Thermal Habitat Use and Evidence of Seasonal Migration by Rocky Mountain Tailed Frogs, *Ascaphus montanus*, in Montana

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Adams, Susan B., and Christopher A. Frissell. 2001. Thermal habitat use and evidence of seasonal migration by Rocky Mountain Tailed Frogs, *Ascaphus montanus*, in Montana. Canadian Field-Naturalist 115(2): 251–256.

All life stages of Rocky Mountain Tailed Frogs (*Ascaphus montanus*) occurred in a reach of Moore Creek, Montana, where water temperatures exceeded those previously reported for *Ascaphus* in the wild. However, relative density of *Ascaphus* in the warmest reach, immediately downstream of a lake outlet, was lower than in cooler reaches downstream. Although we observed larvae and frogs in water temperatures up to 21°C, cold groundwater seeps contributed to a spatially complex thermal structure in the warmest stream reach. Frogs congregating near a cold seep and nesting in a groundwater-influenced site were likely using behavioral thermoregulation. At a stream weir in the warmest reach, we captured 32 Tailed Frogs moving downstream and none upstream, in September and October 1997. Because no migration was evident at five other weirs where summer water temperatures remained below 16°C, we propose that the frogs moving through upper Moore Creek migrated seasonally to avoid the high temperatures. The mature frogs may spend summers in the small, cold lake inlet streams, moving downstream in the fall to overwinter. Behavioral studies would be necessary to determine the extent to which individuals limit their overall thermal exposure in such spatially complex environments. Migration in response to local, seasonally changing habitat suitability could explain the diverse, and apparently contradictory, movement patterns (or lack thereof) among *Ascaphus* populations reported in the literature. Future studies of *Ascaphus* movements could benefit by accounting for seasonal changes in habitat suitability and by quantifying in-stream movements.

Key Words: *Ascaphus montanus*, Tailed Frog, amphibian, water temperature, thermal complexity, habitat, movements, migration, behavior.

Tailed Frogs (*Ascaphus truei* and *A. montanus*[1]) live in cold, rocky streams in the Pacific Northwest and northern Rocky Mountains (Nussbaum et al. 1983) of the USA and in southwestern Canada. Although important to understanding the species' habitat use, population dynamics, gene flow, and recolonization abilities, *Ascaphus* movements are not well documented. Mark-recapture studies directed at detecting movements of transformed *Ascaphus* have concluded that site fidelity is high among mature individuals (Daugherty and Sheldon 1982a) or have been inconclusive (Metter 1964a). Three reports suggested that transformed frogs migrated seasonally; however, direct evidence of movement was lacking (Metter 1964a; Landreth and Ferguson 1967; Brown 1975). Such inconsistencies could reflect either shortcomings in the studies or spatial and temporal variations in movement patterns.

Thermal tolerances and tolerance ranges of *Ascaphus* are lower than for any other anuran studied in North America (reviewed by Claussen 1973). Reports of *Ascaphus* occurrence are generally from streams with maximal temperatures not exceeding 16°C (Franz and Lee 1970; Welsh 1990). Laboratory experiments suggest that thermal tolerances vary among the life history stages. Critical examinations of whether temperature actually limits *Ascaphus* distributions are lacking.

In Rocky Mountain *Ascaphus* populations, individuals transform at age 4, first mature at age 8 and can live for 14 or more years (Daugherty and Sheldon 1982b). The frogs typically mate in the fall (but see Wernz 1969), and females retain sperm until the following July when they lay eggs (Metter 1964b). Eggs usually hatch in late summer, but larvae apparently remain in the nest site until the following summer (Metter 1964a; Brown 1975). This implies that eggs and larvae experience the thermal regime at the nest site throughout an entire year.

Incidental to a study of introduced Brook Trout (*Salvelinus fontinalis*) in two Montana streams (Adams 1999), we made new observations on *Ascaphus* seasonal movements and occurrence in warm water temperatures. We subsequently assessed *Ascaphus* relative abundances and water temperatures throughout one stream-lake network to determine how water temperature was related to summer distributions of each life stage and to timing of downstream frog movements.

[1]Nielson et al. (2001) recommended that inland populations of Tailed Frogs be recognized as a distinct species (*Ascaphus montanus*). Minor inconsistencies between our text and the existence of two distinct *Ascaphus* species occur because our paper was already in press when we read Nielson et al. (2001).

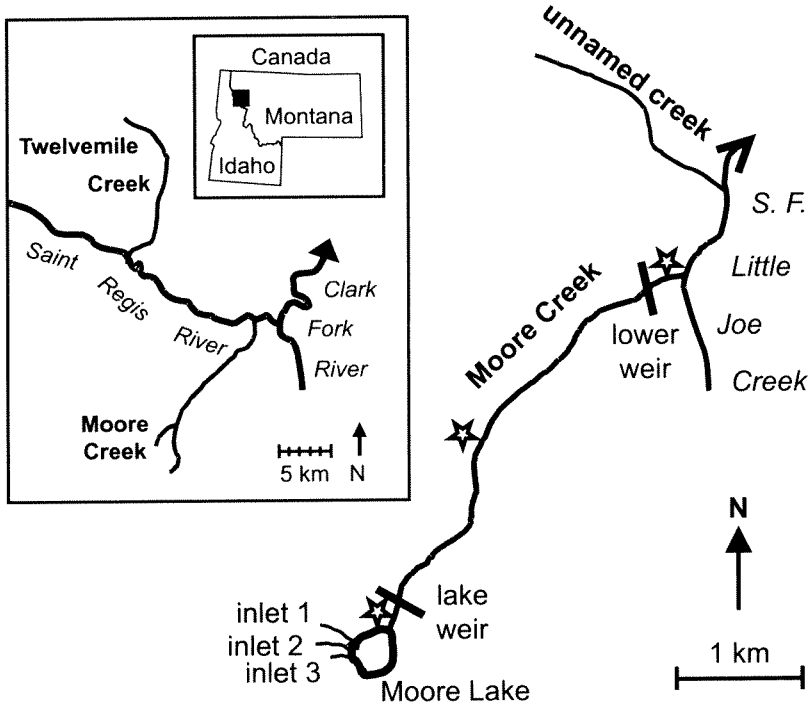

FIGURE 1. Locations of Moore and Twelvemile creeks in Mineral County, Montana, USA, and detail of Moore Creek showing locations of weirs (bars) and temperature recorders (stars). The lake weir was about 75 m downstream of the lake outlet and 5 m downstream of the upper temperature recorder. The lower weir was 120 m upstream of the confluence with South Fork Little Joe Creek.

Materials and Methods

Moore Creek (St. Regis River drainage, Mineral County, Montana, 47°11'N, 115°15'W) is 3.2 km long and is fed by Moore Lake, a 16-m deep, 5.3 hectare, headwater lake at 1620 m elevation. About 320 m of shoreline separates the closest of three, small, lake-inlet streams from the outlet stream (Figure 1). During late summer low flows, average wetted stream widths ranged from 1.8 m near the lake outlet to 3.2 m near the mouth, channel slopes ranged from 10 to 19%, and average maximum pool depth near the lake outlet was 0.23 m. Riparian vegetation was predominantly Western Redcedar (*Thuja plicata*) forest. Twelvemile Creek is larger, longer (22.6 km), and more moderately sloped than Moore Creek with wetted widths ranging from 1.8 to 9.6 m in summer and channel slopes from 1.3 to 8.1 %.

We intermittently counted Tailed Frogs trapped at two weirs in Moore Creek (Figure 1) from 6 August to 9 October 1997 (dates shown in Figure 2) and at four weirs in Twelvemile Creek from July through late September 1997. We checked traps every 2 to 3 days during operation, and the longest period without counting frogs was 12 to 28 September, 1997. The weirs, constructed of 6.35 mm hardware cloth, consisted of two traps facing in opposite directions and connected to each other and to shore by a fence (see Figure 1b in Gowan and Fausch 1996). An apron buried in the substrate prevented animals from easily passing under the weir. Each trap box was a 60 × 60 × 60 cm cube with a funnel extending almost to the back. Large rocks in the traps provided shelter and velocity refugia for captured animals, and lids minimized predation. After identification, animals were released beyond the weir in the direction they were moving when trapped.

We located *Ascaphus* via snorkeling and electrofishing targeting Brook Trout in Moore and Twelvemile creeks in 1997 and via visual surveys targeting *Ascaphus* in Moore Creek in 1998. In July 1998, students assisted with day and night searches for *Ascaphus* along sections of the lake inlet streams, the lakeshore between Moore Creek and the inlet, Moore Creek, and an unnamed creek near Moore Creek (Figure 1). We performed timed searches, turning over streambed rocks and visually scanning both the streambed and stream banks within 2 meters of the stream. The results are intended only for describing *Ascaphus* distribution and for a qualitative comparison of relative densities among reaches.

The lakeshore, one inlet stream, and the uppermost Moore Creek reach were again searched during the night (and Moore Creek also during day) of 7–8 October 1998.

Hobo-Temp® data loggers recorded stream temperatures from 31 July 1997 to 8 October 1998 (with several gaps) at three locations each in Moore (Figure 1) and Twelvemile creeks. Using a digital thermometer, we took a longitudinal temperature profile in Moore Creek downstream of the lake outlet on 28 July 1998 and took focal point temperatures at some *Ascaphus* locations.

Results and Discussion

Adult movements

At the lake weir in Moore Creek, we trapped 32 frogs moving downstream and one moving upstream. As the trapping period progressed, the number of adult *Ascaphus* moving downstream into the trap increased from no frogs for the period of 7 August through 3 September 1997 to nine frogs on 6 October, three days before the weir was removed (Figure 2). The sex ratio of captured frogs was male biased (chi square = 6.1250, p = 0.0133).

The timing of frog captures coincided with a drop in water temperature (Figure 2). The frogs began moving downstream into the trap when average daily stream temperatures dropped below 16°C, and most were captured when average temperatures fell below 14°C (Figure 2). Whenever frogs were recorded in the trap, the maximum daily temperature had not exceeded 16.5°C during at least one day of the two-to-three-day trapping interval.

The pattern of frog captures suggests that a directed, seasonal migration was occurring in upper Moore Creek. The seasonality of the movement is clear from the complete absence of any frogs in the downstream trap for at least the first month of operation. Although there was unquestionable directionality of capture in the traps, concluding that a downstream migration was actually occurring depends on two assumptions: (1) that the weir was not biased against capture or retention of frogs moving upstream, and (2) that the frogs were not moving upstream over land.

We caught no frogs at the lower weir in Moore Creek or at any of the weirs in Twelvemile Creek, although the frogs and larvae were present throughout both creeks (Figure 3) (Franz 1970; S. Adams, personal observation). Thus, *Ascaphus* movement patterns can vary not only among, but also within, streams. The limited literature on *Ascaphus* movements also indicates that movement patterns may vary considerably among drainages. Daugherty and Sheldon (1982a) found no evidence of seasonal or directed movements by mature Tailed Frogs in

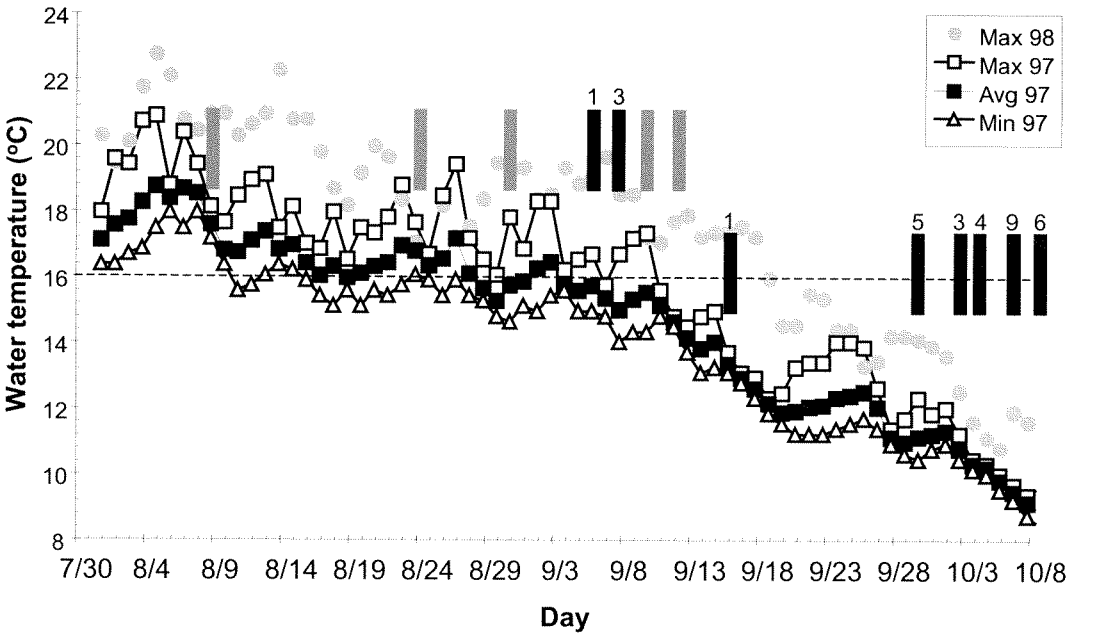

FIGURE 2. Average (avg), maximum (max), and minimum (min) daily stream temperatures 5 m upstream of the "lake weir" in Moore Creek, Montana, 1997 and 1998. Vertical bars indicate dates in 1997 when frogs were counted in traps at the "lake weir". Grey bars represent the absence and black bars the presence of frogs moving downstream. Each bar represents 2 to 3 days of trapping. Numbers of frogs counted are indicated above bars.

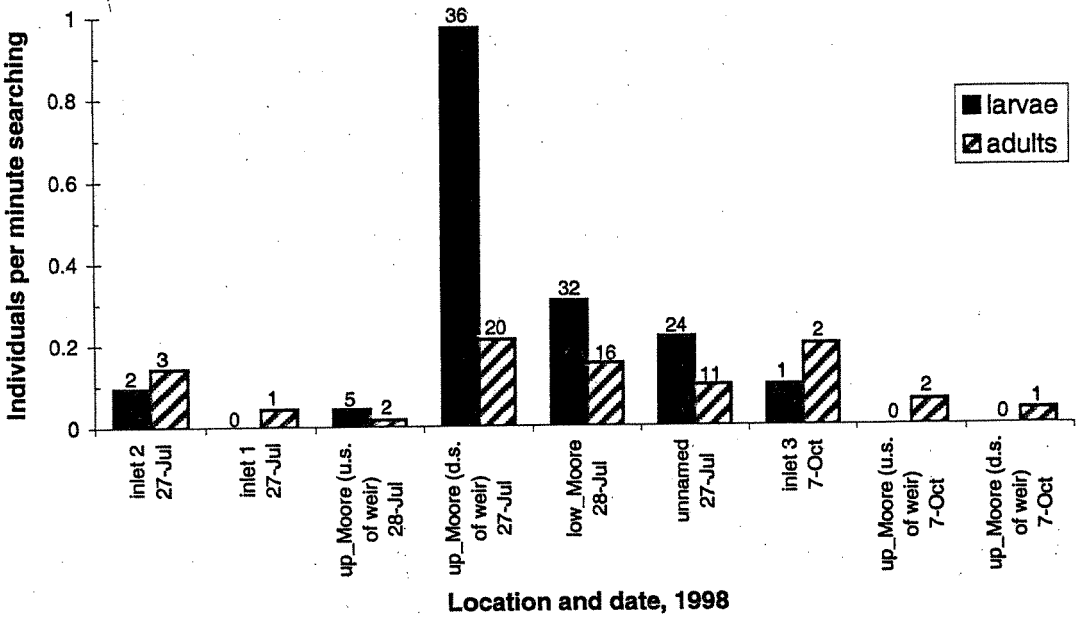

FIGURE 3. Numbers of *Ascaphus* larvae and adults per minute spent searching by each team during night surveys. Numbers above bars are the total numbers of individuals observed during each survey. Inlet 3 was surveyed only in October. u.s. = upstream; d.s. = downstream.

Butler Creek (Montana) and concluded that the frogs exhibited extreme philopatry; however, their annual summer sampling period may have ended too early to detect an autumn migration. By contrast, based on seasonal changes in densities of adult *Ascaphus*, Metter (1964a) hypothesized that adults moved from the Touchet River (Washington) into more shaded tributaries in the late summer. In the Palouse River (Idaho) and tributaries during the same time period, though, he found no seasonal differences in frog densities. Brown (1975) observed aggregations of up to 20 females in "small, shallow tributaries" of Razor Hone Creek, Washington, in late July and suggested that females may move into the warmer tributaries to lay eggs. However, evidence of actual upstream movements was lacking. Landreth and Ferguson (1967) suspected that frogs moved downstream out of small, intermittent creeks to the Lostine River, Oregon, to mate, but again, had no direct evidence of migration. If Tailed Frogs migrate in response to local conditions, diverse movements among sites would be expected.

Stream temperatures and Ascaphus distribution

The average August stream temperature at the upper Moore Creek temperature recording location exceeded 16°C both summers (Table 1). Average daily temperatures exceeded 18°C for at least 5 days in 1997 and 20 days in 1998 (Figure 2), and we likely missed recording many of the warmest days both years. Water temperatures taken during the day and night of 28 July 1998 were 5 to 10°C cooler in the lake inlet streams than in the lake outlet, a pattern that persisted into at least October. Significant water cooling occurred downstream of the lake at both within-reach and whole-stream scales. Water temperatures declined with distance downstream of the lake over 200 m on one warm afternoon (Figure 4), and average August water temperatures at the middle and downstream temperature recording sites were about 7°C cooler than at the site near the lake (Table 1).

Ascaphus larvae and adults were found in all stream sections surveyed except lake inlet 1, where only an adult was found (Figure 3), but none were found along the lake shore. In upper Moore Creek, we observed numerous larvae in water temperatures of 19.5–20.0°C, and several were found in temperatures of 21°C (focal point temperatures). Several

TABLE 1. Stream-scale changes in water temperatures along Moore Creek, Montana, during August 1997 (and 1998 in parentheses). Temperature recording sites were about 0.7, 1.4, and 3.2 km downstream of the lake outlet.

Location	Average	Minimum	Maximum	Maximum daily range
upstream	20.9 (22.8)	16.9 (18.4)	14.6 (15.2)	3.9 (4.1)
middle	12.6	9.7	7.1	2.2
downstream	12.5 (13.9)	10.0 (10.7)	7.5 (7.8)	2.6 (2.5)

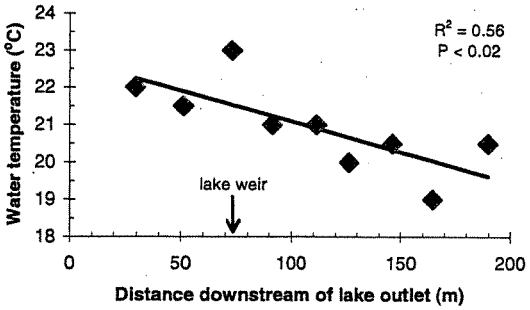

FIGURE 4. Reach-scale changes in water temperatures within 200 m of the Moore Lake outlet. Temperatures were taken on 28 July 1998 between 1235 and 1410 hours, beginning at the outlet and proceeding downstream.

adult frogs also occupied water that was between 19 and 21°C, although most frogs we found were at least partially out of the water.

Maximum stream temperatures in upper Moore Creek were 4.6°C higher than the highest temperature (18.2°C) we found reported where adult *Ascaphus* occurred in nature (Landreth and Ferguson 1967). Reported tolerances of transformed *Ascaphus* in experimental settings are inconsistent but suggest that the frogs may tolerate temperatures of 20°C (Landreth and Ferguson 1967) to 24°C (Claussen 1973). However, low frog densities in the warmest stream reach relative to other reaches and movement through the warmest reach in the fall suggest that high summer temperatures near the lake outlet created an unfavorable summer environment for the frogs.

Ascaphus larvae have been reported in sites with higher water temperatures than have transformed frogs, but not as high as those in upper Moore Creek. Low densities of *Ascaphus* larvae occurred in deforested watersheds of Mount Saint Helens (Washington) where average maximum and mean stream temperatures were 19.5 and 14.4°C, respectively, in late summer (Hawkins et al. 1988). Although maximum summer temperatures in the Washington streams were nearly as high as in upper Moore Creek in 1997, average temperatures were considerably lower. In laboratory experiments larvae survived for a day at 22°C (Metter 1966) and sometimes occupied such temperatures in a thermal gradient (de Vlaming and Bury 1970).

We found a deeply buried nest of *Ascaphus* eggs near the lake weir in Moore Creek on 30 July 1997. On 28 July 1998, we discovered a second nest shallowly buried in a riffle about 30 m downstream of the weir. The majority of embryos appeared viable in both nests. Water temperature in the middle of the pool containing the first nest was 17.4°C at the time of egg collection; however, cold ground water seeping through a bedrock fissure in the substrate less than 1 m upstream of the nest probably moderated temperatures at the nest microsite. When we found the second nest, water temperature was 20.2°C at the nest site and 20.9°C at the opposite side of the pool. *Ascaphus* embryos developed normally in laboratory experiments at temperatures between about 5.0 and 18.5°C, but not at higher temperatures (Brown 1975).

Thermal Complexity

We documented *Ascaphus* response to the spatially complex temperature patterns in upper Moore Creek at both the reach and microhabitat scales. The relative density of both larvae and adults was much higher downstream of the lake weir, where water was cooler, than upstream during July 1998 (Figure 3). However, the relationship between water temperature and *Ascaphus* densities may be confounded by the higher density of Brook Trout upstream than downstream of the weir (unpublished data). The largest aggregation of adult frogs (6 frogs) found was at a cold water pocket (about 9 cm^2) in a mossy bank adjacent to a stream pool. Water temperature was 20–21°C in the pool but was 5.3°C in the pocket. No frogs were found in or along the warmer areas of the pool.

The timing and location of frog captures in weirs suggests that many frogs avoided high water temperatures by migrating. No frogs from upstream of the lake weir were captured until temperatures declined to levels more typically associated with Tailed Frog use. Although two frogs were found in the warm waters upstream of the weir in the summer, higher frog densities occurred in the cold, lake inlet streams (Figure 3). At the other five weirs, stream temperatures remained below 16°C throughout summer 1997, and we found no evidence of migration.

We hypothesize that many of the frogs captured in the lake weir spend the summer in the cold, lake inlet streams (and perhaps in spring seeps around the lake shore), thereby avoiding localized, high summer temperatures in the outlet stream. When lake surface, outlet stream, and air temperatures cool in the fall, the frogs migrate through or around the lake and down the outlet creek to mate and overwinter. Because of their small size, the inlet streams may not provide sufficient overwinter or nesting habitats that are evidently available in the outlet stream. The *Ascaphus* that remain in the warmest reach during summer may persist due to the availability of cool refugia.

Further behavioral studies would be necessary to determine if individuals rely on cool microsites to limit their overall thermal exposure in warm stream reaches; presently, we cannot conclude that occurrence of individuals in warm water implies long-term tolerance of such temperatures. Behavioral responses to thermal heterogeneity and other vari-

able habitat features may help explain the diversity of movement patterns reported in the literature. Future studies of *Ascaphus* movements could benefit by accounting for seasonal changes in habitat suitability and by quantifying in-stream movements rather than focusing primarily on terrestrial movements.

Acknowledgments

S. Adams received partial funding from the USDA Forest Service, Rocky Mountain Research Station. W. Lowe, A. Sheldon, B. Rieman, and anonymous reviewers provided helpful suggestions on early versions of the manuscript. K. Keegan, A. Stephens, L. Rosenthal, and L. Steinbach assisted with weir operations. C.A.F.'s 1998 Ecology and Conservation of Aquatic Vertebrates class (U of Montana, Flathead Lake Biological Station) collected distribution data: S. Brazier, A. Chilton, M. Cucchiara, H. Dean, M. Drum, R. Elliott, T. Mesa, M. Sireniawski, T. Van Roosmalen, and assistant T. Bansak.

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Received 1 August 2000
Accepted 27 April 2001
Updated 15 October 2001