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DISPERSAL OF NEWLY METAMORPHOSED AND JUVENILE WESTERN TOADS (*ANAXYRUS BOREAS*) IN NORTHEASTERN OREGON, USA

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***Abstract.*—The decline of *Anaxyrus boreas*, the Western Toad, in portions of its range has accentuated the need for additional information on all life stages of this species. My objectives in this study were to identify patterns of dispersal, mortality factors, and conservation concerns for toadlets (i.e., newly metamorphosed toads) and juvenile (one-year old) toads. Toadlets dispersed up to 2,720 m from the breeding site within eight weeks of transformation in one of three study areas in northeastern Oregon during 2006–2008. Toadlets traveled an average of 84 m/day and dispersed along drainages with intermittent or permanent water associated with streams, seeps, and marshy areas. Juveniles were detected 1,070-2,720 m from the breeding sites in all study areas. Desiccation, avian predation, trampling by vehicles and cattle, and chytridiomycosis were causes of mortality of toadlets. Conservation concerns identified in this study include (1) shoreline structure of reservoirs; (2) retention of water in reservoirs until after transformation; (3) protection from vehicle mortality; and (4) minimization of water loss in streams and pools along dispersal routes.**

Key Words.— Anaxyrus boreas; Boreal Toad; dispersal; habitat selection; juvenile; mortality; northeastern Oregon; toadlet; Western Toad

INTRODUCTION

Populations of the Western or Boreal Toad, *Anaxyrus boreas* (formerly *Bufo boreas*), have declined in many parts of its range including the central Rocky Mountains (Carey 1993; Corn et al. 1997; Livo and Yeakley 1997), California Great Central Valley (Fisher and Shaffer 1996), northern Utah (Thompson et al. 2003), the northern Great Basin (Wente et al. 2005), and Montana (Werner et al. 1998; Maxell et al. 2003). The U.S. Fish and Wildlife Service (1991) lists the Rocky Mountain populations of *Anaxyrus boreas* as a candidate species for listing as endangered in Colorado, New Mexico, and Wyoming. The population status of *A. boreas* in northeastern Oregon is unknown, although 18 of 43 high elevation lakes sampled in 2000 and 2001 contained *A. boreas* eggs or larvae with an average of 4.0 and 2.6 egg strings per lake for lakes with and without fish, respectively (Bull and Marx 2002).

Little information exists on dispersal of *Anaxyrus boreas* toadlets (i.e., newly metamorphosed toads) and juvenile (one-year old) toads because their small size makes permanently and/or individually marking them problematic (Carey et al. 2005). Recruitment is dependent on successful dispersal of toadlets from breeding sites to overwintering sites, followed by survival until reproduction. Recolonization of sites where breeding populations have disappeared is dependent on immigration of juveniles or adults from neighboring breeding sites. Information on the effects of emigration and immigration on population dynamics is of great value in managing individual amphibian species (Biek et al. 2002). The objectives of this study were to identify toadlet and juvenile dispersal patterns, mortality factors, and conservation concerns in northeastern Oregon.

METHODS

***Study sites.*—**During 2006–2008, I monitored toadlets and juvenile toads at three breeding sites on the Wallowa-Whitman National Forest in Baker County in northeastern Oregon: Balm Creek Reservoir (Balm; 44°58’55” N, 117°29’73” W), Pine Creek Reservoir (Pine; 44°49’30” N, 118°4’58” W), and Fish Lake Reservoir (Fish; 45°2’92”N, 117°5’41”W). These sites are in mountainous, forested terrain with undulating uplands and moderately or steeply walled drainages at elevations of 1,368 to 1,992 m (Table 1). Study sites were selected based on the presence of at least 50 adult toads and accessibility by vehicle during breeding activity. Forests surrounding Pine and Fish consist primarily of Lodgepole Pine (*Pinus contorta*), Subalpine Fir (*Abies lasiocarpa*), and Western Larch (*Larix occidentalis*) and at Balm forests of Ponderosa Pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), and Grand Fir (*A. grandis*) surrounded the reservoir. Vegetation also includes grasses and sedges with some alder (*Alnus* spp.) at Balm and willow (*Salix* spp.) at Fish. Pine Reservoir differs from the other two reservoirs in being located in a basin surrounded by near-vertical cliffs on the south and west sides and a

TABLE 1. Site characteristics and weather conditions at three *Anaxyrus boreas* study areas in northeastern Oregon, 2006-2008.

	Study area		
Variable	**Balm**	**Pine**	**Fish**
Elevation (m)	1368	1966	1992
Reservoir size (ha)	36	12.1	34.8
Water level at metamorphosis (% capacity of reservoir)			
2006	100%	100%	unknown
2007	50%	1%	60%
2008	85%	1%	85%
No. days >3.9 ºC in 2007[a]	81	44	41
Mean daily temperature in August 2007	15.1 ºC	11.5 ºC	12.8 ºC
Snow water equivalent (cm)			
April, May 2006	61, 38	46, 27	85, 35
April, May 2007	27, 0	14,0	47, 23
April, May 2008	64, 21	49, 20	59, 40
Accumulated precipitation (cm)			
May-September 2006	16.0	20.1	10.9
May-September 2007	12.4	12.2	13.7
May-September 2008	20.6	19.1	12.2
SNOTEL site and number	Taylor Green, 812	Bourne, 361	Schneider Meadows, 736

[a]Between transformation and 20 September 2007

FIGURE 1. Pine *Anaxyrus boreas* study area showing breeding sites along shore, forested slope used for juvenile dispersal, and near-vertical cliffs inhibiting toad movements in northeastern Oregon. (Photographed by Evelyn Bull)

steep drop-off on the east side with a gentler and forested slope on the north side (15–60%; Fig.1).

Two distinct periods of precipitation occur in these study areas, the first as snow from October or November to March and the second as rain during March-May. Frost can occur any month of the year. Moisture within the growing season (May through September) results from thunder storms. An average of 106 cm precipitation and 500 cm of snowfall occurs at the weather station closest to Balm and Fish (Cornucopia, Oregon; 45º00’N 117º12’W; recorded in 1949–1972). An average of 52 cm precipitation and 231 cm of snowfall occurs at the weather station closest to Pine (Rock Creek, Oregon; 44º55’N 118º04’W; recorded in 1948-2007).

Most of the water in the three reservoirs comes from spring run-off, although at least one perennial stream flows into each reservoir. The three reservoirs are used for cropland irrigation downstream which results in the reservoirs being partially drained in some summers. Abundant streams, springs, or seeps are common within 1 km of Fish and Pine, while streams at Balm are more intermittent and retain pools sporadically up to 2.7 km from the reservoir throughout the summer. Drainages in all three areas contain substrate dominated by gravel and cobble.

To determine how weather variables influenced the maximum dispersal distance or size of toadlets and juveniles, I recorded: (1) active period (number of days when the maximum daily temperature in the 2007 growing season was > 3.9ºC); (2) mean daily temperature in August 2007; and (3) snow water equivalent in April and May in 2006–2008. The active period was defined by Muths et al. (2006) as temperatures > 3.9ºC in *A. boreas* and by Mullally (1952) as > 3ºC in *A. boreas halophilus*. The active period was determined from data loggers (Onset Computer Corporation, Cape Cod, Massachusetts, USA) recording ambient air temperature at two-hour intervals from the date of first transformation until 20 September 2007. Data loggers were placed in the shade and 5 cm above the ground within 100 m of breeding sites. Mean daily temperature, accumulated precipitation, and snow water equivalent were taken from the SNOTEL site nearest each study site (within 6–13 km and 211–372 m in elevation; Table 1). Snow water equivalent was used as a relative measure of snow accumulation (Corn 2003).

***Breeding and larval activity*.—**I monitored breeding activity at Balm and Fish during 2006–2008, and at Pine in 2007 and 2008. I tallied the number of gravid females by capturing all toads detected and marking them with PIT (passive integrated transponders) tags at Balm and Fish; I estimated the number of egg strings at Pine by walking the shoreline and counting the number of strings and gravid females detected. More than 90% of the females were in amplexus, thus verifying that they were gravid. During breeding activity, I visited Balm daily, Fish every two to three days, and Pine once a week to quantify the number of toads. I estimated number of larvae within one week of transformation at each site on one occasion to get an estimate of the number of toadlets; I also estimated the percentage of the reservoir that contained water using the high water mark as a reference line. Counts of larvae were used instead of toadlets because some toadlets left the reservoirs before all the larvae had transformed making quantification difficult. I walked the shoreline at each reservoir and at each section of shoreline that contained transforming larvae. I counted the number of larvae in a meter-square area and then measured the length and width of that section of shoreline with larvae to get an estimate of the total number of larvae in that section. I then summed all the numbers of larvae in the different sections of shoreline. This method provided a relative number of transforming larvae and toadlets at each site each year. During transformation, I visited Balm every three to four days, and Fish and Pine every one to three weeks.

***Toadlet dispersal*.—**I monitored movements of toadlets to identify the paths of dispersal and rate of travel. I defined toadlets as toads having transformed that season, and juveniles as having overwintered at least once. When both age groups were present, I defined juveniles as toads 29–50 mm snout-vent length (SVL) and > 1.6 g at Balm, and as toads 24–50 mm SVL and at least 1.1 g at Pine and Fish; toadlets were smaller than these values. The size difference in the definition of a juvenile at Balm and at Pine/Fish corresponds to the 5 mm difference in toadlet size at transformation. When both toadlets and second-year juveniles were present, I based the cutoff sizes on the size classes that were clearly a product of that year’s metamorphosis.

Once toadlets had transformed and initiated dispersal, I located routes of dispersal by driving or walking all accessible roads, trails, and drainages with permanent or intermittent water flowing within 2 km of each reservoir. Once toadlets were located traveling up a drainage, I searched all the sources of water at least 0.5 km beyond the toadlet found farthest from the reservoir. I surveyed for toads on roads and trails when possible because toadlets are easier to detect on surfaces with low vegetation. I monitored toadlet dispersal at least once a week at Balm, every two weeks at Pine, and every four weeks at Fish. Wildfires prevented access to Fish in 2006. I believe the dispersal I identified was from the three breeding sites I monitored. In earlier studies (Bull and Marx 2002; Bull 2006), the area within 3 km of each reservoir was searched extensively for additional breeding sites. At Balm only one shallow temporary pool contained one egg string in two years, and no additional breeding sites were found at Pine. At Fish, one to three egg strings were found in three additional breeding sites but these were located in different drainages than where the dispersal from Fish was documented.

After I identified routes of dispersal, I established 3–4 monitoring stations spaced approximately 200–400 m apart within each drainage to document toadlet movements every 1–2 weeks at Balm and Pine. The stations were selected subjectively with the following characteristics: (1) presence of toadlets in the drainage within a week of the onset of dispersal; (2) water or moist soil within 3 m; (3) low vegetation to facilitate counting toadlets; and (4) accessibility. Monitoring sites were systematically selected because the requirement for rehydration likely influenced toadlet movements. By checking the monitoring stations, I determined the station farthest up the drainage with toadlets and then searched another 200 m beyond to determine the farthest dispersal from the breeding sites.

The high number of toadlets at Balm allowed me to determine rate of travel with two methods. First, I located the farthest distance toadlets traveled in each of four drainages twice a week in the month of July 2007, measured the distance traveled between consecutive visits, and calculated the distance traveled per day. Second, 3,446 toadlets were marked in late August 2007 with visible implant fluorescent elastomer tags (Northwest Marine Technology, Inc., Tumwater, Washington, USA; Nauwelaerts et al. 2000). I marked toadlets that were captured within a 50-m radius at one site in each of three drainages. Toadlets were "batch" marked with a unique color in each drainage. The rate of travel was calculated for a recaptured (marked) toadlet by determining the distance from the original capture site (edge of the 50-m radius) and number of days since it was marked.

To determine if toadlets were dispersing outside of drainages, I searched transects perpendicular to drainages and across landscapes at Balm. I searched 40 50-m transects in August and September 2006 and 24 transects in July and August 2007. Transects were located perpendicular to the drainage and ran 50 m in both directions and started outside the wetted stream channel that contained toadlets. Any toadlet seen within 2 m on either side of the 50-m transect was counted.

Because Pine and Fish had numerous seeps and springs, in addition to streams, I searched for toadlets on a broader scale. At Pine I searched all sources of water for toadlets on the 60-ha forested north slope that was surrounded by cliffs and rock scree in August and/or September 2006–2008 (four times in 2006 and twice in 2007 and 2008). I hiked 6 km along four transects at 75-m intervals in the 60-ha slope between the forest edge and the reservoir searching all habitats for toadlets. Two transects also traversed the rock hillside 50 and 100 m above the forest edge. At Fish I searched 4 km of transects traversing wet and dry habitats radiating within 2 km of the three breeding sites in September 2007 and 2008.

General habitat characteristics of drainages used by toadlets for dispersing were recorded including: intermittent or permanent stream, the wetted channel width, channel substrate (percentage of gravel, cobble and boulder), distance to an open road, ground cover (type, height, and percent coverage), presence of grazing, percent canopy closure, and slope aspect and gradient.

Juveniles.—During 2006–2008, I simultaneously searched for juveniles and toadlets within 1–3 km of the three reservoirs looking at the ground surface and under logs and rocks at seeps/springs and along streams during the day in June. Night searches occurred on four nights in July and August at Balm and on one night in July at Pine in 2007.

I marked 711 juveniles with visible implant elastomer and 70 juveniles over 31 mm SVL with PIT tags (8 mm tags) in two drainages at Balm in late June and early July 2007. I attempted to recapture marked juveniles every 2 weeks to determine their movements.

At each site with juveniles, I recorded the following characteristics in a 4-m radius circular plot: date, UTM, number of toads seen within plot, vegetation type (forest, wet meadow, dry slope, rock, stream), diameter of a meadow if one was present, distance and direction to oviposition site (m), distance to water and kind of water, percentage ground cover (grass, forb, log, rock, water, bare), presence of moss, height of ground cover, percentage slope, aspect, distance to forest edge, percentage canopy closure, and number of burrows and shelter a juvenile toad could use (> 2-cm diameter hole). To determine available habitat, I sampled the habitat at a plot 30 m away from the toad location. Direction from the toad location was determined by using a random azimuth from the second hand of a watch. Habitats in occupied and available plots were compared using Wilcoxon matched-pairs signed-ranks test for continuous variables and chi-square tests for categorical variables (Zar 1999) with an alpha level of 0.05.

Mortality and disease.—Mortality of toadlets and juveniles and the suspected cause (desiccation, trampling, vehicles, predation, and chytridiomycosis) were documented as I walked along the shoreline and along dispersal routes on each visit to the three study sites. Dead toads were typically difficult to find, so my observations are opportunistic and may not be accurate counts of mortality that occurred. Once toadlets started dispersing, road crossings (three at Balm, two at Fish, and one at Pine) were checked for toadlets, and the number of dead observed were counted. Balm and Fish were accessible to all vehicles, while Pine was accessible to all terrain vehicles only.

Pine was drained just prior to transformation in 2007 and 2008, and I searched the dry reservoir for dead larvae. I concentrated on the low depressions where the last water would have occurred and counted the number of dead larvae in a meter-square area and multiplied that by the length and width of the depression with dead larvae.

TABLE 2. Population characteristics of *Anaxyrus boreas* and maximum dispersal distance of immature toads at three study areas in northeastern Oregon, 2006–2008.

	Study area		
Variable	**Balm**	**Pine**	**Fish**
Maximum toadlet dispersal distance (m)	2,720	400	570
Maximum juvenile dispersal distance (m)	2,720	1,070	2,420
No. egg strings or gravid females			
2006	156	unknown	50
2007	168	>15	41
2008	136	>15	84
Initiation of ovipositing			
2006	11 May	unknown	27 June
2007	23 April	30 May	29 May
2008	16 May	20 June	25 June
Date of first metamorphosis			
2006	14 July	24 August	After 17 August
2007	2 July	8 August	10 August
2008	23 July	5 September	18 August
Estimated no. of toadlets			
2006	750,000	90,000	unknown
2007	200,000	4,000	6,000
2008	50,000	4,000	5,000

To assay for *Batrachochytrium dendrobatidis* (*Bd*), amphibian chytrid fungus, I took swab samples of live toadlets and/or juveniles at each study area each year (except Fish in 2007) using techniques described by Livo (2004. Methods for obtaining *Bd* samples for PCR [polymerase chain reaction] testing. Department of Integrative Physiology, University of Colorado, Boulder, Colorado, USA). A PCR assay (Annis et al. 2004) was used to determine the presence of *Bd* (Pisces Molecular, Boulder, Colorado, USA). Four dead toadlets and one sick juvenile were sent to the USGS National Wildlife Health Center (Madison, Wisconsin, USA) for determination of cause of death.

RESULTS

Breeding of *Anaxyrus boreas* at these sites occurred during or after snowmelt, although the date varied by as much as 27 days among years (Table 2). Numbers of egg strings or gravid females ranged from 15 to 168, which directly determined the number of embryos by site (Table 2). The relative survival of embryos and larvae varied among years at the different sites and was likely influenced by weather. In 2006, deep snow pack resulted in the reservoirs filled to capacity at breeding and remaining full until larvae transformed with high survival of embryos, larvae, and toadlets. In 2007, shallower snow pack and less precipitation may have resulted in earlier transformation and fewer toadlets detected. In 2008, deep snow pack, a late spring, and a cooler summer may have resulted in later breeding and transformation and poorer survival of larvae. Pine Reservoir was drained before transformation in both 2007 and 2008 resulting in poor survival, although about 4,000 toadlets transformed in a small pool that remained near the dam each year.

Toadlet dispersal.—Maximum dispersal of toadlets during 2006–2008 was 2720 m at Balm, 400 m at Pine, and 570 m at Fish (Figs. 2-3). In this study thousands of toadlets were detected dispersing along drainages with water in all three areas. I did not detect additional dispersal in heavily vegetated areas away from water but visibility was limited. Toadlets at Balm had 81 days in an active period between transformation and 20 September 2007, in contrast to 44 days at Pine and 41 days at Fish. Mean daily temperature in August 2007 ranged from 11.5ºC at Pine to 15.1ºC at Balm (Table 1).

At Balm in 2006 when higher precipitation and a heavier snowpack occurred compared to 2007 (Table 1), more than 750,000 toadlets dispersed along five drainages with permanent or intermittent water. In all years toadlets at Balm dispersed from breeding sites to the farthest point with water in four intermittent streams. Toadlets (unmarked) at Balm traveled an average of 84 m a day in one drainage, and 87 m a day in a second drainage between 2 and 30 July 2007 based on the farthest points of dispersal in each drainage. One color-marked toadlet traveled 610 m upstream in 7 days, which equates to 87 m per day.

Each year toadlets at Pine dispersed up to 400 m from the breeding sites along streambed channels with intermittent water in a flat, grassy meadow surrounded by steep terrain to the base of steep slopes. Two permanent streams with a steep gradient (35–60%) flowed into the meadow, yet toadlets were not detected along these streams beyond the meadow. More than 90,000 toadlets transformed in August 2006 when the

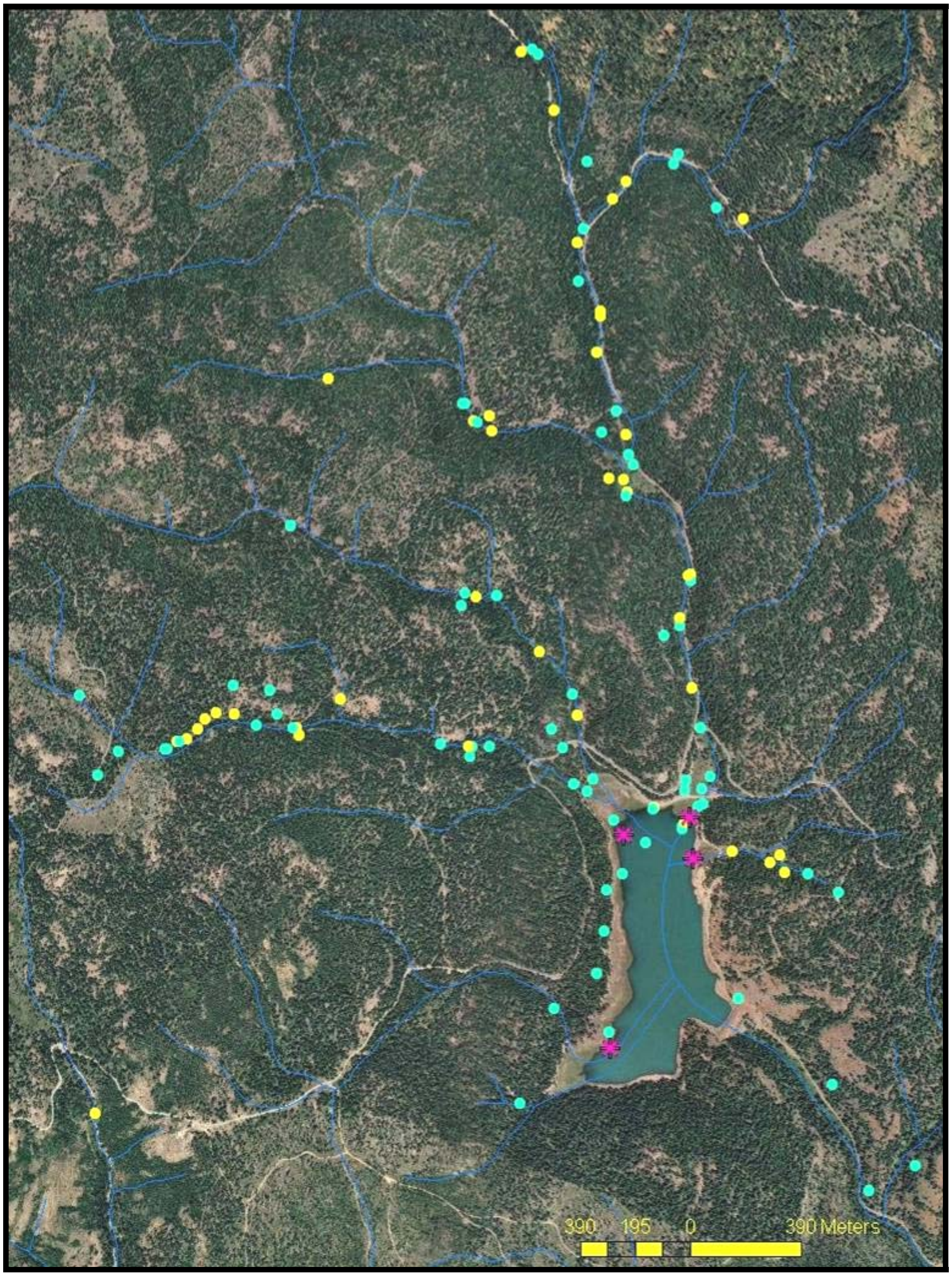

FIGURE 2. Locations of dispersing *Anaxyrus boreas* toadlets (green points) and juveniles (yellow points) at Balm in northeastern Oregon 2006–2008. Oviposition sites are shown as pink stars and streams as blue lines. (Figure created by Barbara Wales)

reservoir was at full capacity compared to an estimated 4,000 toadlets in 2007 and 2008 when the reservoir was drained. At Fish toadlets dispersed to the north and east along three permanent streams and an irrigation ditch into seven wet meadows up to 570 m north of Fish.

More than 99% of observed toadlets dispersed along drainages with water, although 40 toadlets were detected along eight of 40 transects 10–50 m from streams at Balm in 2006. No toadlets were found outside stream channels or wet areas at Pine and Fish. At the three study sites there were four intermittent and nine permanent streams, and dispersal was detected along 12 of them.

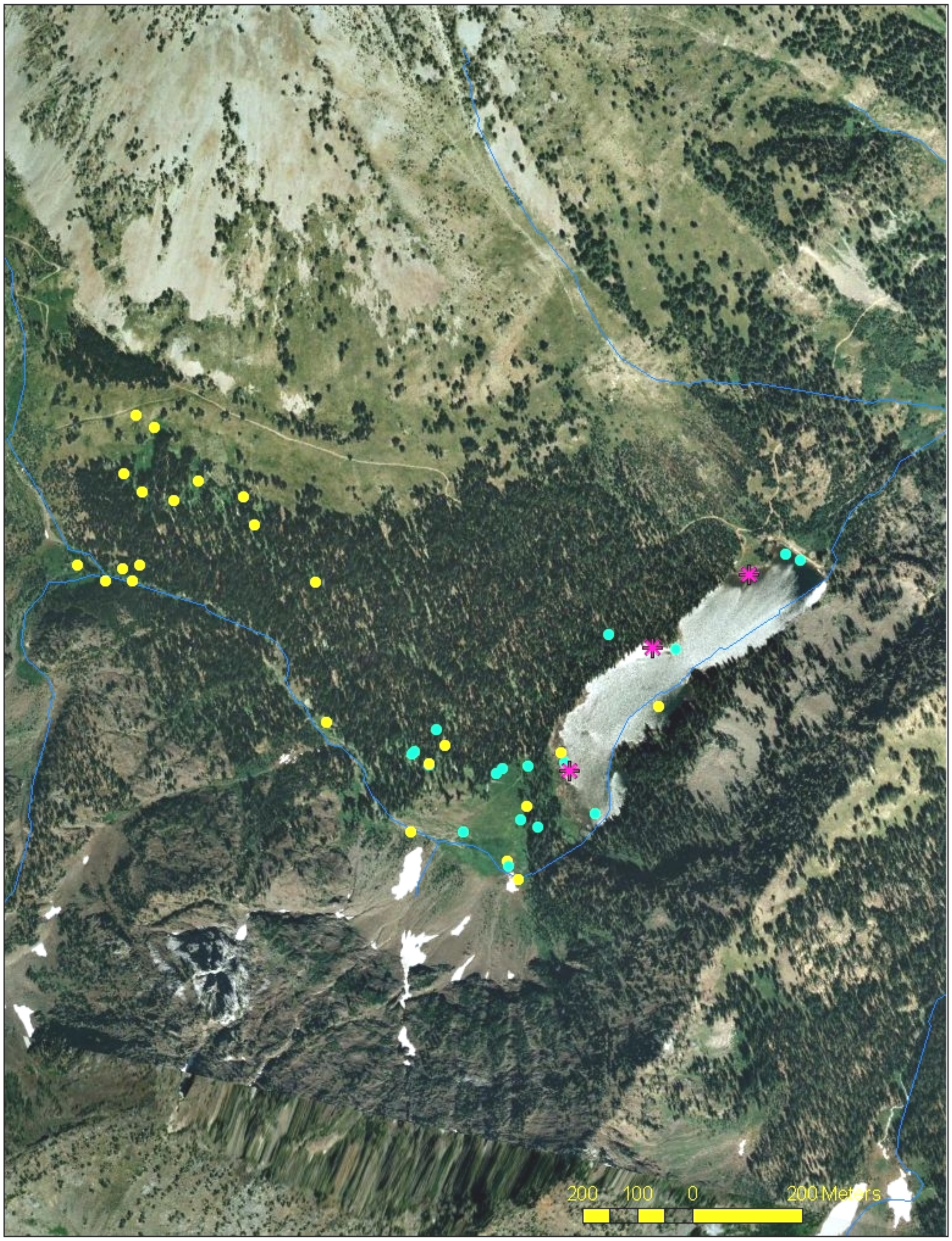

FIGURE 3. Locations of dispersing *Anaxyrus boreas* toadlets (green points) and juveniles (yellow points) at Pine in northeastern Oregon, 2006–2008. Oviposition sites are shown as pink stars and streams as blue lines. (Figure created by Barbara Wales)

The wetted stream channels used for dispersal ranged from 0.3 to 4 m in width and averaged 0.9 m. The primary substrate was cobble in six of the streams, gravel in four, and mud in two. The primary ground vegetation along dispersal routes was heavily grazed grass at Balm; tall, ungrazed sedge at Pine; and partially grazed sedge at Fish. Dense stands of alder were present in 10–20% of four of the five streams in Balm. On the portions of the streams used by toadlets, the overall slope gradient ranged from 2 to 8% at Balm and Pine. Near-vertical cliffs, 5–6 m tall, did not hinder dispersal at three locations in Balm (Fig. 4).

***Juveniles*.—**The maximum distances juveniles were located from the breeding sites were 2,720 m at Balm, 1070 m at Pine, and 2,420 m at Fish (Table 2). One color-marked juvenile was located 840 m upstream 40 days later (21 m/day) at Balm. Numbers of juveniles detected varied by year with more than 1,000 in 2007 and 10 in 2008 at Balm, 108–200 detected each year at Pine, and 35 in 2008 and 1 in 2007 at Fish. Only 16 juveniles were detected at Balm at night in July and August 2007.

Juveniles (n = 60 plots) were always associated with water, either in wet meadows (50%), along streams (33%), or in seeps or springs (17%), whereas available plots (i.e., without toads) occurred in forests (70%), dry meadows (23%), rock slides (5%), and wet meadows (2%). Compared to available plots, juveniles selected sites closer to water, farther from forests, with a lower canopy closure, gentler slopes, taller ground cover, more grass ground cover, fewer logs and shrubs, and more shelters (Table 3; Fig. 5). The presence of water at all juvenile plots explained the presence of moss at 85% of these plots in contrast to only 3% of the available plots.

FIGURE 4. Dispersing *Anaxyrus boreas* toadlets scaled these cliffs in a drainage in northeastern Oregon. (Photographed by Evelyn Bull)

***Mortality and disease*.—**Mortality of toadlets and juveniles in these study sites largely resulted from predation, vehicles, desiccation, trampling, and chytridiomycosis. Gray Jays (*Perisoreus canadensis*), American Robins (*Turdus migratorius*), and Killdeers (*Charadrius vociferous*) were observed preying on toadlets near the breeding sites. Vehicles killed thousands of toadlets at Balm in 2006 when toadlets crossed roads traveling away from the reservoir. All terrain vehicles appeared to be responsible for killing hundreds of toadlets near the breeding sites at Balm and Pine based on vehicle tracks. More than 50 toadlets and one juvenile were found dead in cattle tracks at Balm. More than 300 desiccated toadlets were found in a 1 m^2 area in a dry streambed at Balm.

Desiccation caused mortality in larvae at Pine. I counted more than 20,000 dead larvae on the dry reservoir in 2008 after it was drained for irrigation just prior to transformation.

Chytridiomycosis occurs in adult toads at these sites (Bull 2006) and was confirmed in four dead toadlets and one sick juvenile at Balm in September 2007 (USGS 2007). Toadlets or juveniles tested positive for *Bd* at Balm (15 of 34 sampled), Pine (8 of 22), and Fish (2 of 10).

TABLE 3. Mean values (SE) of habitat characteristics at 60 4-m radius plots occupied by juvenile *Anaxyrus boreas* and at 60 plots in available habitat at Balm and Pine in northeastern Oregon, 2006-2008. Statistical values of comparisons are also provided.

Characteristics	**Toad locations**	**Available habitat**	***Z* value, *P***
Distance to water (m)	1.40 (0.81)	46.8 (6.65)	-6.11, $P < 0.001$
Distance to forest (m)	11.38 (1.67)	8.78 (2.79)	-3.10, $P < 0.001$
Percentage slope	12.82 (1.68)	25.45 (2.68)	-4.92, $P < 0.036$
Percentage canopy closure	12.46 (2.48)	57.67 (4.51)	-5.94, $P < 0.001$
Number of burrows	0.80 (0.39)	1.71 (0.48)	-2.23, $P = 0.03$
Number of shelters	14.08 (1.92)	7.57 (1.46)	-3.51, $P < 0.001$
Height of ground cover (cm)	32.59 (4.20)	19.20 (2.71)	-2.07, $P = 0.04$
Percentage ground cover			
Grass	42.3 (3.14)	13.4 (2.74)	-4.85, $P < 0.001$
Log	7.97 (1.20)	16.83 (2.69)	-2.94, $P < 0.001$
Water	13.5 (1.78)	0.5 (0.5)	-5.69, $P < 0.001$
Shrubs	3.75 (1.66)	17.03 (4.28)	-2.75, $P = 0.01$
Bare	11.19 (2.27)	36.92 (3.13)	-4.98, $P < 0.001$

FIGURE 5. Juvenile *Anaxyrus boreas* occurred in wet grassy meadows with high solar radiation at Pine in northeastern Oregon. (Photographed by Evelyn Bull)

DISCUSSION

Survival of embryos and larvae to transformation and the timing of transformation differed among years. The greatest survival occurred in 2006 and was associated with high water levels at Balm and Pine as a result of a deep snow pack (high snow water equivalent) and high precipitation. Survival was poorest and development was earliest in 2007 when water levels were low and development was latest in 2008, probably due to a late spring and cool summer. These observations are consistent with Kiesecker et al. (2001) who reported that reductions in water depth caused high mortality of embryos by increasing their exposure to UV-B radiation and vulnerability to *Saprolegnia ferax* infections. Newman (1992) found that development is accelerated and metamorphosis occurs quickly when the risk of desiccation is high, and development may be prolonged if the risk of desiccation is low.

Dispersal.—Juveniles and toadlets in my study dispersed greater distances than previously reported. The distance that juveniles dispersed was similar to the mean distance radio-tagged female toads traveled from the breeding sites in Balm (2,823 m) and Fish (2067 m) in an earlier study (Bull 2006). Muths and Nanjappa (2005) stated that toadlets may remain along the border of their natal wetland to overwinter or may move to nearby terrestrial sites or wetlands. In Colorado, reintroduced *A. boreas* toadlets had dispersed 350–600 m by July and August from the reintroduction area where tadpoles were released (Scherff-Norris. 1999. Final report: Experimental reintroduction of Boreal Toads, *Bufo boreas boreas*. Colorado Division of Wildlife, Denver, Colorado, USA). Of 605 *Bufo calamita* toadlets released in 1991 in Germany, all had dispersed from breeding areas within four weeks and recaptured toadlets had traveled about 400 m (Sinsch 1997a). In Indiana, the median linear distance moved between metamorphosis and a juvenile life stage was 174 m in *A. woodhousei fowleri* (Breden 1987). In Germany, the maximum distance traveled between the release and recovery site by marked (dipole reflector tags) *B. calamita* and *B. viridis* toadlets was 588 m and 665 m, respectively (Leskovar and Sinsch 2005).

The distance toadlets dispersed in my study was apparently influenced by the time between metamorphosis and overwintering, ambient air temperature, and the amount of habitat with moisture. Toadlets at Balm were able to disperse more than 2,000 m farther than those at Pine and Fish because they metamorphosed 5–6 weeks earlier, ambient air temperatures were warmer, and there was moist habitat for dispersal up to the farthest distance that toadlets moved (Table 1). Toadlets at Pine and Fish transformed later and had shorter and cooler active periods than at Balm.

Toadlets at Balm dispersed 2,720 m to the end of surface water in four of five drainages, which was where it appeared that suitable moist habitat ended. This observation is consistent with Loeffler (2001. Conservation plan and agreement for the management and recovery of the southern Rocky Mountain population of the Boreal Toad [*Bufo boreas boreas*]. Boreal Toad Recovery Team, Colorado Division of Wildlife, Boulder, Colorado, USA), who reported that toadlets moved both upstream and downstream but were restricted in movement by available moist habitat. In contrast, there were moist habitats 600 m and more than 3,000 m beyond where toadlets were found at Pine and Fish in September, respectively. The high altitude and late transformation likely hindered more extensive dispersal in these areas.

Toadlets at Balm travel long distances even though there are many risks involved and they appear to leave suitable habitat behind. The high density of toadlets at breeding sites may necessitate dispersing to find better food resources, more suitable water sources, and better cover from predators concentrated near the breeding sites. Dispersal can enhance genetic diversity and emigration to establish new populations when suitable sites are encountered.

Habitat.**—**Although juvenile habitat is poorly known, Livo (1998. Investigations of Boreal Toad tadpole ecology. Colorado Division of Wildlife Boreal Toad Research Progress Report 1995–1997) suggested that juveniles probably use the same habitat as adults, but wetter, due to their susceptibility to desiccation. My observations of adults and juveniles within 10 m of each other on five occasions support this idea, although adult toads were moving to the streams at night from drier habitats, while the juveniles were adjacent to the streams day and night.

Carey et al. (2005) stated that temperature is the primary determinant of growth in toadlets and hydration is critical. Juveniles in my study used sites with water, little tree canopy, gentle slopes, dense grass and forb cover, and south- and west-facing slopes, thereby maximizing both temperature and hydration. Wet meadows occurred where the terrain was gentle enough for the water to pool in contrast to steep terrain where the water flowed quickly in narrow channels. The moisture and moss in these wet meadows reduced the risk of desiccation for these small toads. The high moisture content in the wet meadows prohibited trees from becoming established, which resulted in high solar radiation. The moisture and solar radiation resulted in dense growth of grasses, forbs, and mosses, which likely provided abundant cover and prey for toads. The available paired plots typically occurred in the forested stands surrounding the wet meadows, which were shaded, cooler, and lacked ground vegetation (Table 3). Although slope aspect did not differ between occupied and available plots because of their close proximity, sites with toads were on slopes that received the maximum amount of radiation, which extended the active period for the toads and increased their growth due to the warm temperatures.

Mortality and disease**.—**High mortality of toadlets occurs because toadlets are highly vulnerable to desiccation, predation, and intraspecific competition due to high densities in the vicinity of ponds (Sinsch 1997b), and due to warm summer temperatures plus xeric conditions (Scherer et al. 2005). In the Cascade Mountains in Oregon, 95–99% of *A. boreas* young die or disappear in the first year of life (Samollow 1980).

I detected mortality of toadlets due to vehicles, desiccation, predation, and *Bd* at Balm, although the magnitude of the mortality is not known. Substantial mortality of larvae from desiccation occurred at Pine when the reservoir was drained.

Eigenbrod et al. (2008) found that *A. americanus* was negatively associated with traffic density in Canada. In contrast, *Bd* may have been responsible for the considerable mortality detected at Balm in 2007 (4–12 weeks after transforming) based on the emaciated condition of toadlets and juveniles, mobility problems, and the confirmation of *Bd* from both swab samples and diagnostic reports (USGS 2007). An experimental study found that lethal chytridiomycosis could be induced in toadlets and death occurred within 5–7 weeks (Carey et al. 2006). Direct body contact was not necessary for transmission of *Bd* (Carey et al. 2006) and water could remain infective for up to seven weeks (Johnson and Speare 2003).

Conservation concerns.**—**Water sources for reproduction, dispersal, and rehydration are essential for the survival of *A. boreas* and other amphibians. For the long term, networks of ponds are essential to maintain viable, self-adjusting metapopulations of amphibians breeding in temporary ponds (Griffiths 1998). The structure of the water body, namely a shallow sloping shoreline that provides shallow warm water, particularly on the south-facing shore, is a critical issue. Maintaining water in reservoirs until after metamorphosis could improve survival of eggs, larvae, and toadlets. Draining reservoirs prior to larval transformation could have a significant impact on the toad populations, particularly if it occurs in multiple years. Adopting management strategies that retain water in reservoirs and in streams or seeps used for dispersal could extend movements and improve survival of toadlets, as well as adult toads.

I found thousands of dead, flattened toadlets on the roads at Balm and Pine, although with the high numbers of surviving toadlets this observation did not represent a substantial source of mortality at these sites. Road closures have been effective at protecting amphibians during migratory events to or from breeding sites (Timm et al. 2007). Culverts of the appropriate size and placement could be effective in funneling the dispersing toadlets under the roads along creeks at Balm, as has been done for turtles in Florida (Aresco 2005).

There appeared to be a detrimental impact of cattle on the survival of toadlets and juveniles in this study because of their use of water from the few remaining pools in stream beds during dispersal in a dry year. Cattle were observed drinking in small pools with toadlets at Balm that were subsequently dry and did not have toadlets on subsequent surveys. If survival of toadlets and juveniles is a conservation objective, particularly if toad numbers are low and water is limiting, it would be beneficial to prohibit cattle from accessing dispersal routes of toadlets to retain water in the drainages. This management activity could promote greater dispersal, recruitment, and immigration.

The long-term effect of the presence of *Bd* on all life stages of toads in these study areas is unknown, although *Bd* is believed to have caused substantial mortality in toads in the Rocky Mountains (Carey et al. 2005). Additional research is needed to verify that the substantial toadlet mortality at Balm in some years is caused by *Bd* and the factors that influence its prevalence.

This study has identified extensive dispersal of toadlets and juveniles and the importance of streams, seeps, springs, and appropriate habitat in their movements. Dispersal opportunities are likely critical for survival, recruitment, immigration, genetic exchange, and the long-term health of a population.

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