A R T I C L E

Wildfire influences individual growth and breeding dispersal, but not survival and recruitment in a montane amphibian

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Abstract

Global wildfire regimes are changing rapidly, with widespread increases in the size, frequency, duration, and severity of wildfires. Whereas the effects of wildfire on ecological state variables such as occupancy, abundance, and species diversity are relatively well documented, changes in population vital rates (e.g., survival, recruitment) and individual responses (e.g., growth, movement) to wildfire are more limited because of the detailed information needed on the same individuals both pre- and post-fire. We capitalized on the 2018 Roosevelt wildfire, which occurred during our 6-year (2015–2020) capture–mark–recapture study of boreal toads (*Anaxyrus boreas boreas*; $n = 1415$) in the Bridger-Teton National Forest, USA, to evaluate the responses of population vital rates and individual metrics to wildfire. We employed robust design capture–recapture models to compare the growth, dispersal, survival, and recruitment of adult boreal toads pre- and post-fire at burned versus unburned sites. At burned locations, growth increased 2 years post-fire compared with the year directly following wildfire and was higher 2 years post-fire than any other interval during our study period. Boreal toads dispersed to alternative breeding patches more at burned sites than unburned sites and dispersal increased 2 years post-fire compared with the year directly following wildfire. Annual survival and recruitment neither differed between pre- and post-fire years nor among pre-fire years, the year following wildfire, and 2 years post-fire. We demonstrate that, in certain contexts, dispersal can play a major role in changes to state variables (e.g., abundance) after wildfire, as opposed to other vital rates such as survival and recruitment. Our study represents an important step toward understanding the biological processes that underlie observed patterns in state variables following wildfire, which ultimately will be critical for the effective management of species in landscapes experiencing shifts in fire activity.

INTRODUCTION

Environmental disturbances play a central role in structuring ecological communities (Connell, 1978; Sousa, 1984). Human activity is causing rapid changes to global disturbance regimes, and the current knowledge of species responses to disturbance events may not accurately reflect how these effects manifest under future conditions (Johnstone et al., 2016; Turner, 2010). For instance, wildfire can be an important natural disturbance in many systems that promote biodiversity, landscape heterogeneity, and ecosystem services (Driscoll et al., 2010; van Wilgen et al., 1996). However, the size and frequency of wildfires have increased rapidly in recent decades (Dennison et al., 2014; Littell et al., 2009; Westerling, 2016), exceeding the limits of historical fire regimes (Kasischke & Turetsky, 2006; Kelly et al., 2013). Anthropogenic influences, such as human-induced climate change, moreover, are expected to continue to increase the number of large wildfires and the duration of fire season across the western United States and other temperate forest biomes (Abatzoglou & Williams, 2016; Krawchuk et al., 2009; Liu et al., 2010; Sommerfeld et al., 2018). Careful study of how organisms respond to wildfire will therefore be critical for the effective management of species in landscapes experiencing shifts in fire activity.

Wildlife studies would ideally assess the effects of wildfire using a before–after/control–impact (BACI; Stewart-Oaten et al., 1986; Underwood, 1992) approach, whereby pre- and post-fire metrics are compared at burned (impact) versus unburned (control) sites, or across sites with varying degrees of burn severity (e.g., Smucker et al., 2005; Vieira et al., 2004). Pre- and post-fire comparisons using the BACI design are relatively common for ecological state variables, such as changes in abundance/density (Converse et al., 2006; Duarte et al., 2017; Sestrich et al., 2011), occupancy/distribution (Dunham et al., 2007; Hossack & Corn, 2007; Jones et al., 2016; Sestrich et al., 2011), and species diversity/community composition (Brehme et al., 2011; Brown et al., 2015; DiCarlo et al., 2019; Pastro et al., 2011). By contrast, changes in population vital rates (e.g., survival, recruitment) and individual responses (e.g., growth, dispersal) to wildfire are seldom studied. The biological processes underlying observed patterns in state variables are therefore often unknown.

Documenting vital rates and individual responses to disturbances such as wildfire is rare because comparisons necessitate detailed information on known individuals both pre- and post-fire. Because of the logistical difficulties and unpredictability of wildfires, most studies are opportunistic and capitalize on being in the "right place at the right time" (Gade et al., 2019; Smucker et al., 2005). To capture vital rates and individual responses, wildfires must therefore occur by chance during the middle of studies that collect data on the same organisms through time, such as intensive capture–mark–recapture efforts (e.g., Rockweit et al., 2017; Webb & Shine, 2008).

We capitalized on the 2018 Roosevelt wildfire, which occurred during our 6-year (2015–2020) capture–mark–recapture study of boreal toads (*Anaxyrus boreas boreas*) in the Bridger-Teton National Forest in western Wyoming, United States. Whereas the fire burned some of our study sites with high severity, other sites remained unburned such that we were able to use a BACI design to examine the responses of population vital rates and individual metrics to wildfire. Such work is timely, as amphibians are currently the most threatened vertebrate class globally (Catenazzi, 2015) and many species evolved in landscapes projected to experience shifts in wildfire regimes (Hossack & Pilliod, 2011). For instance, although low-severity fires maintain diverse amphibian communities in fire-adapted ecosystems (Means, 2006; Russell et al., 1999), the implications of high-severity fires are poorly understood (Bury, 2004; Pilliod et al., 2003). Given that most amphibians are moisture-sensitive, many species may be particularly vulnerable to the dry conditions resulting from high-severity fires (Hossack, Lowe, & Corn, 2013). Lastly, whereas responses in state variables such as occupancy, abundance, and species diversity are well documented in amphibians (Brown et al., 2014; Chelgren et al., 2011; Hossack & Honeycutt, 2017; Rochester et al., 2010), changes in vital rates and individual metrics in response to wildfire remain poorly documented.

We investigated population vital rates and individual responses of adult boreal toads to a large wildfire. Specifically, we compared pre- and post-fire changes in body mass (hereafter, growth) and rates of dispersal, survival, and recruitment at sites that burned with high severity and nearby sites that were unburned. We did not expect direct mortality from fire, as amphibians can often retreat underground or seek aquatic refuges (Friend, 1993; Pilliod et al., 2003). Rather, we expected the effects of wildfire to manifest indirectly via changes to habitat conditions and quality (Hossack & Pilliod, 2011). For instance, post-fire

landslides and other sedimentation events can reduce breeding habitat in highly aquatic species (Backlin et al., 2004; Parker, 2006), and changes to canopy/vegetation cover and microclimate can negatively affect taxa that are sensitive to disturbances such as plethodontid salamanders (Gade et al., 2019; Rochester et al., 2010).

Boreal toads, by contrast, often respond positively to disturbance (Crisafulli et al., 2005; Pearl & Bowerman, 2006), prefer open habitats (Bull, 2006), and perform optimally at relatively warm temperatures (e.g., maximal growth and energy ingestion at ∼27°C; Lillywhite et al., 1973). Indeed, in western Montana, boreal toad occupancy increased shortly after large wildfires (Hossack & Corn, 2007; Hossack, Lowe, & Corn, 2013), and individuals preferred severely burned areas to moderately burned forests (Guscio et al., 2008). Boreal toad populations also display greater genetic connectivity near the areas affected by wildfire than the populations farther from burned areas (Murphy et al., 2010), suggesting wildfire may increase landscape connectivity and facilitate dispersal between subpopulations. Furthermore, boreal toads are challenged with *Batrachochytrium dendrobatidis* (*Bd*) in and near our study area (Barrile, Chalfoun, & Walters, 2021a; Pilliod et al., 2010), a fungal pathogen implicated in global amphibian declines (Scheele et al., 2019). Following wildfire, boreal toads found in warmer, recently burned areas (Hossack et al., 2009) were significantly less likely to be infected with *Bd* than toads in cooler, unburned areas (Hossack, Lowe, Ware, & Corn, 2013). Warmer, drier microclimates after wildfire may decrease the prevalence of the temperature- and moisture-sensitive fungus in the environment and/or provide opportunity for toads to clear infection via behavioral fever (Barrile, Chalfoun, & Walters, 2021b). For all the reasons stated above, we predicted that rates of growth, dispersal, survival, and recruitment in boreal toads would increase following wildfire in our study area.

METHODS

Study area

We studied boreal toads at four stream segments in the Bridger-Teton National Forest, two in the northern Wyoming Range (∼1.1 km reach at Buck Creek and ∼0.4 km reach at Chall Creek; 42°59′ N, 110°24′ W) and two in the northern Wind River Range (∼0.2 km reach at Lower Gypsum Creek and ∼0.3 km reach at Upper Gypsum Creek; 43°16′ N, 109°57′ W) (Figure 1). Sites in the Wind River Range were at slightly higher elevations (Lower Gypsum Creek = 2509 m; Upper Gypsum Creek = 2671 m) than Wyoming Range sites (Buck Creek = 2487 m; Chall Creek = 2441 m). The landscape

was similar between the two ranges: both contained mixed-conifer and aspen (*Populus tremuloides*) forests, sagebrush (*Artemisia tridentata*) and subalpine meadows, and riparian areas with willow (*Salix* spp.) complexes. Beaver ponds were common in montane stream channels and provided breeding habitat for boreal toads and other amphibians.

Capture–mark–recapture surveys

Boreal toads congregate at breeding ponds shortly after snowmelt in the spring (∼mid-May) and continue spawning through mid to late June. We conducted standardized visual encounter surveys to hand-capture toads at breeding sites within our four stream segments at night during the breeding season (May–June) in 2015–2020. Captured individuals were sexed by the presence of darkened nuptial pads on the thumbs of males, weighed using a precision spring scale (Pesola 20100 micro-line balance; Pesola Präzisionswaagen AG, Schindellegi, Switzerland), and marked using passive integrated transponder tags (8 × 1.2 mm FDX tag; Oregon RFID, Portland, OR, USA) for individual identification. We tagged adult males only, assuming individuals ≤15 g were juveniles. We excluded female toads because they do not remain at breeding sites post-amplexus and often skip breeding years (Muths et al., 2010), both of which could bias demographic estimates.

We sampled all active or abandoned beaver ponds along each stream segment with signs of boreal toad breeding (e.g., egg clutches, amplectant pairs), which included four clustered ponds (i.e., four ponds in close proximity) at both Buck and Chall creeks, and two and three clustered ponds at Lower Gypsum and Upper Gypsum Creeks, respectively (Figure 1c,d). We refer to each cluster of ponds within our core study reaches as the "primary site" (yellow circles in Figure 1c,d) because we also surveyed at breeding ponds outside of our core study area (see the *Surveys at alternative sites* section below) and refer to those ponds as "alternative sites" (black circles in Figure 1c,d). We surveyed all ponds within primary sites at a given stream during each nighttime survey and conducted multiple recapture surveys within each breeding season at all streams (mean = 5 surveys per stream, per year; range = 3–9).

Wildfire

On 15 September 2018, the Roosevelt wildfire ignited and burned 24,893 ha of land, the majority of which was in the Bridger-Teton National Forest. Whereas our study
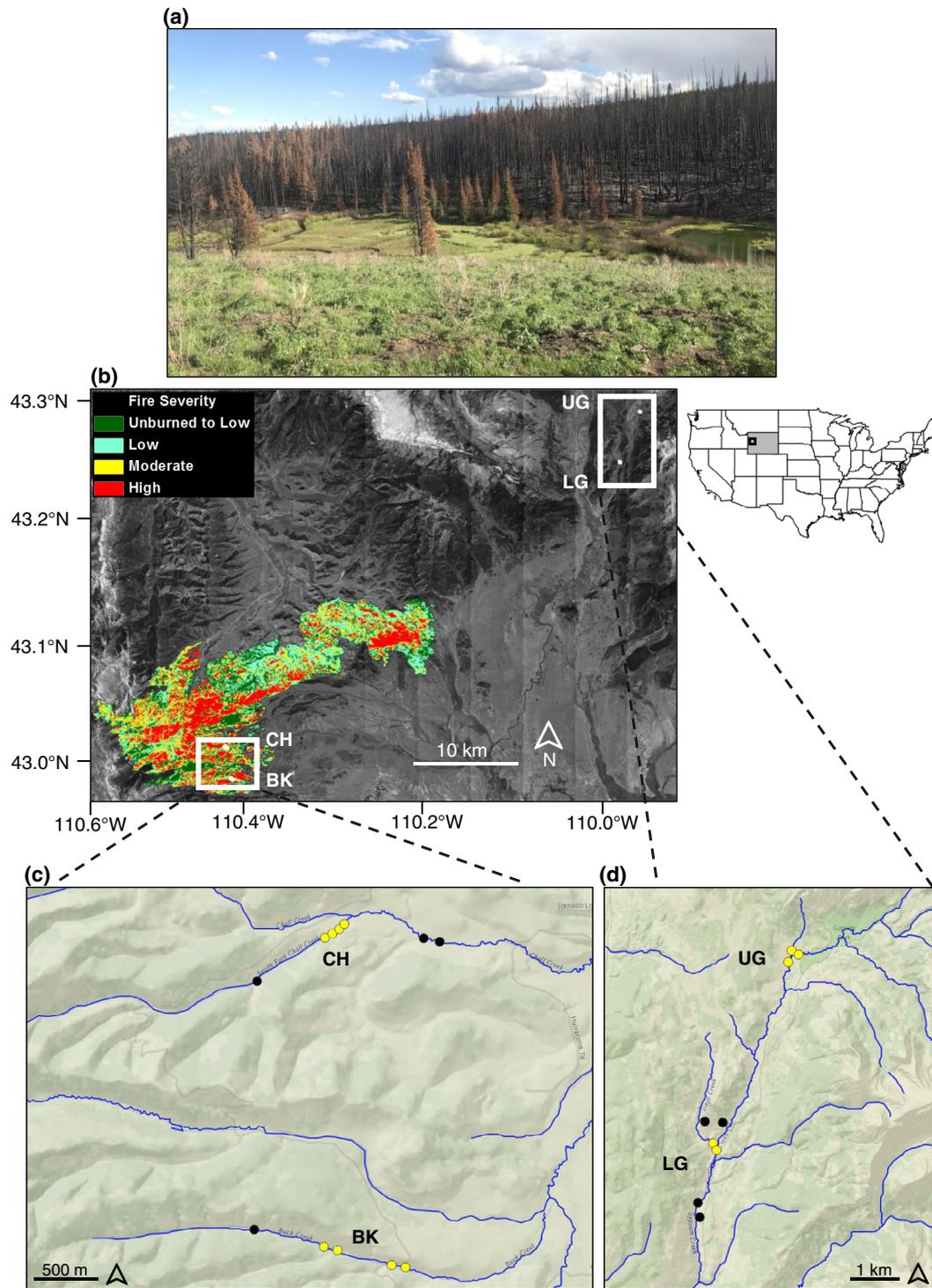
FIGURE 1 (a) Photograph of Buck Creek from August 2019 illustrating the influence of the Roosevelt wildfire on the overall landscape, including the fire's proximity to boreal toad breeding sites (e.g., pond located at center-right in the image). (b) Map displaying the location of our four study streams: Buck (BK) and Chall (CH) creeks in the Wyoming Range and Lower Gypsum (LG) and Upper Gypsum (UG) Creeks in the Wind River Range. Also pictured in (b) is the extent of the Roosevelt wildfire, including burn severity categories developed by the Monitoring Trends in Burn Severity project. (c, d) Breeding ponds included in our capture–recapture surveys at (c) Buck and Chall creeks and (d) Lower Gypsum and Upper Gypsum Creeks. Yellow circles represent primary sites within our core study area; black circles represent alternative ponds outside our core study area.

sites at Buck and Chall creeks burned (Figure 1a,b), sites along Lower and Upper Gypsum Creeks were unburned (Figure 1b). Furthermore, because all of our sites along Buck and Chall creeks were in or within 100 m of high-severity burns, as classified by the Monitoring Trends in Burn Severity project (Eidenshink et al., 2007), we did not differentiate among burn severities, but rather characterized sites at Buck and Chall creeks as "burned" and sites at Lower and Upper Gypsum Creeks as "unburned."

Surveys at alternative sites

During the early spring of 2017, high snowmelt runoff destroyed beaver dams within our core study reaches, which degraded the quality of breeding habitat at many of our primary sites (Barrile, Walters, et al., 2021). Because boreal toad dispersal can increase following wildfire (Hossack & Corn, 2007; Hossack, Lowe, & Corn, 2013), we predicted that fire-induced habitat changes (e.g., increased landscape permeability; Rochester et al., 2010) and/or enhanced growth would provide individuals the opportunity to depart low-quality breeding ponds (i.e., primary sites) and colonize alternative breeding ponds (hereafter, alternative sites) outside of our core study area (e.g., areas with recent beaver activity). The process of dispersal typically is described as the unidirectional movement of an individual from birth to its first breeding patch (i.e., natal dispersal), or among successive breeding patches (i.e., breeding dispersal; Clobert et al., 2009; Matthysen, 2012). Importantly, breeding dispersal often consists of three main components within amphibian metapopulations (Perret et al., 2003): (1) transience (i.e., nomadic individuals with a fugitive presence in any given breeding patch); (2) local dispersal of resident individuals (non-transients) to breeding patches within the studied area; and (3) permanent emigration, or dispersal of non-transient individuals to breeding patches outside of the studied area. We focused on the second component (i.e., local dispersal) of breeding dispersal, as we aimed to characterize how wildfire influenced toad movement from our core study area to alternative breeding patches. We therefore defined breeding dispersal as the movement of an adult toad between primary and alternative sites between years. Although we focused specifically on local dispersal, we accounted for transience in our demographic models and acknowledged that permanent emigration was confounded with mortality in our study (see the *Survival* section below for details).

To capture movements between primary and alternative sites in our marked population, we surveyed all beaver ponds within 1.5 km of our core study area during 2019 and 2020. We selected a 1.5-km search radius based on a 2015 pilot study in which adult toads were radio-tracked and moved a maximum distance of 1.5 km from the breeding ponds at which transmitters were attached (G. M. Barrile, unpublished data). Surveys at burned locations included three alternative sites at Chall Creek (950, 990, and 1112 m from the study area) and one at Buck Creek (410 m from the study area), and surveys at unburned locations included four alternative sites at Lower Gypsum Creek (290, 370, 1070, and 1450 m from the study area) (Figure 1c,d). No alternative beaver ponds occurred within 1.5 km of our study area at Upper Gypsum Creek; thus, we excluded individuals at Upper Gypsum Creek from dispersal models (see the *Breeding dispersal* section below). We conducted 2–3 recapture surveys of marked individuals at each alternative breeding pond at both burned and unburned sites during 2019 and 2020 (i.e., 2–3 surveys per site, per year). We did not tag new individuals during surveys at alternative sites, rather we simply captured individuals and, if marked previously, recorded each unique tag number.

Growth

To obtain a metric of individual growth, we calculated the percent change in body mass between consecutive years in each toad for which we acquired the requisite information (i.e., toads captured in consecutive years at some interval during the study period). We then compared the percent change in body mass over time in all toads that were captured in any two consecutive years. Given that boreal toads are presumed to exhibit indeterminate growth (Duellman & Trueb, 1985), we were confident that percent change in body mass served as an appropriate proxy for individual growth. Toad body mass depends heavily on water absorption and bladder storage (Jørgensen, 1994), such that urination after handling toads captured in ponds could have altered individual body mass. We presumed that biased measurements due to urination were not an issue in our study, as we placed toads in Ziploc bags immediately after capture, where they remained throughout weighing (i.e., water loss from urination was captured within the bag and therefore included in the measurement of body mass). To test this assumption and ensure that measurements were consistent and repeatable within a year, we calculated the difference in body mass values obtained from each individual that we captured multiple times within any given breeding season (Appendix S1: Figure S1).

Survival

Our mark–recapture surveys produced capture data at two distinct temporal periods (within and among breeding

seasons), thereby comprising a robust design. Robust designs consider multi-season studies of open populations as series of short-term studies of closed populations, allowing for demographic estimates that are robust to sources of variation in capture probabilities (Kendall et al., 1997). We used robust design models with a Huggins estimator to analyze our mark–recapture dataset. The Huggins estimator is an extension of the robust design model that conditions abundance out of the likelihood and permits the modeling of capture probability as a function of individual covariates (Huggins, 1989). Our first set of robust design models estimated apparent survival (φ; "apparent" because mortality cannot be separated from permanent emigration) and temporary emigration (the probability a toad was absent from a breeding pond in a given year) between primary periods (i.e., breeding seasons) and capture probability (p) within primary periods. Estimating temporary emigration involved two gamma parameters, γ_i'' and γ_i'. In this study, γ_i'' denotes the probability that a toad available for capture within our study area at time $i-1$ moved off of the study area temporarily and thus was unavailable for capture at time i (e.g., if a toad skipped a breeding attempt and did not return to the breeding pond at time i; Muths et al., 2006). γ_i' signifies the probability a toad that was not within our study area at time $i-1$ (i.e., unavailable for capture) remained outside of the study area and thus was also unavailable for capture at time i (e.g., if a toad continued to skip breeding attempts in consecutive years). Both parameters assume that the individual is alive, but temporarily unavailable for capture. Importantly, temporary emigration differs from permanent emigration (i.e., when animals leave the sampling area and never return) by assuming that individuals return to the study area during subsequent sampling occasions. Modeling temporary emigration helps account for differences in capture probability between individuals inside and temporarily outside the study area, which results in less-biased capture probabilities and thus less bias in estimates of survival probability (Fujiwara & Caswell, 2002).

Rather than fitting an extremely large model set incorporating all plausible combinations for model parameters, we adopted a step-down approach (Lebreton et al., 1992) to identify supported models and test the influence of wildfire on boreal toad survival. We first fixed survival and temporary emigration parameters at a high dimensionality (φ, γ_i'', and γ_i' varied over time) while identifying the most parsimonious structure for capture probability (Doherty et al., 2012; Lebreton et al., 1992). To avoid confounding parameters, we constrained the last two γ_i'' values and the last two γ_i' values to equal one another such that all survival and temporary emigration parameters were identifiable (Muths et al., 2006). We ran models in which capture probability remained constant or varied by year (i.e., breeding season), capture occasion, stream, and mountain range (Buck + Chall creeks = Wyoming Range; Lower Gypsum + Upper Gypsum Creeks = Wind River Range), including additive and interactive combinations of these variables (14 total structures; Appendix S1: Table S1). Given that toad body condition and size could have influenced detectability, we also included models wherein capture probability varied by toad body mass, using the average mass for individuals captured and weighed on multiple occasions within a given breeding season.

We next identified the most parsimonious structure(s) for temporary emigration. Our model set included no temporary emigration (parameters fixed to zero), time-constant, time-dependent, stream-dependent, and range-dependent (Wyoming vs. Wind River Range) models, including additive and interactive combinations. For each model structure, we distinguished between random and Markovian patterns of temporary emigration (Muths et al., 2006). Under random emigration, the probability of temporary emigration at time i would be the same regardless of whether an individual was present or absent from the study area at $i-1$, such that $\gamma_i'' = \gamma_i'$ in our random models (eight structures; Appendix S1: Table S2). Under Markovian emigration, by contrast, an individual that is absent from the study area at $i-1$ would have a different probability of temporary emigration at time i than an individual that was present in the study area at $i-1$ (Bailey et al., 2004), such that $\gamma_i'' \neq \gamma_i'$ and gamma parameters were estimated separately in our Markovian models (nine structures; Appendix S1: Table S2).

Finally, retaining the most parsimonious structures for capture probability and temporary emigration, we tested whether wildfire influenced boreal toad survival by estimating apparent survival pre- and post-fire at both burned and unburned sites (i.e., sites in the Wyoming Range vs. sites in the Wind River Range). Because animals can display time-lagged responses to wildfire (Hossack, Lowe, & Corn, 2013; Smucker et al., 2005), we created an additional variable to explore potential differences in survival among pre-fire years (2015–2018), 1 year after wildfire (2018–2019), and 2 years post-fire (2019–2020). We also considered time-constant and time-dependent models for survival, including interactions with site location (i.e., between mountain ranges). Given the presence of transient individuals in other amphibian systems (Frétey et al., 2004; Schmidt et al., 2007), including some boreal toad populations (Muths et al., 2018), we expected some degree of transience in our system. We defined transient individuals as newly captured toads that were marked, released, and then

permanently emigrated from our study area, such that those nomadic toads were no longer available for encounter during subsequent surveys (Pradel et al., 1997). Resident (adult males that remained in our study area) survival probability can be negatively biased if transience is not modeled appropriately (e.g., if transience exists in the population, estimated apparent survival will be lower following first capture). We therefore fit each model structure for survival both with and without transience (16 total models). We incorporated transience into survival models following the methods employed by Muths et al. (2018) (see appendix S2 in Muths et al., 2018, for details). We also excluded individuals that dispersed to alternative breeding ponds outside of our core study area from survival models to further avoid biases when estimating the survival of resident individuals.

During each step of the modeling procedure described above (i.e., capture probability, temporary emigration, and apparent survival), we dropped models that did not converge or models with singular parameters. We used Akaike information criterion corrected for small sample size (AIC$_c$) or quasi-AIC$_c$ (QAIC$_c$; depending on whether overdispersion was present) model selection to compare and rank models and to calculate model weights (Burnham et al., 2011). Robust design analyses were conducted using Program MARK (White & Burnham, 1999), with models constructed via the RMark package (version 2.2.7; Laake, 2013) in R version 4.1.1 (R Core Team, 2021). We used our global structures and the median $\hat{c}$ approach to adjust for possible overdispersion in the capture–recapture data (White & Burnham, 1999).

Recruitment

We fit reverse-time capture–recapture models (Pradel, 1996) to evaluate the potential effects of wildfire on boreal toad recruitment. We used the robust design parameterization of the Pradel model with a Huggins estimator (Huggins, 1989), which estimated apparent survival (φ) and recruitment rate (f) between primary periods (i.e., breeding seasons) and capture probability (p) within primary periods. The recruitment rate (f) represents the number of individuals added to the breeding population at time $t + 1$ per animal in the breeding population at time t. Given that we used the same capture–recapture dataset that we used to estimate survival in the previous section, we retained the most parsimonious structures for φ and p from the survival procedure when modeling recruitment. Further, we considered the same model structures as in the survival procedure, and models were parameterized and selected using the same methods as described in the *Survival* section above.

Breeding dispersal

To assess the breeding dispersal of boreal toads in response to wildfire, we fit multi-state robust design capture–recapture models (hereafter, multi-state models) with a Huggins estimator (Huggins, 1989). Our multi-state models estimated apparent survival (φ) and state-transition probabilities (ψ) between primary periods (i.e., breeding seasons) and capture probability (p) within primary periods. "States" in our models refers to individual breeding ponds and transition probabilities represent the probability of moving from one breeding site to another between seasons. Because we were concerned with dispersal outside of our core study area, we only included transitions from "primary sites" to "alternative sites" (and vice versa) and excluded transitions among primary sites (i.e., ponds within our core study area signified state "A" and alternative ponds signified state "B" in which breeding dispersal was defined by transitions between states A and B).

We retained the most parsimonious structures for φ and p from the survival procedure when modeling dispersal. We also included structures wherein capture probability differed between states to account for potential variation in sampling effort between primary and alternative sites. We considered models in which transition probability remained constant or varied by toad body mass (the average for each individual), year (2018–2019 vs. 2019–2020), and mountain range (burned vs. unburned sites), including additive and interactive combinations of these variables (14 structures; Appendix S1: Table S3). We excluded capture histories from Upper Gypsum Creek in multi-state models as no alternative ponds occurred within 1.5 km of our original study area at this location. Further, we fixed the transition probability to zero during 2015–2018 because we did not survey at alternative sites (state B) until 2019. We also did not observe any individuals previously marked at primary sites returning to primary sites after being captured at alternative sites, so we fixed this transition (from state B to state A) to zero to improve parameter estimation and model convergence. Transition probability therefore represents the probability of an individual moving from a primary site to an alternative site between years (from state A to state B). Given that we did not tag unmarked toads encountered at alternative sites, some unaccounted-for individuals may have dispersed from alternative to primary sites between breeding seasons. Those individuals should have been captured and marked during our surveys at primary sites (unless they evaded capture), however, and thus counted as recruits (via immigration) in our reverse-time models (see the *Recruitment* section above). All multi-state models were parameterized and selected using the same methods as described in the *Survival* section above.

RESULTS

Capture–mark–recapture surveys

We captured and tagged 1415 unique individuals during 2015–2020: 352 adult male boreal toads during 30 capture surveys at Buck Creek, 844 toads during 35 surveys at Chall Creek, 141 toads during 24 surveys at Lower Gypsum Creek, and 78 toads during 19 surveys at Upper Gypsum Creek. We surveyed all four streams multiple times in each year (2015–2020), with the exception of Upper Gypsum Creek, which we did not survey in 2020. We captured 53 of our marked individuals at alternative breeding ponds during 2019 and 2020 and therefore excluded capture histories of those individuals from survival analysis.

Growth

The mean difference in body mass measurements from individuals captured multiple times within a breeding season was 2.06 g, with almost half of all observations (819 of 1757) between 0 and 1 g (Appendix S1: Figure S1). For context, the mean body mass of tagged individuals was 28 g. We therefore maintain that body mass represents a repeatable measurement within a year and proceeded with percent change in body mass as a metric for individual growth. Body mass did not influence our detectability of toads (Appendix S1: Table S1), moreover, which further increased our confidence that body mass measurements were not biased (e.g., larger individuals were not more likely to be captured).

The annual percent change in body mass of adult male boreal toads ($n = 422$) varied over time during our study period at burned and unburned sites (Figure 2). Notably, growth was elevated 2 years post-fire (2019–2020) compared with the year directly following wildfire (2018–2019) at burned sites, whereas growth did not appear to differ between the same temporal intervals at unburned sites. Furthermore, the percent change in body mass at burned sites was higher between 2019 and 2020 (2 years post-fire) than any other interval during our study period (Figure 2).

Survival

We found evidence of overdispersion ($\hat{c} = 2.13$) in the robust design model (with temporary emigration) containing the most general structures for all parameters. We therefore used QAIC$_c$ to compare models and calculate model weights, and report adjusted standard errors for all parameter estimates using $\hat{c}$ from the general
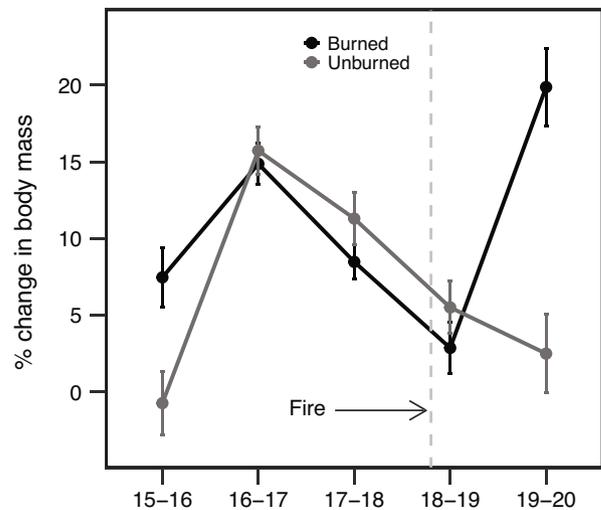

FIGURE 2 The annual percent change in body mass (i.e., growth) of adult male boreal toads varied over time at burned and unburned sites in the Bridger-Teton National Forest, USA, during 2015–2020. Growth was elevated at burned sites 2 years post-fire (2019–2020) compared with the year directly following wildfire (2018–2019), whereas growth at unburned sites did not appear to differ between these same intervals. Furthermore, growth 2 years post-fire at burned sites was higher than any other interval during our study period. Mean values (dots) and standard errors (error bars) represent the growth of all individuals that were captured in any two consecutive years ($n = 422$) during 2015–2020. The vertical dotted line and pointed arrow indicate the timing of the Roosevelt wildfire (September 2018).

model. The best-supported structure for capture probability (model weight, $w = 1.0$) indicated variation among streams and secondary capture occasions (i.e., surveys within the breeding season; Appendix S1: Table S1). Capture probability ranged from 0.07 to 0.51 (mean = 0.24) and was generally higher at sites in the Wind River Range and during surveys earlier in the breeding season. The most parsimonious structures for γ_i'' and γ_i' (model weight, $w = 0.98$) indicated that boreal toads displayed a Markovian pattern of temporary emigration whereby $\gamma_i'' \neq \gamma_i'$ and both parameters varied by mountain range (Appendix S1: Table S2). At sites in the Wind River Range, whereas the probability that an individual is absent at time i if present at time $i-1$ (i.e., γ_i'') was 0.17 (95% CI = 0.09, 0.29), the probability that an individual is absent from the study area at time i if absent at $i-1$ (i.e., γ_i') was 0.28 (95% CI = 0.02, 0.89). Temporary emigration was considerably higher at sites in the Wyoming Range, as γ_i'' was 0.42 (95% CI = 0.35, 0.49) and γ_i' was 0.97 (95% CI = 0.91, 0.99).

The best-supported model for survival probability (model weight, $w = 0.34$) indicated variation between mountain ranges (Table 1), with higher mean survival at sites in the Wind River Range (0.76; 95% CI = 0.68, 0.83)

TABLE 1 Model selection results including model structure, quasi-Akaike information criterion corrected for small sample size (QAIC$_c$), ΔQAIC$_c$, model weights (Wt), number of parameters (K), and Qdeviance (-2 log-likelihood/$\hat{c}$) from robust design capture–recapture models used to estimate the apparent survival probability (φ) of adult boreal toads ($n = 1362$) at four stream segments in the Bridger-Teton National Forest, USA, during 2015–2020.

Model	QAIC$_c$	ΔQAIC$_c$	Model Wt	K	Qdeviance
φ(range + 2a)	7863.53	0.00	0.34	35	8843.68
φ(tsf + range + 2a)	7865.20	1.67	0.15	37	8841.26
φ(prepost + range + 2a)	7865.54	2.02	0.12	36	8843.65
φ(range)	7865.92	2.39	0.10	34	8848.11
φ(year + 2a)	7867.08	3.55	0.06	38	8841.10
φ(prepost × range + 2a)	7867.20	3.68	0.05	37	8843.27
φ(prepost + range)	7867.50	3.97	0.05	35	8847.65
φ(tsf + range)	7867.70	4.17	0.04	36	8845.81
φ(year + range + 2a)	7868.98	5.46	0.02	39	8840.95
φ(tsf × range + 2a)	7869.03	5.51	0.02	39	8841.00
φ(year)	7869.44	5.91	0.02	37	8845.50
φ(prepost × range)	7869.54	6.01	0.02	36	8847.64
φ(year + range)	7871.46	7.94	0.01	38	8845.48
φ(year × range + 2a)	7876.64	13.11	0	43	8840.41

Note: We investigated apparent survival (φ) structures that varied spatially between mountain ranges (range) and temporally among all years (year), between pre- and post-fire years (prepost), and among pre-fire years (2015–2018), 1 year after wildfire (2018–2019), and 2 years post-fire (2019–2020) (i.e., time since fire [tsf]). We considered all additive (+) and interactive (×) combinations of spatial and temporal variables and fit each model structure both without and with transience (denoted 2a). Models that did not converge or contained singular parameters were omitted from model selection and do not appear in the table. All models included the best-supported structures for temporary emigration, γ_i''(range) and γ_i'(range) (Appendix S1: Table S2), and capture probability, p(survey × site) (Appendix S1: Table S1), where survey indicates capture occasions within a year and site represents each of our four study streams.

compared with sites in the Wyoming Range (0.69; 95% CI = 0.34, 0.90). The second and third best-supported models (model weight, w = 0.15 and 0.12, respectively) included the potential effects of wildfire on boreal toad survival and indicated that annual survival probability did not differ between pre- and post-fire years (Figure 3a) nor among pre-fire years, the year following wildfire, and 2 years post-fire (Figure 3b). Four of the top five models for survival, including the best-supported model, also included the transience parameter (denoted as 2a in Table 1), suggesting that accounting for transient adults was important for modeling the survival of resident individuals. Transience varied only slightly between mountain ranges: the proportion of transients was 0.15 at sites in the Wind River Range and 0.19 at sites in the Wyoming Range. All reported survival estimates (e.g., Figure 3) reflect those of resident individuals only.

Recruitment

We found evidence of overdispersion ($\hat{c}$ = 2.39) in the reverse-time model containing the most general structures for all parameters. We therefore used QAIC$_c$ to

compare models and calculate model weights, and adjusted standard errors for all parameter estimates using $\hat{c}$ from the general model. The best-supported model for recruitment rate (model weight, w = 0.98; Table 2) indicated variation over time (i.e., by year) and between mountain ranges (Figure 4). No other reverse-time models were supported by our data (e.g., little to no model weight; Table 2), including those with potential effects of wildfire, suggesting that wildfire did not influence boreal toad recruitment at primary sites during our study period.

Breeding dispersal

We found evidence of overdispersion ($\hat{c}$ = 2.32) in the multi-state model containing the most general structures for all parameters. We therefore used QAIC$_c$ to compare models and calculate model weights, and we adjusted standard errors for all parameter estimates using $\hat{c}$ from the general model. Capture probability did not differ between states (primary vs. alternative sites), as none of the multi-state models with this structure carried any model weight (Appendix S1: Table S3), and mean capture
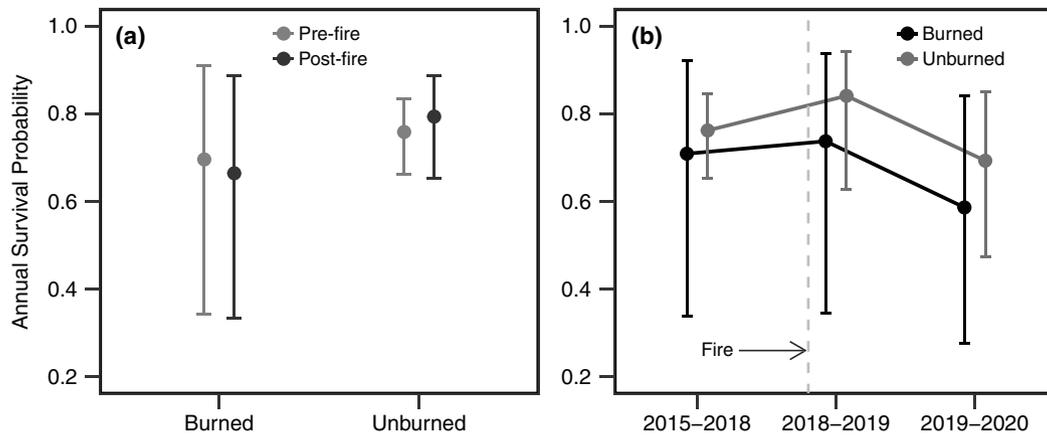
FIGURE 3 Apparent survival of adult male boreal toads ($n = 1362$) did not differ (a) between pre- and post-fire years or (b) among pre-fire years (2015–2018), the year following wildfire (2018–2019), and 2 years post-fire (2019–2020) at both burned and unburned sites in the Bridger-Teton National Forest, USA. Mean predicted survival estimates (dots) and 95% CIs (error bars) of resident individuals were derived from (a) the third best-supported model for survival (model weight, $w = 0.12$) and (b) the second best-supported model for survival (model weight, $w = 0.15$; Table 1). The vertical dotted line and pointed arrow in (b) indicate the timing of the Roosevelt wildfire (September 2018).

TABLE 2 Model selection results including model structure, quasi-Akaike information criterion corrected for small sample size (QAIC$_c$), ΔQAIC$_c$, model weights (Wt), number of parameters (K), and Qdeviance (-2 log-likelihood/$\hat{c}$) from reverse-time capture–recapture models used to estimate the recruitment rate (f) of adult boreal toads ($n = 1415$) at four stream segments in the Bridger-Teton National Forest, USA, during 2015–2020.

Model	QAIC$_c$	ΔQAIC$_c$	Model Wt	K	Qdeviance
f(year $\times$ range)	9052.16	0.00	0.98	41	3212.02
f(year + range)	9059.94	7.78	0.02	37	3227.99
f(year)	9071.88	19.72	0.00	36	3241.98
f(tsf $\times$ range)	9097.59	45.43	0.00	37	3265.64
f(prepost + range)	9099.83	47.67	0.00	34	3274.01
f(prepost $\times$ range)	9100.24	48.08	0.00	35	3272.39
f(tsf + range)	9100.92	48.77	0.00	35	3273.07
f(range)	9111.55	59.39	0.00	33	3287.78

Note: We investigated structures for recruitment rate (f) that varied spatially between mountain ranges (range) and temporally among all years (year), between pre- and post-fire years (prepost), and among pre-fire years (2015–2018), 1 year after wildfire (2018–2019), and 2 years post-fire (2019–2020) (i.e., time since fire; tsf). We considered all additive (+) and interactive ($\times$) combinations of spatial and temporal variables. Models that did not converge or contained singular parameters were omitted from model selection and do not appear in the table. All models included the best-supported structures from our modeling procedure for annual survival, including survival probability, φ(range + 2a), where 2a denotes transience, and capture probability, p(survey $\times$ site), where survey indicates capture occasions within a year and site represents each of our four study streams.

probability was only slightly higher at primary (0.20; 95% CI = 0.19, 0.21) compared with alternative sites (0.18; 95% CI = 0.13, 0.26). The best-supported model for dispersal (model weight, $w = 0.48$; Appendix S1: Table S3) indicated variation over time (2018–2019 vs. 2019–2020) and between mountain ranges. Boreal toads dispersed from primary sites to alternative sites more at burned sites than unburned sites on average (Figure 5). Furthermore, mean dispersal probability increased 2 years post-fire (2019–2020) compared with the year directly following wildfire (2018–2019) at burned

sites, whereas mean dispersal was similar over this same interval at unburned sites (Figure 5).

DISCUSSION

Understanding how organisms and populations respond to wildfire is critical for the effective conservation and management of species in landscapes experiencing shifts in fire activity. We compared the growth, dispersal,
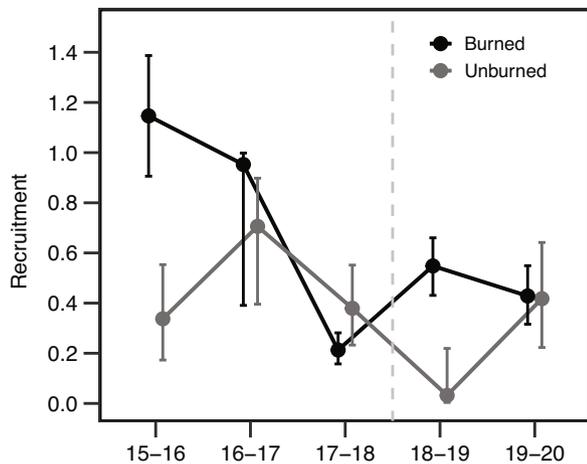
FIGURE 4 The rate of recruitment into the adult male breeding population of boreal toads ($n = 1415$) varied over time and between mountain ranges (i.e., burned vs. unburned sites) in the Bridger-Teton National Forest, USA, during 2015–2020. Mean predicted estimates (dots) and 95% CIs (error bars) were derived from the best-supported reverse-time capture–recapture model for recruitment (model weight, $w = 0.98$; Table 2). The vertical dotted line indicates the timing of the Roosevelt wildfire (September 2018).
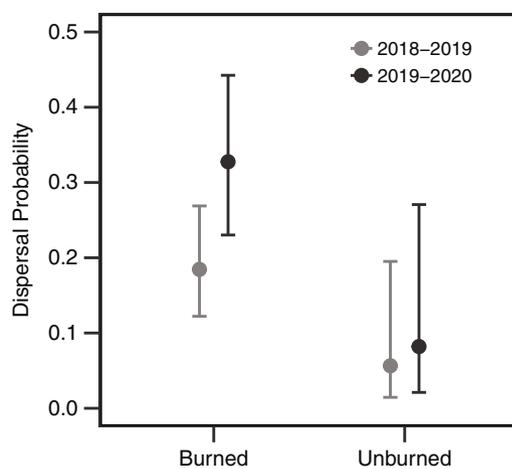
FIGURE 5 The mean probability that adult male boreal toads ($n = 1337$) dispersed to alternative ponds outside of our core study area increased 2 years post-fire (2019–2020) compared with the year directly following wildfire (2018–2019) at burned and unburned sites in the Bridger-Teton National Forest, USA, with a greater increase at burned sites than unburned sites. Mean predicted estimates (dots) and 95% CIs (error bars) were derived from the best-supported multi-state capture–recapture model for dispersal (model weight, $w = 0.48$; Appendix S1: Table S3).

survival, and recruitment of adult boreal toads pre- and post-fire at burned versus unburned sites. At burned locations, growth increased 2 years post-fire compared with the year directly following wildfire and was higher 2 years post-fire than any other interval during our study period. Breeding dispersal also increased

2 years post-fire at burned sites, as some boreal toads departed from our core study area and colonized alternative breeding habitat. Wildfire did not influence survival and recruitment, by contrast, as capture–recapture models that included the effect of wildfire were either not supported by our data or indicated no differences between pre- and post-fire years. Overall, our results suggest that wildfire did not influence the population's vital rates of survival and recruitment in our system, but did influence individual metrics such as growth and movement behavior.

The Roosevelt wildfire ignited (15 September 2018) toward the end of the growing season of boreal toads in our study area. Toads emerged from hibernacula during mid-May and remained active until entering overwintering sites around mid-October (Barrile, Chalfoun, & Walters, 2021b). Given that boreal toads often overwinter in upland forested habitats (e.g., deep in tree root canals: Browne & Paszkowski, 2010)—areas that burned with high severity during the Roosevelt wildfire—individuals may have been forced into hibernacula earlier than usual during the fall of 2018 at burned sites. Toads therefore may have missed opportunities for growth during the end of the active season, which could explain the slight decrease in growth when we sampled those individuals during the spring of 2019 (Figure 2), shortly after they emerged from hibernacula. Alternatively, preferred hibernacula may have been unavailable or destroyed during the wildfire, forcing toads to travel greater distances and/or settle in suboptimal overwintering habitat, both of which could have impacted growth between 2018 and 2019. Slightly reduced growth directly after wildfire was contrary to our prediction, but is logical given the timing of both the wildfire and our field sampling.

Increased growth 2 years post-fire at burned sites was consistent with our predictions, which were based on the expected effects of wildfire on environmental conditions and the preferred temperatures and habitats of boreal toads (e.g., as described in Bull, 2006; Guscio et al., 2008; Lillywhite et al., 1973). Burned areas typically are warmer and within the preferred temperature range of boreal toads than unburned areas, particularly in important refuge habitats such as small mammal burrows (Hossack et al., 2009). Environmental temperatures can remain elevated in burned areas for at least 3 years post-fire (Hossack et al., 2009), providing favorable thermal opportunities to promote growth and other processes such as digestion, fertility, and immunity (Barrile, Chalfoun, & Walters, 2021b; Hossack, Lowe, Ware, & Corn, 2013). Growth ultimately is contingent on the availability of food resources, however, which for boreal toads includes primarily arthropods, principally ants (Formicidae), beetles (Coleoptera), and spiders (Bull, 2006; Bull & Hayes, 2009;

Campbell, 1970). Wildfire can increase the diversity and abundance of arthropods and other invertebrates (Bess et al., 2002; Buddle et al., 2006; Ferrenberg et al., 2019; Jackson et al., 2012), and high-severity fires can result in an extended "fire pulse" characterized by a flux of invertebrate prey to aquatic and terrestrial habitats (Harris et al., 2018; Malison & Baxter, 2010; Silins et al., 2014). Post-fire increases in prey availability therefore may have stimulated the growth of boreal toads between 2019 and 2020 at burned sites in our study area. Furthermore, elevated environmental temperatures may have interacted synergistically with more abundant food resources (e.g., improved digestion and energy incorporation) to increase post-fire growth in boreal toads.

Improved growth 2 years post-fire may have contributed to the increase in dispersal to alternative sites between 2019 and 2020 at burned sites. Larger amphibians and those in better body condition often exhibit greater emigration propensity because of enhanced locomotor capacity and decreased desiccation risk because of a reduced surface-to-volume ratio (reviewed by Cayuela et al., 2020). We unfortunately could not link growth with breeding dispersal in our study as we did not obtain body mass measurements from individuals recaptured at alternative sites, and multi-state models that included the influence of toad body mass on dispersal failed to converge (Appendix S1: Table S3). Nevertheless, greater dispersal 2 years post-fire in our study is consistent with the rapid colonization rates of previously unoccupied wetlands by boreal toads following several wildfires in Glacier National Park, USA (Hossack & Corn, 2007; Hossack, Lowe, & Corn, 2013).

Dispersal by boreal toads also can increase following disturbances other than wildfire (volcanic eruptions: Crisafulli et al., 2005; excavated ponds: Pearl & Bowerman, 2006), including after the extreme flooding event that occurred in our system during the spring of 2017. After high snowmelt runoff destroyed several beaver dams at primary sites, many boreal toads departed from these degraded breeding ponds affected by flooding and settled in higher quality breeding ponds that supported successful metamorphosis (Barrile, Walters, et al., 2021). Although we did not quantify how wildfire influenced the quality of breeding ponds in this study, post-fire landslides and debris flows may have increased sedimentation of beaver impoundments (Backlin et al., 2004; Parker, 2006), reducing the quality of breeding habitat and triggering departure. Alternative sites colonized by boreal toads were not outside the burn perimeter in our study, however, though we suspect that fire-induced habitat changes (e.g., increased bare ground, decreased leaf litter and shrub cover, warmer stopover refugia; Hossack et al., 2009; Rochester et al., 2010) likely facilitated movement to alternative ponds, provided that toads were able to retain adequate body water while moving through these

habitats (Bartelt et al., 2010; Bartelt & Peterson, 2005). Indeed, if wildfire increases landscape permeability, boreal toads may be capable of longer-distance dispersal movements post-fire (e.g., colonization of previously unoccupied streams, range expansion), particularly larger females that are able to travel greater distances (Bull, 2006). Experimental manipulations involving fire treatments would help clarify how male and female boreal toads move through burned landscapes and which habitat features enhance dispersal capacity.

Contrary to our prediction that survival would increase post-fire, capture–recapture models that included the potential effects of wildfire indicated no differences in survival between pre- and post-fire years. This result was surprising as boreal toads perform optimally at higher temperatures (e.g., growth, digestion; Lillywhite et al., 1973), prefer open and severely burned areas (Bull, 2006; Guscio et al., 2008), and exhibit improved immunity and disease resistance in warmer habitats (Barrile, Chalfoun, & Walters, 2021b; Hossack, Lowe, Ware, & Corn, 2013), all of which we expected to increase survival rates. Nonetheless, survival was best explained by mountain range (Wyoming Range vs. Wind River Range), which likely was due to regional differences in climatic regimes and disease prevalence. The influence of climate and disease on boreal toad survival was examined previously (Barrile, Chalfoun, & Walters, 2021a) and fell outside of the scope of this study. Climate can influence how animals respond to disease and wildfire (Cohen et al., 2019; Crowther et al., 2018), however, and interactions among wildfire, climate, and disease would comprise an intriguing line of future inquiry.

Recruitment of boreal toads also was not influenced by wildfire during our study period. We expected recruitment via immigration into our study area given that boreal toad dispersal tends to increase post-disturbance (Barrile, Walters, et al., 2021; Crisafulli et al., 2005) and fire-induced habitat changes likely increased landscape permeability (Rochester et al., 2010). Many of the breeding ponds within our study streams were degraded from spring flooding during 2017, however, such that emigration out of our system may have been more common than immigration into our system. Furthermore, male boreal toads do not become reproductively mature until around 3–5 years of age (Carey et al., 2005), so perhaps the influence of wildfire on in situ recruitment of locally born individuals into the adult breeding population would not manifest until several years after our study period. Recruitment rate instead was best explained by spatial and temporal variables during our study; recruitment varied among years and between mountain ranges, which likely reflects annual changes to the hydrological dynamics of breeding ponds due to variation in regional precipitation (Lambert et al., 2016).

Abundance was a derived parameter in our capture–recapture models. Extracting abundance estimates from the top reverse-time model for survival and recruitment (Table 2) revealed temporal variability in the number of breeding males at each study stream (Appendix S1: Figure S2). Whereas our results indicate relative temporal stability in annual survival, recruitment rates varied considerably over time, suggesting that changes in abundance in our system were largely associated with annual variation in recruitment. Furthermore, decreases in abundance likely were attributable to increased dispersal following disturbance events: flooding at all sites during the spring of 2017 and wildfire at burned sites (Buck and Chall creeks) during the fall of 2018, though post-fire dispersal did not manifest fully until 2019–2020. We are confident that dispersal was in part a response to wildfire and not solely due to the extreme flooding because similar flooding occurred at unburned locations where we observed less dispersal to alternative ponds during 2018–2020. Notably, the dispersal-induced decrease in abundance did not occur until 2018–2019 at Lower Gypsum Creek because most beaver dams at that study reach did not breach until the spring of 2018 (Appendix S1: Figure S2).

Higher abundances at burned sites (Appendix S1: Figure S2) may partially explain greater movement to alternative sites (i.e., density-dependent dispersal), though it would not account for the increase in dispersal 2 years post-fire. Rather, our results for transience and temporary emigration may help better contextualize dispersal in relation to wildfire. First, the proportion of transients in our system (0.15 and 0.19 at Wind River and Wyoming Range sites, respectively) was consistent with reports from boreal toad populations in Colorado, USA, where 10%–20% of newly marked individuals were transients (Muths et al., 2018). Furthermore, a detailed examination of capture histories from individuals that we observed dispersing from primary to alternative sites revealed that 11 of 53 individuals (~20%) were captured only once at primary sites prior to capture at alternative sites, thus would have qualified as transients had we never surveyed at alternative sites. Taken together, these results suggest that ~10%–20% of individuals across boreal toad populations exhibit nomadic behavior, such that transience and local dispersal constitute two separate processes within metapopulations. For instance, the 42 of 53 non-transient toads (toads captured in more than 1 year prior to departing primary sites) that moved to alternative sites were most likely resident individuals that dispersed in part in response to wildfire. Increased movement by resident individuals post-disturbance contributes to a growing body of research that suggests

context-dependent dispersal is relatively common in pond-breeding amphibians (e.g., Boualit et al., 2019; Cayuela et al., 2018; Tournier et al., 2017).

In contrast to transience, temporary emigration at our sites differed dramatically from boreal toad populations in Colorado. Temporary emigration was rare and random (i.e., non-Markovian) in Colorado populations, with males seldom absent from the breeding pond in consecutive years (Muths et al., 2006). By contrast, our results strongly indicated Markovian temporary emigration, with a high probability of skipping breeding in consecutive years (γ_i' was 0.28 and 0.97 at Wind River and Wyoming Range sites, respectively). We suspect that greater disturbance at our study sites (compared with sites in Colorado) partially explains the higher rates of temporary emigration. Further, although temporary emigration presumes that individuals will return to the study area, high temporary emigration likely correlates to some degree with increased dispersal. For example, a higher probability of skipped breeding at burned sites compared with unburned sites is consistent with our finding of greater dispersal at burned sites, further indicating that wildfire facilitated movement across the landscape.

Similar to temporary emigration, breeding dispersal was rare in Colorado populations, with 0.01–0.02 constituting the highest probability of dispersal, which was between sites within 1 km of one another (Muths et al., 2018). Boreal toads in our study area dispersed much more frequently, particularly at burned sites (e.g., mean dispersal >0.3 2 years post-fire), and movements did not depend on distance to alternative sites. For instance, two alternative ponds at Lower Gypsum Creek (unburned site) were in closer proximity to primary sites than any alternative ponds were to primary sites at burned locations, yet dispersal to alternative sites was lower at Lower Gypsum Creek compared with burned sites. This finding reinforces the notion that wildfire played a key role in dispersal behavior within our studied metapopulations. Notably, individuals may not have dispersed to alternative sites if reproductive habitat within our core study area was of high quality (e.g., breeding ponds supported successful metamorphosis), rather than degraded from spring flooding during 2017. In other words, fire-induced habitat changes (e.g., increased landscape permeability) and enhanced growth during 2019–2020 may have provided opportunity for individuals to depart low-quality breeding habitat. Future studies therefore could consider the quality of habitat resources pre- versus post-disturbance to better predict the likelihood of disturbance-induced dispersal (i.e., individuals may depart low but not high-quality habitats after disturbance).

Historical wildfire regimes in our study area were characterized by infrequent (>200-year return interval),

high-severity fires, whereby subalpine and boreal forests would recover long before another burn (Jager et al., 2021; Turner & Romme, 1994). In the near term, however, wildfire frequency, severity, and area burned are predicted to increase (Hagmann et al., 2021), which could affect overwintering sites in upland habitat and critical riparian corridors, which were strongly preferred by boreal toads during the summer foraging season (July–September; Barrile, Chalfoun, & Walters, 2021b). Further, boreal toads at our study sites bred almost exclusively in beaver ponds within riparian corridors. Efforts to maintain beaver populations in our system may help protect riparian habitat from fire-induced habitat changes, as beaver-dammed riparian corridors remain relatively unaffected by wildfire compared with corridors without beaver damming (Fairfax & Whittle, 2020). Finally, wildfire also may interact with other key disturbances in our system, including extreme flooding and livestock grazing, both of which can influence riparian habitat and the quality of breeding ponds (Barrile, Walters, et al., 2021; Barrile, Walters, & Chalfoun, 2022; Fesenmyer et al., 2018). Determining how wildfire, grazing, and flooding independently and interactively influence the quality of breeding ponds and the dispersal pathways between them likely will be critical for predicting how boreal toads will respond in an uncertain future.

As global wildfire regimes continue to change (Hagmann et al., 2021; Krawchuk et al., 2009), identifying which vital rates are responsible for changes in state variables (e.g., occupancy, abundance) pre- versus post-fire will be critical for developing targeted management actions. We demonstrate that, in certain contexts, dispersal can play a major role in changes to state variables after wildfire, as opposed to other vital rates such as survival and recruitment. Our results suggest that improved growth following wildfire may have facilitated dispersal in our system (e.g., via increased locomotor capacity), highlighting the importance of individual metrics in understanding population responses to disturbance. Increased growth and dispersal did not occur until 2 years post-fire, moreover, underscoring the need to consider time-lagged responses in wildfire dynamics and disturbance ecology (Smucker et al., 2005). The ability to study individual and population responses to wildfire will remain opportunistic, as pre- versus post-fire comparisons necessitate fires occurring by chance during the study period. Greater investment in long-term projects (consistent sampling over a number of years) such as mark–recapture efforts would provide more serendipitous opportunities to understand species responses and inform conservation efforts in landscapes experiencing shifts in fire activity.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Barrile, Chalfoun, et al., 2022) are available from Dryad: https://doi.org/10.5061/dryad.rv15dv49j.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.