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WILDFIRE EFFECTS ON WATER TEMPERATURE AND SELECTION OF BREEDING SITES BY THE BOREAL TOAD (*BUFO BOREAS*) IN SEASONAL WETLANDS

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***Abstract.*—Disturbances can significantly affect the thermal regime and community structure of wetlands. We investigated the effect of a wildfire on water temperature of seasonal, montane wetlands after documenting the colonization of recently burned wetlands by the Boreal Toad (*Bufo boreas boreas*). We compared the daily mean temperature, daily maximum temperature, and accumulated growing degree·days measured on the north shore of three classes of wetlands: unburned wetlands, burned wetlands that were colonized by breeding toads, and burned wetlands that were not colonized. We hypothesized that toads colonized burned wetlands because they were warmer than unburned wetlands and selected specific burned wetlands because they were warmer than neighboring burned sites. There was weak evidence that toads selected burned wetlands with higher temperature maxima; however, the differences were small (≤ 1°C) and were not supported when accounting for geography and wetland features. We also found no evidence that burning the forest around wetlands increased water temperatures two and three years after the fire. Unburned wetlands had higher daily mean and maximum temperatures and accrued more growing degree·days than either class of burned wetlands. Temperature differences among groups of wetlands seemed to be driven by subtle differences in geography. We suspect we did not find warmer temperatures in burned wetlands because all of the wetlands we monitored already had open canopies and the fire likely resulted in only small increases in incident radiation**.

Key Words.—Boreal Toad; *Bufo boreas*; degree·days; fire; forest disturbance; Glacier National Park, water temperature, wetlands

INTRODUCTION

The distribution of organisms is a product of numerous interacting factors, including the choice of breeding sites by adults (Pulliam and Danielson 1991; Resetarits 2005). Individuals respond to several environmental cues to choose among and within potential breeding sites for characteristics that may confer greater fitness. Temperature affects many biological processes of larval amphibians and thus should be a strong selective force on life history traits (Moore 1939; Berven et al. 1979; Skelly 2004). Preference for warmer water is likely to be especially strong in temporary or cold environments, where there is often less time for larvae to develop and leave natal sites (Berven et al. 1979; Newman 1992; Merilä et al. 2000).

Variation in forest canopy cover affects the selection of breeding sites by amphibians because water temperature is strongly associated with insolation (Werner and Glennemeier 1999; Skelly and Friedenburg 2000; Batzer et al. 2000). Insolation often increases after forest disturbance such as logging or beaver activity (Chen et al. 1999; Skelly and Freidenburg 2000). Wildfire was historically the dominant disturbance regime across much of western North America and greatly affected the formation and function of ecosystems (Arno 1980; Hessburg and Agee 2003). Even though its role has been supplanted in many areas, fire—or the lack of fire—is still central to the distribution of most taxa in the region (e.g., Hutto 1995; Smith 2000). Skelly (2004) suggested changes in thermal regimes of wetlands could promote rapid local evolutionary change in developmental rates of the Wood Frog (*Rana sylvatica*). There may have been similar selection pressures on developmental rates of lentic amphibians under historical fire regimes in the West.

Wildfires can significantly increase stream temperatures, depending upon the extent and severity of disturbance and size of stream (Royer and Minshall 1997; Dunham et al. 2007). Comparable investigations into the effects on wetlands have not been conducted, but like headwater streams, wetlands may be tightly coupled with their catchments (Batzer et al. 2000; Palik et al. 2001). The frequency and duration of large wildfires in forests of the western U.S. have already increased in some areas (Westerling et al. 2006). Changes to fire regimes are expected to continue under future climate scenarios (McKenzie et al. 2004;

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Westerling et al. 2006), which could affect numerous physical and biological interactions in wetlands. For example, changes in wetland temperature would likely affect selection of breeding sites, growth and developmental rates, timing of emergence, or fertility of resident ectotherms (Huey 1991; Williams 1996).

The Boreal Toad (*Bufo boreas boreas*) colonized several previously unoccupied wetlands the year after the wetlands burned in a mixed-severity wildfire in Glacier National Park (NP), Montana (Hossack and Corn 2007). One hypothesis to explain the colonization pattern was that toads selected burned wetlands because the fire reduced shading vegetation and increased water temperatures. Prior work in the park showed that *B. boreas* was more likely to breed in water bodies that receive more sunlight (Hossack et al. 2006). We investigated the effect of wildfire on temperature of seasonal montane wetlands during the second and third years after the fire. We compared the daily mean temperature, daily maximum temperature, and accumulated growing degree·days of burned wetlands that were colonized by *B. boreas*, neighboring burned wetlands that were not colonized, and the nearest unburned wetlands that were not occupied by *B. boreas*. Our objectives were to determine whether *B. boreas* selected wetlands based on temperature, and whether burned wetlands were warmer than unburned wetlands.

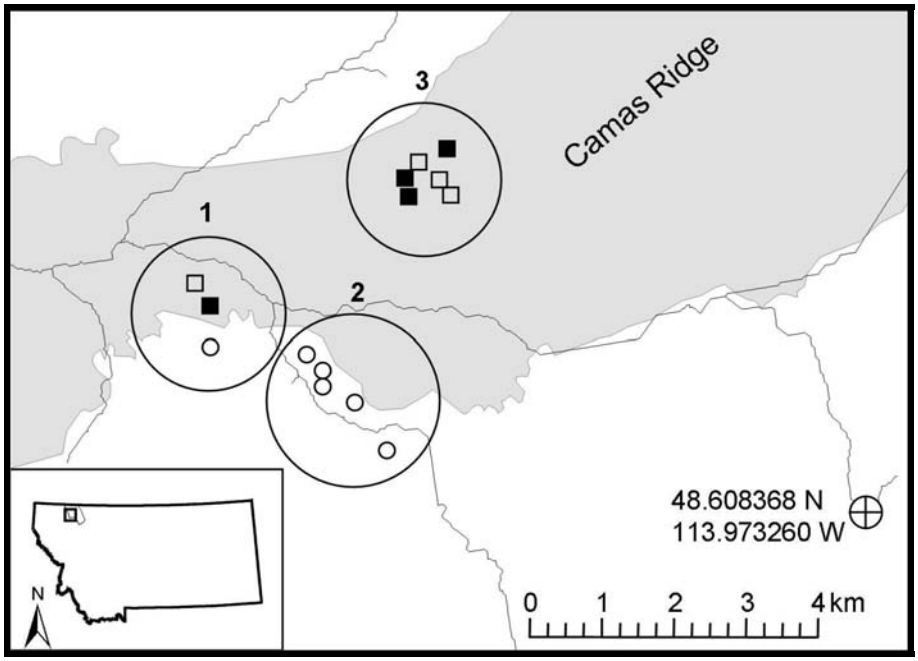

FIGURE 1. Location of study wetlands monitored for temperature (2003 and 2004) in and around the perimeter of the 2001 Moose Fire perimeter (shaded) in Glacier National Park, Montana, USA. Small circles indicate unburned wetlands, squares indicate burned wetlands, and black squares indicate wetlands colonized by breeding Boreal Toads (*Bufo boreas*) after the fire. The number above each large circle specifies the three clusters of wetlands used in the analysis (see Table 1).

MATERIALS AND METHODS

Study Area.—The Moose Fire was ignited by lightning on 14 August 2001 on the Flathead National Forest. It moved into Glacier NP and burned an area where we had collected data on amphibian occupancy of wetlands since 1999 (Hossack and Corn 2007; Fig. 1). The mixed-severity, stand-replacement fire burned ca. 9,830 ha in the park in an area of mixed conifer forests that were historically replaced by fire every 140-340 years (Barrett et al. 1991). Due to the naturally long fire intervals, fire suppression has not greatly altered the natural succession of forest stands in this area (Barrett et al. 1991) and the Moose Fire was an average landscape-scale fire relative to previous fires in the North Fork Valley during the last 400 years (Barrett 2002). The burned wetlands were surrounded primarily by forest that burned patchily with low and moderate severity (see Key and Benson 2005 for definitions). The unburned wetlands were surrounded by mature forest stands that grew after fires in 1866 and 1926.

Forests in the northwest portion of the park are densely populated with shallow wetlands. Most of these wetlands fill with snowmelt in the spring, have near-neutral pH, support extensive emergent vegetation communities (predominately sedges [*Carex* spp.]), and typically dry by mid-summer (Fig. 2). The study area receives approximately 73 cm of precipitation annually (Western Regional Climate Center 2007. Available from http://www.wrcc.dri.edu/ [Accessed 09 February 2008].]), mostly as snow, and is underlain by Precambrian sedimentary rocks covered with unconsolidated glacial tills (Alt and Hyndman 1973). All wetlands monitored for temperature had substrates of fine sediments and > 50% coverage by emergent vegetation (Fig. 2).

Wetland Temperature.—We measured post-fire differences in water temperature during 2003 and 2004. Wetlands were selected based on the distribution of *B. boreas* breeding sites within the Moose Fire perimeter in

FIGURE. 2. A typical seasonal wetland on the west side of Glacier National Park, Montana, USA, 10 months after being burned by a mixed-severity wildfire. The trees on the right burned with high severity. The trees in the center burned with moderate severity. (USGS photo).

2002, which enabled us to measure differences relative to burn status and to determine if burned wetlands that were colonized after the fire were warmer than burned wetlands that were not colonized. We installed temperature loggers during late May to early June, when *B. boreas* typically breeds in the study area.

In 2003, we randomly selected four burned wetlands that were occupied by *B. boreas* in 2002 and the nearest four burned and four unburned wetlands that were not occupied. We assumed all wetlands were potential breeding sites because *B. boreas* uses a wide range of habitats (Nussbaum et al. 1983). We have never documented *B. boreas* breeding in heavily shaded wetlands in Glacier NP (Blake Hossack, pers. obs.), but all of the wetlands in this study had open canopies. We added two randomly selected unburned wetlands in 2004 after some results in 2003 that we suspected could be spurious (i.e., unburned wetlands were warmer).

Because we used *B. boreas* breeding sites as the basis for site selection, the group of selected wetlands fell into three distinct geographic clusters: one where all wetlands were burned (n = 6), one with a mix of burned and unburned wetlands (n = 3), and one where no wetlands burned (n = 3 in 2003 and n = 5 in 2005; Fig. 1). The unburned wetlands have not been occupied by *B. boreas* since at least 1999 (Hossack and Corn 2007). Only one burned wetland colonized by *B. boreas* in 2002 was close to the southern boundary of the fire perimeter, near the unburned wetlands that we monitored. A 1999 wildfire that abutted the northern perimeter of the Moose Fire prevented us from selecting reference sites closer to most of the wetlands that were colonized by toads.

We characterized wetlands according to shading, maximum depth, and size. We measured the angle to the horizon (every 20° at bearings from 90-270°) using a clinometer from the north shore of each wetland to provide an index of shading by surrounding trees and topography (Diamond et al. 2005). Mean length and width were based on bank-full dimensions calculated from several measurements taken with a range finder. The average elevation of burned and unburned wetlands was 1174 m and 1149 m, respectively.

To measure water temperature, three data loggers (Maxim Thermochron iButton DS1921G-F50 [Sunnyvale, California, USA]; resolution = 0.5° C, accuracy = ± 1° C) were tethered to a pole and suspended at 5-cm depth below a fishing bobber at different locations along the north shoreline, where toads in Glacier NP typically oviposit (Blake Hossack, pers. obs.). Placement of loggers in wetlands was not standardized. Instead, we sought a balance between selecting the general area where we thought toads, if present, would oviposit, and the need to have the loggers far enough from shore that they would not get stranded before the end of June. The temperature loggers were typically within 3 m of the shore. Average wetland depth where the loggers were deployed was similar in burned (18.4 cm, 20.7 cm) and unburned (17.7 cm, 22.8 cm) areas in 2003 and 2004, respectively.

One logger in a shielded container was suspended above the center of the wetland and recorded air temperature. For wetland loggers that eventually became stranded, air temperature was used to determine the date of stranding. When a wetland logger became stranded, its nighttime temperature equaled the air temperature. We did not analyze air temperature because wildlife frequently disturbed the shields. Loggers exposed to the sun provide erroneous measurements of air temperature.

Loggers recorded temperature every 30 min in 2003 (period of record: 03 June to 30 June) and every 60 min in 2004 (period of record: 20 May to 30 June), providing 24 hr temperature profiles. Using 60 min intervals in 2004 allowed us to extend the recording season with little loss of information. Earlier deployment of temperature loggers also allowed us to determine if burned wetlands warmed earlier in the season than unburned wetlands.

One wetland dried before the end of the recording period in 2003; its period of record was 03 June to 23 June. Instrument failure or disturbance by animals resulted in the loss of one logger in 2003, one logger in two wetlands in 2004, and two loggers in a wetland in 2004. All three loggers were disturbed in one burned

TABLE 1. Mean (SD) and range (below) of values for mean angle to the southern horizon, maximum depth, and area in unburned wetlands without Boreal Toads (*Bufo boreas*), burned wetlands without toads, and burned wetlands that were colonized in 2002 (Table 1a) and for the 3 geographic clusters of wetlands in Glacier National Park, Montana, USA (see Fig. 1).

1a.

Treatment Group	n	Horizon (º)	Max. Depth (cm)	Area (m^2)
unburned, no toads	6	36 (9) 22–48	30 (6) 22–39	1073 (1520) 204–4149
burned, no toads	4	22 (7) 14–29	37 (12) 22–51	555 (508) 79–1203
burned, with toads	4	19 (1) 17–20	26 (6) 19–32	1498 (1542) 400–3762

1b.

Wetland Cluster	n	Horizon (º)	Max. Depth (cm)	Area (m^2)
1	3	22 (3) 19–25	27 (4) 22–30	1839 (2001) 662–4149
2	5	38 (7) 32–48)	29 (7) 22–39	458 (220) 204–756
3	6	20 (10) 14–29	33 (12) 19–50	1141 (1369) 79–3762

wetland in 2004, eliminating the wetland from the analysis for that year.

Water temperature varies widely within wetlands. It is important to note that we did not necessarily measure the maximum temperature in each wetland, which generally occurs at shoreline. Using three loggers deployed at 5-cm depth provided a standardized measure among wetlands and would be less sensitive to fluctuations in water levels that might leave shoreline loggers stranded.

Analysis.—We compared daily mean and maximum temperatures of the average values of all loggers in each wetland using a repeated measures model fitted by maximum likelihood methods (PROC MIXED, SAS 9.1). The covariance in within-wetland temperatures was modeled using a first-order autoregressive structure (AR[1]; Littell et al. 2006). Because we used *B. boreas* breeding sites as the basis of our selection method, burn status of wetlands was partially confounded with geographic location (the three clusters mentioned above), and the location of wetlands seemed to be associated with wetland temperature. Therefore, we used a model comparison approach to determine which covariates provided the best description of the data by fitting four models to each dependent variable: wetland cluster, wetland cluster + treatment group, wetland characteristics (area, maximum depth, and horizon), and wetland cluster + treatment group + wetland characteristics. Maximum depth and mean angle to the southern horizon were square-root transformed prior to analysis; wetland area was log transformed. The wetland characteristics model ignores geographic and fire effects and measures whether temperature was simply a function of wetland features. Models were ranked according to differences in the second-order Akaike's Information Criterion (ΔAICc) and model weights (w_i; Burnham and Anderson 2002). Model weights represent the probability that a model is the best of those being considered for the dataset (Burnham and Anderson 2002).

We also calculated growing degree·days to show the cumulative differences in water temperature across the season. Growing degree·days represent the number of degrees above developmental zero each day (e.g., Berven et al. 1979). Field and laboratory measurements of *B. boreas* larvae in Colorado suggested a developmental zero of 8° C (Paul Corn, unpubl. data). Degree·days were calculated by subtracting 8° C from each temperature record (any records < 8° C were set to 0), dividing by 48 or 24 (the number of 30-min or 60-min recording intervals per day) and then summing for each day. Daily values were summed to produce seasonal growing degree·days for each group of wetlands.

RESULTS

There was substantial variation in wetland characteristic. With a couple of exceptions, however, the mean and range of measurements were overlapped extensively among treatment groups and wetland clusters. Unburned wetlands had greater angles to the local horizon; this relationship was also present in wetland Cluster 2, where five of the six unburned wetlands were located (Table 1, Fig. 1). Burned wetlands that were not colonized by toads tended to be smaller than other wetlands, as were wetlands in Cluster 2 (Table 1, Fig. 1). The remaining unburned wetland, in Cluster 1, was the largest wetland monitored and more than doubled the mean for all unburned wetlands when they were grouped together. Across all wetlands, potential shading from trees and topography was weakly correlated with wetland size (Pearson's r = -0.16) and maximum depth (r = 0.06). Wetland size and maximum depth were also weakly correlated (r = -0.14).

The daily mean temperature of burned wetlands that were colonized by *B. boreas* was cooler than burned wetlands that were not colonized, although there was variation between years (Table 2). There was weak evidence that toads selected burned wetlands with higher

TABLE 2. Mean (SE), range, and growing degree·days accumulated at 5-cm depth in 2003 and 2004 in unburned wetlands without Boreal Toads (*Bufo boreas*), burned wetlands without *B. boreas*, and burned wetlands that were colonized by *B. boreas* in Glacier National Park, Montana, USA. Temperature was recorded every 30 minutes from 03 June to 30 June 2003 and hourly from 20 May to 30 June 2004. Data from one unburned wetland with only a 22 day temperature record in 2003 were excluded from the degree·day calculations.

Treatment Group	Year	n	Daily Mean ºC	Daily Max ºC	Range ºC	Degree·Days
unburned, no toads	2003	4	17.1 (0.14)	24.2 (0.94)	8.5–32.4	260.4 (12.80)
burned, no toads	2003	4	16.3 (0.11)	21.7 (0.72)	9.1–28.3	232.1 (14.60)
burned, with toads	2003	4	15.8 (0.12)	22.1 (0.81)	8.1–30.0	219.6 (11.40)
unburned, no toads	2004	6	14.7 (0.13)	18.8 (0.62)	7.4–26.4	280.4 (19.92)
burned, no toads	2004	3	13.9 (0.10)	18.0 (0.52)	7.7–23.4	246.5 (30.83)
burned, with toads	2004	4	13.8 (0.12)	19.0 (0.65)	6.3–25.4	258.7 (20.57)

maximum temperatures than neighboring burned wetlands (Table 2); however, the differences were small and were not supported when accounting for geography and wetland characteristics. No model for either daily mean or maximum temperatures was clearly the best for a given dataset, and there was little difference in the amount of variation any model explained. For each dataset, however, the model that described only the geographic location of wetlands received the most support (Table 3). The wetland characteristics model received moderate support in the analysis of daily maximum temperature because deeper wetlands tended to have lower maximum temperatures ($b_{[depth]}$ = -0.13, SE = 0.06).

We found no evidence that the fire increased wetland temperatures. We did not reanalyze the data with the two groups of burned wetlands combined because it was evident that unburned wetlands had higher daily mean and maximum temperatures and accumulated more degree·days during both years (Table 2). Temperatures varied widely within and among days, with daily amplitudes up to 20° C (Fig. 3). Temperature of unburned wetlands exceeded that of burned wetlands by up to 3-4° C on the warmest days, especially in 2003, which was sunnier than 2004. Unburned wetlands generally also had lower minima (Fig. 3), although the lowest temperatures during both years were in burned wetlands colonized by *B. boreas* (Table 2). The difference in the temperature profiles of burned and unburned wetlands increased with time in 2003 (linear regression: $b_{[date]}$ = -0.09, SE = 0.03) but not in 2004 ($b_{[date]}$ = 0.01, SE = 0.01; Fig. 3). Despite the much warmer temperatures in 2003 than 2004, accumulated degree·days of the 10 wetlands for which we have a complete dataset for both years were strongly correlated (r = 0.93), which indicates the relative differences among wetlands are likely consistent.

Most of the variation in temperature was at the level of individual wetlands. There was little difference in the amount of variation explained by the fitted models. The Wetland Cluster models received the most support, in part because they were the most parsimonious. Wetlands in the only area with a mix of burned and unburned wetlands had the highest average temperature of the three clusters during both years. This cluster had two of the three warmest wetlands in 2003, three of the

TABLE 3. Models used to evaluate the selection of burned wetlands by the Boreal Toad (*Bufo boreas*) and the effect of wildfire on wetland temperature in Glacier National Park, Montana, USA. Models are ranked according to differences in AIC_c and model weights (w_i). Wetland Cluster refers to the 3 geographic groups of wetlands (see Figure 1), Treatment Group describes the 3 types of wetlands monitored (unburned without toads, burned without toads, and burned with toads), and Wetland Characteristics includes the mean southern horizon, maximum depth, and area of each wetland.

Model	-2log(L)	Δ AIC_c	w_i
Daily Mean Temperature			
Wetland Cluster	3190.2	0.0	0.77
Wetland Cluster + Treatment Group	3189.3	3.2	0.16
Wetland Characteristics	3193.3	5.1	0.06
Wetland Cluster + Treatment Group + Wetland Characteristics	3187.9	7.9	0.01
Daily Maximum Temperature			
Wetland Cluster	4461.0	0.0	0.45
Wetland Characteristics	4459.4	0.4	0.37
Wetland Cluster + Treatment Group	4459.6	2.7	0.12
Wetland Cluster + Treatment Group + Wetland Characteristics	4454.5	3.7	0.07

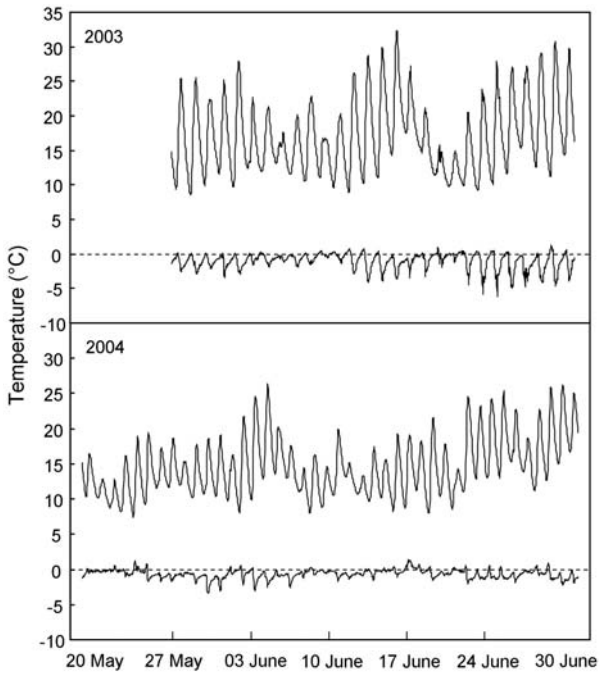

FIGURE. 3. Daily temperature profiles of unburned wetlands (upper line) and the difference between unburned and burned wetlands (lower line) in 2003 and 2004 in Glacier National Park, Montana, USA,.

four warmest wetlands in 2004, and the warmest of all burned wetlands that was monitored. The cluster where all wetlands burned had the coolest temperatures and lowest accumulated degree·days during both years even though they had less landscape shading than wetlands in the area where no wetlands burned.

DISCUSSION

We found little evidence that the fire affected the temperature of burned wetlands colonized by *B. boreas* or of burned wetlands in general. Wetlands colonized by toads differed by ≤ 0.5° C compared to neighboring burned wetlands that were not colonized, and unburned wetlands were more frequently within the preferred temperature range of *B. boreas* tadpoles (28-34° C; Beiswenger 1978). No wetlands approached the lethal limits for *B. boreas* tadpoles of 36-40° C (Karlstrom 1962; Beiswenger 1978), at least at 5-cm depth. There was weak evidence that toads may have selected burned wetlands with higher temperature maxima, similar to the selection by the Natterjack Toad (*B. calamita*) in Britain of shallow wetlands that experienced greater daytime heating (Banks and Beebee 1987). The differences in maximum temperature of wetlands colonized by *B. boreas* were small however, and were less than in several unburned wetlands where we have never detected breeding. In the cluster of wetlands that contained one unburned wetland, one burned wetland that was not colonized by *B. boreas*, and one burned wetland that was colonized by *B. boreas*, the occupied wetland had the lowest daily mean and maximum temperatures. The occupied wetland was < 450 m from these other sites. *Bufo boreas* is a vagile amphibian (Bartelt et al. 2004; Bull 2006) that readily colonizes new ponds or areas (Pearl and Bowerman 2006; Hossack and Corn 2007). Therefore, we doubt that any wetland in our study area was inaccessible, and it seems unlikely that water temperature was the proximate mechanism for the colonization of specific wetlands.

Responses of temperature to landscape disturbance will depend upon the physical setting, wetland characteristics, and nature of disturbance. Peak temperatures in open canopied ponds can be ≥ 15° C higher than in neighboring undisturbed wetlands (Skelly and Freidenburg 2000). Small wetlands where the deciduous canopy has been opened are commonly 2-5° C warmer than closed canopy ponds (Werner and Glennemeier 1999; Skelly and Freidenburg 2000). Across a range of wetland sizes and characteristics, however, gradients in water temperature are often more subtle (Batzer et al. 2000) or are not detected (Battle and Golladay 2003). We suspect we did not find an effect of wildfire on temperature in part because all of the wetlands we monitored had open canopies. The fire likely resulted in only small increases in incident solar radiation on the north shore, where we measured water temperature. More notable differences in temperature would likely occur where small wetlands were more heavily shaded by surrounding forest.

The geographic location of our study wetlands had a greater influence on water temperature than burn status. Small differences in geography, topography, and forest structure can significantly affect microclimate and may have resulted in differences in energy flux or wind patterns among the clusters of wetlands (Chen et al. 1999). There was more topographic variation in the area where we monitored only burned wetlands. The topography did not result in greater wetland shading but may have resulted in greater winds that can cool water bodies. Wetlands with the warmest temperatures were in flatter topography; even there however, unburned wetlands were warmer than burned wetlands.

Maximum depth was the only wetland characteristic associated with temperature. We expected the mean angle of the southern horizon, an index of potential landscape shading, to be correlated with temperature because of the documented relationship between wetland shading and temperature. The gradient in landscape shading around our wetlands may have been insufficient to affect the thermal characteristics of wetlands we studied. Across a larger range of water bodies in Glacier NP, landscape shading reduced incident radiation on the summer solstice by an average of 16% (Diamond et al. 2005). We suspect that land management activities such

as logging could have a larger effect on temperature of small wetlands, because more of the canopy may be removed than by fire. Surprisingly, however, there are few studies on which to base this comparison. The effects of land management and disturbance on temperature regimes of small wetlands are unknown for most ecosystems (Batzer et al. 2000; Palik et al. 2001).

Our conclusions are tempered because our study design was partially confounded and we could not completely control for geography while assessing the effect of the fire. The distribution of wetlands colonized by *B. boreas*, combined with a 1999 fire that bordered the northern portion of our study area, precluded a spatially balanced experimental design. We also assume that the results during the second and third years after the fire are similar to what we would have seen the year after the fire. The strong concordance in accumulated degree·days in the same wetlands in 2003 and 2004 suggests that this assumption is valid. It is possible that the blackened substrate in recently burned wetlands provided an initial temperature boost during the spring after the fire. If that was the case, then the effect of fire on water temperature was brief.

Our results do not offer a likely explanation into why *B. boreas* colonized several wetlands after they burned. Toads may have been responding primarily to changes in the terrestrial environment. Observations of *B. boreas* in Glacier NP equipped with transmitters revealed a preference for summer activity in severely burned habitats (Guscio et al., in press), and physical models that simulated their operative body temperature indicated that recent fires provide better thermal environments (Blake Hossack et al., unpubl. data). The increased breeding activity in burned wetlands likely has more than one easily identified cause. Our results also do not show that the Moose Fire resulted in warmer wetland temperatures. Instead, heterogeneity in wetlands, the surrounding landscape, and weather between years had a larger effect on water temperature than burn status.

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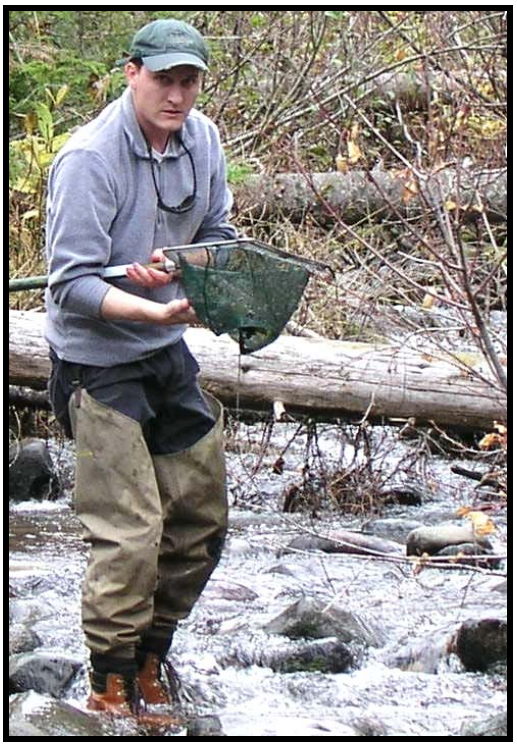

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