
HABITAT USE BY YOSEMITE TOADS: LIFE HISTORY TRAITS AND IMPLICATIONS FOR CONSERVATION

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Abstract.—In the 1970s we studied habitat use and reproductive biology in Yosemite Toads (*Bufo canorus*) in the Sierra Nevada Mountains of California. Our surveys of four zones of terrestrial habitat in the post-breeding period provided a sample of 654 toads and revealed population and gender differences in distribution. Wet-meadow bottoms containing breeding pools were occupied by the majority (immatures and adults combined = 58%). Interestingly, the next most occupied zone was at the highest part of the meadow environment where it contacted talus slopes, more than 800 m from the nearest breeding pools (immature and adults combined = 26%). Adult females tended to be located there (108 of 237; 46%), but not adult males (7 of 225; 3%). Ovaries of post-breeding females were only partially developed before they entered hibernation. This suggests that storing enough energy during the brief high altitude summer to provide for both hibernation and reproduction in successive years is difficult and may cause irregular breeding in *B. canorus*, especially in females because they invest more than males in gonadal mass. We hypothesize that this asymmetry in energy requirements of adults may be the fundamental cause of differential dispersal.

Key Words.—*Bufo canorus*; core areas; habitat splitting; ovarian cycles; Yosemite Toad

INTRODUCTION

Within the past few decades concern about global declines and even extinctions of amphibian populations has motivated herpetologists to identify the causal agents of mortality and regulatory agencies have developed management plans to protect the health and reproductive success of endangered populations. Usually these plans are designed to protect water quality and breeding sites, including small buffer zones around them (Semlitsch and Bodie 2003; Cushman 2006; Gamble et al. 2006; Goates 2006; Goates et al. 2007). Conservation efforts of this type have frequently shown good results (Halliday 2005), but in the long run they may be ineffective unless heavily used core areas of terrestrial habitat are also protected (Semlitsch 2002; Trenham 2001; Trenham et al. 2003; Cushman 2006; Browne and Paszkowski 2010). At present identification of these core areas is difficult because post-breeding dispersal patterns are largely unknown for most amphibian species (Halliday 2005). This ignorance is being rapidly dispelled, however, in one interesting group, the montane-dwelling bufonids. Recent studies of their mobility and terrestrial habitat preferences are yielding important and perhaps unexpected data. For example, individuals of *Bufo boreas* in the Rocky Mountains (Bartelt 2000; Muths

2003; Bartelt et al. 2004; Bull 2006; Goates 2006) and *B. bufo* in the Austrian Alps (Sztatecsny and Schabetsberger 2005), particularly females, commonly moved a kilometer or more away from wetland breeding sites before taking up summer residence, sometimes in discrete, delineated patches.

Herein we present information, gathered several decades ago, on the behavior, distribution, and physiology of another high altitude *Bufo* species, the Yosemite Toad (*B. canorus*). Our data are consistent with those reported for other bufonids and lead us to hypothesize that sexually disparate migrations in adults may be related to irregular participation in breeding and to maximization of fecundity. They also support the principle that conservation regulations, such as those aimed at high altitude populations, should be landscape based.

MATERIALS AND METHODS

From 1971 to 1977 we conducted mark-recapture (toe clipping and hand capturing) and breeding-biology studies of *B. canorus* on a large subalpine meadow at Tioga Pass (3,018 m altitude) on the eastern Sierran slope in Mono County, California, USA. We also visited four other sites with substantial *B. canorus*

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breeding activity, also located in Mono County but away from roads, several times each summer. These were at Mildred Lake (2,975 m altitude), Hoover Lake (3,042 m), Saddlebag Lake (3,085 m), and Frog Lakes (3,170 m). From 1976 to 1979, Cindy Kagarise Sherman continued to mark individuals while conducting daily behavioral studies on Tioga Pass meadow, especially at the northern end (see map in Kagarise Sherman 1980). Before and concurrent with her work, we sampled adult females with known breeding histories in 1971, 1972, 1976, and 1977 to measure seasonal changes in ovarian mass. We categorized females as pre-breeding if they entered monitored breeding pools and as post-breeding if we collected them subsequent to oviposition in those pools during that same summer. Following etherization,

we removed ovaries, immersed them in Bouin's fixative and weighed them later in the laboratory with a torsion balance to the nearest milligram.

While searching for marked individuals at Tioga Pass and the other four sites mentioned above, we sometimes found adults on rocky hillsides hundreds of meters from breeding pools. Thus, to obtain data on dispersal in an organized manner, in 1976 and 1977 during the post-breeding period (breeding activity had ceased in both of those years by about 20 June), we conducted seven surveys in the afternoon (*B. canorus* is diurnally active) on a portion of Tioga Pass habitat located almost midway between the boundary of Yosemite National Park and the southern end of Tioga Lake (Fig. 1). The survey area, selected for its substantial size and

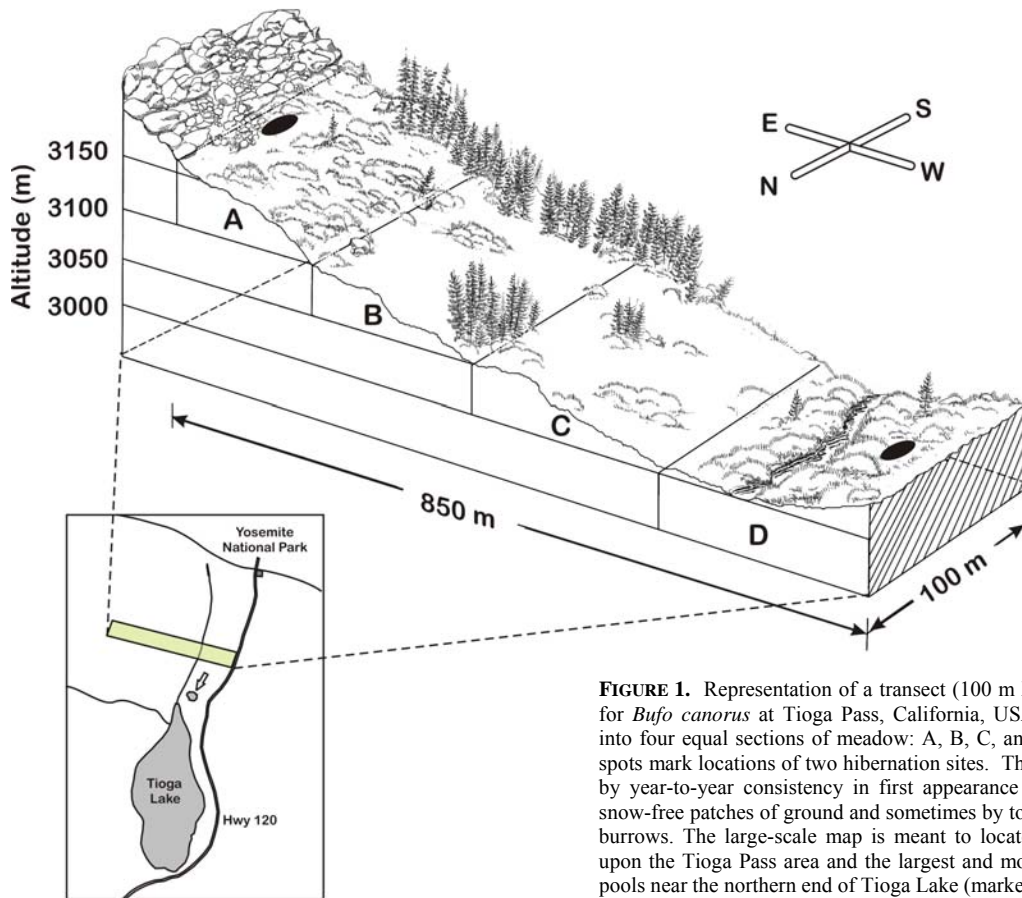


FIGURE 1. Representation of a transect (100 m X 850 m) searched for *Bufo canorus* at Tioga Pass, California, USA, and its division into four equal sections of meadow: A, B, C, and D. Oblong black spots mark locations of two hibernation sites. These were identified by year-to-year consistency in first appearance of toads on small snow-free patches of ground and sometimes by toads emerging from burrows. The large-scale map is meant to locate both the transect upon the Tioga Pass area and the largest and most visited breeding pools near the northern end of Tioga Lake (marked by an arrow).

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continuity, encompassed a swath of lush meadow dominated by willows (*Salix* sp.) and herbaceous vegetation 100 m wide that extended from Highway 120 on the west up to the bottom of a large talus slope on the east, a distance of 850 m. We marked boundaries with flagging tied onto bushes. We conducted surveys in 1976 on 19 and 27 July, and 2, 5, and 7 August; dates in 1977 were 2 and 23 August. Previously marked toads

were identified by toe-clip pattern; unmarked ones were toe-clipped, age was determined as immature or as adult if snout-vent length exceeded 60 mm (see Kagarise Sherman 1980), and sex was determined by coloration (*B. canorus* adults are at least 3 y of age and sexually dichromatic). All individuals were located on a map of the survey area and released *in situ*.

RESULTS

Habitat use.—We handled 654 toads during the seven surveys; 192 immatures and 462 adults. Among the latter were 237 females and 225 males. Division of the area searched into four equally spaced sections (A, B, C, D; Fig. 1) and a tally of individuals found within each shows that they were found in all sections, but that their distribution varied (Fig. 2). The majority, 382 (58%), occurred on the meadow bottom (section D) and the next largest group, 168 (26%), at the upper eastern edge (section A). Section D is bisected by a small stream with many associated streamlets and contains the boggy areas and tarns used for breeding. By comparison the eastern slope (A, B, C) is drier once the snow has melted off and, within the transect area, contains only one small spring and no sites suitable for spawning.

Male and female adults were unequally distributed across this habitat (Fig. 2). The proportion of toads that were adult females was highest in section A (64%) and lowest in section D (19%), and these proportions were significantly different ($\chi^2 = 81.5$, $df = 3$, $P < 0.001$), whereas proportions of males tended to be the opposite of those observed in females. Proportions of males ranged from a low of 4% of all individuals found in section A to a high of 54% of those in section D, and were significantly different ($\chi^2 = 107.8$, $df = 3$, $P < 0.001$). The distribution of the sexes along the transect was significantly different ($\chi^2 = 190.1$, $df = 3$, $P < 0.001$). In contrast, immature toads (age one or two years) formed a relatively constant proportion of individuals found in each section; 27% to 40%, and differences were not significant ($\chi^2 = 2.9$, $df = 3$, $P = 0.410$). Adults, both sexes combined, consistently repre-



FIGURE 2. Percentage of total number of *Bufo canorus* found in each section depicted in Fig. 1, according to age and sex. Sample sizes shown next to plotted points.

sented about two-thirds of all toads in each section and immatures (sex unknown) the remaining one-third.

Ovarian cycling.—Mean ovarian mass of 10 pre-breeding individuals was 20.1% of total body mass (Fig. 3). Ovaries of 16 post-breeding females increased in size from 5.2% of body mass in June to 9.7% in September (Fig. 3). Compared to pre-breeding females, ovaries of individuals in the first months after spawning were reduced in size and the ova contained therein were small and unpigmented.

DISCUSSION

Life-history strategies.—Dispersal behavior has seldom been measured directly in amphibians (Smith and Green 2005; Trenham and Shaffer 2005) although advances in technology are rectifying this. For example, information on dispersal of juveniles is now being obtained from microsatellite markers (Palo et al. 2004) and post-breeding migrations by adults are being monitored by miniaturized telemetry systems. Radio-tracking data show that *B. canorus* sometimes moved hundreds of meters within a single 24-h period (Martin 2008). The same was true of *B. boreas*. Furthermore, females traveled greater distances from breeding sites than males (Bartelt 2000; Muths 2003; Bartelt et al. 2004; Bull 2006) and had home ranges that were four times larger (Muths 2003). Locomotor abilities of migrating *Bufo* spp. also include being able to navigate

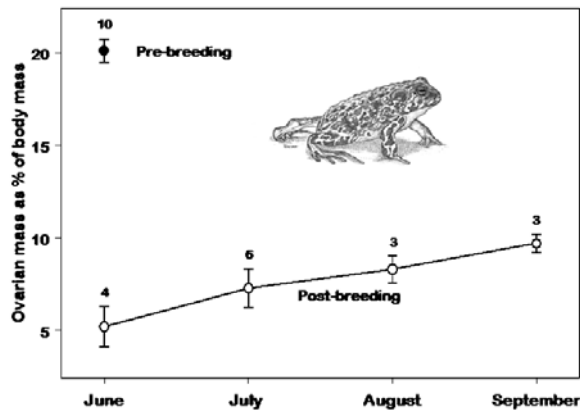


FIGURE 3. Ovarian mass, as percentage of body mass, in *Bufo canorus* collected as they entered breeding pools (pre-breeding) and during the summer months following a spawning session (post-breeding). Data points show means \pm 1 SE and numbers give sample sizes. The illustration of a female crossing a large expanse of snow was drawn by MEP from a photograph.

large snow fields (Kagarise Sherman and Morton 1984) as well as talus slopes and cliff faces (Sztatecsny and Schabetsberger 2005).

Until now movements by *B. canorus* at our primary study site, Tioga Pass, have only been reported for adults within section D between the hibernation site marked there and breeding pools located about 200 m down the meadow to the north (Kagarise Sherman 1980). Migration distances to breeding sites may often be considerably greater than this particularly for adult females and juveniles that dispersed to the interface between meadow and talus slope. We observed juveniles emerging from their first hibernation only a few meters from breeding sites, but they dispersed across the landscape that summer and the following one demonstrating early vagility in *B. canorus*.

Female anurans inhabiting the temperate zone usually breed annually and their cycle includes a post-ovulatory resting period of two to three months during which the ovaries remain quiescent (Jørgensen et al. 1979). Growth then resumes and by the time of hibernation ovaries are close to breeding size (Jørgensen et al. 1979). This pattern did not apply uniformly to adult females of *B. canorus* because some entered hibernation (usually in September and early October) with undeveloped ovaries that weighed about 10% of body mass, half the percentage of those that entered wetlands to breed. In contrast, testes were always less than 1% of body mass in adult males (Morton 1982). It appears likely that short summer seasons with near-freezing nocturnal conditions at high altitude often force irregular breeding.

It is likely that there is simply not enough time or available energy for adults, especially females, to accumulate reserves sufficient for hibernation and for consecutive annual reproductive cycles. This hypothesis is supported by data on visitation frequencies of individually marked *B. canorus* to their traditional Tioga Pass breeding sites (Kagarise Sherman 1980). It was found that 182 of 216 marked females (84%) bred just once during a four-year study and that only three individuals (1%) spawned in all four years. Individual males were about twice as likely as females to enter breeding sites annually (both sexes were site-tenacious), but they sometimes also skipped one or more years between breeding attempts. The data we present on ovarian mass and reproductive timing in *B. canorus* are similar to those found in *B. boreas* (Carey et al. 2005), and although these schedules might seem unusual for small vertebrates, they probably are not. Intermittent reproduction appears to be a normal life-history trait of iteroparous ectotherms (Bull and Shine 1979), particularly in those living at high altitude (Turner 1960; Heusser 1968; Olson 1992; Morrison and Hero 2003; Carey et al. 2005).

At Tioga Pass conditions at the edges of talus slopes appear to be particularly suitable for summering females because they tended to cluster there. Dry and rocky areas such as these may provide hibernation sites (Bull 2006; Martin 2008), refuge from predators, or microclimates favorable for basking and feeding. The adults with the greatest fat content ever sampled at Tioga Pass were females found near the edge of a talus slope (Morton 1981). Given Muths' (2003) data on *B. boreas*, it might also be that talus slopes are simply barriers to additional dispersal. Muths found that radio-tagged females, but not males, sometimes moved 2 km or more from their breeding ponds. We suspect that certain patches of summer habitat are sought out and occupied because they promote improved body condition. This may help to increase fitness by decreasing the frequency of skipped breeding cycles.

Conservation implications.—Numbers of *B. canorus* visiting breeding pools that we studied at Tioga Pass over a 20-year period (1971-1990) began to decrease in the late 1970s and continued through the 1980s, and in 1990 only one egg mass was located (Kagarise Sherman and Morton 1993). During the next five summers we remained at Tioga Pass to study avian reproduction, but we also checked frequently for *B. canorus* activity. No evidence of their spawning was found and only rarely did we encounter a live individual. Across the range of

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B. canorus, 50% of populations had vanished by 1994 (Jennings and Hays 1994; as cited by Davidson and Fellers 2005), with most disappearances occurring at lower elevations on the western slope of the Sierra (Davidson et al. 2002).

Chytrid fungus has been strongly implicated in the demise of *B. boreas* in Colorado (Muths et al. 2003). At our study sites, however, no single cause for the decrease in toad numbers could be identified: drought, disease (chytridiomycosis and bacillary septicemia), predation, and silting in of tarns used for spawning were all possible factors (Kagarise Sherman and Morton 1993; Green and Kagarise Sherman 2001). Leading hypotheses for range-wide declines of *B. canorus* are disease, airborne contaminants, and livestock grazing (Davidson and Fellers 2005; Martin 2008). *Bufo canorus* live almost completely on federally managed lands, much of it designated wilderness, but the U. S. Fish and Wildlife Service considers the species to be only moderately threatened and has precluded it from listing (U. S. Fish and Wildlife Service 2002). The U. S. Forest Service does recognize *B. canorus* as “sensitive” and is taking steps to protect wet-meadow breeding habitat through limitations on grazing and pesticide applications (Davidson and Fellers 2005). As our study shows, protection should be extended to include patches of terrestrial habitat that can be located many hundreds of meters away from breeding sites, as well as landscape connectivity among such areas. This might be particularly crucial for juveniles and adult females that may live continuously for several consecutive years at a time in these drier terrestrial locations. Migrations to “high-quality” summer habitat (higher vegetation diversity and abundance of food) have also been observed in *B. bufo* in the Austrian Alps (Sztatecsny and Schabetsberger 2005), so use of widely disconnected patches of habitat might be a common feature of bufonid behavior in high altitude environments. Finally, we suggest that information on high-altitude amphibians as a group, which includes urodeles (Funk and Dunlap 1999; Schabetsberger et al. 2004) as well as anurans, is now of enough quality for development of biologically based models that could be used for predicting consequences of habitat loss and fragmentation especially when it causes a disconnection between habitats used by different life-history stages (Cushman 2006; Becker et al. 2007).

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MARIA ELENA PEREYRA is an Assistant Professor of Biological Sciences at the University of Tulsa. Her research interests focus on the physiological and behavioral ecology of reproduction in vertebrates, and the ecological and evolutionary processes that shape biological diversity. Current projects include long term studies centering on the reproductive ecology of subalpine passerine birds in northern British Columbia and endocrine mechanisms regulating overwintering behaviors and physiology of birds in the southern Great Plains. (Photographed by Martin L. Morton)