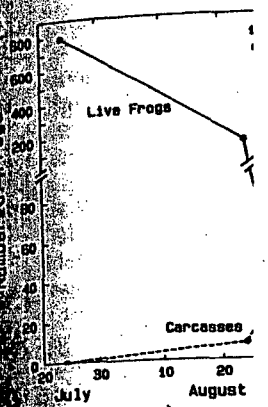
This study focused on a population of *R. muscosa* inhabiting a lake (referred to as Ridge Lake) at 3425 m elevation in Kings Canyon National Park, Tulare County, California (36°37′22″N, 118°36′36″W; Bradford, 1984). This lake (4.8 m deep, 0.65 ha) lies near the top of a ridge, contains no rooted vegetation, and has a shoreline composed almost entirely of granite rocks. The surrounding vegetation is alpine fell-fields (Munz and Keck, 1965).

Comparative data are also reported for a population of *R. muscosa* in Table Meadows, Sequoia National Park, 2.8 km SW of Ridge Lake (36°37′5″N, 118°38′13″W; Bradford, 1984). This site lies at lower elevation (3100 m) in a basin more protected from the wind, contains a stream and a number of small ponds with rooted vegetation along shore, and has a shoreline largely overhung with willows or dense grass. The regional plant community is subalpine forest (Munz and Keck, 1965). Both Ridge Lake and Table Meadows lie in the Tablelands area described by Bradford (1983, 1984, 1989).

These sites were visited several times during the summer of 1978, approximately weekly during the summer of 1979, and once in 1989. Both frogs and tadpoles were censused in Ridge Lake by counting individuals near or on shore during midday. Nearly all individuals could be censused in this way because both frogs and tadpoles seek the warmer thermal regimes near shore (Bradford, 1984). Ridge Lake was also searched for dead frogs on shore and throughout the lake. Carcasses were removed when found.

RESULTS

Mortality of Frogs.—Throughout the summer of 1978 and early summer of 1979, virtually no mortality was evident at Ridge Lake, where frogs were abundant. In late August 1979, however, dead frogs were found and the number of live



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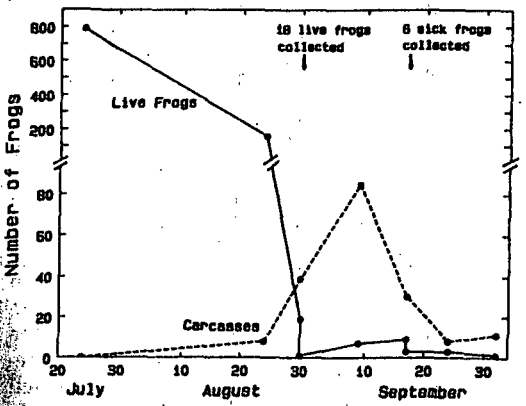

FIG. 1. Numbers of live frogs present and frog carcasses collected in Ridge Lake during summer, 1979.

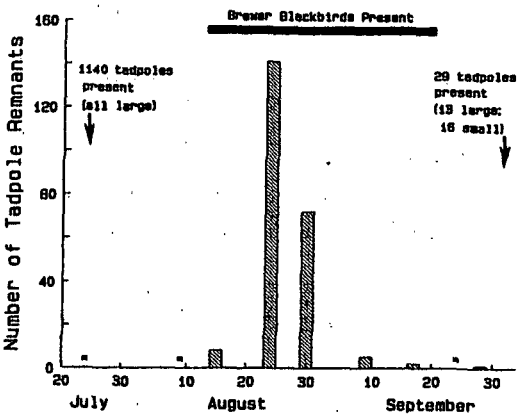

FIG. 2. Numbers of tadpole carcasses collected at Ridge Lake during summer, 1979. Asterisks indicate that no tadpole remains were found on indicated dates.

frogs present was conspicuously diminished from the previous level of 790 individuals (Fig. 1). By the end of August the number of live frogs dropped to about 20. The number of live frogs remained very low, and only one individual was found in early October. There were no exceptional climatic events during this period although heavy storms and reduced temperatures occurred during mid August.

Many carcasses were found during the time of obvious population decline (Fig. 1). Carcasses were almost invariably intact, showing no sign of injury or predation other than occasional scavenging by aquatic insects. Carcasses were found primarily on the lake bottom near shore, but 34% were found on land. Only 201 carcasses were found, whereas approximately 790 frogs disappeared.

During late August and September, individual frogs were occasionally found in a sick or moribund condition. Many were on land and did not show the typical escape response toward water. Affected individuals were emaciated, sluggish, and poorly coordinated, and the ventral surface of the thighs and sometimes the forearms and toes were abnormally red with enlarged capillaries or hemorrhages. These symptoms are consistent with those associated with "red-leg" disease, as caused by the bacterium *Aeromonas hydrophila* (Dusi, 1949; Gibbs et al., 1966; Nyman, 1986).

Three affected individuals were collected and transported to Los Angeles for examination by a veterinary pathologist. Analysis of blood from two specimens revealed *Aeromonas hydrophila* and *Enterobacter aerogenes* in one specimen, and *E. aerogenes* and *E. agglomerans* in the other.

In Table Meadows, sick and dead frogs were also found at the same time as the die-off of frogs in Ridge Lake. Although an accurate determination of population change was not possible because of the greater difficulty in finding individuals at this site, and the indistinct boundaries of the population, it was evident that mortality in this population was not as substantial as in Ridge Lake. It appeared that most of the small frogs (ca. 40) succumbed, whereas the larger adults (ca. 20) survived. In two other populations visited during the summer of 1979 in the Tablelands regions (i.e., within 8 km of Ridge Lake), and in two populations 25 km away, frogs appeared to be unaffected by disease.

Tadpole Mortality.—*In early summer of 1979* ca. 1100 large tadpoles (probably two years old) were present in Ridge Lake (Fig. 2). In contrast, only 29 individuals were found at the end of the summer. These remaining tadpoles probably represented individuals from the present summer ("small") and the previous summer ("large").

During midsummer tadpoles began metamorphosis and often sat at the water's edge. Brewer's blackbirds were frequently observed feeding on these individuals, and appeared to have little difficulty approaching and capturing them. Upon capturing a tadpole, a blackbird typically consumed it in pieces, but commonly left behind the skeleton and skin of the hind legs. These carcass remnants, which were collected from the lake area approximately weekly, indicated that blackbird predation was most intense in late August (Fig. 2). A total of 229 tadpoles was represented by the remnants found.

Between 14 August and 20 September 4 to 8 Brewer's blackbirds were always present at Ridge Lake, and they apparently consumed every transforming tadpole, as no dead tadpoles or juveniles were found. There was no evidence that tadpoles were infected with red-leg disease. Aberrant swimming behavior and physi-

cal features associated with this disease (Nyman, 1986) did not occur.

Brewer's blackbirds were also present throughout most of the summer at Table Meadows, and predation on *R. muscosa* tadpoles was observed. In contrast to Ridge Lake, however, blackbirds did not succeed in consuming all metamorphosing tadpoles, as 34 recently-metamorphosed individuals were observed. Blackbirds searched for tadpoles among the willows and sedges along the shoreline in Table Meadows, whereas this vegetation was absent in Ridge Lake.

Extinction of the Ridge Lake Population.—The Ridge Lake site was not surveyed again until 1989, at which time neither frogs nor tadpoles were present. However, a number of medium-sized adult *R. muscosa* were observed by a biologist in 1983 (L. M. Moe, pers. comm.), indicating that the population survived the mass mortality of 1979. Interestingly, of the two other lake populations in the Tablelands region which contained adults in 1979, one had gone extinct by 1989 and the other contained only young tadpoles. In addition, a population of *R. muscosa* persisted in Table Meadows in 1989. However, this population appeared tenuous because only metamorphosing tadpoles or recently-metamorphosed individuals were observed. No young of the year or reproductive-size adults were present.

Discussion

Mass mortality in high-elevation populations of *R. muscosa* may not be uncommon. In addition to the mortality factors of disease and predation described above, winterkill due to oxygen depletion apparently results in periodic catastrophic mortality, at least of metamorphosed individuals (Bradford, 1983). Several aspects of the biology of *R. muscosa* are probably significant in allowing the species to persist at high elevation despite these periodic die-offs. Firstly, the mass mortality events observed appear to occur irregularly in time and space, and these and other mortality factors often affect only one cohort of a population (e.g., frogs, metamorphosing tadpoles, or young tadpoles). Secondly, tadpoles of *R. muscosa* require two to three summers to reach metamorphosis at high elevation (Zweifel, 1955; Cory, 1962; Bradford, pers. obs.). Thus individuals killed as adults or juveniles may be replaced by tadpoles during the following one to three summers. Thirdly, should a population become extinct, recolonization from other populations may occur. Although *R. muscosa* occurs almost exclusively near permanent water, juveniles are occasionally found in small, intermittent tributary streams (pers. obs.). Thus recolonization may occur by juvenile frogs following streams or rivulets connecting permanent bodies of water.

Unfortunately local recolonization is now largely precluded in much of the range of *R. muscosa* in the Sierra Nevada because of introduced fishes. Several species of fishes, notably trout (*Salmo* spp.) and charr (*Salvelinus* spp.) have been widely introduced into lakes and streams throughout the Sierra Nevada at high elevation where formerly no fish occurred (Hubbs and Wallis, 1948; Christenson, 1977). Because both fish and *R. muscosa* are tied to permanent water, and fish feed on young stages of *R. muscosa*, the presence of introduced fishes generally precludes the persistence of *R. muscosa* (Grinnell and Storer, 1924; Bradford, 1989). Historically, the avenue for recolonization of Ridge Lake would have been the intermittent outlet stream that drains to two lakes that contained *R. muscosa* populations in 1978. However both of these populations became extinct between 1978 and 1989, and fish are resident below these two lakes (pers. obs.). Thus it is unlikely that populations of *R. muscosa* will ever be reestablished in these lakes.

Anthropogenic factors have been suggested for the extensive population declines among ranid frogs in western North America, and in amphibians in general (Hayes and Jennings, 1986; Barinaga, 1990). At Ridge Lake it was not possible to determine whether the die-off of adult *R. muscosa* with red-leg disease was induced by natural or unnatural factors. Although infection by the red-leg pathogen (*Aeromonas hydrophila*) may be common among amphibians in natural conditions (Dusi, 1949; Nyman, 1986), the disease may occur in response to various stresses (Gibbs et al., 1966; Nyman, 1986). *Aeromonas hydrophila* is often isolated from natural waters containing healthy amphibian populations and from the intestines of healthy animals (Gibbs et al., 1966; Nyman, 1986). It seems reasonable to speculate that the initial outbreak of disease at Ridge Lake was due to natural factors such as crowding. Adult *R. muscosa* have been observed in high densities (Grinnell and Storer, 1924; Bradford, 1984), and disease may be a common and natural population control factor.

Intense predation by Brewer's blackbirds on amphibians in the high Sierra Nevada appears to be a natural phenomenon. Although this species has increased in numbers in central California due to extensive agricultural activities, Brewer's blackbirds have been regular summer visitors to the high-elevation lakes and meadows for a long time (Dawson, 1923; Grinnell and Miller, 1944; Sumner and Dixon, 1953). The success of blackbirds in extirpating the population of metamorphosing *R. muscosa* in 1979 in Ridge Lake can be explained by the vulnera-

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bility of metamorphosing anurans to predation (Arnold and Wassersug, 1978), the lack of protective vegetative cover in this lake, and the high density of metamorphosing individuals that made it profitable for a group of blackbirds to concentrate at the site. Intense predation on concentrated prey has been observed in other predator/anuran systems, including anurans containing high levels of toxic skin secretions (Olson, 1989).

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