

Factors Limiting the Recovery of Boreal Toads (*Bufo b. boreas*)

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Boreal toads (*Bufo b. boreas*) are widely distributed over much of the mountainous western United States. Populations in the Southern Rocky Mountains suffered extensive declines in the late 1970s through early 1980s (Carey, 1993). At the time, these mass mortalities were thought to be associated with a bacterial infection (Carey, 1993). Although the few populations that survived the mass die-offs were not systematically monitored until at least 1993, no mass mortalities had been observed until 1996 when die-offs were observed. A mycotic skin infection associated with a chytrid fungus is now causing mortality of toads in at least two of the populations (M.S. Jones and D.E. Green, unpublished data; Muths et al., 2003). Boreal toads are now absent throughout large areas of their former distribution in Colorado and southern Wyoming and may be extinct in New Mexico (Corn et al., 1989; Carey, 1993; Stuart and Painter, 1994). These toads are classified as "endangered" by Colorado and New Mexico and are designated as a protected non-game species in Wyoming. The U.S. Fish and Wildlife Service has categorized the Southern Rocky Mountain populations for federal listing and is currently reviewing their designation as a "warranted but precluded" species for possible listing in the next few years. For the management of boreal toads and their habitats, a Boreal Toad Recovery Team was formed by the Colorado Division of Wildlife in 1995 as part of a collaborative effort with federal agencies within the United States' departments of the Interior and Agriculture and with agencies in two adjoining states. To date, conservation agreements have been signed by eight state and federal agencies and by the Colorado Natural Heritage Program.

Although boreal toads were considered common throughout their range in Colorado, no comprehensive surveys of the numbers and sizes of their populations were conducted prior to mass die-offs in the 1970s. Surveys completed in the late 1980s to early 1990s, however, indicated that the toads were still present in only one of 377 historical sites in parts of western Colorado (Hammerson, 1992) and in about 17% of previously known sites in the Colorado Front Range (Corn et al., 1989). Once common in Rocky Mountain National Park, boreal toads are now found at only seven localities, with just two or three of these populations likely to be reproducing successfully each year (Corn et al., 1997). Intensive surveys by the Boreal Toad Recovery Team since 1995 have found about 50 breeding sites

comprising 25 distinct populations within Colorado (Loeffler, unpublished data). Of these populations, most are small (fewer than five egg clutches laid per year) and may not survive over the long term.

Efforts to restore population sizes and expand the geographical distribution of boreal toads in the southern Rocky Mountains have involved considerable person-hours and financial commitments. Special care has been taken to protect habitats and, when feasible, to improve sites where breeding populations currently exist. However, initial attempts to repatriate these toads in historic habitats in which boreal toads were present before 1975 have generally proven unsuccessful (Carey, unpublished data; Muths et al., 2003). It is too early to determine if recent repatriations will establish breeding populations (Scherff-Norris, 1999), but these efforts will likely continue. Despite the best human intentions and efforts, the recovery of former population sizes and the historical distribution of boreal toads will greatly depend on its own life history characteristics. However, as we will review in this paper, environmental factors affect many life history attributes in a manner that poses serious obstacles for recovery.

Geographical Locations and Time Periods of Observations

Data presented in this study were gathered at several localities in Colorado (Fig. 31-1), both before and after the mass mortalities of the 1970s–80s. Boreal toads were studied prior to their population crash, which started in 1973 or 1974 in the East River Valley of the West Elk Mountains, near Crested Butte, Colorado (106° 59' W, 38° 58' N; Carey, 1993). A map of the breeding sites, located at altitudes between 2990 and 3550 m within the East River Valley, has been published in Carey (1993). Data collected at these sites are designated as "West Elk Mountains."

Two sites in the North Fork of the Big Thompson River within Rocky Mountain National Park have been monitored intensively since 1991 (Corn et al., 1997; Corn, 1998). Kettle Tarn (40° 30' N, 105° 31' W, 2810 m) is a shallow glacial kettle pond. Lost Lake (3,266 m) is a drainage lake. Data from these sites are identified as "RMNP."

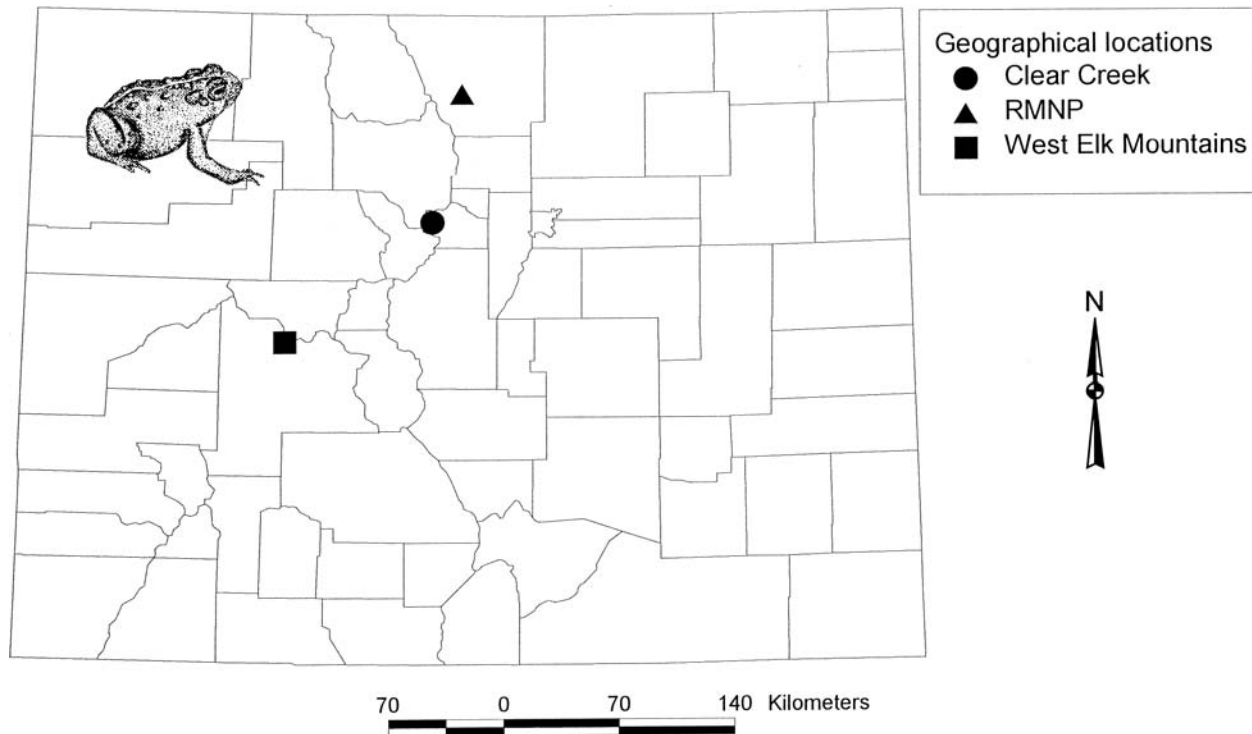


FIGURE 31-1 Colorado sites at which boreal toad life history characteristics reported in this study were observed. Observations were conducted at West Elk Mountains (1971–76), Rocky Mountain National Park (RMNP; 1991–present), and Clear Creek (1995–present).

Several sites in the vicinity of Woods Mountain (39° 43' N, 105° 50' W), Clear Creek County, have been monitored since 1995. The most intensively studied sites are in the Urad Valley (Woods Creek drainage); including sites informally known as Hesbo, Lower Urad, Treatment, Donut, Anne's Pond, and Upper Urad. In West Fork, the adjacent drainage, we collected information from sites informally known as Power Alley, JSP, and 1 Pond. The Herman Gulch and Mt. Bethel sites are located in the Clear Creek drainage. All locations are at elevations between 3,048 and 3,170 m. Data from these sites are designated as "Clear Creek."

Environmental Characteristics

Boreal toad populations in the Southern Rocky Mountains historically were found between approximately 2,500 and 3,600 m (Campbell, 1970c,d; Livo and Yackley, 1997). Breeding sites range from large lakes, beaver ponds, and glacial kettle ponds to temporary pools formed by snowmelt in depressions such as tire ruts. The high montane environment where the toads live is dominated by cold temperatures; snow generally covers the ground for six to eight months. In response, boreal toads hibernate in locations such as rodent burrows, cavities in dams of beaver ponds, and under the overhanging edges of stream banks (Campbell, 1970c; Jones and Goettl, 1998). Emergence is governed by snowmelt, which can occur anytime between mid-May through late June. During the short summer growing season, boreal toads must accumulate sufficient energy to sustain basic metabolism, growth, and reproduction. At this time, the daily body temperatures of boreal toads fluctuate from near freezing to around 30 °C, depending on cloud conditions and behavioral

tendencies (Carey, 1978). High body temperatures, which foster high rates of passage and absorption of food through the digestive tract, circulation of blood, immune function, and overall metabolism (Carey, 1976, 1979; Maniero and Carey, 1997), are achieved by basking in direct sunlight. However, frequent cloud cover during the day reduces body temperatures to 10–20 °C, and body temperatures fall to near freezing during summer nights (Carey, 1978). In addition to support of basic metabolic and reproductive functions, boreal toads must also store energy in the form of fat and glycogen, some of which is used to survive the subsequent winter. Toads enter hibernation sometime between late August and early October, depending upon weather conditions. Therefore, the combination of short growing seasons and cold summer temperatures lowers cumulative metabolic rate and restricts the rate of accumulation of energy by the toads.

We believe these environmental factors are major determinants of the life history characteristics of boreal toads. These factors differ from those encountered by lowland *Bufo* populations, and they likely limit the ability of Southern Rocky Mountain populations to recover from mass mortalities.

Life History Attributes

Timing of Breeding

At all three locations (Fig. 31-1), breeding has almost always occurred in the spring or early summer when the snow melted from most, if not all, of the body of water. However, in one unusual case, a clutch was laid in August (Fetkavitch and Livo, 1998). Because snow usually melts earlier at lower altitudes, breeding commences earlier at lower locations. We observed

TABLE 31-1
Clutch Sizes and Sizes of *Bufo boreas* Females at Three Localities in Colorado

Locality	Mean + SE Clutch Size	n	Range	Female Snout-Vent Length (mm)
West Elk Mountains	5897 ± 363	21	3,239–8,663	72.5–87.2
RMNP	8155 ± 954	4	6,655–10,872	83.0–84.0
Clear Creek	7440 ± 435	13	4887–9333	71.7–83.95
Overall mean	6661 ± 294	38		

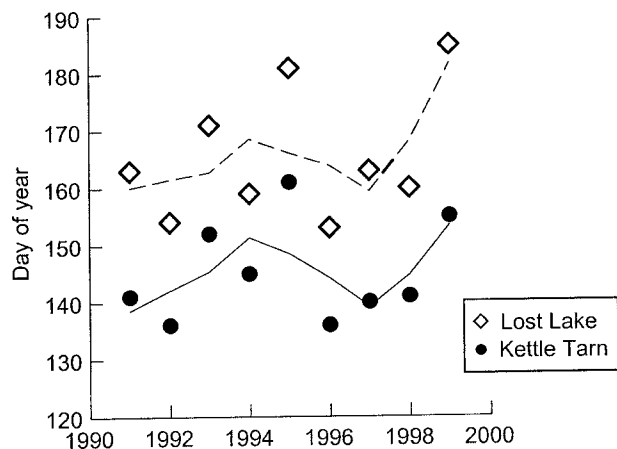


FIGURE 31-2 Dates of peak breeding activity by boreal toads at two locations in Rocky Mountain National Park, Colorado. Trend lines were drawn using LOWESS regression (Cleveland, 1979).

considerable variation in the timing of breeding by toads at two sites along the North Fork of the Big Thompson River in Rocky Mountain National Park (Fig. 31-2). From 1991–99, the date of peak breeding activity at Kettle Tarn averaged 24 May, but varied from 15 May 1992 and 1996 to 10 June 1995. At Lost Lake, breeding peaked, on average, around 13 June. The onset of breeding at Lost Lake varied from 1 June 1996, to 4 July 1996, to 10 June 1995 (Fig. 31-2).

Between 1971–75 in the West Elk Mountains, the earliest date on which egg laying began was May 25. Frequently, no breeding occurred at the highest elevations (3,550 m) until the end of June. Breeding was initiated at lower elevation sites in Clear Creek County (such as Hesbo and Herman Gulch) from mid- to late May and at higher elevations from late May to early June.

Reproductive Size

The minimum snout-vent length recorded for a breeding female was 71.7 at the Urad Valley site of the Clear Creek population and 72.5 mm at the West Elk Mountains populations. In the Clear Creek population, the mean snout-vent length of breeding females and males was 77.6 ± 1.1 and 67.0 ± 1.1 mm, respectively, but a 55-mm male was caught in amplexus in the Clear Creek population (Livo, 1999). In the West Elk

Mountains, mass and snout-vent length of breeding females captured immediately after egg laying averaged 46.1 ± 1.4 g (range 37.9–52.7 g) and 78.6 ± 3.3 mm (range 72.5–87.2 mm), respectively.

Clutch Size

Three different methods were used to estimate clutch size. To investigate clutch size in the West Elk Mountains during the 1973–74 breeding season, males and females in amplexus were located just prior to egg laying. A thread was tied around the hind foot of each female to prevent her from leaving the breeding site before her snout-vent length and body mass could be determined. Snout-vent length and body mass were measured with vernier calipers and an Ohaus balance. After egg laying was completed, eggs were gathered in a plastic container and counted. Because this method disrupted the protective properties of the egg jelly, egg masses treated in this manner usually developed fungal infections and few larvae hatched. Therefore, although this procedure provides an accurate count, we do not recommend it for future studies of clutch size, especially on endangered or threatened species.

Clutch sizes at RMNP were recorded *in situ* by gently pulling the egg string through the observer's hands and counting the eggs. The jelly was largely undisturbed by this process and hatching success appeared normal.

Prior to egg laying, pairs of boreal toads found in amplexus during the 1999 breeding season in the Urad Valley of Clear Creek County were placed in a 30×44 cm plastic container. The eggs of each clutch were arranged in a single layer and photographed. (For details on the method used to estimate egg number from the photographs see Livo [1999].) Diameters of 20 eggs from two positions in each egg mass were measured using a dissecting microscope with an ocular micrometer. All toads and resulting eggs were released in the ponds at which the toads were captured. Using this procedure, no unusual fungal infections were noted and hatching rates of these clutches approached those of undisturbed clutches.

An overall mean clutch size (number of eggs per clutch) calculated for the three boreal toad populations was $6,661 \pm 294$ eggs (Table 31-1). The number of eggs in 21 clutches laid between 1973–74 in the West Elk Mountains was significantly lower (ANOVA, $F = 5.46$, $p = 0.009$) than the average clutch sizes in Clear Creek and RMNP (Table 31-2).

TABLE 31-2
 Known Sources of Complete Boreal Toad (*Bufo boreas*) Embryo and Tadpole Mortality at Seven Breeding Sites in Clear Creek County in 1999

	Hesbo	Donut	Lower Urad	Power Alley	Anne's Pond	Mt. Bethel	Herman Gulch	Total
Freezing	4							4
Desiccation				1	21		6 ^a	28
Sterility	2							2
Water quality							4 ^a	4
Fungus		3						3
Temperatures			2					2
Unknown						1		1
Total egg masses	23	17	2	1	21	2	10	76

^a Egg masses in pools were moved to more permanent pools to prevent desiccation; poor water quality was probably the cause of mortality of eggs found covered with fungus.

NOTE: Numbers are egg masses.

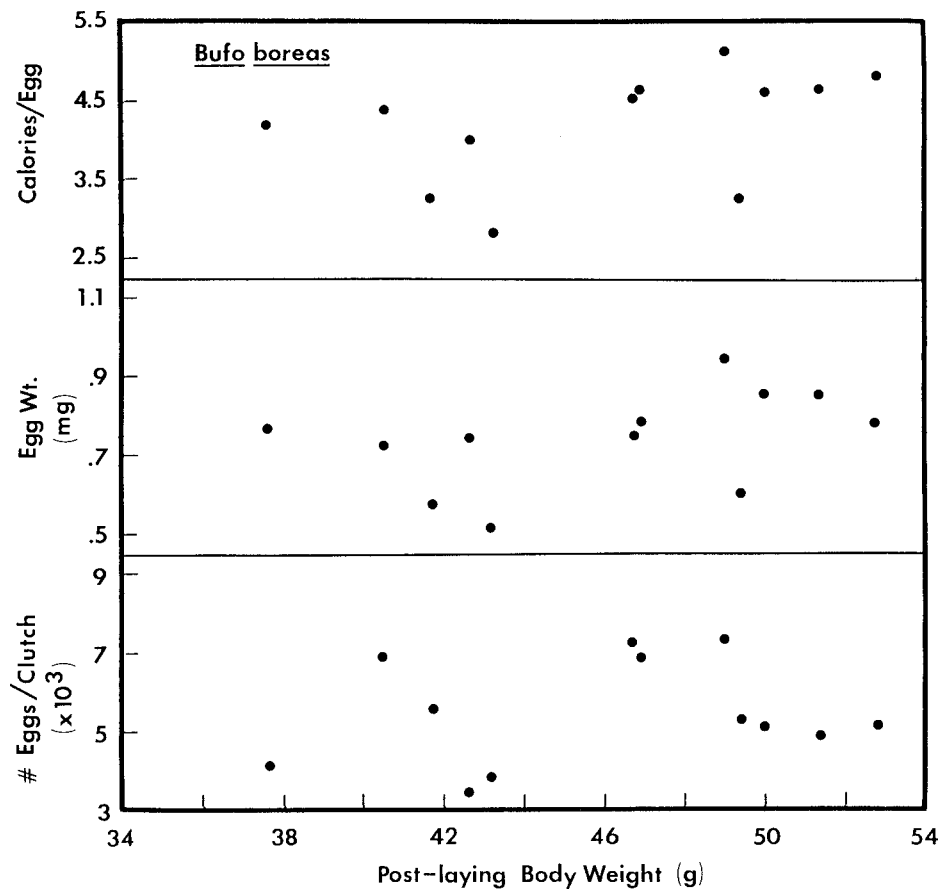


FIGURE 31-3 Caloric content per egg, dry egg mass, and number of eggs per clutch as a function of post-reproductive body mass of females in the West Elk Mountains. Each female provided one point for each variable.

The mean initial mass of 70 ± 3 g of 12 females in the Clear Creek population decreased an average of 17 ± 1 g following egg laying, representing an average loss of 24 ± 5 percent of the initial body mass. A significant positive relationship existed between the initial mass of 12 females

and the number of eggs they produced ($r = 0.851$, $df = 10$, $p < 0.01$).

Within individual populations, such as the West Elk population, no significant relation existed between clutch size and either female post-breeding body mass ($p = 0.22$; Fig. 31-3) or

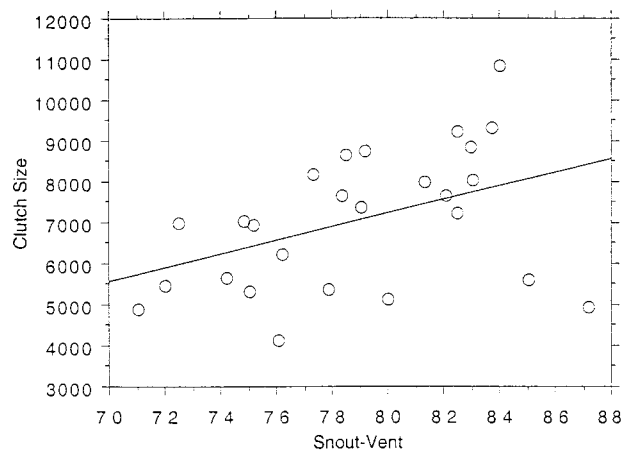


FIGURE 31-4 Clutch size of individual females as a function of snout-vent length (mm). Data were combined from populations in the West Elk Mountains, RMNP, and Clear Creek. The least-square regression equation best describing the relation between clutch size and snout-vent length (SVL) is "Clutch Size = -6046.2 + 166.2 Snout-vent Length;" it is shown by the thin line.

snout-vent length ($p = 0.70$). However, when data were combined for the three populations, a significant ($r = 0.43$, $df = 25$, $p = 0.03$) relation existed between clutch size and female snout-vent length (Fig. 31-4).

Egg Characteristics

Ten eggs from each of 18 clutches gathered from the West Elk Range were freeze-dried for 4 days until they reached constant mass. These were then weighed on a Mettler balance, accurate to 0.001 g, to determine dry mass. The values from the ten eggs were averaged for an estimate of the dry egg mass for a given clutch. Dry eggs from each clutch were combined and homogenized into pellets for analysis of caloric content. The caloric contents of three pellets per clutch were analyzed with a Phillips microbomb calorimeter, calibrated with benzoic acid. The average of the results from the three pellets was used as the estimate of caloric content per g egg. The caloric content per clutch was obtained by multiplying the clutch size by the dry egg mass to obtain dry clutch mass, and then multiplying that value by the caloric content per g egg mass. (Average values will be presented throughout this paper as mean \pm SE. Least squares regression lines were calculated to define the relation of various types of fecundity data to body mass or snout-vent length.)

Mean egg diameter at the Urad site in Clear Creek County was 1.6 ± 0.07 mm. A negative correlation between egg diameter and number of eggs per clutch existed at that location ($r = -0.524$, $df = 11$, $p < 0.05$). Total volume for an egg mass can be estimated as $(3.14 \times n \times d^3) \times 6^{-1}$, where n is the egg number and d is the mean egg diameter in mm. A significant, positive relationship existed between total egg mass volume and female snout-vent length ($r = 0.604$, $df = 11$, $p < 0.05$). Mean egg diameter and female snout-vent length were not significantly related ($r = -0.505$, $df = 11$, $p > 0.05$).

Dry mass of eggs laid in the West Elk Mountains averaged 0.74 ± 0.02 mg (range 0.51–0.94 mg). The dry mass of a clutch averaged 4.40 ± 0.21 g (range 1.96–6.94 g). Mean caloric content per egg and per clutch were 4.18 ± 0.03 cal (range 2.80–5.12) and $24,786 \pm 1,818$ cal (range 10,782–43,108),

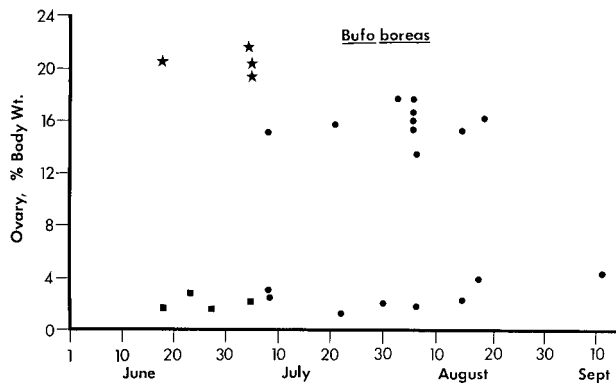


FIGURE 31-5 Ovarian masses of female boreal toads (% body weight) captured between 1972–74 in the West Elk Mountains. Ovary masses of females captured in amplexus before ovulation and those that just finished laying eggs are represented by stars and squares, respectively. Ovarian masses of those that were captured after breeding are shown by circles. Each symbol represents the value for a single female.

respectively. Calories per egg, dry egg mass, or calories per clutch were not significantly related to either female post-breeding body mass (Fig. 31-3) or to snout-vent length.

Frequency of Breeding

Several lines of evidence indicate that boreal toad females rarely, if ever, breed two years in a row. First, morphological evidence indicates that the ovaries of some females of breeding size contain only immature, pre-vitellogenic oocytes during a given summer, and that these females could not lay eggs the subsequent summer. In the West Elk Mountains, ovarian masses of females in amplexus prior to ovulation ranged between 19–22% body mass (Fig. 31-5). These ovaries were dominated by large, highly pigmented oocytes. Ovaries collected from females just after laying a clutch averaged 1–3% of body mass and contained non-pigmented, immature oocytes, and atretic oocytes (those that began vitellogenesis, but then stopped development and were not ovulated; Fig. 31-5). Ovaries of females collected after the breeding season fell into two categories: (1) ovaries weighing between 1–3% of body mass and containing non-pigmented oocytes and atretic follicles and (2) ovaries weighing between 13–17% of body mass and containing pigmented oocytes that were undergoing vitellogenesis. These data suggest that the ovaries of females collected in July and August and weighing 1–3% of body mass are in a "resting" condition, in which no oocytes are being prepared for breeding the following year. Ovaries of other females are enlarged with oocytes undergoing vitellogenesis in preparation for laying the following summer.

Mark-recapture studies provide a second line of evidence supporting the idea that female boreal toads do not usually breed every year. Adult toads inhabiting the North Fork of the Big Thompson River in RMNP have been marked using PIT tags since 1991 (Corn et al., 1997). Far more males than females are actually captured. In the North Fork (Kettle Tarn, Lost Lake, and other localities) from 1991–98, 874 males (691 recaptures) and 246 females (31 recaptures) were marked, but the mean estimated population sizes (412 ± 17.5 males and 591 ± 314.4 females) were not significantly different. Females had lower capture probabilities (0.098 ± 0.054 , hence the poor precision of the estimate) than did males (0.49 ± 0.02), and

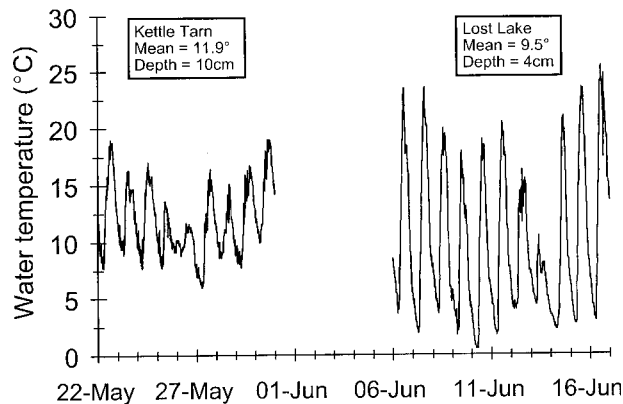


FIGURE 31-6 1994 water temperatures at two egg deposition sites in RMNP. Temperatures were recorded at 10–12 min intervals using thermometers and single-channel data loggers (Corn, 1998).

most recaptures of females occurred after breeding. From 1991–98, only 6 of the 31 recaptures were of female toads marked during one breeding season and recaptured in a later breeding season.

Finally, the ratio of effective to total population size supports the idea that boreal toad females rarely, if ever, breed two years in a row. The number of egg masses averages 12% of the estimated number of males at Kettle Tarn and Lost Lake. Given that the sex ratio for a population is probably close to 1:1, the low number of females breeding in a given year indicates that most do not breed in consecutive years.

Thermal Influences on Egg and Tadpole Development

Boreal toads typically lay eggs on the north, northwest, or northeastern shores of large ponds or lakes—areas that receive the most daily sunlight. In most cases, egg laying occurs in shallow water (< 10 cm) on gently sloping pond edges. Solar radiation warms shallow water to temperatures as high as 30 °C during the day, but water temperatures often cool to near freezing at night. Therefore, eggs of boreal toads are exposed to considerable fluctuations in daily temperatures (Fig. 31-6).

The importance of egg laying in sunlit, shallow water is highlighted by the fact that tadpole development does not occur at constant, cold temperatures and requires high water temperatures for at least a portion of the day. As an experiment, we removed four groups of about 50 eggs each from a clutch of eggs laid on 2 June 1973 in the West Elk Mountains. Remaining eggs were left in the field to develop. It snowed on day 2 and day 5, and the pond froze on day 7. The eggs left in these conditions did not show any development past Gosner stage 4 (Gosner, 1960), and all these eggs died when the pond froze (Fig. 31-7). The four groups that were taken to a laboratory at the Rocky Mountain Biological Laboratory were acclimated to one of four temperatures (10 °C, 15 °C, or 30 °C) and a cyclical regime of 12 hours at 10 °C and 12 hours at 30 °C. Embryos showed no development past stage 4 at a constant temperature of 10 °C (Fig. 31-7). Development was most rapid at 30 °C and was slowest at 15 °C. Development of embryos/larvae exposed to the fluctuating thermal regime (which most closely represented typical daily changes in temperature) was intermediate between the rate at 30 °C and 15 °C. Therefore, exposure to 10 °C was not harmful to the embryos as long as they experienced warmer temperatures

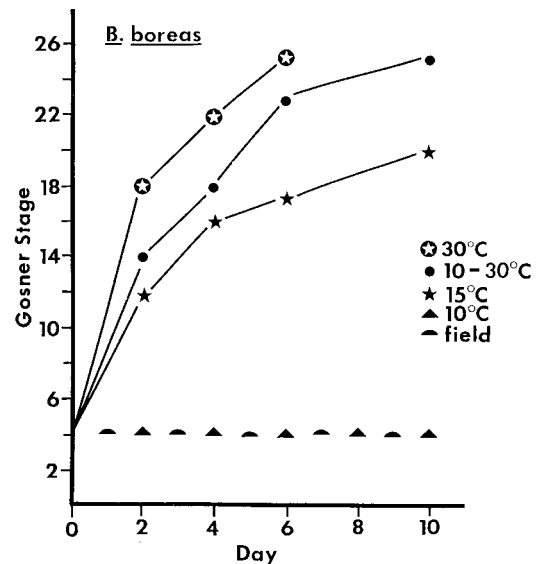


FIGURE 31-7 Effect of temperature on median Gosner (1960) stage of boreal toad embryos held at a variety of temperatures (in the field under a natural thermal regime which involved two snowstorms and eventual freezing of the pond); constant temperatures of 10 °C, 15 °C, 30 °C and a 12-hour alternating cycle of 10 °C to 30 °C for 10 days.

for a portion of the day, but it did retard development to some degree. These data indicate that cooler water temperatures, like those associated with cloud cover and/or late season snowstorms, can delay development of larvae to metamorphosis. Therefore, failure to undergo metamorphosis before freezing temperatures occur in the fall can result not only from heavy spring snowpacks that delay egg laying, but also from unusually cold summer temperatures that retard egg and embryo development.

In Clear Creek County, the Lower Urad site is across a dirt road from the Hesbo site. Although the two sites are located at the same elevation and experience the same atmospheric conditions, thermal regimes differ substantially. The Lower Urad site is a cold, stream-fed reservoir; the Hesbo site is a temporary pool that warms considerably during the summer. In 1999, females deposited two egg masses at the Lower Urad site during the same time that breeding was underway at the Hesbo site. Metamorphosis at the Hesbo site began on August 13, 81 days after the first eggs had been deposited. In contrast, no tadpoles developed to metamorphosis at the colder Lower Urad site (Table 31-3).

Breeding Success

Boreal toads suffer high mortality at both the egg and larval stages. Desiccation of egg masses appears to be the single largest source of egg mortality. For instance, 15 clutches laid in 1973 at the top of Schofield Pass in the West Elk Mountains were destroyed when a June drought caused the pond to dry. In 44 out of 76 clutches that suffered complete mortality at the Clear Creek County sites, pond desiccation caused over half of the cases (Table 31-2). Corn (1998) reported a loss of 5 of 35 egg masses laid at Lost Lake in 1994 due to dropping water levels.

Egg masses can also be lost when water levels rise rapidly. In 1995 at Kettle Tarn, an abnormally high amount of snow fell during May and delayed breeding. However, some pairs bred

TABLE 31-3
 Dates of Egg Deposition and Onset of Metamorphosis of Boreal Toads at Clear Creek County
 Breeding Sites

Site	Year	Egg Deposition Date	Date of Metamorphosis	Approximate Days Elapsed
Hesbo	1999	24 May	13 August	81
Hesbo	1998	20 May	5 August	77
Donut	1999	3 June	20 August	78
Donut	1998	2 June	12 August	71
Donut	1997	4 June	26 August	83
Mt. Bethel	1998	2 June	20 August	79
Mt. Bethel	1997	2 June	2 September	92
Mt. Bethel	1996	29 May	21 August	84
Herman Gulch	1998	16 May	6 August	82
Herman Gulch	1997	22 May	18 August	88
Anne's Pond	1998	2 June	5 August	64
Anne's Pond	1997	4 June	26 August	83

early; the resulting massive snowmelt raised the level of the pond by at least 50 cm and, subsequently, no trace of the early egg masses was observed. Other factors, such as gamete sterility, water quality, and fungal infections also contribute to high egg mortality at boreal toad breeding sites (Table 31-2).

Some mortality of boreal toad larvae occurs because they are unable to metamorphose before their breeding pond freezes in the fall (Fetkavitch and Livo, 1998). If egg laying is delayed by a heavy winter snowpack, or if larval development is retarded by unusually cold summer days, larvae may not have enough time to complete metamorphosis. In general, at lower elevations in RMNP, variation in breeding dates does not affect the eventual metamorphosis by tadpoles. Breeding occurs an average of 20 days earlier at the lower elevation Kettle Tarn site in RMNP than the higher Lost Lake locality. Additionally, water temperatures are warmer and tadpoles develop faster at the lower altitude site (Corn and Muths, unpublished data). Breeding was delayed by heavy spring snowpack at Lost Lake in 1995 and 1999, and no tadpoles were observed to have metamorphosed in either year. In most years at Lost Lake, at least some tadpoles metamorphose; however, almost every year at this site we observe small tadpoles in September and October that would be unable to reach metamorphosis prior to freeze-up. Many of the shallower pools at this site held tadpoles and metamorphic animals killed by freezing or drying.

Predation is another major source of mortality of boreal toad larvae. Major predators of boreal toad tadpoles and toadlets include several species of birds (Campbell, 1970c; Beiswenger, 1981; Jones et al., 1999; Livo, 1999). Spotted sandpipers (*Actitis macularia*) consumed numerous metamorphosing toadlets in Clear Creek County and virtually eliminated all the toadlets at one site (Jones et al., 1999). Mallard ducks (*Anas platyrhynchos*) consumed all the tadpoles at several sites in the Denny Creek drainage of Chaffee County (C. Fetkavitch, unpublished data). Other predators include terrestrial garter snakes (*Thamnophis elegans*), tiger salamanders (*Ambystoma tigrinum*), and predaceous diving beetle larvae (*Dytiscus* sp.; Reese, 1969; Campbell, 1970c; Livo, 1999).

Metamorphosis

In the Clear Creek County sites, metamorphosis begins within 64–92 days after egg laying (Table 31-3). Typical body masses and snout-vent lengths of newly metamorphosed boreal toads at these sites were about 0.30–0.35 g and 15 mm, respectively. Comparable values for toadlets in the West Elk Mountains averaged 0.25 g and 13.1 mm, respectively. These differences probably represent normal variability in boreal toad metamorphosis because considerable site-to-site and year-to-year variation in size at metamorphosis exists within Clear Creek populations (Fig. 31-8). When toadlet sizes at two Clear Creek sites were compared between years, the production of smaller toadlets occurred in the comparatively hotter, drier summer. No significant relation ($r = 0.58$, $df = 9$, $p < 0.05$) existed between toadlet mass at metamorphosis and the minimum length of the larval period at five sites in the Clear Creek area.

Some variation in size at metamorphosis is due to genetic differences in growth rates, even among siblings. About 200 eggs from a single clutch laid at one of the Clear Creek sites were raised in the laboratory at 25 °C with food for larvae provided *ad libitum*. An opportunity for raising body temperature above 25 °C was provided in one corner of the cage by a heat lamp. Body masses of the newly metamorphosed toadlets varied from 0.42–1.16 g.

Due to colder mean temperatures, tadpoles at higher elevations frequently have difficulty completing development before winter. Although we do not have quantitative data addressing this issue, we believe that survival through metamorphosis is only one of a series of hurdles that are encountered by young boreal toads. The fact that many more toadlets are usually observed soon after metamorphosis in the late summer or fall than are found the following spring suggests that considerable mortality occurs during their first winter.

Growth of Metamorphosed Individuals

Temperature is the primary determinant of growth rate in metamorphosed boreal toads. Forty-five sub-adult boreal toads

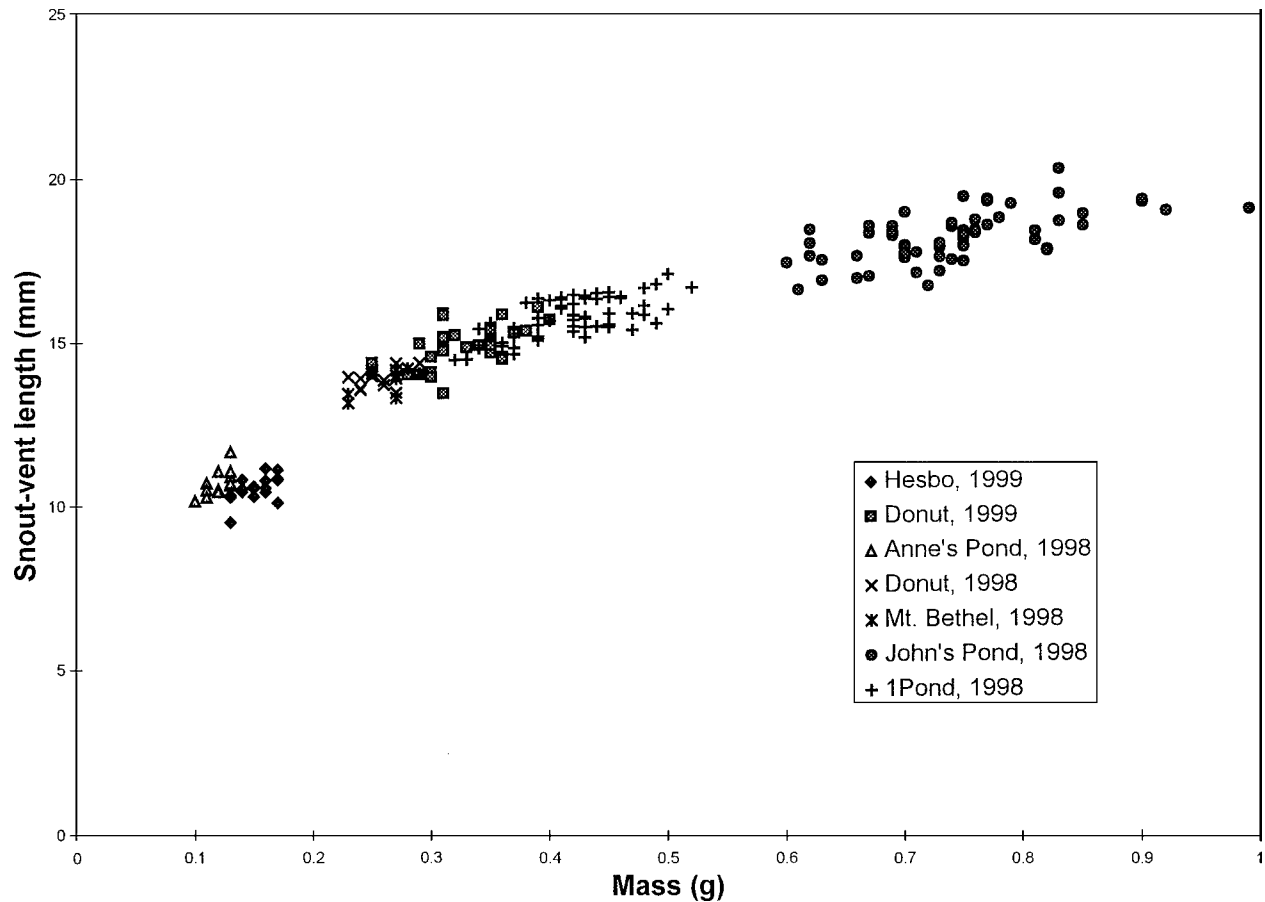


FIGURE 31-8 Variation in mass of newly metamorphosed boreal toad toadlets at various sites in Clear Creek County.

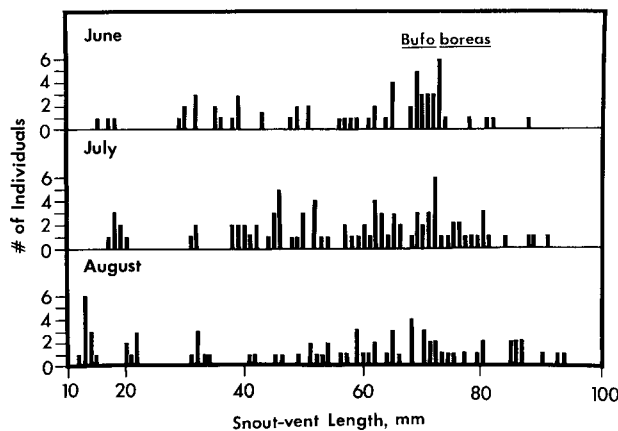


FIGURE 31-9 Number of boreal toads of various snout-vent lengths that were captured from June through August, 1971–74. These individuals were captured at the Trail 401 breeding area near the Rocky Mountain Biological Laboratory in the West Elk Mountains (for a map, see Carey, 1993).

collected in the West Elk Mountains in 1972 were divided randomly into three groups. Initial mass and snout-vent lengths of all 45 toads averaged 10.82 ± 0.4 g and 47.71 ± 1.4 mm, respectively. Fifteen toads were held at 7°C , another 15 at 25°C , and a third 15 were exposed to temperatures that cycled between 7°C and 25°C every 12 hours. The cyclical thermal

regime most closely approximates the change in body temperatures that would be experienced by boreal toads in their montane habitat during the summer (Carey, 1978). For the 4-week duration of the experiment, food (*Tenebrio* larvae) and access to water were provided *ad libitum*. Although the toads held at 7°C consumed food, they lost an average of 3% body mass, and snout-vent length did not increase during the 4-week trial. Body mass and snout-vent length of the toads held on the cyclical $7\text{--}25^\circ\text{C}$ regime increased an average of 29% and 4%, respectively, over the values at the beginning of the experiment. Toads held at a constant 25°C for the four-week period gained an average of 40% of initial body mass. Snout-vent lengths of these animals increased an average of 7%. Therefore, growth of metamorphosed boreal toads does not occur at the cold temperatures that prevail at night during the summer in their montane habitat. The high body temperatures achieved during daytime basking contribute importantly to the rate of growth of these toads in the field. Growth rates of the toads exposed to the cyclical regime in this experiment are more rapid than those observed in the field (see below) because cloud cover precludes basking on some summer days and the amount of food supplied in this experiment likely exceeded that available in the field.

A continuum of post-metamorphic sizes exists in boreal toad populations that produce some metamorphic young each year or nearly each year (Fig. 31-9). A total of 102 metamorphosed toads from the Trail 401 population in the West Elk Mountains were toe-clipped over three summers between 1971–73. Of that number, 25 marked individuals were recaptured at approximately the

TABLE 31-4
Average (\pm SE) Increase in Snout-vent Length (mm) Per Year of Various Sizes of *B. boreas* from the West Elk Mountains

Snout-vent length (mm) at first capture:					
10–20 mm	30–40 mm	40–50 mm	50–60 mm	60–70 mm	70+ mm
8.0 (1)	8.0 \pm 1.1 (5)	6.86 \pm 1.5 (7)	7.38 \pm 0.9 (8)	5.67 \pm 0.9 (3)	0.17 \pm 0.4 (5)

NOTE: A value for a particular animal was placed in the size category in which snout-vent length fell the year the animal was first captured. No data were available for the 20–30 mm size range. Sexes of individuals could not be determined until they were about 50 mm. All individuals within the 70+ category were females. Sample size is given in parentheses.

same time each summer at least one year after they were marked. Snout-vent lengths of these individuals were measured (Table 31-4). As judged by a one-way ANOVA, the average annual increase in length does not significantly change until the toads reach about 70 mm, when growth nearly ceases. Based on our values (Table 31-4), it would take an average of 4–5 years for a male, and about 6–7 years for a female, to reach the minimum breeding size. The differences in growth rates among siblings described above, however, suggest that some individuals may reach sexual maturity more rapidly than most of their age cohort.

Movements of Metamorphosed Individuals

Because newly metamorphosed and juvenile toads cannot be marked permanently and individually marked, no information exists concerning the movements of these toads in the years before they breed. When individuals in these age groups have been repatriated into historical habitats in which no known breeding populations have existed for a number of years, they have gradually disappeared from the site. We do not know whether they have died or dispersed to other areas, or if they will ever return to breed.

Because adult toads that were PIT-tagged at Lost Lake in RMNP have been caught a year or two later 8 km downstream at Kettle Tarn, we know that some movement of older toads occurs. However, data from the Clear Creek sites indicate that most breeding adults tend to remain (at least for several summers) in the same valley in which they participated in breeding. At these sites, 26 toads (9 males and 17 females) were radio-tagged between May and June 1998, with Holohil BD-2G radio transmitters that weighed 2 g and had a projected battery life of 6 months. A harness composed of fishing leader in vinyl tubing was used to fasten a radio around the waist of each toad. Toads were monitored once per week from May until hibernation. Locations were recorded in Universal Transverse Mercator (UTM) coordinates using a Trimble Pathfinder Basic Plus global positions system (GPS). Locations were imported into the ARC/INFO program for analysis.

Movements after breeding depended in part upon the type of habitats surrounding the breeding pond. If wetlands existed next to the pond, toads remained closer to the breeding site; if no wetlands existed, toads tended to move uphill to relatively moist areas that provided protection in the form of rodent burrows, overhanging shrubs, and other habitat features.

Movements varied considerably among individuals (Figs. 31-10, 31-11). Females left breeding sites immediately after breeding and, compared to males, they moved longer distances and more quickly from the breeding site. Females also had a greater tendency to move upland than males. After breeding

terminated, males tended to move a greater distance per day (14.1 m per day) than females (6.3 m per day), but the averages do not differ statistically due to the effect of large individual variability. The maximum (summed between location points) distances traveled by radio-tracked toads during the summer of 1999 was 5,756 m in 70 days (82.2 m/d) by one female, and 6,485 m in 106 days (61.2 m/d) for another female. None of the adults monitored with radio telemetry left the valley in which breeding occurred (Jones, 1999).

Interpopulation and Interspecific Comparisons

The three investigations that contributed data to this paper approached the study of boreal toad life histories from different directions. Clutch size was the only common variable that was examined in all three studies. Therefore, it is difficult to determine whether the RMNP and Clear Creek populations possessed variations in life history attributes that may have contributed to their ability to survive the mass die-offs that occurred throughout most of the Colorado Rockies during the 1970s. Mean clutch size of the West Elk Mountain populations was significantly lower than those found in RMNP and Clear Creek. The meaning of this difference cannot be determined at this time.

Annual Period of Activity

The Southern Rocky Mountain environment in which boreal toads breed is characterized by short, snow-free growing seasons that last from approximately mid-May through late September. The near freezing temperatures during summer nights restrict prey activity and the rate of digestion and absorption. In contrast, in the lowland temperate habitats experienced by many other *Bufo*, moderate temperatures foster nocturnal feeding and digestion (Carey, 1976). Therefore, the amount of time in which boreal toad females can accumulate the energy and nutrients necessary for egg production is relatively limited. Lowland Great Plains toads (*B. cognatus*) breed as early as March (Bragg, 1937b, 1940a; Krupa, 1994), and red-spotted toads (*B. punctatus*) breed in late April through early May in Kansas (Smith, 1934). Neither of these species enters hibernation until late October, at the earliest. Low altitude, high latitude European toads (*B. bufo*) are active in Denmark from April through early November (Jørgensen et al., 1979).

The seasonality and thermal environment of boreal toads in the southern Rockies is most similar to that of Yosemite toads (*B. canorus*) in the Sierra Nevada of California. Yosemite toads are primarily found between 2,500–3,000 m, with an upper altitudinal

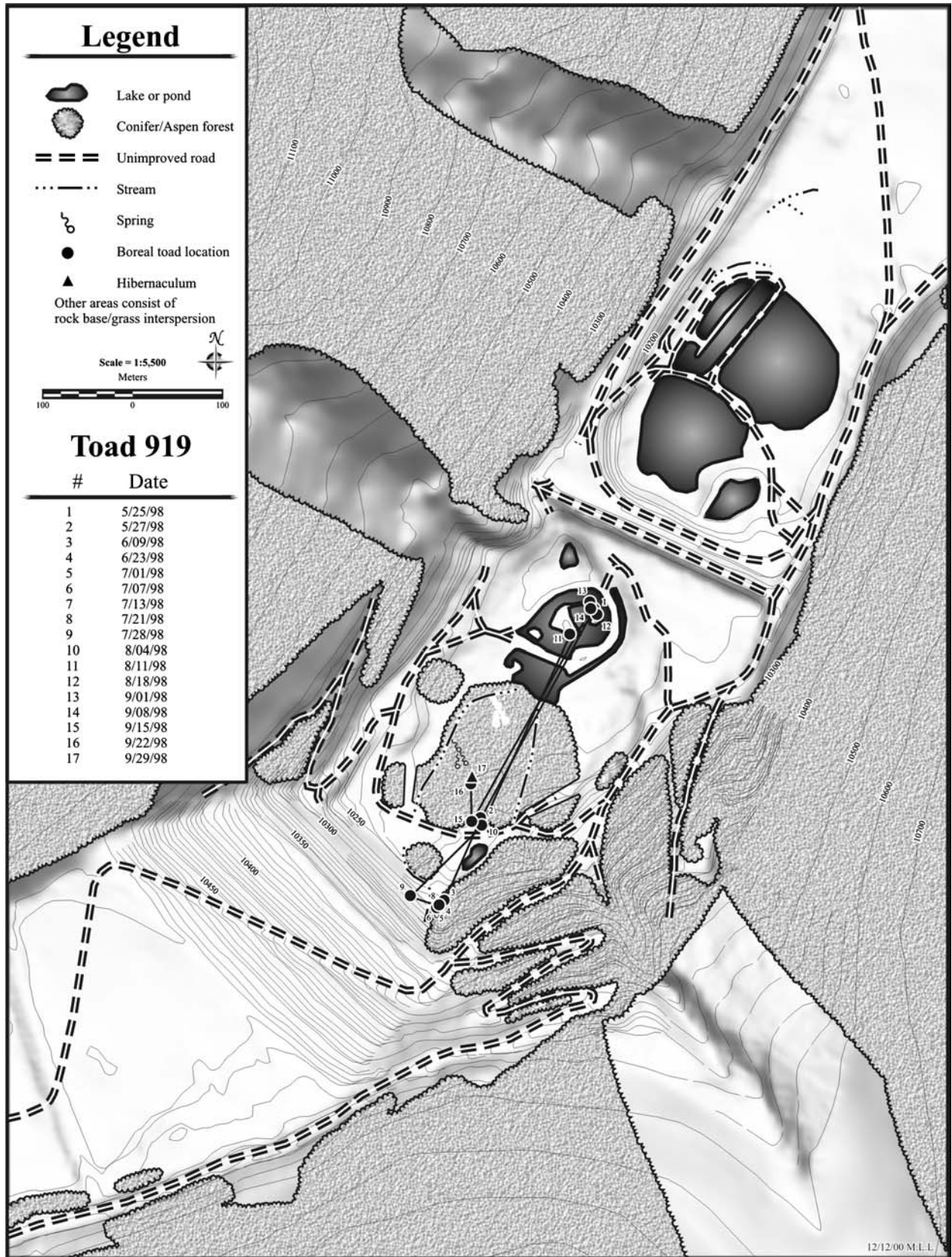


FIGURE 31-10 1998 movements, measured by radio telemetry, of Toad 919 (adult male) at the Henderson/Urad study area in Clear Creek County.

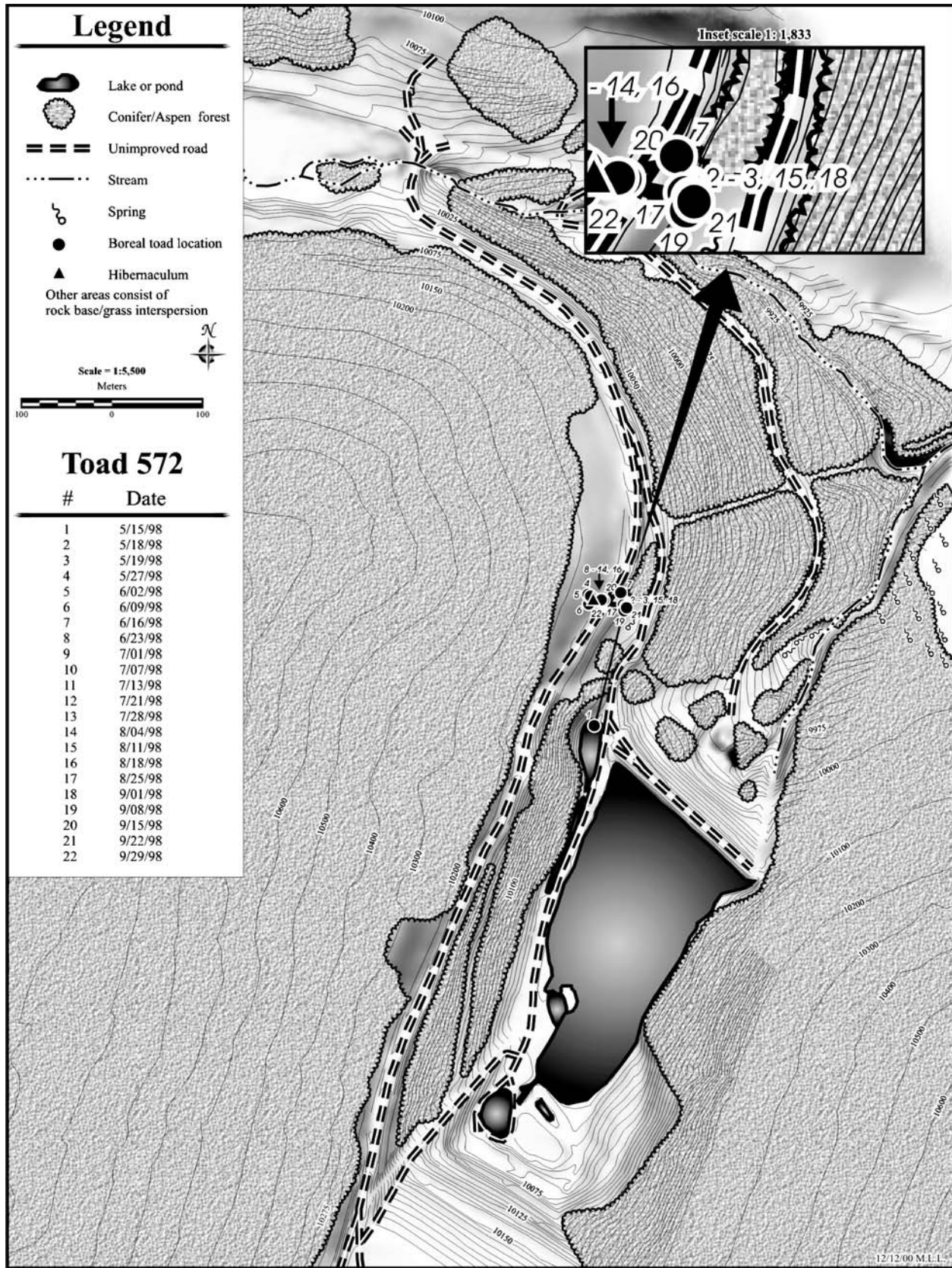


FIGURE 31-11 1998 movements, measured by radio telemetry, of Toad 572 (adult female) at the Henderson/Urad study area in Clear Creek County.

limit of about 3,450 m (Karlstrom, 1962; Fellers and Davidson, this volume, part II). Heavy snow accumulations (300–400 cm depth on 1 April; Morton and Allan, 1990) are not unusual in the habitats of Yosemite toads and can delay emergence from hibernation into July. Populations of Yosemite toads in the lower portion of their altitudinal range are active typically from late May through early October. In contrast, the activity periods of high altitude populations may be restricted by one to two months (Karlstrom, 1962).

Clutch and Egg Characteristics

Females can be expected to experience natural selection both for number of offspring and fitness of offspring (Smith and Fretwell, 1974; Wilbur, 1977c). Consequently, in many anuran species there are positive correlations between female size and egg number and size (Crump, 1974; Ryser, 1988; Corn and Livo, 1990; Tejedo, 1992). Although clutch size is significantly related to body size in Great Plains toads (Krupa, 1994), common toads (*B. bufo*) and natterjack toads (*B. calamita*) in Britain (Banks and Beebee, 1986), and a number of other temperate anurans (Jørgensen et al., 1979), interestingly, there is no correlation in several tropical anurans (Lang, 1995). In our data set, the association between clutch size and female body size in boreal toads was significant only when data from all three study sites were combined; within each population, no significant relation existed. Furthermore, caloric content per egg and egg weight were not significantly related to female size (Fig. 31-3). Although larger boreal toad females may be physiologically capable of laying larger clutches or increasing egg mass or caloric content per egg in some years, snowpack, cold summer temperatures, and/or other environmental factors that affect food availability may prevent them from producing additional eggs.

Many low altitude, temperate *Bufo* females appear to lay eggs every year, or in some species, such as Great Plains toads, even occasionally produce more than one clutch per season. (Krupa, 1994). Most of our data support the hypothesis that boreal toad females do not breed every year. A similar finding was reached by Olson (1992), who studied three populations of boreal toads in Oregon at altitudes ranging from 1,200–2,000 m. She marked over 1,700 female toads during a five-year period, between 1982–86. Only 88 of these females were recaptured in a subsequent year. Of those that returned to breed, 80% skipped at least one year between breeding events. In contrast, males in Oregon and in our Clear Creek populations bred each year. The males tended to return to the same breeding pond each year; only 6% of the males switched breeding sites at least once during a five-year period at the Urad Valley. Biennial breeding is common in other montane amphibians. European toads in Switzerland typically lay eggs every other year (Heusser, 1968), while they undergo vitellogenesis each summer in preparation for egg laying in the subsequent spring in lowland Denmark (Jørgensen et al., 1979). Female northwestern salamanders (*Ambystoma gracile*) breed annually in low altitude (100 m) populations in British Columbia, whereas those at 1,200 m spawn biennially (Eagleson, 1976).

Montane *Bufo* theoretically might respond to the restriction in the yearly accumulation of energy and materials for egg synthesis with a reduction in clutch size or alteration in the energy and material content of the egg, but their egg and clutch sizes are not abnormal compared to other *Bufo*. The mean egg diameter of boreal toads (1.6 mm at Clear Creek

TABLE 31-5
Clutch Sizes and Snout-vent Lengths of Female *Bufo* of Various Species

<i>Species</i>	<i>Snout-Vent Length (mm)</i>	<i>Clutch Size (reference)</i>
<i>B. alvarius</i>	87–178 ^b	7,500–8,000 ^b
<i>B. americanus</i>	56–100 ^b	4,000–8,000 ^b 20,603 ^c
	56–76 ^d	1,700–5,600 ^d
<i>B. arenarum</i>		23,000 ^e
<i>B. boreas</i>	72–87 ^a	6,661 ^a
<i>B. boreas halophilus</i>	60–120 ^b	16,500 ^f
<i>B. cognatus</i>	60–99 ^b	19,617 ^g
	80	9,376 ^k
	60–115	1,342–45,054 ^k
<i>B. canorus</i>	45–75 ^b	1,500–2,000 ^h
<i>B. punctatus</i>	42–64 ^b	30–5,000 ⁱ
<i>B. quercicus</i>	20–32 ^b	600–800 ^j
<i>B. terrestris</i>	44–92 ^b	2,500–3,000 ^b
<i>B. fowleri</i>	56–82 ^b	8,000 ^b
		2,500–10,300 ^l
		5,000–10,000 ^f
<i>B. woodhousii</i>	58–118 ^b	25,644 ^c

^aThis study; ^bWright and Wright, 1949; ^cSmith, 1934; ^dCollins, 1975; ^ede Allende and Orias, 1955; ^fLivezey and Wright, 1947; ^gBragg, 1937; ^hKarlstrom and Livezey, 1955; ⁱTevis, 1966; ^jClarke, 1973; ^kKrupka, 1994.

sites) falls within the range of egg sizes of various lowland *Bufo*: 1.0 mm in oak toads (*B. quercicus*) to 2.0 mm in California toads (*B. boreas halophilus*; Karlstrom, 1962; see other references in Jørgensen et al., 1979). Examples of egg diameters of other lowland North American bufonids are 1.2 mm in Great Plains toads (Bragg, 1940a) and 1.43 mm in American toads (*B. americanus*; Smith, 1934).

The range of clutch sizes (number of eggs laid) of boreal toads generally matches those of other, similarly sized bufonids (Table 31-5). Another indication that the clutch size of boreal toads is similar to those of other bufonids is ovarian mass relative to body size (Fig. 31-5). The pre-laying and post-laying values for ovarian mass as a proportion of body mass are similar to those of European toads (Jørgensen et al., 1979) and Fowler's toads (*B. fowleri* in Georgia; Bush, 1963). The ovaries of pre-breeding European toads in Denmark weigh 18–19% of body mass, and after breeding about 2.5%. However, the ovarian cycles of European and boreal toads diverge following egg laying. While the ovaries of boreal toads contain only undeveloped and atretic oocytes for at least a year after breeding, vitellogenesis of oocytes of European toads begins after a short resting period of a month or two, culminating with ovaries weighing about 14% of body mass prior to hibernation. Ovarian mass remains constant during hibernation. After emergence from hibernation, final maturation of the eggs increases ovary mass to the pre-laying value (Jørgensen et al., 1979).

Although egg and clutch sizes of boreal toads do not differ appreciably from those of low altitude bufonids, Yosemite toads apparently have reduced clutch size in favor of larger eggs. Yosemite toads lay the largest eggs (2.1 mm) and among the smallest clutch sizes of any North American bufonid (Karlstrom, 1962; Table 31-5). Other montane species appear to lay larger eggs at higher altitudes, but data on clutch size are lacking. For example, European common frogs (*Rana temporaria*) lay larger eggs at higher latitudes and altitudes (Koszlowska, 1971; Koskela and Pasanen, 1975), and western chorus frogs (*Pseudacris triseriata*) in the Colorado Rockies show the same pattern (Pettus and Angleton, 1967). These authors speculate that a relatively large egg size might contribute to more rapid development and faster metamorphosis, a characteristic that could prove advantageous for tadpoles that must complete metamorphosis in one, short season. We hypothesize that this reasoning holds for boreal toads.

Egg diameter is inversely correlated with clutch size in both European (Jørgensen et al., 1979) and boreal toads. Coefficients of variation for intraclutch egg diameters in boreal toads range from 4.1–12.9%. Jørgensen et al. (1979) noted considerable interclutch variation in egg size within a population of European toads. Crump (1984) suggested that intraclutch variation in egg size may be a form of “bet-hedging” as a means of dealing with environmental uncertainty.

If boreal toads were able to lay eggs every year, and if egg diameter and caloric content were maintained, the limitations on energy acquisition forced by the short growing seasons and cold night temperatures would require a reduction in clutch size. Some of the clutches in the West Elk population were small enough that they could potentially represent reproductive output by females selected to lay smaller clutches more frequently. Until more data become available from PIT-tagged individuals, however, this possibility will remain untested. However, the tendency of most females to skip years between breeding results in the possibility that a female may successfully produce young only rarely in her lifetime because egg and larval mortality are so high. This tendency contributes to the difficulty in recovery of boreal toad populations.

Survival to Metamorphosis

The tendency of boreal toads to lay eggs in the shallow areas of large bodies of water or in small puddles that warm rapidly on sunny days is related to the fact that developing larvae require temperatures above 10 °C (Fig. 31-7). Comparative data are lacking on thermal minima for development in other *Bufo*. Similarly, no data on comparative size at metamorphosis exist in other *Bufo*. Several factors (including food availability, tadpole density, site permanence, degree of predation pressure, and temperature) interact in a complex manner to influence anuran size at metamorphosis (Wilbur and Collins, 1973; Brockelman, 1975; Smith-Gill and Berven, 1979; Werner, 1986; Pfennig et al., 1991; Tejedo and Reques, 1994; Reques and Tejedo, 1995; Newman, 1998).

Many causes of egg and larval mortality in boreal toad populations in the southern Rockies are identical to those of lowland species of *Bufo* and include desiccation, predation, infertility, and disease. For example, a population of Great Plains toads suffered high larval mortality due to desiccation (Krupa, 1994). As noted by Burger and Bragg (1947, p. 62), boreal toads “exercise little discrimination in the selection of breeding sites.” While smaller puddles provide thermal advantages by

warming rapidly during the day (Young and Zimmerman, 1956), they commonly dry before the larvae can metamorphose unless summer rains are unusually frequent.

One source of larval mortality of boreal toads in the southern Rockies appears to differ from lowland *Bufo*. If egg laying is delayed by spring snowmelt and/or if growth is retarded due to unusually cold summer temperatures, some larvae do not have time to metamorphose before the pond freezes in the fall. In common with larvae of Yosemite toads (Karlstrom, 1962), boreal toad larvae do not survive the winter under ice. The minimal larval period of boreal toads in the Clear Creek population varied from 64–92 days (Table 31-3). The average length of time to metamorphosis (71 days) for Yosemite toads in the Sierra Nevada falls within this range (Karlstrom, 1962). Larval periods of lowland *Bufo*, however, are considerably shorter, due in part to relatively high average temperatures, particularly at night (e.g., 49 days for Great Plains toads; Bragg, 1940a; Krupa, 1994; and 45 days for Woodhouse’s toads [*B. woodhousii*]; Carey, unpublished data). Metamorphosis in these species can occur as early as mid-June through July, long before ponds freeze. One unusual case of mortality recorded elsewhere (Oregon) in the range of boreal toads has not been observed (but is plausible) for boreal toad populations in the Southern Rocky Mountains: boreal toad clutches in shallow water were washed out of the water onto the shore by a seiche (wave) generated when a massive snow bank fell into the water on the opposite side of a pond (Ferguson, 1954a).

Because of the different causes of mortality and the difficulty of tracking the number of eggs that develop through metamorphosis, we cannot estimate the average survival of boreal toad clutches that do not suffer complete mortality. Estimates for survival through metamorphosis for various species of *Bufo*, *Rana*, and *Ambystoma* range from 1–13% (Miller, 1909, cited in Bragg, 1940a; J. D. Anderson et al., 1971; Shoop, 1974).

Growth

Metamorphosed boreal toads of all ages, including newly metamorphosed toads, bask for considerable amounts of time each day (Lillywhite, 1974a; Carey, 1978; Muths and Corn, 1997). In newly metamorphic toadlets, this behavior differs from that of larger, older toads in that toadlets will aggregate in piles. These aggregations maximize body temperatures while minimizing water loss (Livo, 1998). Furthermore, these aggregations may be particularly important for protecting toadlets from the damaging effects of UV-B light. Newly metamorphosed Woodhouse’s toads will bask, but do not appear to form aggregations (Carey, unpublished data).

In North America, post-metamorphic growth is rapid in lowland anuran populations. Canadian toads (*B. hemiophrys*) in Minnesota metamorphose in late June to early July. Before hibernation in mid-September, they grow to an average of 31 mm SVL. In their second year, they reach an average length of 51 mm; they are able to breed in their third summer (second year) of life (Breckenridge and Tester, 1961). Great Plains toads reach their minimal breeding size (60 mm for females, somewhat smaller for males) by their second full year (Krupa, 1994), as do Wyoming toads (*B. baxteri*; Corn, unpublished data). Breeding desert bufonids, including Great Plains toads, red-spotted toads, and Sonoran Desert toads (*B. alvarius*) are between 2–4 years old (Sullivan and Fernandez, 1999). In species in which the females become sexually mature at larger sizes than males,

the size differential may result from faster growth rates in females (Krupa, 1994) or extra seasons of growth.

Boreal toads in the Southern Rocky Mountains, however, need considerably more than 2–4 years to reach sexual maturity. The minimal size at breeding for males and females in the West Elk Mountains and Clear Creek populations was about 55 and 70 mm, respectively. Our estimates that males and females take at least 4–5 years and 6–7 years, respectively, to become sexually mature is difficult to verify with PIT tags, because these devices cannot be applied until an individual reaches a critical size, usually over 10 g (about 40 mm). Olson (1992) estimated that the age at maturity of male and female boreal toads in a population at 2,000 m in the Oregon Cascades was 3 years and 4–5 years, respectively, but it is unclear on what measurements this estimate is based. Male Yosemite toads in the Sierra Nevada were thought to need 3 years to grow to sexual maturity at 53–68 mm (Karlstrom, 1962). The slow rate of growth of boreal toads to sexual maturity is, however, correlated with a long life span. Data appear to be unavailable on the longevity of other toad populations, but boreal toads in Oregon are thought to live at least 10–11 years (Olson, 1992). Measurement of growth rings in toes of museum specimens by D. M. Green (personal communication) indicates that one boreal toad female was at least 13 years at death.

Growth rates of boreal toads above 70 mm are markedly lower than rates of smaller individuals (Table 31-4). A similar drop in growth rates of larger, sexually mature individuals occurs in wood frogs (*Rana sylvatica*; Bellis, 1961a). Depending on the rate of growth during those later years, the largest individuals caught in this study could be considerably older than 10 years. We predict that boreal toads grow only in the summer. Even if low temperatures did not retard or prevent growth, other *Bufo* appear to cease growth in the fall, even if kept at warm temperatures (Jørgensen, 1983). We also predict that growth rates are not homogeneous throughout the active season. Food supplies may be lacking early in the season after emergence from hibernation and exponential rates of liver glycogen deposition in preparation for hibernation would also limit energy availability for growth in late summer (Carey, unpublished data).

Movements of Metamorphosed Individuals

We are unsure about the movements of pre-adult boreal toads from the time they metamorphose until they breed. A large number of toadlets were reintroduced to Lost Lake, in Boulder County, Colorado, in 1996 and 1997. A few were recaptured in 1998, having survived at least one winter (Scherff-Norris, 1999). At least some toadlets from this reintroduction experiment were observed as far away as 600 m (straight-line distance) from Lost Lake, indicating that some individuals may have dispersed (Scherff-Norris, 1999). However, no information is available concerning the long-term geographical distribution or survival of introduced toadlets.

The tendencies of radio-telemetered boreal toad adults to remain in the vicinity of breeding localities, and movements within those localities during the summer after breeding, are similar to that of Canadian toads (Breckenridge and Tester, 1961). Adult male boreal toads may exhibit more breeding site fidelity than females (this study; Olson, 1992).

Boreal toad habitat occurs in the valleys of all mountain ranges in Colorado. Historically, at least several breeding areas typically occurred within a valley or just over an adjacent ridge.

Therefore, an individual dispersing from one breeding area would likely encounter another breeding site within a short distance. Prior to the mass mortalities in the 1970s, movement of individuals from one breeding area to another would have fostered genetic exchange and establishment of new populations. Currently, many of the remaining sites at which breeding still occurs are isolated from others by long distances or by unsuitable habitat between mountain ranges. Individuals dispersing away from these isolated sites may not find another breeding site in their lifetime and could therefore represent a genetic loss to the population.

The loss of individuals by dispersal is particularly critical for boreal toad recovery because many of the remaining populations are very small (one to five clutches laid per year). The Allee effect may increase the likelihood of extinctions for small and low-density populations through the reduced ability of dispersing individuals to find mates (Courchamp et al., 1999; Stephens and Sutherland, 1999). Surveys at historical boreal toad breeding sites sometimes find small numbers of individuals but no evidence of current breeding. In these situations, the individuals tend to be females rather than males, an observation that may reflect a longer lifespan of females or their possible tendency to disperse greater distances than males.

Final Comments

The sizes and numbers of boreal toad populations in the southern Rockies dramatically dropped in the late 1970s through early 1980s. The few populations that remain began to be monitored in 1993, and further mass mortalities were not observed until the last few years. A mycotic skin infection associated with a chytrid fungus is now causing mortality of toads in at least two metapopulations (Jones and Green, unpublished data). The etiology of these fungal infections matches the pattern of the previous die-offs; in particular, metamorphosed individuals, including breeding adults, succumb. This epidemic, combined with the environment and life history of this species, challenge the recovery of these toads.

One aspect of the current recovery effort involves the repatriation of eggs, larvae, or metamorphosed toadlets from existing breeding areas into historical habitat. Translocation efforts for anurans have generally proved unsuccessful (Dodd and Seigel, 1991). For example, no new populations of Houston toads (*B. houstonensis*) became established as of 1991 despite the translocation of 500,000 individuals of various life history stages (Dodd and Seigel, 1991). In some cases, insufficient time has elapsed to evaluate the success of translocation efforts. Since 1996, approximately 10,000 Wyoming toads have been released in southern Wyoming in an effort to restore this endangered species (Spencer, 1999). However, survival rates of these repatriated individuals typically have been low (Jennings and Anderson, 1997; Spencer, 1999). Some reports of successful translocations of *Bufo* exist (Beebee, 1996; Denton et al., 1997). Unfortunately, species of *Bufo* and other anurans that have been involved in successful translocations typically require less time to reach sexual maturity and have higher reproductive outputs than boreal toads. Therefore, the life history characteristics of boreal toads may restrict the success of this technique to help these toads recover their former geographical distribution.

Global climate change may also affect the long-term prospects for recovery of boreal toad populations in the southern Rocky Mountains. Global mean temperatures are predicted

to increase 1–5 °C during the next 100 years, primarily due to the greenhouse effect of increasing atmospheric CO₂ concentrations, and distributions of vertebrates are predicted to move north or to higher elevation (Schneider and Root, 1998). For a variety of reasons, global change is expected to decrease the survival of species with small populations and limited dispersal ability (e.g., boreal toads), but warming temperatures could possibly benefit high-elevation populations of boreal toads in two ways. First, earlier breeding due to warmer spring temperatures would provide more time to complete metamorphosis. Indeed, some British amphibians, including natterjack toads, are breeding significantly earlier now than they did 20 years ago (Beebee, 1995). However, there has yet been no trend toward earlier breeding during the 1990s among boreal toads in Rocky Mountain National Park (Fig. 31-2). Second, warmer summer temperatures would allow faster rates of development by tadpoles, again resulting in greater chances to escape aquatic environments that are lethal during winter. However, summer temperatures in the Front Range of Colorado, including Rocky Mountain National Park, are actually decreasing, possibly due to the influence of increased agriculture and urbanization on the plains to the east (Stohlgren et al., 1998). Thus, it is not apparent that a more favorable thermal environment yet exists for high-elevation populations of boreal toads, and we do not expect that hypothesized benefits will measurably increase the probability of survival for boreal toads in the Southern Rockies.

Summary

Boreal toad (*B. b. boreas*) populations in the southern Rocky Mountains suffered dramatic declines in the late 1970s through early 1980s. Recovery efforts to protect the few remaining populations began in 1995. Many aspects of the life

history of these toads, such as clutch size, size at maturity, and wet egg mass, mirror those of low altitude, temperate *Bufo*. However, environmental factors in the montane environment of these toads, such as short growing seasons and cold nighttime summer temperatures, force changes in other life history characteristics that restrict the ability of boreal toads to recover their original geographic distribution or population sizes. Breeding starts one to three months later than in lowland *Bufo* in temperate climates, and boreal toads are forced into hibernation one to three months sooner than lowland counterparts. Population recruitment is limited by the prolonged length of the larval period, mortality of larvae that fail to complete metamorphosis before onset of freezing temperatures in fall, slow growth rates of metamorphosed toads to breeding size, and the tendencies of females to skip one or more years between breeding. Although many adult toads of both sexes appear to remain near breeding sites, dispersal of metamorphosed individuals from isolated populations will additionally limit population size. These factors, plus the recent resurgence of outbreaks of infectious disease, create enormous challenges for the recovery of boreal toads in the Southern Rocky Mountains.

Acknowledgments

The research presented in this paper was supported by grants from Great Outdoors Colorado, the Colorado Division of Wildlife, the National Science Foundation, and the Rackham Graduate School of the University of Michigan. Bud Stiles assisted with the fieldwork. We thank the personnel of the Rocky Mountain Biological Laboratory for their assistance throughout the study on boreal toads from 1971–76. We thank David Armstrong, David Chiszar, Gregory Carey, Ruth Bernstein, and Alan de Quieroz for their assistance to Lauren Livo.