

Informed breeding dispersal following stochastic changes to patch quality in a pond-breeding amphibian

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Abstract

1. The unidirectional movement of animals between breeding patches (i.e. breeding dispersal) has profound implications for the ecological and evolutionary dynamics of spatially structured populations. In spatiotemporally variable environments, individuals are expected to adjust their dispersal decisions according to information gathered on the environmental and/or social cues that reflect the fitness prospects in a given breeding patch (i.e. informed dispersal).
2. A paucity of empirical work limited our understanding of the ability of animals to depart from low-quality breeding patches and settle in high-quality breeding patches. We examined the capacity of individuals to respond to stochastic changes in habitat quality via informed breeding dispersal in a pond-breeding amphibian.
3. We conducted a 5-year (2015–2019) capture–recapture study of boreal toads *Anaxyrus boreas boreas* ($n = 1,100$) that breed in beaver ponds in western Wyoming, USA. During early spring of 2017, an extreme flooding event destroyed several beaver dams and resulted in the loss of breeding habitat. We used multi-state models to investigate how temporal changes in pond characteristics influenced breeding dispersal, and determine whether movement decisions were in accordance with prospects for reproductive fitness.
4. Boreal toads more often departed from low-quality breeding ponds (without successful metamorphosis) and settled in high-quality breeding ponds (with successful metamorphosis). Movement decisions were context-dependent and associated with pond characteristics altered by beaver dam destruction. Individuals were more likely to depart from shallow ponds with high vegetation cover and settle in deep ponds with low vegetation cover. The probability of metamorphosis was related to the same environmental cues, suggesting that boreal toads assess the fitness prospects of a breeding patch and adjust movement decisions accordingly (i.e. informed breeding dispersal).
5. We demonstrated that stochastic variability in environmental conditions and habitat quality can underpin dispersal behaviour in amphibians. Our study highlighted the mechanistic linkages between habitat change, movement behaviour and prospects for reproductive performance, which is critical for understanding how wild animals respond to rapid environmental change.

KEYWORDS

amphibian, *Anaxyrus boreas*, capture–recapture, context-dependent dispersal, dynamic landscapes, environmental change, movement behaviour, multi-state models

1 | INTRODUCTION

Understanding how organisms respond to environmental change is a fundamental challenge for ecologists and wildlife managers. Primary responses to environmental change are echoed in the mantra ‘move, adapt, acclimate or die’ (Beever et al., 2017; Williams et al., 2008). When conditions at a location deteriorate such that survival and/or reproduction are no longer viable, dispersal to higher quality patches (i.e. ‘move’) may represent the only sustainable response to changing conditions. Dispersal describes 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), potentially resulting in gene flow (Ronce, 2007). Breeding dispersal, for instance, can allow individuals to escape rapid declines in the quality of breeding resources and colonize new patches with higher reproductive potential (Dugger et al., 2010; Williams et al., 1993).

Dispersal is expected to evolve when the fitness benefit of relocating exceeds its direct and indirect costs (Bonte et al., 2012; Stamps et al., 2005). Breeding dispersal, in particular, is thought to be driven primarily by spatiotemporal variation in the quality of breeding resources (McPeck & Holt, 1992; Reigada et al., 2015). Individuals should therefore adjust their movement decisions in accordance with information gathered on the fitness prospects in a given breeding patch (i.e. ‘informed dispersal’; Clobert et al., 2009). Yet, a paucity of empirical work limits our understanding of the ability of animals to depart from low-quality breeding patches and settle in high-quality breeding patches (with the exception of some nomadic birds; e.g. Fernández-Chacón et al., 2013; Péron et al., 2010; Williams et al., 1993). Further, although dispersal behaviour is characterized well in relation to environmental conditions (i.e. ‘context-dependent dispersal’; Matthysen, 2012) (e.g. Kuussaari et al., 2016; Studts et al., 2008), a common assumption is that patch characteristics remain static over time. Quantifying dispersal in relation to temporal changes in patch characteristics would better reflect the conditions of dynamic environments (Cayuela et al., 2018). Moreover, a better understanding of how animals disperse in response to environmental change at breeding patches, and particularly whether movement decisions are in accordance with prospects for reproductive fitness, would help establish mechanistic linkages between habitat change, individual movement and reproductive potential.

Pond-breeding amphibians provide an excellent biological model to study breeding dispersal as ponds often are clustered in space, and movements from one pond to another are frequent and dependent upon environmental conditions (Joly, 2019). Indeed, dispersal in pond-breeding amphibians has received increased attention in recent decades (for a review, see Cayuela, Valenzuela-Sánchez, et al., 2020), including how movement decisions correlate with

reproductive success and environmental change (Boualit et al., 2019; Cayuela, Pradel, et al., 2018). Such work is timely, as amphibians are the most threatened vertebrate class globally (Catenazzi, 2015) and understanding their movement ecology is critical in developing effective conservation measures (Bailey & Muths, 2019; Joly, 2019).

We used pond-breeding amphibians to examine the capacity of individuals to respond to stochastic changes in habitat quality via informed breeding dispersal. The process of dispersal consists of three phases (Baguette & Van Dyck, 2007), namely departure (emigration), transience (transfer within the landscape matrix) and settlement (immigration). Our specific objectives were to assess the environmental conditions and cues associated with both the departure and settlement phases of dispersal, and determine whether movement decisions were in accordance with reproductive potential (here defined as departure from low-quality patches and settlement in high-quality patches).

We used a 5-year (2015–2019) capture–recapture dataset of boreal toads *Anaxyrus boreas boreas* that breed in beaver ponds in western Wyoming to address these questions. Prior to the spring breeding season in 2017, high snowmelt runoff breached several beaver dams, resulting in the draining of ponds and functional loss of breeding habitat. Stochastic variability in habitat quality at beaver ponds during this period provided a natural experiment with which to test how shifting environmental conditions influenced breeding dispersal. We expected higher rates of departure after dramatic change in breeding habitat conditions (context-dependent dispersal) and settlement in ponds with conditions conducive to the production of metamorphs (here defined as tadpoles that successfully transform from the aquatic to the terrestrial morphology). We reasoned that ponds with successful metamorphosis were of higher quality and ponds with unsuccessful metamorphosis were of lower quality and expected individuals to disperse from ponds with unsuccessful metamorphosis to ponds with successful metamorphosis (informed dispersal). Finally, we suspected that individuals assessed the quality of breeding patches based on environmental cues associated with habitat changes following the collapse of beaver dams. We therefore predicted that pond characteristics associated with dispersal decisions would also influence the probability of metamorphosis.

2 | MATERIALS AND METHODS

2.1 | Study area

We studied boreal toads at two stream segments (~1.4 km reach at Buck Creek and ~0.4 km reach at Chall Creek) within the South Beaver Creek watershed in the Bridger-Teton National Forest, western Wyoming (42°59'N, 110°24'W) during 2015–2019 (Figure 1). The area has a continental subarctic climate and receives a mean of 1,900 mm

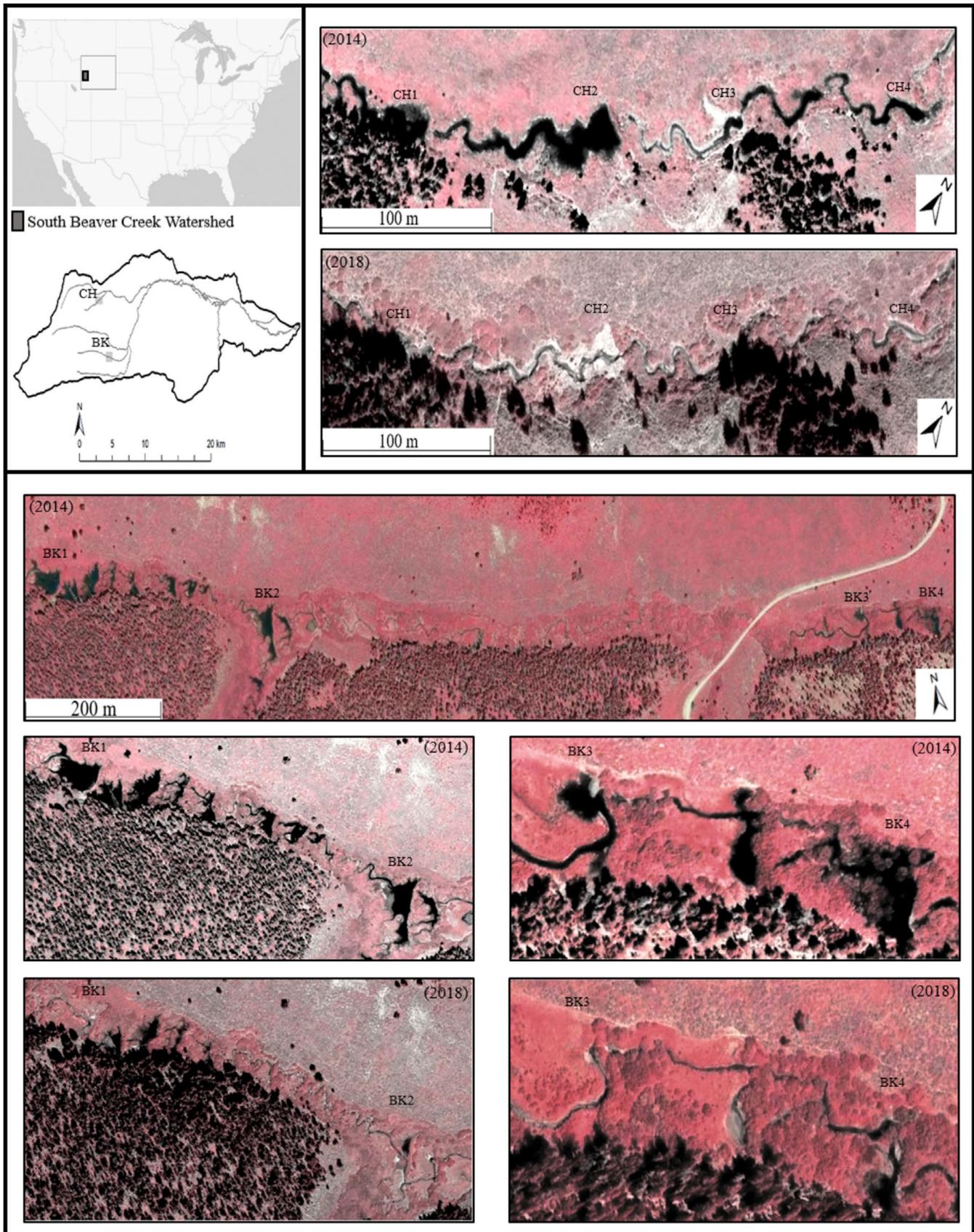


FIGURE 1 Infrared aerial satellite imagery of Chall (CH) and Buck (BK) creeks in the South Beaver Creek watershed, western Wyoming. Images from 2014 (July) and 2018 (August) demonstrate habitat change at breeding sites, primarily the result of beaver dam collapse and pond draining. Streams flow left to right with sites denoted by creek (CH/BK) and number (1–4)

of precipitation annually, most of which (c. 1,600 mm) falls as snow between October and May. The average elevation was 2,500 m and mean daily temperatures ranged from -13°C in January to $+15^{\circ}\text{C}$ in July (climate data summarized from 1982 to 2019 at Blind Bull Summit SNOTEL station, located within 15 km of both study streams). The landscape was composed of mixed-conifer and aspen (*Populus tremuloides*) forest, sagebrush *Artemisia tridentata*, 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 amphibian species. We sampled boreal toads at eight breeding sites, four at Buck Creek and four at Chall Creek (Figure 1). All sites were active or once-active beaver ponds and separated by ≥ 100 m.

2.2 | Habitat change

The collapse of beaver dams as a result of high snowmelt runoff in early spring of 2017 triggered a successional process whereby

ponds drained, followed by the establishment of herbaceous vegetation and progression towards meadow habitat (Little et al., 2012; Naiman et al., 1988). During each breeding season (2015–2019), we recorded the following three variables associated with wetland succession: (a) percent emergent vegetation (vegetation piercing the surface of the water) cover (vegetation) using ocular estimates from quadrat sampling throughout the entire pond surface; (b) pond surface area (area) using a handheld GPS to trace the perimeter of each pond (and subsequently calculated area from perimeter measurements); and (c) maximum depth of each pond (depth) using a metre stick. We standardized measurements temporally by conducting habitat assessments during June 9–21 each year. Generally, change in pond conditions prior to the 2017 flood (2015–2016) was minimal, with dramatic changes immediately following the flood, and gradual changes in the two post-flooding years (2018–2019) (Figure 2; Table S1). Several ponds were less affected by the flooding event, with dams remaining partially intact. We used capture–recapture data to examine whether individuals

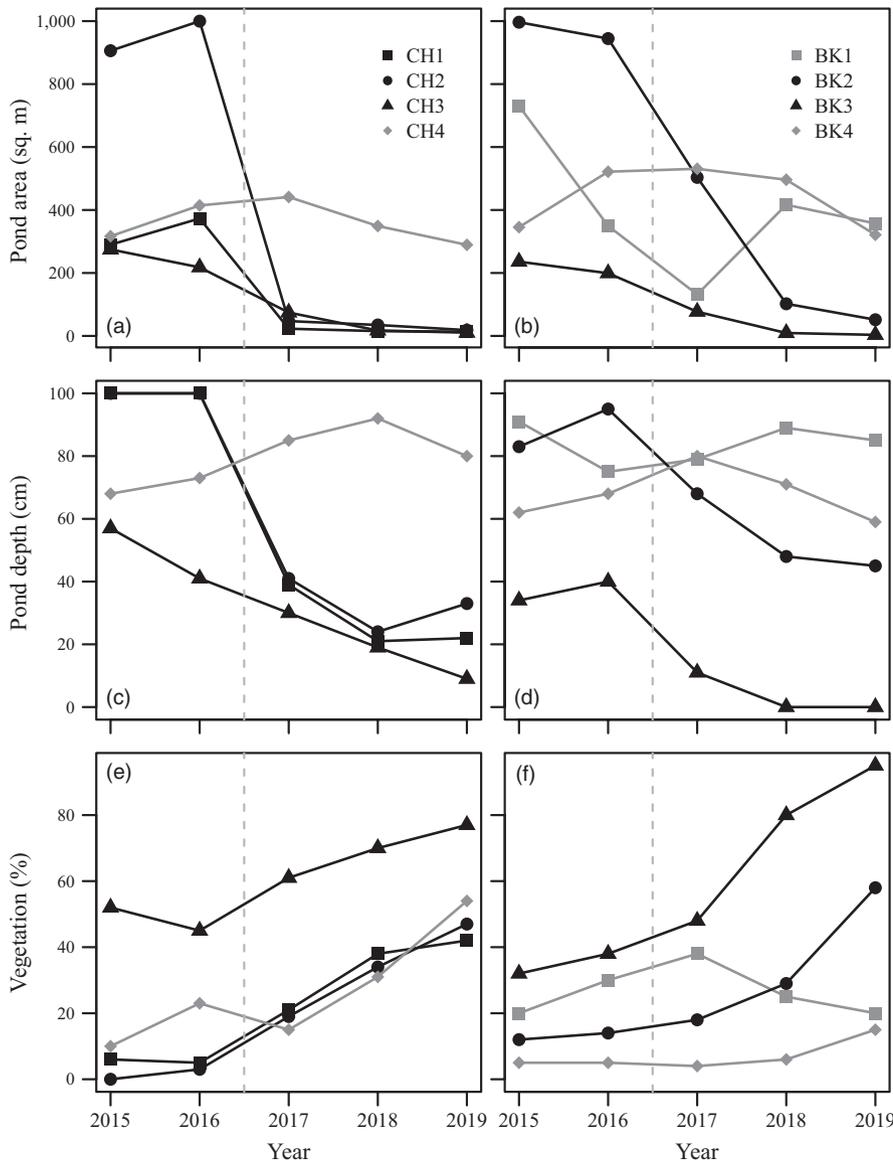


FIGURE 2 Change in environmental conditions at beaver ponds used as breeding sites by boreal toads at (a, c, e) Chall Creek (CH) and (b, d, f) Buck Creek (BK) in the Bridger-Teton National Forest, USA, during 2015–2019. The vertical dotted line signifies the timing of the extreme flooding event (early spring of 2017) that collapsed beaver dams. Black lines indicate ponds in which dams were completely destroyed and grey lines indicate ponds in which dams remained partially intact

departed from degraded ponds and settled in ponds less affected by flooding.

2.3 | Capture–Mark–Recapture surveys

Boreal toads congregate at breeding ponds shortly after snowmelt in the spring (~early May) and continue spawning through mid to late June. We conducted standardized visual encounter surveys to hand-capture toads at our eight breeding sites at night during peak breeding in 2015–2019. Captured individuals were sexed by the presence of darkened nuptial pads on the thumbs of males and marked using passive integrated transponder tags (8 mm × 1.2 mm FDX tag; Oregon RFID) for individual identification. We tagged adult males only, assuming individuals ≤ 55 mm were juveniles (Carey et al., 2005). 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 four sites at either Buck Creek or Chall Creek during each nighttime survey and conducted multiple recapture surveys within each breeding season at both streams (mean = 6 surveys, range = 3–9).

2.4 | Statistical analysis

Our sampling method produced capture–recapture data at two distinct temporal scales (within- and among 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 the sources of variation in capture probabilities (Kendall et al., 1997). We used multi-state closed robust design (hereafter, multi-state) models with a Huggins estimator to analyse 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 modelling of capture probability as a function of individual covariates (Huggins, 1989). Our multi-state models estimated apparent survival (ϕ ; 'apparent' because mortality cannot be separated from permanent emigration) and state-transition probabilities (ψ) between primary periods (i.e. breeding seasons) and capture probability (p) within primary periods. 'States' in our models refer to individual breeding ponds and transition probabilities represented the probability of moving from one breeding site to another between seasons (i.e. breeding dispersal). This modelling approach assumes that no site transitions occurred within a breeding season (Chabanne et al., 2017); however, 3.4% of the captures violated this assumption. To minimize this violation, if an individual was captured in two different sites within a breeding period, we retained captures matching the second site recorded in that season (i.e. ignored captures at the first site), assuming individuals departed from the first site and settled in the second.

In model parameterization, transition probability is conditional on survival (e.g. transition probability ψ_t^{rs} represents the probability an individual in state r at time t survives and moves to state s

at time $t + 1$). Therefore, although transition probability was our focal parameter and we considered survival probability a nuisance parameter, survival had to be modelled appropriately for reliable estimates of transition probabilities. Rather than fitting an extremely large model set incorporating all plausible combinations for model parameters, we adopted a stepwise approach to identify supported models. We fixed the survival and transition parameters at a high dimensionality (ϕ and ψ varied over time and among breeding ponds) while identifying the most parsimonious structure for capture probability (Doherty et al., 2012; Lebreton et al., 1992). We ran models in which capture probability remained constant or varied by year (i.e. breeding season), capture occasion and across sites (i.e. each breeding pond), including additive and interactive combinations of these structures (13 structures; Tables S2 and S3). Retaining the most parsimonious structure for capture probability (highest AIC_c weight; Burnham et al., 2011), we next identified the most parsimonious structure for survival. Our model set for survival included constant, time-dependent and site-dependent models, including additive and interactive combinations of these variables (five structures; Tables S4 and S5). We then retained the best structures for capture and survival probability when modelling transition probability, which was our parameter of interest. We fit all capture–recapture models separately for Buck and Chall creeks because there was no documented movement between drainages. Further, at each step of the modelling procedure, we dropped models that did not converge or with singular parameters. All multi-state analyses were conducted using Program MARK (White & Burnham, 1999), with models constructed via the RMark package (Laake, 2013) in Program R (R Core Team, 2020). To our knowledge, a goodness-of-fit test is not available for these model types when including site-specific and time-varying covariates, so we used our general structures and the median \hat{c} approach to adjust for possible overdispersion (White & Burnham, 1999).

2.5 | Departure phase

To determine how environmental conditions influenced the departure phase of dispersal in boreal toads, we fit multi-state models that included the three field-derived habitat metrics described above (*vegetation*, *area* and *depth*). Because we were interested in movement in relation to current environmental conditions and responses to stochastic change, we fit three models that included values for each habitat metric at time t and three models that included the differences between years of each habitat metric (i.e. value at time $t - 1$). Our three habitat metrics were highly correlated (all Pearson's correlation coefficients $> |0.65|$), so we did not include multiple covariates in a single model, and instead fit six univariate models. Covariate values in the departure models corresponded to the pond occupied by an individual toad prior to dispersal, thus the transition parameter was effectively transformed into a departure probability (i.e. probability of transitioning given the covariate values at the departure site).

2.6 | Settlement phase

To determine how environmental conditions influenced the settlement phase of dispersal, we again fit multi-state models that included the three field-derived habitat metrics (*vegetation*, *area* and *depth*). In contrast with departure models, covariate values in the settlement models corresponded to the pond occupied by an individual after dispersal, effectively transforming the transition parameter into the probability of settlement (i.e. probability of transitioning given the covariate values at the settlement site). In the RMark package, this coding is achieved by assigning the covariate values from each breeding pond and time period to the appropriate 'tostratum' argument, which corresponds to the settlement site, rather than the 'stratum' argument, which corresponds to the departure site. We fit three multi-state models that included the conditions in a given breeding season for *vegetation*, *area* and *depth*. Settlement decisions in boreal toads also may relate to the distance from departure locations (Muths et al., 2018). We therefore fit a fourth model that included the proximity (Euclidean distance) between departure and settlement sites.

2.7 | Breeding dispersal and metamorphosis

We conducted standardized visual encounter surveys at breeding sites from July to September (period when tadpoles metamorphose) during each year (three surveys per site, one in each month) and recorded detection or non-detection of metamorphs within a 5-m buffer around the perimeter of each pond (Muths et al., 2014). Given the frequency of our visits to each pond, we expected to observe the presence or absence of metamorphs with a high detectability. To confirm the assumption of a low false-negative error rate, we built site-occupancy models to estimate the detection probability of metamorphs (MacKenzie et al., 2002; Tyre et al., 2003). Our sampling included multiple visits to each breeding pond both within and among years, constituting a robust design, and we assumed that metamorphosis commenced prior to our first surveys in each year (~mid-July). We used the Gamma parameterization of the robust design occupancy model (RDOccupPG model in RMark), such that models included a parameter denoting the probability of an unoccupied site becoming occupied (i.e. the probability of a pond with unsuccessful metamorphosis at time t supporting successful metamorphosis at time $t + 1$), which we held constant across space and time. We reasoned that occupancy (i.e. probability of successful metamorphosis) was dependent on the year and the breeding pond, thus allowed occupancy to vary across time and space. If the overall detection probability (i.e. constant detection probability) was higher than 0.9, we were comfortable using metamorph presence (1) or absence (0) as a binary variable in subsequent analyses.

Ponds that successfully produced any metamorphs were considered high quality and ponds with unsuccessful metamorphosis were considered low quality. To determine whether dispersal decisions

were in accordance with prospects for reproductive fitness, we fit multi-state models that included the quality of breeding habitat at both the departure and settlement ponds. However, to account for alternative explanations for dispersal behaviour, we fit nine competing models in this procedure. We fit a model in which ψ was constant over time and among breeding ponds, models in which ψ varied over time and among breeding ponds (including additive and interactive combinations of these parameters), models in which either departure or settlement was related to the quality of breeding ponds, and a model in which both departure and settlement were related to the quality of breeding ponds. In models that included the quality of breeding patches, the presence/absence of metamorphs at the departure site corresponded to time t while the presence/absence of metamorphs at the settlement site corresponded to time $t + 1$.

2.8 | Pond characteristics and habitat quality

To investigate whether environmental conditions associated with dispersal were reliable indicators of the quality of breeding habitat (i.e. the presence/absence of metamorphs), we modelled the probability of metamorphosis as a function of our three field-derived habitat metrics (*vegetation*, *area* and *depth*). We parameterized generalized linear mixed-effects models with binomial error distributions (logit link function), specifying breeding pond as a random intercept. Model parameters were estimated using maximum likelihood in the lme4 package (*glmer* function) in Program R (R Core Team, 2020). Data from Buck and Chall creeks were combined in this analysis.

3 | RESULTS

We captured 317 adult male toads during 27 capture surveys at Buck Creek and 783 toads during 32 surveys at Chall Creek across the 5-year study period (2015–2019). We found little evidence of overdispersion ($\hat{c} = 1.96$ and 2.12 in global models for Buck and Chall Creek respectively) and thus used AIC_c to compare models and calculate model weights. The best-supported structure for capture probability was the same at Buck (model weight, $w = 0.84$) and Chall ($w = 0.99$) creeks and indicated variation among years, capture occasions and breeding ponds (Tables S2 and S3). Mean capture probability was generally higher at Buck (0.24, range = 0.04–0.41) than Chall (0.14, range = 0.04–0.36) Creek. Whereas the most parsimonious structure for survival indicated variation among breeding ponds at Buck Creek ($w = 0.43$; Table S4), survival was best modelled as constant across space and time at Chall Creek ($w = 0.66$; Table S5). Site BK1 produced the highest mean survival (0.58, $SE = 0.06$) and site BK4 produced the lowest mean survival (0.32, $SE = 0.07$) at Buck Creek, with sites BK2 and BK3 producing intermediate survival estimates (0.53, $SE = 0.03$ and 0.42, $SE = 0.08$ respectively). Mean apparent survival at Chall Creek (0.36, $SE = 0.02$) was relatively low compared to Buck Creek.

3.1 | Departure phase

The top two models for departure probability at Buck Creek (and the only two models with model weight) included pond depth (model weight, $w = 0.65$) and the change in emergent vegetation cover in ponds between year t and $t + 1$ ($w = 0.35$) (Table 1). Boreal toads were more likely to depart from shallow ponds ($\beta = -0.06$, $SE = 0.01$; Figure 3a) and ponds with increasing emergent vegetation cover ($\beta = 0.11$, $SE = 0.02$) than deep ponds with stable or decreasing amounts of emergent vegetation. The top two models for departure probability at Chall Creek (and the only two models with model weight) included the change in pond depth between year t and $t + 1$ ($w = 0.67$) and pond depth in year t ($w = 0.33$) (Table 1). Similar to

boreal toads at Buck Creek, individuals at Chall Creek were more likely to depart from shallow ponds than deep ponds ($\beta = -0.02$, $SE = 0.01$). However, the strongest signal at Chall Creek was departure in response to the decrease in pond depth between years ($\beta = -0.03$, $SE = 0.01$; Figure 3b).

3.2 | Settlement phase

The best-supported model for settlement probability at Buck Creek (model weight, $w = 0.99$) included the effect of emergent vegetation cover ($\beta = -0.04$, $SE = 0.01$) (Table 1). Transient boreal toads at Buck Creek were more likely to settle in breeding ponds with low

TABLE 1 Parameter estimates (β) with standard errors (SE) and model selection results including model name, AIC_c , ΔAIC_c , model weights, number of parameters (K) and $-2\log(L)$ for four separate transition probability (ψ) procedures, using multi-state capture-recapture models to estimate departure and settlement of breeding ponds by adult boreal toads ($n = 1,100$) at Buck and Chall creeks in the Bridger-Teton National Forest, USA, during 2015–2019. Parameter coefficients with 95% confidence intervals that did not overlap zero are bolded

Model	β	SE	AIC_c	ΔAIC_c	Model Wt	K	$-2\log(L)$
Buck Creek							
Departure							
$\psi(\text{depth})$	-0.057	0.011	3,938.60	0.00	0.65	22	3,893.39
$\psi(\Delta \text{vegetation})$	0.107	0.018	3,939.84	1.24	0.35	22	3,894.62
$\psi(\text{area})$	-0.004	0.001	3,951.89	13.29	0	22	3,906.67
$\psi(\text{vegetation})$	0.095	0.021	3,952.18	13.57	0	22	3,906.96
$\psi(\Delta \text{area})$	0.002	0.001	3,975.44	36.84	0	22	3,930.22
$\psi(\Delta \text{depth})$	0.012	0.014	3,980.16	41.56	0	22	3,934.95
Settlement							
$\psi(\text{vegetation})$	-0.037	0.011	3,963.58	0.00	0.99	22	3,918.36
$\psi(\text{depth})$	0.015	0.007	3,975.13	11.55	0	22	3,929.91
$\psi(\text{area})$	0.006	0.001	3,976.09	12.51	0	22	3,930.87
$\psi(\text{distance})$	-0.750	0.431	3,977.96	14.37	0	22	3,932.74
Chall Creek							
Departure							
$\psi(\Delta \text{depth})$	-0.025	0.006	8,179.34	0.00	0.67	19	8,140.85
$\psi(\text{depth})$	-0.020	0.005	8,180.75	1.41	0.33	19	8,142.25
$\psi(\text{area})$	-0.001	0.000	8,193.78	14.44	0	19	8,155.29
$\psi(\text{vegetation})$	0.016	0.007	8,194.01	14.67	0	19	8,155.51
$\psi(\Delta \text{area})$	-0.001	0.000	8,194.06	14.72	0	19	8,155.56
$\psi(\Delta \text{vegetation})$	0.021	0.018	8,197.67	18.33	0	19	8,159.18
Settlement							
$\psi(\text{depth})$	0.029	0.004	8,140.08	0.00	1	19	8,101.59
$\psi(\text{area})$	0.003	0.001	8,160.53	20.45	0	19	8,122.04
$\psi(\text{vegetation})$	-0.031	0.007	8,178.10	38.02	0	19	8,139.60
$\psi(\text{distance})$	0.348	1.591	8,198.93	58.85	0	19	8,160.43

Notes: Transition probability (ψ) was modelled as a function of three pond characteristics: percent emergent vegetation cover (*vegetation*), pond surface area (*area*) and maximum water depth (*depth*). Additionally, departure was modelled as a function of the change in pond characteristics between time t and time $t + 1$ (indicated by the Δ symbol preceding variable names) and settlement was modelled as a function of the Euclidean distance between ponds (*distance*). Note that models cannot be compared across streams (Buck vs. Chall Creek) nor transitions (departure vs. settlement). All models included the best-supported structures for survival probability, $\phi(\text{site})$ at Buck Creek and $\phi(\cdot)$ at Chall Creek, and capture probability, $p(\text{survey} + t + \text{site})$, which was the same at both streams. *Survey* indicates capture occasions within a year, t indicates variation between years, *site* indicates each breeding pond and ' \cdot ' indicates the parameter remained constant across space and time.

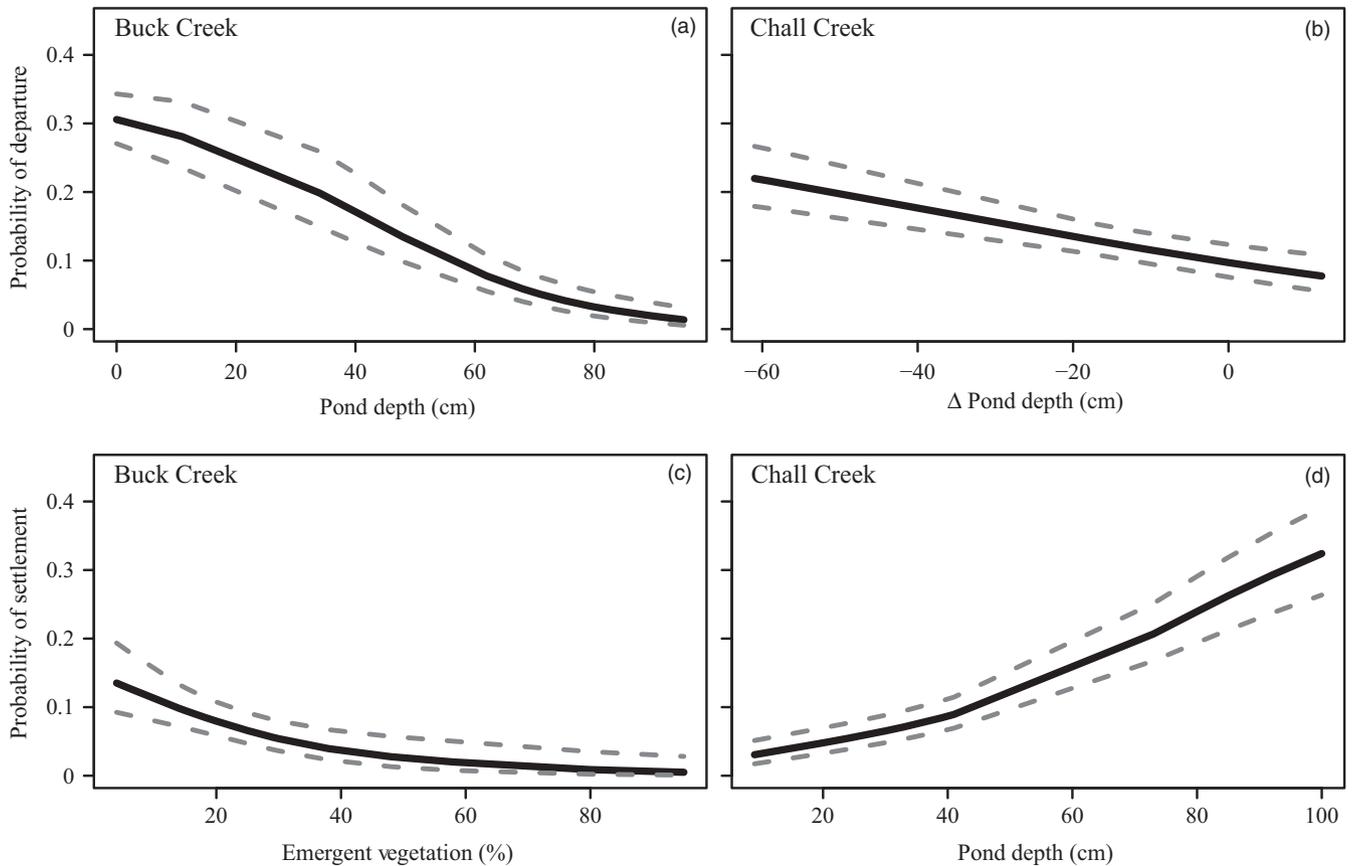


FIGURE 3 The probability that boreal toads departed breeding ponds decreased with (a) increasing pond depth at Buck Creek and increased with (b) greater decreases in pond depth between year t and year $t + 1$ at Chall Creek in the Bridger-Teton National Forest, USA, during 2015–2019. The probability that transient boreal toads settled in breeding ponds decreased with (c) increasing emergent vegetation cover at Buck Creek and increased with (d) increasing pond depth at Chall Creek. Mean predicted values (solid lines) and 95% confidence intervals (dashed lines) were derived from multi-state capture–recapture analyses: results in (a) and (c) were derived from the top model for departure and settlement at Buck Creek and results in (b) and (d) were derived from the top model for departure and settlement at Chall Creek (see Table 1)

emergent vegetation cover than ponds with high vegetation cover (Figure 3c). The best-supported model for settlement probability at Chall Creek ($w = 1.00$) included the effect of pond depth ($\beta = 0.03$, $SE = 0.004$) (Table 1). Transient boreal toads at Chall Creek were more likely to settle in deep breeding ponds than shallow ponds (Figure 3d).

3.3 | Breeding dispersal and metamorphosis

We conducted 120 surveys for boreal toad metamorphs during July–September in 2015–2019 (three surveys in each year at all eight breeding ponds). The mean detection probability of metamorphs was 0.94 (95% CI = 0.83, 0.98), indicating a low false-negative error rate, thus we used metamorph presence/absence in models of breeding dispersal.

The best-supported model for dispersal probability (of the nine competing models in this step) included the presence/absence of metamorphs at the departure site and the settlement site at both Buck and Chall creeks (model weight, $w = 0.96$ and 0.82 respectively;

Tables S6 and S7). Boreal toads were more likely to depart from sites without successful metamorphosis at time t and settle in sites with successful metamorphosis at time $t + 1$ compared with all other alternatives (Figure 4). Moreover, toads were least likely to disperse from sites with metamorphosis to sites without metamorphosis (i.e. maladaptive behaviour with respect to reproductive potential) at both Buck and Chall creeks (Figure 4).

3.4 | Pond characteristics and habitat quality

At Buck Creek, two of four sites produced metamorphs in all years except 2018, in which only BK4 supported successful metamorphosis. At Chall Creek, two of four sites and three of four sites produced metamorphs in 2015 and 2016 respectively. During 2017–2019, however, only CH4 supported successful metamorphosis (Table S1). The probability of metamorphosis increased in deeper ponds ($\beta_{\text{depth}} = 0.21$, $SE = 0.11$) with higher surface area ($\beta_{\text{area}} = 0.02$, $SE = 0.01$) and decreased in ponds with a greater amount of emergent vegetation cover ($\beta_{\text{vegetation}} = -0.10$, $SE = 0.03$) (Figure 5).

4 | DISCUSSION

Dispersal is a key ecological and evolutionary process that influences the demography and gene flow of spatially structured populations (Ronce, 2007; Thomas & Kunin, 1999). In spatially structured amphibian populations that experience habitat patch turnover, for

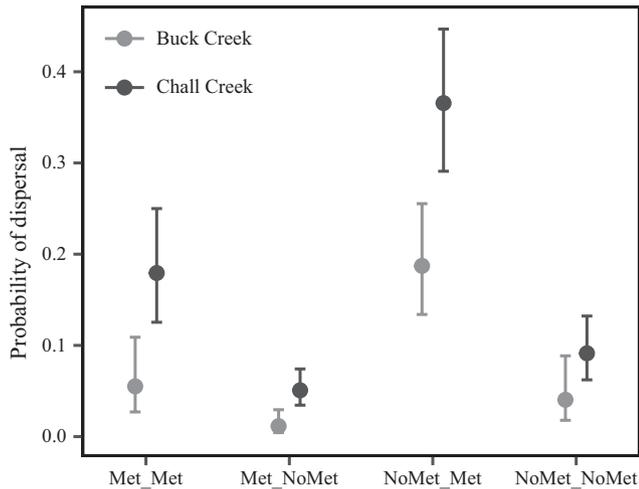


FIGURE 4 Dispersal probability of adult male boreal toads in relation to whether metamorphs were present or absent at breeding ponds at Buck Creek and Chall Creek in the Bridger-Teton National Forest, USA, during 2015–2019. ‘Met’ denotes a pond that produced metamorphs in a given year while ‘NoMet’ indicates unsuccessful metamorphosis. The left side of x-axis labels signifies the site from which adult toads departed in year t , whereas the right side represents the settlement site in year $t + 1$ (e.g. ‘NoMet_Met’ represents the probability of movement from a site without metamorphosis in year t to a site with successful metamorphosis in year $t + 1$). Mean estimates (dots) and 95% confidence intervals (error bars) were derived from a multi-state analysis in which transition probability was modelled as a function of the presence/absence of metamorphs at both the departure and settlement locations (top models in Tables S6 and S7)

example, simulations of context-dependent, compared to random, breeding dispersal decreased the extinction risk of populations (Cayuela, Besnard, et al., 2020). Yet, the capacity of amphibians to disperse according to information gathered on the prospects for reproductive fitness in a given breeding patch (i.e. informed breeding dispersal) is unclear and supported by very few empirical examples (e.g. Boualil et al., 2019). Our study provides a robust example of both context-dependent and informed breeding dispersal in a pond-breeding amphibian. Adult boreal toads exhibited the ability to depart from ponds with unsuccessful metamorphosis and settle in ponds with successful metamorphosis. Further, pond characteristics that influenced the probability of metamorphosis also influenced departure and settlement decisions. Shallow ponds with high amounts of emergent vegetation cover were associated with a low probability of metamorphosis. Indeed, boreal toads were more likely to depart from shallow ponds with high amounts of emergent vegetation and settle in deep ponds with low amounts of emergent vegetation. Boreal toads therefore likely gather information on pond depth and vegetative cover to assess the fitness prospects of a breeding patch and adjust movement decisions accordingly.

Water depth and emergent vegetation may indicate the hydro-period length of breeding ponds and thus the risk of offspring desiccation. In experimentally manipulated waterbodies, yellow-bellied toads *Bombina variegata* were more likely to depart from waterbodies with a short hydroperiod (Tournier et al., 2017). Although beaver ponds in our system did not dry completely like other waterbodies (e.g. ephemeral wetlands), reproductive failure often resulted from the desiccation of egg clutches and tadpoles stranded on pond fringes (G.M. Barrile, pers. obs.). Adult boreal toads therefore may adjust dispersal decisions to avoid reproductive failure due to desiccation.

In addition to environmental conditions at time t , boreal toads also dispersed between breeding ponds in response to environmental change (conditions at t – conditions at $t - 1$). Change in pond characteristics between time $t - 1$ and time t may simply correlate with

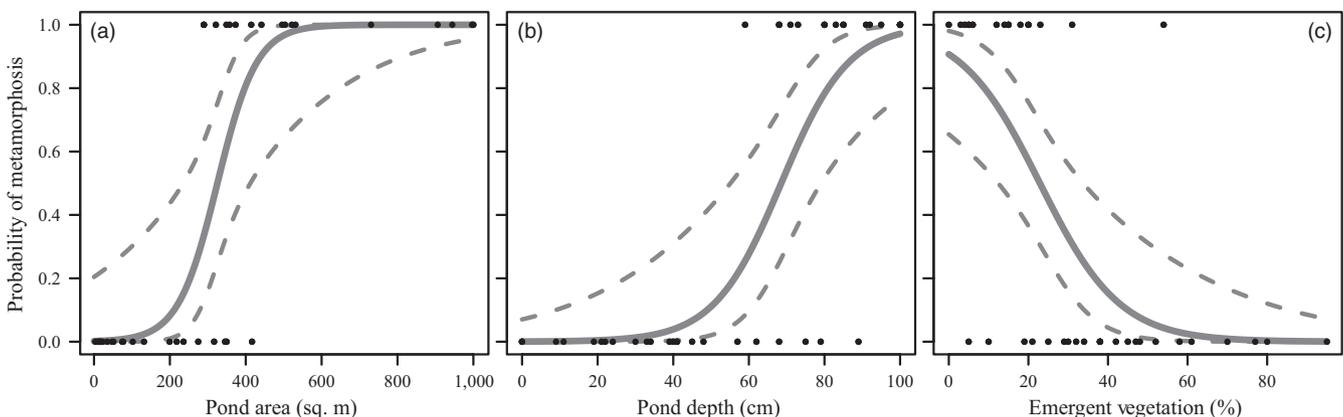


FIGURE 5 The probability of metamorphosis in boreal toad tadpoles increased with (a) higher surface area and (b) greater maximum depth and decreased with (c) higher amounts of emergent vegetation cover in breeding ponds at Buck Creek and Chall Creek in the Bridger-Teton National Forest, USA, during 2015–2019. Mean predicted values (solid lines) and 95% confidence intervals (dashed lines) were derived from univariate generalized linear mixed-effects models specifying site (i.e. breeding pond) as a random intercept

environmental cues at time t (e.g. a rapid decrease in pond depth between years likely results in a shallow pond in the subsequent year, which then provides the actual biological cue for breeding success and dispersal). Alternatively, like several other taxonomic groups, amphibians may use memory of past conditions to inform movement decisions (Börger et al., 2008; Merkle et al., 2014), such as comparing current breeding conditions to previous breeding conditions. For instance, the directionality of habitat change (e.g. increase in emergent vegetation) may indicate a directional change in the quality of breeding habitat. Memory-driven movement processes are difficult to distinguish from reactive sensory-driven behaviours (Fagan et al., 2013), however. Targeted analyses to differentiate between these alternatives in amphibian systems would comprise an intriguing line of future inquiry.

Environmental cues were likely not the only mechanism underlying dispersal behaviour. Movement decisions may also relate to phenotypic characteristics such as body condition (i.e. 'phenotype/condition-dependent dispersal'; Clobert et al., 2009) and public information (Boulinier et al., 2008) such as conspecific (Cayuela et al., 2019; Gamble et al., 2007) and/or heterospecific density (Cayuela et al., 2018). Perhaps, for instance, only individuals above a certain quality or condition threshold (e.g. body size; Denoël et al., 2018) were able to pay the costs associated with dispersal. Furthermore, the number of conspecifics or heterospecifics at a site may be assessed more readily than environmental conditions. The presence of others may not reliably indicate the quality of breeding habitat (Van Horne, 1983), however, and settlement in crowded patches could subject dispersers to density-dependent processes such as competition (Buxton & Sperry, 2017) and disease transmission (e.g. chytrid fungus *Batrachochytrium dendrobatidis* in our system; Barrile et al., 2021).

Notably, we could not explicitly link dispersal between breeding sites to reproductive success as we did not have information on the reproductive performance of individuals. Dispersal may have constituted an adaptive behaviour if individuals bred successfully after settling in high-quality ponds, provided that the relative fitness benefits outweighed the costs associated with such movements (e.g. desiccation, predation, energy expenditure; Bonte et al., 2012). Further, not all individuals dispersed during our study period, and we often observed adult males returning to familiar breeding patches that offered little to no reproductive potential. Remaining in poor quality habitat may not be maladaptive, again depending on the costs associated with dispersal. Importantly, with respect to the population level, however, in systems wherein breeding patches have a limited life span (e.g. beaver ponds in our system), simulations suggest that spatially structured amphibian populations cannot persist without dispersal (Cayuela, Besnard, et al., 2020). The long-term persistence of boreal toad populations in our study area will therefore depend strongly on beaver activity creating suitable breeding ponds within the reach of toad colonization.

Although the proximity of breeding ponds did not influence movement decisions during our study (Table 1), this result likely reflects the spatial scale of our system, as increased distance typically

presents a major impediment to dispersal in anuran species (Cayuela, Valenzuela-Sánchez, et al., 2020), including adult boreal toads (Muths et al., 2018). Structural connectivity among breeding ponds also is important for matrix permeability and facilitating dispersal (Muths et al., 2018). For instance, boreal toads strongly preferred riparian habitat in our system (Barrile et al., 2021) and likely followed the favourable thermal and hydric conditions of riparian corridors during dispersal (Murphy et al., 2010). Efforts to maintain beaver populations and preserve multiple dispersal pathways (Grant et al., 2010) between breeding ponds are therefore likely to be important for the conservation of boreal toads and other organisms that rely on beaver-modified habitats (Hossack et al., 2015).

Advances in multi-state and multi-event modelling have expanded the toolbox with which to analyse and understand dispersal (Cayuela, Rougemont, et al., 2018) and have been applied in several capture-recapture studies of pond-breeding amphibians (Cayuela et al., 2016; Denoël et al., 2018; Grant et al., 2010; Muths et al., 2018). Recent developments in multi-event models provide the flexibility to integrate temporal covariates (Cayuela, Pradel, et al., 2018); however, applications thus far included change in patch characteristics over time between qualitative states only (e.g. habitat type A transitions to habitat type B). Our analysis expands the framework and detail through which we understand animal dispersal by incorporating temporal changes in continuous patch characteristics, which better reflect the conditions organisms experience in dynamic ecosystems. We report that dispersal rates can covary with changing environmental conditions within habitat patches. Furthermore, we set dispersal in a probabilistic framework such that managers can better forecast and plan for increased movement (e.g. block traffic during road crossings) and predict dispersal between sites with specific characteristics (Bailey & Muths, 2019).

Mobile animals should track high-quality resources to maximize individual fitness (Bowler & Benton, 2005). Elk *Cervus elaphus* migrating in concordance with plant phenology increases body fat, for example, which is an important correlate of reproduction and survival in most ungulates (Middleton et al., 2018). Our study suggests that animals can track high-quality resources via unidirectional movements such as dispersal to alternative breeding habitat. This is especially important in systems wherein breeding patches can appear and disappear through stochastic processes, as dispersal decisions can determine population demography and long-term viability (Cayuela, Besnard, et al., 2020). For example, subpopulation abundance (i.e. abundance at each pond) was a derived parameter in our multi-state models. Extracting abundance estimates from the top model for dispersal at each stream (model including the presence/absence of metamorphs at departure and settlement sites; Tables S6 and S7) revealed temporal variability in the number of breeding males in each subpopulation (Figure S1). Our results suggest that increases in abundance at ponds such as BK4 and CH4 are in part due to immigration from other ponds (e.g. BK3 and CH2) and might help maintain overall population stability. We could not, however, quantify the relative contributions of dispersal versus in situ recruitment to increases in subpopulation abundance. Distinguishing between locally born individuals that have

never dispersed and individuals that either dispersed prior to their first breeding (i.e. natal dispersal) or after their first breeding (i.e. breeding dispersal) but prior to their capture is a limitation in many amphibian species because of difficulty marking and surveying individuals from metamorphosis to death. A clearer understanding of the demographic implications of amphibian dispersal decisions is therefore needed (Cayuela, Valenzuela-Sánchez, et al., 2020), particularly if movement behaviour is to be integrated into management decisions (Bailey & Muths, 2019).

We demonstrate that stochastic variability in patch quality and conditions can underpin dispersal behaviour in amphibians. Dispersal rates therefore can vary considerably depending on the environmental context, suggesting that movement among subpopulations may fluctuate over time, particularly in spatially structured populations experiencing unpredictable environments (Cayuela et al., 2016). Our results further demonstrate that some amphibians can respond to environmental change via informed dispersal (i.e. in accordance with prospects for reproductive fitness), whereby individuals depart low-quality breeding patches and settle in high-quality breeding patches. Creating new suitable environments (e.g. facilitating beaver activity in our system) and increasing the structural connectivity among patches could be important conservation tools for enabling dispersal to higher quality breeding habitats. Our study highlights the mechanistic linkages between habitat change, individual movement behaviour and reproductive potential. Understanding such evolved linkages will be critical for the maintenance of wild populations and species into the future, especially in the light of the extent of human-induced rapid environmental change (Sih et al., 2011).

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AUTHORS' CONTRIBUTIONS

A.D.C. and A.W. secured funding; G.M.B. and M.W. conceived the original idea and collected the data; G.M.B. conducted the analyses and led the writing of the manuscript. All the authors contributed substantially to revisions and gave final approval for submission and publication.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.2ngf1vhnc> (Barrile, Walters, et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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