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Climate-associated decline of body condition in a fossorial salamander

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Abstract

Temperate ectotherms have responded to recent environmental change, likely due to the direct and indirect effects of temperature on key life cycle events. Yet, a substantial number of ectotherms are fossorial, spending the vast majority of their lives in subterranean microhabitats that are assumed to be buffered against environmental change. Here, we examine whether seasonal climatic conditions influence body condition (a measure of general health and vigor), reproductive output, and breeding phenology in a northern population of fossorial salamander (Spotted Salamander, *Ambystoma maculatum*). We found that breeding body condition declined over a 12-year monitoring period (2008–2019) with warmer summer and autumn temperatures at least partly responsible for the observed decline in body condition. Our findings are consistent with the hypothesis that elevated metabolism drives the negative association between temperature and condition. Population-level reproduction, assessed via egg mass counts, showed high interannual variation and was weakly influenced by autumn temperatures. Salamander breeding phenology was strongly correlated with lake ice melt but showed no long-term temporal trend (1986–2019). Climatic warming in the region, which has been and is forecasted to be strongest in the summer and autumn, is predicted to lead to a 5%–27% decline in salamander body condition under realistic near-future climate scenarios. Although the subterranean environment offers a thermal buffer, the observed decline in condition and relatively strong effect of summer temperature on body condition suggest that fossorial salamanders are sensitive to the effects of a warming climate. Given the diversity of fossorial taxa, heightened attention to the vulnerability of subterranean microhabitat refugia and their inhabitants is warranted amid global climatic change.

KEYWORDS
Ambystoma maculatum, body condition, climate change, ecophysiology, metabolic rate, microhabitat, phenology, reproduction

1 | INTRODUCTION

Global climate change is unequivocal, and rates of observed and predicted temperature increases are greater at higher latitudes (Intergovernmental Panel on Climate Change, 2014). High- and mid-latitude regions have experienced rapid environmental change

over the past half-century, including increases in mean air and surface temperature, extreme high temperature events, decreases in the number of frost-free days, and decreases in ice cover (Bartolai et al., 2015; Cohen et al., 2014). The short post-glacial history of the Northern hemisphere mid-latitudes, combined with regional geology, climate, and varied habitat types, makes this region the

northern range edge of many cold-adapted ectotherms (Lesbarrères et al., 2014; Seburn & Bishop, 2007; Sunday et al., 2011). Some of these temperate, cold-adapted species may respond to climate change with latitudinal and altitudinal range shifts, and indeed, such shifts are increasingly documented among terrestrial species (Chen et al., 2011; Hughes, 2000; Walther et al., 2002). However, not all taxonomic groups are highly mobile and capable of rapid or long-distance dispersal in response to unfavorable environmental conditions. For instance, the slow dispersal of many ectothermic vertebrates, including some amphibians, relative to the accelerating rate of climate change imposes hard limitations on geographic range shifts as a response to climate change (Blaustein et al., 2010).

Amphibians—especially high latitude, mid latitude, and northern range edge populations—are expected to respond strongly to climate change due to their specific reproductive requirements, complex life histories, and often short breeding period (Daszak et al., 2005; Fitzpatrick et al., 2020). Climate-induced shifts in reproductive timing and biology are very well reported for anurans (Beebee, 1995a, 1995b; Gibbs & Breisch, 2001; Klaus & Lougheed, 2013; McCarty, 2001; Sheridan et al., 2018; Terhivuo, 1988; Todd et al., 2011; Tryjanowski et al., 2006; Walpole et al., 2012). Of broader concern, however, is that climatic change is negatively impacting amphibian populations by reducing net resource acquisition rates of individuals and/or inducing physiological (temperature and/or water) stress, leading to lower body condition and curtailed reproductive efforts. Decreases in anuran body size, body condition, and fecundity, for example, have been attributed to increases in temperatures or proxy measures thereof (Benard, 2015; Lannoo & Stiles, 2017; Reading, 2007; Sheridan et al., 2018). Amphibian responses to a changing environment are complex and have been shown to vary in a number of ways. For example, warmer winters were correlated with an increase in body size in two species of European ranid frogs (Tryjanowski et al., 2006). Annual drought severity, including the interplay of temperature and precipitation, was correlated with decline in Crawfish Frog (*Lithobates areolatus*) body condition and fecundity (Lannoo & Stiles, 2017). Regional changes in frost-free days and precipitation across North America explain sex-specific responses in body size, including body size increases and decreases, in the Wood Frog (*Lithobates sylvaticus*) over the past century (Sheridan et al., 2018). Climatic warming and drying have been implicated in reducing body size of plethodontid salamanders in eastern North America (Caruso et al., 2014; but see Connette et al., 2015). In sum, there is strong evidence that the breeding biology and life cycles of amphibians, among other taxa, are responding to rapid climate change.

The cryptic and relatively fossorial nature of many amphibians has generally impeded research into relationships between climate change and biology (but see Beebee, 1995a, 1995b; Kirk et al., 2019; Kusano & Inoue, 2008; Todd et al., 2011). Yet, fossorial lifestyles are common in amphibians: an estimated 11% of known amphibian species (723 spp.) associate with underground environments, including 7% of frogs (397 spp. of Anura), 23% of salamanders (145 spp. of Caudata), and 97% of caecilians (181 spp. of Gymnophiona; Oliveira et al., 2017). Although non-fossorial amphibians are likely to bear

the brunt of rapid warming, fossorial species have been largely overlooked in climate change studies, perhaps owing to the untested assumption that they are safeguarded by living in a thermally buffered underground environment. Subterranean-dwelling *Ambystoma* salamanders, for instance, demonstrate strong dependence on temperature and precipitation to signal aboveground migration and breeding, but bouts of surface activity are short (Blanchard, 1930; Douglas, 1979; Sexton et al., 1990). Thus, subterranean microhabitat use may mediate exposure to thermal and moisture extremes, thereby allowing individuals to persist within their physiological tolerances in otherwise inhospitable ambient environments (Moore et al., 2018; Scheffers et al., 2013; Scheffers, Edwards, et al., 2014). Fossorial lifestyles in amphibians are, in fact, broadly associated with temperate regions characterized by climatic variability, high temperature variation, and/or low precipitation (Oliveira & Scheffers, 2019), suggesting that below-ground microhabitat use mediates climatic extremes, allowing persistence in challenging above-ground environments.

If fossorial salamanders demonstrate sensitivity to climatic change, then there could be broad repercussions, as salamanders contribute important ecological roles, including trophic structuring, leaf litter and soil nutrient cycling, and carbon sequestration (Best & Welsh, 2014; Davic & Welsh, 2004). The goal of this study is to explore the thermal sensitivity of body condition (i.e., general health, vigor) and key lifecycle events of a fossorial amphibian, leveraging a long-term dataset on the Spotted Salamander (*Ambystoma maculatum*; Shaw, 1802). Since 1986, Spotted Salamander reproductive biology and breeding phenology has been studied non-continuously in their northern distribution in Algonquin Provincial Park, Ontario, Canada. Concurrent with global and regional climate change, changes in seasonal temperature and precipitation have occurred in Algonquin Provincial Park over the past half-century (Lemieux et al., 2007; Ridgway et al., 2018; Waite & Strickland, 2006). Our first objective was to estimate the relationship between annual climate (temperature, precipitation, and ice conditions) and body condition, population-level reproductive output, and breeding phenology for the Spotted Salamander. Our second objective was to predict trends in salamander breeding body condition under realistic near future (2050–2100) climate scenarios. Our third objective was to estimate longitudinal trends in the reproductive biology of the Spotted Salamander.

2 | METHODS

2.1 | Study species and area

The Spotted Salamander (*A. maculatum*) is a medium-bodied member of the mole salamander group and is widespread in the forests of eastern North America. The species is a not true burrower (Semlitsch, 1983), instead relying on the burrows created by small mammals (e.g., *Blanaria*, *Peromyscus*, *Tamias*; Faccio, 2003; Kleeberger & Werner, 1983; Madison, 1997; Montieth & Paton, 2006; Windmiller, 1996).

Brief periods of aboveground activity, limited to late winter/early spring breeding and autumn movement, are strongly cued by weather, namely rainfall and spring thaw at northern latitudes (Baldauf, 1952; Madison, 1997; Sexton et al., 1990). Spotted Salamanders are not freeze-tolerant and overwinter below the frost line (Madison, 1997). Breeding occurs in shallow water and females can lay multiple egg masses during a single spring reproductive period (Petranka, 2010). Long-term observations suggest that females in our study population do not breed annually and/or are highly transient at the breeding site (P.D. Moldowan, unpublished data).

Bat Lake in western Algonquin Provincial Park is a naturally acidic (pH 4.6) and fishless kettle bog with permanent water (3.4 ha open-water surface area; mean depth: 4.5 m; maximum depth: 8.3 m; Hoeniger, 1986) in the low latitude boreal wetland region (Zoltai et al., 1988) of Ontario, Canada. The region is characterized by a relatively high elevation (300–600 m above sea level) that is wetter and cooler than the surrounding landscape (150 m). The active season for Spotted Salamanders in the region, defined as the non-freezing period during which salamanders are post-breeding and presumed feeding, spans approximately ordinal day 140–288 (May 20–October 15). This northernly location within the Spotted Salamander geographic range, local elevation, and prevailing climatic means that the Bat Lake salamander population effectively lives near a climatic range edge.

2.2 | Data collection

The breeding biology of Spotted Salamander was studied non-continuously from 1986 to 2019 at Bat Lake. Prior to 2008, breeding phenology data (first egg-lay date) were sporadically collected by various observers (1986, R.G. Tozer and D. Strickland in Oldham & Weller, 1989; 1992–1993, D.C. Cunnington, unpublished; 2004–2007 author G.J. Tattersall). Between 2008 and 2019, the capture–mark–recapture study and reproductive monitoring were conducted annually. Each year ($N = 12$; 2008–2019) we conducted salamander trapping using non-baited aquatic funnel traps and egg mass counts, commencing at lake ice-off and continuing daily throughout the duration of the 3- to 4-week spring breeding period. Each year we distributed traps equidistantly (spaced 8–10 m apart) around the perimeter of the lake at fixed locations. Captured salamanders were measured for snout–vent length (SVL) and body mass. Female reproductive status (gravid or spent) was assessed by visually inspecting the venter for abdominal distension and visible ova. Individuals were marked with a single toe clip, digitally photographed, cataloged in a photo identification database, and recaptures were identified by their unique spot pattern using Interactive Individual Identification System Classic software (v. 4.0.2., den Hartog & Reijns, 2020; van Tienhoven et al., 2007). Trapping ended following three consecutive days of no salamander captures, coinciding with the mass emigration of adults out of the lake at the end of the breeding season, or until water temperature at submerged trap depth reached 10°C (as to not risk severe hypoxia in submerged salamanders).

We conducted whole lake egg mass counts, a measure of population-level reproductive output, throughout the annual sampling period by paddling the vegetated perimeter of the lake and counting egg masses with the aid of polarized sunglasses. Egg mass counts ceased when egg mass abundance plateaued and/or salamander captures declined sharply in traps, signifying the end of breeding.

2.3 | Hypothesis testing and statistics

We were interested in whether climatic conditions prior to breeding influence female and male breeding body condition, population-level reproductive output (egg mass abundance), and spring breeding phenology. We therefore identified plausible environmental predictor variables related to the breeding biology and life history of temperate amphibians (Table S1), including environmental conditions from the preceding summer, autumn, winter, and the contemporary spring period. These predictors included mean temperature (°C) and total precipitation (mm) of the summer (July and August), autumn (September and October), pre-winter (November), and spring periods (April and/or May), as well as the number of days from lake surface freeze to thaw (ice-on duration, a proxy for the length of winter and hence salamander dormancy), and the ordinal date of majority lake ice-off (i.e., first breeding opportunity for pond-breeding salamanders; Table S1). Climate data were retrieved from the Algonquin Provincial Park East Gate climate station (45°32′N, 78°16′W; Environment and Climate Change Canada: www.climate.weather.gc.ca) located approximately 30 km east of Bat Lake. Annual ice-off dates were known for Bat Lake, although annual ice-on dates were not available. We used ice-on date and ice-on duration from Lake of Two Rivers (2007–2019), a long-term monitoring site within two kilometers of Bat Lake (R.G. Tozer, unpublished data), as a proxy for Bat Lake. Annual ice-off dates for Bat Lake and Lake of Two Rivers for the period of data overlap (2008–2019) were highly correlated (Pearson correlation: $r = 0.93$, $p < 0.0001$).

Statistical analyses were completed in R statistical software (version 3.6.3, R Development Core Team, 2020). We used an information-theoretic approach (Burnham & Anderson, 2002; Burnham et al., 2011; Nakagawa & Schielzeth., 2013) and developed an ecologically relevant set of candidate models for each response variable, with each unique candidate set addressing one of the three major response variables in our study (body condition, reproductive output, and breeding phenology); below, we broadly describe these hypotheses for each variable (Tables S2–S4). All models in each candidate set were fit with maximum likelihood then ranked according to the second-order Akaike's information criterion (AICc; Burnham & Anderson, 2002). The best-ranked models in each set ($\sum w_i \geq 0.95$; Burnham & Anderson, 2002) were carried forward for model averaging (using subset or "natural averaging," as opposed to full-model averaging; Burnham & Anderson, 2002; Symonds & Moussalli, 2011) using the R package MuMIn (version 1.43.17; Bartoń, 2020).

We tested all response variables for temporal (i.e., year over year) autocorrelation because salamanders may skip years and

accumulate energy for reproduction over multiple seasons (e.g., Bulahova & Berman, 2017; Peacock & Nussbaum, 1973; Yartsev & Kuranova, 2015). We examined the predictor variables of each model for multicollinearity by calculating variance inflation factors (VIF) using the R package car (version 3.0.10, Fox & Weisberg, 2019). All predictors were retained in the models unless stated otherwise.

2.4 | Body condition

Salamander body condition at the time of breeding (late April through mid-May) reflects their state following overwintering, which at the latitude and elevation of our study site means that salamanders have presumably not fed for the preceding 5–6 months, from the onset of freezing temperatures (November) of the preceding year. Female and male breeding body condition for the period of 2008–2019 was calculated as the scaled mass index (SMI; Peig & Green, 2009). The SMI standardizes the mass of an individual to the mean body size of all individuals in the population (female and male datasets were treated independently) while accounting for the SVL–mass allometric relationship (Peig & Green, 2009). The SMI accurately reflects the energy stores (fat) of adult newts and other amphibians (MacCracken & Stebbings, 2012) and output values are interpretable in the same unit of measure as input data (Peig & Green, 2009). To calculate SMI, we plotted ln-transformed mass and ln-transformed SVL, then fitted a line of best fit using standardized major axis regression (Peig & Green, 2009). The slope of this best fit line was carried forward as the scaling exponent for the SMI calculation. We used mean SVL (L_0, as per Peig & Green, 2009) for females and males in calculating SMI for each sex.

We reasoned that the summer and/or autumn temperature in the preceding year may affect fossorial salamander biology by altering ground temperatures, and thus affecting metabolic rate and/or the extent of thermal stress of salamanders while underground. In the absence of a compensatory response in resource acquisition by salamanders, this would result in a negative relationship between temperature and body condition, and no expected relationship between precipitation and body condition. We further reasoned that summer and/or autumn temperature from the preceding year may also affect forest productivity, thereby altering food availability when salamanders forage aboveground. If productivity and resource acquisition outweighed a metabolic or stress response, then this would manifest as a positive relationship between body condition and temperature; furthermore, under the productivity hypothesis, we also expect a positive relationship between body condition and precipitation.

Next, we reasoned that the pre-winter environment (November temperature and precipitation from the preceding year) would be related to annual variation in the length of the foraging period. We predicted that November temperature of the previous year would be positively related to body condition, and that November precipitation would be negatively related to condition, as precipitation in November is overwhelmingly snow (climate data did not differentiate between snow and rain). We predicted that ice-on duration

(i.e., winter duration) would be negatively related to body condition, reasoning that longer winter periods represent a longer non-feeding dormancy period and possibly a shorter pre-November foraging period. We reasoned that warm temperature and high rainfall during late winter/early spring of the contemporaneous breeding year would result in earlier thaw, an earlier onset of salamander breeding, and shortened overwinter fasting period. Therefore, we predicted a positive relationship between body condition and contemporaneous April temperature and precipitation.

Finally, we included ordinal date (i.e., day of year) of capture as a covariate in all models, as salamanders do not feed during breeding and are expending energy continuously. We expected that body condition would decline with ordinal capture date. Reproductive status was included as a grouping variable (yes, gravid; no, spent) in all models of female body condition, as some females were captured before laying and others post-laying. No interactions among variables were included in any model.

Ultimately, these hypotheses and their combinations resulted in a set of 17 ecologically plausible models to explain each female and male body condition from 2009 to 2019 (Tables S1 and S2; body condition data from 2008 were retained for time series analyses but excluded from linear mixed-effect models because relevant precipitation data were not available); female and male data were fit separately. Linear mixed-effects models were fit using the R Package lme4 (version 1.1.23; Bates et al., 2015). Both body condition model sets included individual ID, unique day (unique date of capture; a unique day assignment across all years in the dataset that addresses error unique to a sampling day), and year as random effects to account for the non-independence of these factors on measures of condition (Table S2). Data standardizations were used to improve the biological interpretability of regression coefficients and relative importance of predictors: The response variable (SMI) was scaled (centered then divided by the standard deviation), and all predictor (fixed effect) variables were centered prior to modeling (Schielzeth, 2010).

2.5 | Body condition: Long-term temporal and environmental relationships

We investigated whether a temporal change in body condition occurred over the study period (2008–2019). We used a separate model for each sex with random effects of year, individual ID, unique day, and fixed effects of ordinal date, year, and for females, reproductive status; below we refer to this model as the "Base Model" for each sex, as the model contains the fixed effect of year but no environmental covariates (Table 1). We inferred a temporal change in body condition if confidence intervals on the fixed effect of year (β_{Year}) did not overlap zero.

Next, we explored which environmental covariates, if any, were responsible for driving temporal changes in body condition. Drawing from our model selection procedure with the body condition model set, we sequentially substituted each environmental covariate

TABLE 1 Description of models and results exploring the sensitivity of the parameter β_{Year}, the slope of Spotted Salamander (*Ambystoma maculatum*) body condition over year, to environmental covariates. The base model for each sex does not feature an environmental covariate, whereas subsequent environmental models consider a single environmental covariate; after the addition of the covariate, the qualitative change in the magnitude and direction of β_{Year} relative to the base model is described. In all models, random effects are individual ID, unique day, and year (defined Table S1)

Model description	Fixed effects	Period	$\beta_{Year} \pm$ SE	% change in β_{Year} relative to base model
Females				
Base model F_0	Reprod status, ordinal date, year	2008–19	−0.114 ± 0.0470	—
Env model F_1	Reprod status, ordinal date, year, summer temp	2008–19	−0.0625 ± 0.0445	−45%
Env model F_2	Reprod status, ordinal date, year, autumn temp	2008–19	−0.102 ± 0.0552	−11%
Env model F_3	Reprod status, ordinal date, year, ice in duration	2008–19	−0.117 ± 0.0519	+3%
Env model F_4	Reprod status, ordinal date, year, summer precip	2009–19	−0.135 ± 0.0456[a]	+30%[a]
Males				
Base model M_0	Ordinal date, year	2008–19	−0.146 ± 0.0482	—
Env model M_1	Ordinal date, year, summer temp	2008–19	−0.106 ± 0.0509	−27%
Env model M_2	Ordinal date, year, autumn temp	2008–19	−0.128 ± 0.0556	−12%
Env model M_3	Ordinal date, year, ice in duration	2008–19	−0.141 ± 0.0530	−3%
Env model M_4	Ordinal date, year, april temp	2008–19	−0.125 ± 0.0654	−14%
Env model M_5	Ordinal date, year, summer precip	2009–19	−0.186 ± 0.0473[a]	+22%[a]

[a]Precipitation data were not available in 2007 for pairing with 2008 salamander body condition data. Therefore, Env model F_4 and Env model M_4 are based on the interval 2009–2019. The percent change in $\beta_{Year} \pm$ SE estimates is also based on the interval 2009–2019, where the base model $\beta_{Year} \pm$ SE estimate for females is −0.103 ± 0.0560 and for males is −0.152 ± 0.0594.

identified as important (i.e., where model-averaged confidence intervals did not overlap zero; Figure 1) into the base model, separately for each sex (Table 1). For each substitution, we qualitatively examined how the parameter estimate for the fixed effect of year (β_{Year}) changed relative to that of the base model. Large changes in β_{Year} relative to the base model suggested that an environmental covariate played a role in driving changes in body condition over time. Because we were interested only in parameter estimates, all models were fit with restricted maximum likelihood.

2.6 | Body condition: Forecasting body condition under climate change

Our analyses suggested that increased temperature, particularly summer temperature, was associated with a temporal decline in salamander body condition, and that this association may be dampened by increases in summer precipitation (see Section 3; Table 1). Drawing from this result, we used model-averaged parameter estimates to forecast male body condition under three realistic near-future (2050–2100) climate scenarios for Algonquin Provincial Park (Lemieux et al., 2007; Ridgway et al., 2018): up to 24% increase in mean summer precipitation and up to 3°C increase in each mean summer temperature, mean autumn temperature, and concurrent mean summer and autumn temperature. For simplicity, only male condition was used for forecasting as females had a much lower sample size coupled with multiple reproductive states.

2.7 | Egg mass counts

We assumed that the maximum observed egg mass count at the peak of breeding (2009–2019) was a suitable estimate of population-level reproductive output, as egg mass count should be related to both the number of breeding females and the number of clutches produced per female. Population-level reproductive output may be linked to climatic conditions that favor resource acquisition and body condition, and therefore, the same hypotheses that describe variation in body condition apply to egg mass counts. We included one additional fixed effect in our model set, ice-off date, reasoning that the timing of thaw may be related to how many salamanders arrive to breed (Table S1). Statistical modeling of egg mass counts was relatively simple, given that egg mass count was taken as one value (maximum) per year. Thus, we developed a set of 18 candidate models (Table S3). We compared models using AICc, as above. We also used linear regression to test whether maximum egg mass counts changed during 2008–2019.

2.8 | Spring breeding phenology

Our field observations suggested that annual variation in spring weather patterns is associated with variation in salamander breeding date. Median breeding date, retrospectively calculated as the ordinal date at which half of the maximum egg masses were deposited at Bat Lake, was used as the response variable in the candidate model set.
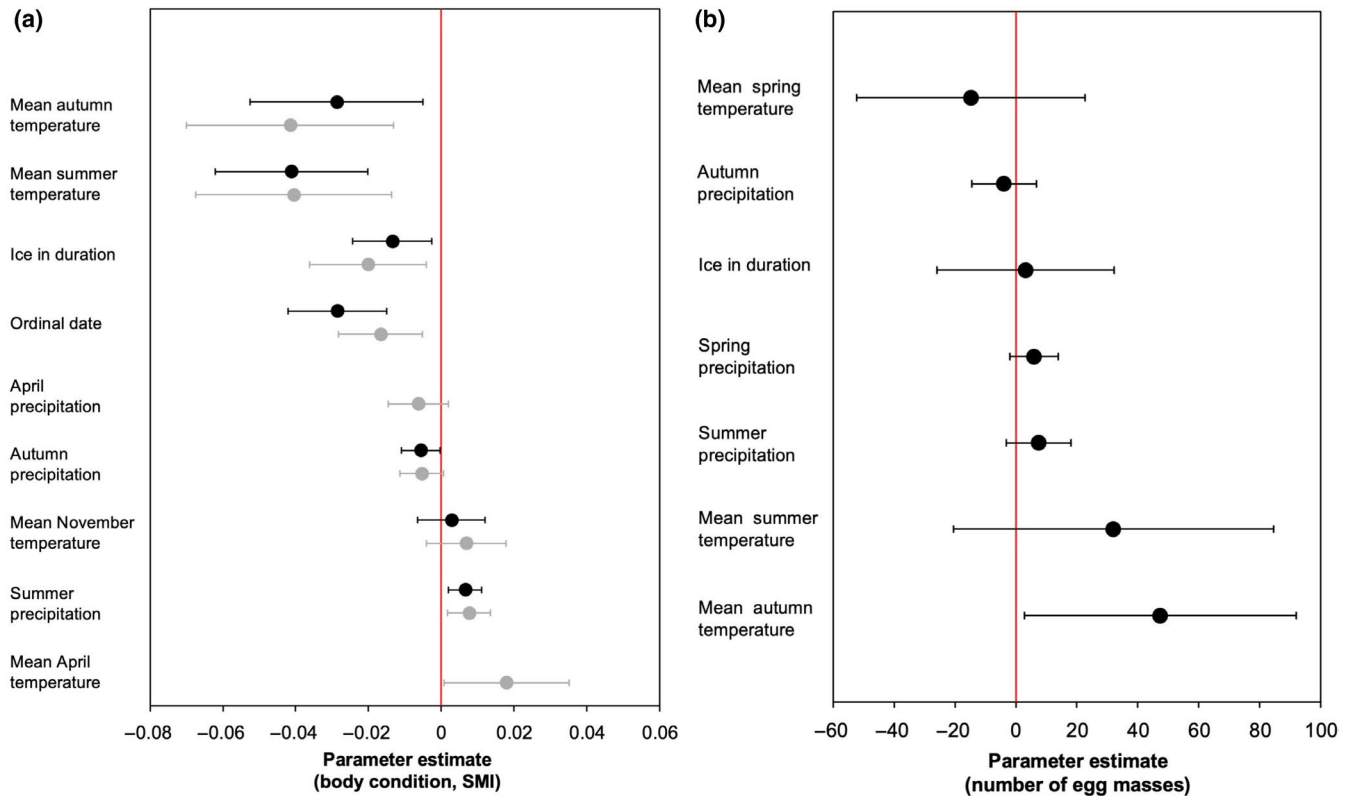
(a)

(b)

FIGURE 1 Parameter estimates from the best-ranked model set ($\sum w_i \geq 0.95$) for (a) female* (black) and male (gray) Spotted Salamander body condition (scaled mass index, SMI; Peig & Green, 2009); (b) egg mass abundance (population-level reproductive output). Adjusted standard error (Burnham & Anderson, 2002: section 4.3.3; Bartoń, 2020: 33, 42) was used to construct 95% confidence intervals of the parameter estimates. In (a) temperature estimates were multiplied by 0.1 before plotting. Also, April precipitation and mean April temperature were present in the best-ranked models of the male dataset, but absent from the corresponding female models (Table S5).
*Gravid parameter estimate (0.49 ± 0.11, 95% CI) not plotted among female body condition parameter estimates because of figure scaling

Median breeding date was selected because it is more robust to outliers compared to start date (Carter et al., 2018) and captures the period of environmental conditions responsible for the onset of major breeding activity. We reasoned that mean temperature and summed precipitation in March, April, and May, as well as Ice-off Date, could affect breeding phenology (2008–2019). We expected temperatures to be negatively associated with breeding date, as high temperature accelerates snow and ice melt. We expected ice-off date to be positively correlated with breeding date, as breeding cannot begin until ice is off the breeding pond. Lastly, we expected precipitation in March and April (usually comprising snow) to be positively associated with breeding date, and precipitation in May (cool rain) to stimulate activity and lead to earlier breeding date. Ultimately, these hypotheses and their combinations resulted in a set of six candidate models (Table S4).

Linear regression was used to test for temporal trends in reproductive phenology using two datasets: annual first egg-lay dates (non-continuous study, 1986–2019, $N = 19$ years) and annual first egg-lay, median egg-lay, and peak egg-lay dates (focal study period, 2008–2019, $N = 12$ years). Finally, because ice-off date was a very strong predictor of salamander breeding (see Section 3), we examined trends in ice-off phenology at Bat Lake (2008–2019, $N = 12$ years)

and nearby Lake of Two Rivers (1973–2019, $N = 44$ years available; R.G. Tozer, unpublished data).

2.9 | Salamander metabolic rate estimation

During the period of August 2017 to September 2020, dataloggers (HOBO TidbiT® v2) recorded temperature every 2 h at three soil depths (shallow/surface, 0 m; mid-depth, 0.5 m; deep, 1.0 m) in the forest surrounding Bat Lake. We used soil thermal profiles from Bat Lake and the Spotted Salamander temperature-metabolic rate relationship reported by Whitford and Hutchison (1967) to estimate metabolic rate for Bat Lake Spotted Salamanders. See the Supporting Information file for full metabolic rate estimation methods.

3 | RESULTS

Over the period of 2008–2019, we recorded 1004 capture events of 956 individual female and 3247 capture events of 2176 individual male Spotted Salamanders. Male-biased capture rates likely resulted from sampling methodology (aquatic funnel traps disproportionately

intercept mate searching males), differential breeding turn-out of the sexes, and/or a male sex bias in the population. Body condition sample sizes are therefore much larger for males than for females.

3.1 | Body condition

The best supported model predicting female body condition included summer temperature, summer precipitation, ice-on (winter) duration, and reproductive status (Model FBC_{13}: $w = 0.60$; Table S5). Although there was model selection uncertainty, Model FBC_{13} was still five to eight times more likely to be the best model compared to the next-best models in the candidate set (Table S5). As with females, male body condition was best predicted by a model that included summer temperature, summer precipitation, and ice-on duration (MBC_{13}: $w = 0.39$, Table S5). A model that included summer temperature, autumn temperature, and November temperature was also competitive in explaining male body condition (MBC_8: $w = 0.19$).

Among model averaged parameter estimates, summer temperature, autumn temperature, ice-on duration, ordinal date, and reproductive status (for females) were important predictors of female and male body condition (Figure 1a). Higher mean summer and autumn temperatures, a longer winter duration, and later spring capture date negatively affected both female and male body condition (Figure 1a). We found no significant temporal (i.e., year over year) autocorrelation in mean female body condition when tested with all three datasets (gravid, spent, and pooled datasets; Figure S1a–c), but mean male body condition demonstrated marginally significant temporal autocorrelation at a 1-year time lag (Figure S1d).

3.2 | Body condition: Long-term temporal and environmental relationships

We found that female body condition declined during 2008–2019 ($\beta_{Year} \pm SE = -0.114 \pm 0.0470$; Figure 2). Substituting summer temperature into the base model resulted in a 45% reduction in the magnitude of the parameter estimate for year ($\beta_{Year} = -0.0625 \pm 0.0445$), whereas little change in β_{Year} was observed when substituting autumn temperature, or ice-in duration (Table 1). Using data from 2009 to 2019 (as no 2007 precipitation data were available to pair with 2008 condition data), body condition declined across time for females, albeit marginally ($\beta_{Year} = -0.104 \pm 0.0560$) and substituting summer precipitation into the base model slightly increased the magnitude of β_{Year} ($\beta_{Year} = -0.135 \pm 0.0456$, a 30% increase; Table 1).

Results were broadly similar for males. Body condition declined during 2008–2019 in males ($\beta_{Year} = -0.146 \pm 0.0482$; Figure 2), and substitution of summer temperature into the base model resulted in a 27% reduction in the magnitude of β_{Year} ($\beta_{Year} = -0.106 \pm 0.0509$). We observed modest changes in β_{Year} when substituting autumn temperature, ice-in duration, and April temperature into the base model (Table 1). Using data from 2009 to 2019 (again, no 2007 precipitation data were available to pair with 2008 condition data), body
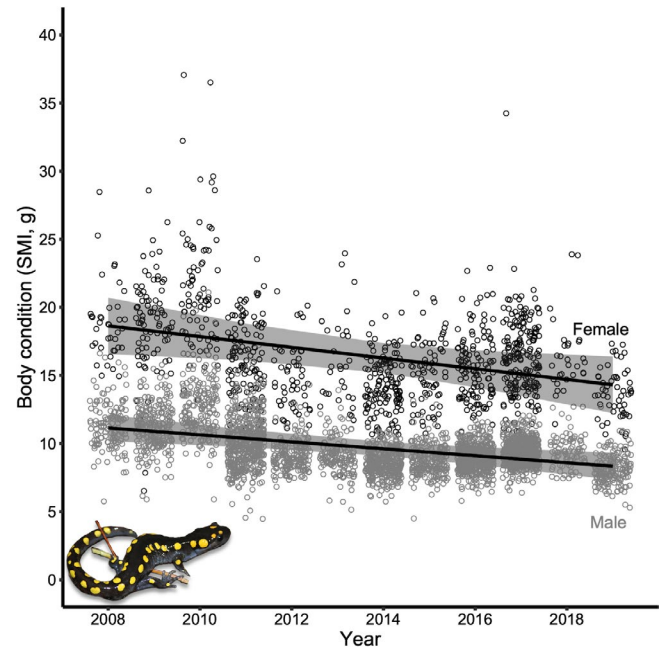
condition declined across time for males ($\beta_{Year} = -0.152 \pm 0.0594$) and substituting summer precipitation increased the magnitude of β_{Year} in the model ($\beta_{Year} = -0.186 \pm 0.0473$, a 22% increase; Table 1). In sum, holding summer temperature constant tended to dampen the temporal decline in condition in females and males, suggesting summer temperature played a role in driving the temporal decline in condition; holding summer precipitation constant tended to exacerbate the decline in condition in males and females, suggesting that annual variation in summer precipitation moderates the temporal decline in condition.

3.3 | Body condition: Forecasting body condition under climate change

Assuming a linear relationship between temperature and body condition loss (and no compensatory response by salamanders), warming of Mean Summer Temperature by 1–3°C is predicted to reduce male breeding body condition by 5%–14% (−0.25 to −0.75 SD of body mass; Figure 3a) for an average breeding condition male ($\bar{x}_{SMI} \pm SD = 9.7 \pm 1.8$ g, all breeding males 2008–2019). Warming of mean autumn temperature by 1–3°C is predicted to cause a body condition decline of 5%–9% for an average condition male (−0.25 to −0.50 SD of body mass; Figure 3b). Simultaneous increases in both mean summer and autumn temperature of 1–3°C are expected to be additive and expedite body condition loss, with declines of 10%–27%
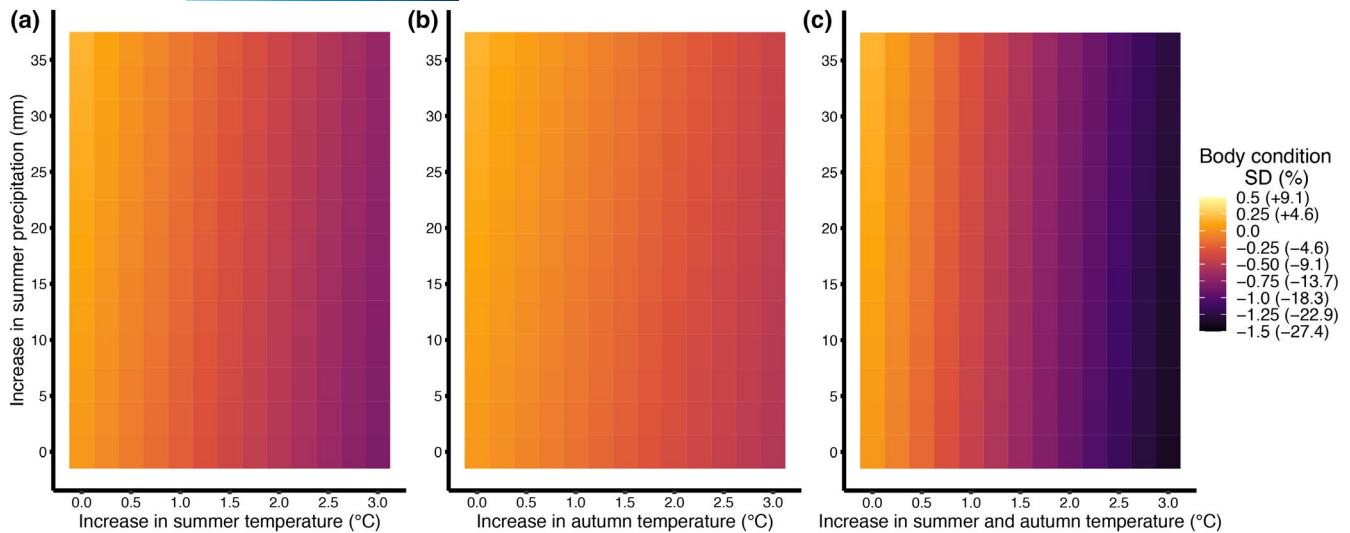
FIGURE 3 Forecast of male Spotted Salamander (*Ambystoma maculatum*) body condition under realistic climate scenarios (2050–2100) for western Algonquin Provincial Park: (a) increasing summer precipitation (up to 36 mm, or 24% increase in mean summer precipitation) and increasing mean summer temperatures (increase up to 3°C); (b) increasing summer precipitation and increasing mean autumn temperatures; and (c) increasing summer precipitation and increasing mean summer and autumn temperatures (synchronous increases up to 3°C in both seasons). Using 2008–2019 climate data as a baseline, the SD in mean annual summer and autumn temperature is 1.1°C and the SD in mean summer precipitation is 50 mm. Therefore, realistic near-future warming of 2–3°C would be approximately ≥2 SD above current seasonal temperatures, whereas realistic near-future summer precipitation increases (20%–24%, equivalent to 30–36 mm) are <1 SD of current values. Near-future climate scenarios are based on Lemieux et al. (2007) and Ridgway et al. (2018)
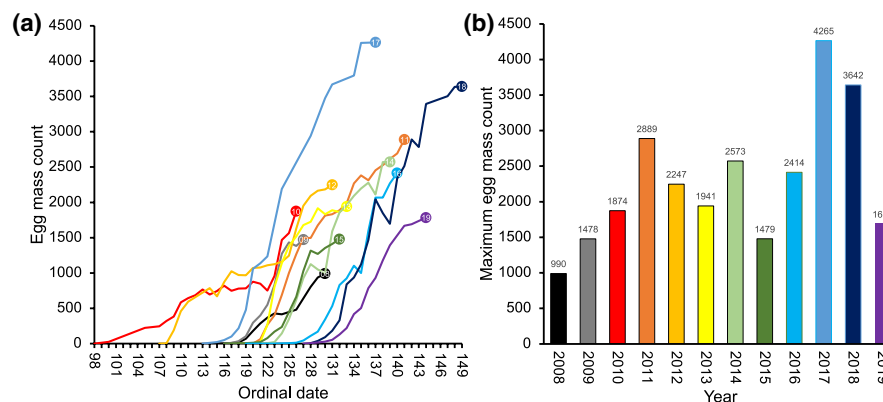

FIGURE 4 Time series of Spotted Salamander (*Ambystoma maculatum*) egg mass abundance at Bat Lake, Algonquin Provincial Park (2008–2019). (a) Daily egg mass counts starting at first egg lay date and extending until maximum (peak) values. During 2008–2019, the earliest breeding start date was ordinal date 98 (April 7, 2010), latest breeding start date was day 129 (May 9, 2019), and the mean first breeding date was day 116 (April 26). Egg mass count values that extended post-peak were excluded to improve visual clarity of the plot. (b) Maximum egg mass count per annum

(−0.50 to −1.50 SD of body mass; Figure 3c). Realistic concurrent increases in precipitation are predicted to offer very little to no buffering of temperature-driven body condition decline (Figure 3).

3.4 | Reproductive output

Maximum egg mass abundance (2008–2019) showed substantial interannual variation across breeding seasons, varying by approximately 400% (Figure 4). A model containing autumn temperature best explained annual egg mass abundance; however, overall support and fit was weak for this model (Model RO_5: $w = 0.38$, $R^2_{adj} = 0.25$) and there was considerable overall model selection uncertainty (Table S6). Model-averaged parameter estimates suggested autumn temperature was positively associated with maximum egg mass abundance, although uncertainty was high (Figure 1b; also see Figure S2). We detected no temporal autocorrelation in annual egg mass abundance (Figure S1e).

3.5 | Spring breeding phenology

During 2008–2019, the mean first breeding date of Spotted Salamanders at Bat Lake was ordinal date 116 (April 26). Across this period, first breeding date varied by 31 days (earliest breeding date: day 98, April 7, 2010; latest: day 129, May 9, 2018). Salamander first breeding date ($r^2_{adj} = 0.29$, $p = 0.04$), median breeding date ($r^2_{adj} = 0.39$, $p = 0.02$), and peak breeding date ($r^2_{adj} = 0.51$, $p = 0.006$) became significantly later during 2008–2019 (Figure 5a); however, the longer time series (1986–2019) showed no trend in first breeding date ($r^2_{adj} = 0$, $p = 0.54$; Figure 5b).

Model selection showed strong support for Model BP_6 in which ice-off date predicted median breeding date ($w = 0.93$, $r^2_{adj} = 0.67$; Table S6). Model averaging was not conducted because Model BP_6 was strongly supported. High levels of collinearity (VIF values up to 6.2) were identified among predictors in models of the breeding phenology model set (Table S4). The variable(s) with high VIF values (VIF > 3.0) in a model were removed and model selection was rerun. The overall outcome of model selection was unaffected, as strong support remained for Model BP_6 as the best-fitting model in the model set.

In subsequent analysis of ice-off dates, we detected a marginally significant delay in Ice-off date for Bat Lake ($r^2_{adj} = 0.27$, $p = 0.047$) at a rate of 1.3 days per year over the 2008–2019 monitoring period ($\beta \pm SE = 1.3 \pm 0.58$ SE). There was no change in ice-off date for the nearby long-term reference site, Lake of Two Rivers, during 1972–2019 ($r^2_{adj} = 0$, $p = 0.90$, $\beta \pm SE = 0.012 \pm 0.099$).

3.6 | Salamander metabolic rate estimation

Ground surface temperature around Bat Lake ranged mostly between 20 and 25°C, occasionally reaching 30°C, in the months of July and August (Figure 6a). Temperatures were 10–15°C at depths of 0.5–1.0 m during summer (Figure 6a). Using soil temperature recorded at

multiple depths and the Spotted Salamander temperature–metabolic rate relationship reported by Whitford and Hutchison (1967), salamanders at shallow depths (14.8°C surface mean temperature) have an estimated metabolic rate 1.3 times that of individuals at mid-depths (10.8°C mean temperature at 0.5 m depth) and 1.6 times that of individuals deep underground (9.1°C mean temperature at 1.0 m depth; Figure 6c) during the active period (May 20–October 15). Metabolic rate estimation highlighted the thermal sensitivity of these fossorial salamanders. For instance, given the Q_{10} value reported for the temperature range of 10–15°C ($Q_{10} = 4.37$; Whitford & Hutchison, 1967), a change of 1, 2, or 3°C results in a 16%, 34%, or 56% change in salamander metabolic rate, respectively.

4 | DISCUSSION

In this study, we explored the association between annual climatic variation, body condition, population-level reproductive output, and breeding phenology in a fossorial salamander over a 12-year period. First, we found that interannual variation in climate is associated with body condition and breeding phenology of salamanders, but climatic variation was not strongly associated with our measure of reproductive output. Second, body condition of females and males declined during the study period, and a slight increase in summer temperature during the study period is likely partly responsible for the decline. Third, associations between temperature and body condition were predicted to be non-trivial under realistic near-future climate change, with up to a 27% decline in body condition for a 3°C seasonal temperature increase and little evidence that precipitation increases will moderate these temperature effects.

Global amphibian diversity is highly structured across vertical strata (fossorial, terrestrial, arboreal), with a large proportion of temperate and arid species occupying subterranean environments (Oliveira et al., 2017; Oliveira & Scheffers, 2019). Microhabitat refugia in combination with behavioral thermoregulation is expected
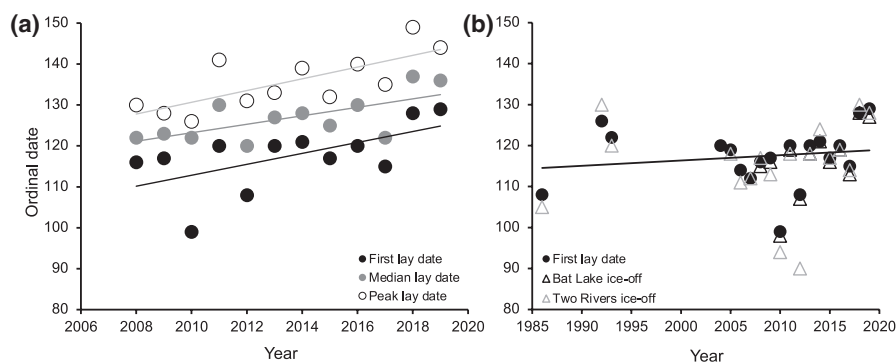

FIGURE 5 Breeding phenology of the Spotted Salamander (*Ambystoma maculatum*) at Bat Lake, Algonquin Provincial Park. (a) First egg-laying date ($r^2_{adj} = 0.29$, $p = 0.04$), median egg-laying date ($r^2_{adj} = 0.39$, $p = 0.02$), and peak egg-laying date ($r^2_{adj} = 0.51$, $p = 0.006$) have become significantly later during the focal study period (2008–2019). (b) Extended dataset of first breeding date (1986–2019) shows no temporal trend (best fit line; $r^2_{adj} = 0$, $p = 0.54$). Ice-off dates at Bat Lake (2008–2019) and nearby reference site, Lake of Two Rivers (1986–2019 shown) are highly correlated ($r = 0.93$, $p < 0.0001$) during years of data overlap (2008–2019). Note close synchrony (typically ≤24 h) between Bat Lake ice-off and first salamander egg-laying
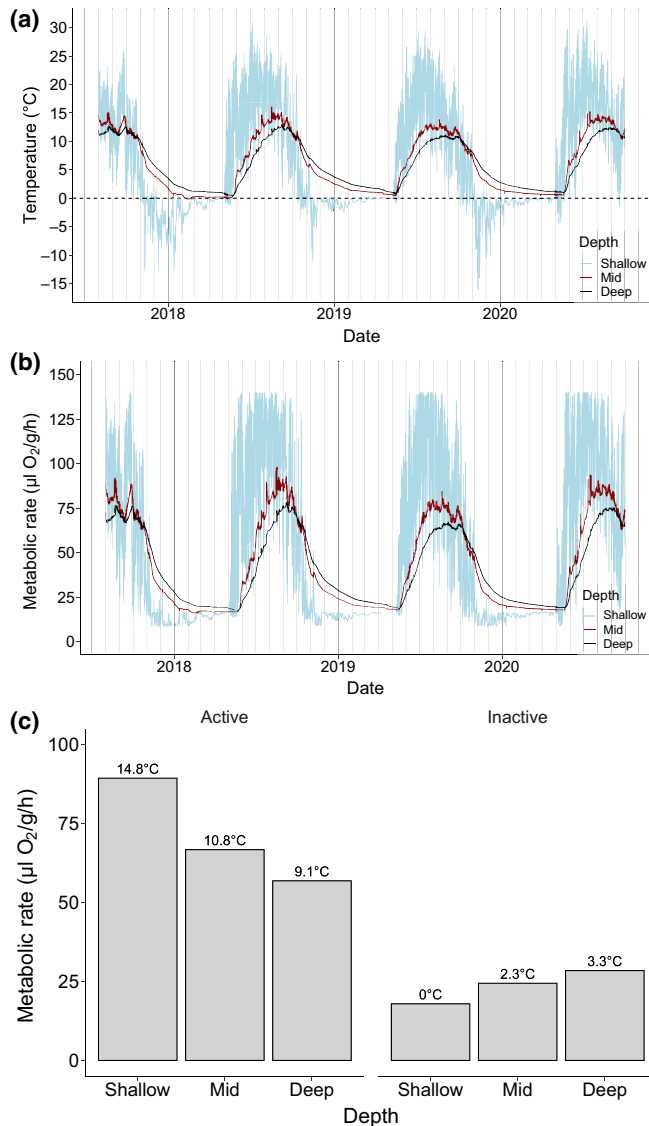
FIGURE 6 Thermal environment and estimated metabolic rate of the Spotted Salamander (*Ambystoma maculatum*). (a) Averaged thermal profile at shallow (surface, 0 m), mid-depth (0.5 m), and deep (1.0 m) soil depths from two temperature monitoring stations at Bat Lake, Algonquin Provincial Park. (b) Estimated Spotted Salamander metabolic rate based on soil thermal profiles. Estimates based on the empirical temperature–metabolic rate relationship reported by Whitford and Hutchison (1967; see Supporting Information). (c) Mean estimated metabolic rate of Spotted Salamanders at varying soil depth across the active and inactive season. For our study population, the active season spanned from ordinal day 140–288 (May 20–October 15) and was defined by the non-freezing period during which salamanders were post-breeding and presumed feeding (In (a) note that that the underground thermal gradient flips direction in mid-May and mid-October). The numerical values presented above each bar are mean soil temperatures at the respective depth and activity period. See Supporting Information for additional information about metabolic rate estimation

to be crucial for individual survival as well as population and species persistence under climate change (Fitzpatrick et al., 2020; Huey & Buckley, 2018; Lara-Reséndiz et al., 2021; Moore et al., 2018;

Scheffers et al., 2013; Scheffers, Edwards, et al., 2014). Amphibians are susceptible to direct threats (thermal and hydric stress), indirect threats (habitat change, food availability, disease risk), and interactions thereof associated with climate change (Blaustein et al., 2010; Lertzman-Lepofsky et al., 2020; Reading, 2007; Rohr & Palmer, 2013), but fossorial species may be buffered from strong climate effects, at least in the short term. This is important because salamanders, and amphibians more broadly, contribute to numerous ecological functions (Best & Welsh, 2014; Davic & Welsh, 2004), particularly in the forests of eastern North America. Nevertheless, given the global distribution, diversity, and ecological roles of fossorial amphibians, heightened attention to the vulnerability of microhabitat refugia is warranted amid global climatic change.

Our study shows that fossorial salamanders are sensitive to temperature increases, with temperature from the preceding summer and autumn negatively affecting breeding body condition. The direction of these relationships is consistent with the interpretation that reduced body condition may be driven by elevated metabolism and/or thermal stress in the summer. Direct monitoring in the forest understory around Bat Lake demonstrated that ground surface temperature ranged consistently between 20 and 25°C in July and August (Figure 6a). Notably, surface temperatures sometimes reached 30°C, which would greatly elevate metabolism (Whitford & Hutchison, 1963, 1967) and likely induce stress, as these temperatures approach the thermal critical maximum of the Spotted Salamander (Gatz, 1971, 1973; Hutchinson, 1961; Pough & Wilson, 1970). Spotted Salamanders often spend the summer and autumn periods at shallow depth (2.5–3 cm below the surface of the leaf litter; Faccio, 2003) in horizontal burrows and runways of small mammals, transitioning to use of deeper vertical burrows for overwintering (Madison, 1997; Montieth & Paton, 2006; salamanders at depths of 30–122 cm are known during summer, Gordon, 1968; Kleeberger & Werner, 1983). Although temperatures are buffered in the subterranean environment, thermal profiles at depths of 0.5–1.0 m at Bat Lake indicated that temperatures still reached 10–15°C during summer (Figure 6a). The temperature sensitivity of metabolic expenditure of Spotted Salamanders at 10–15°C is high (Q_{10} = 4.37 at 10–15°C, based on metabolic rate measured across a temperature range of 5–30°C; Whitford & Hutchison, 1967), which could explain the association between reduced body condition and high active seasonal temperatures. Using soil temperature data, we estimated that salamanders at warmer shallow depths have a metabolic rate 1.3–1.6 times that of individuals at cooler deeper depths (0.5–1.0 m depth; Figure 6c). Furthermore, temperature increases of 1–3°C are estimated to result in sizable increases in salamander metabolic rate (16%–56% change in metabolic rate), suggesting substantive energetic consequences within these commonly encountered spring and summer temperatures. Spotted Salamander microhabitat selection during the active season, including use of areas with deeper leaf litter, high plant and natural object cover, and high small mammal burrow densities, is consistent with preferences for cool damp conditions that would reduce metabolic rate (Faccio, 2003; Montieth & Paton, 2006). Soil temperature profiles (Figure 6a) and metabolic rate

estimates (Figure 6b) suggest that remaining at mid-depths during the inactive (winter) period offers slight advantage for minimizing metabolism while also avoiding freezing temperatures (Figure 6b,c).

During the 12-year study period, the breeding body condition of spent females and males significantly declined (Figure 2). During this period, our study area experienced a slight increase in mean summer temperature ($\beta \pm$ SE = 0.14 $\pm$ 0.081°C, p = 0.11, n = 12 years; Table S8). In our models, holding summer temperature constant dampened the temporal decline in body condition in both sexes (Table 1) and it therefore seems likely that increases in summer temperature are at least partly responsible for the temporal decline in body condition. Longer term temperature trends for Algonquin Park show significant temperature increases (1975–2006, Waite & Strickland, 2006; 1915–2016, Favot et al., 2019). The parameter estimates for temperature–condition relationships in our models (Figure 1a), and projected temperature increases for Algonquin Park over the next half-century (Lemieux et al., 2007; Ridgway et al., 2018), suggest that this trend in declining body condition is expected to continue (Figure 3). We did not model female body condition under near-future climate scenarios given their multiple reproductive states and a smaller sample size. However, given the synchronous decline of body condition in both sexes over the past 12 years (Figure 2) and similar seasonal temperature sensitivities of body condition in both sexes (Figure 1a), it is reasonable to expect that female body condition will continue to decline in a warming climate, as forecasted for males (Figure 3). If female body condition declines continue, individual- and population-level consequences may begin to manifest, such as reduced egg size, clutch size, reproductive frequency, and survival.

The negative relationship between body condition and ice-on (winter) duration can be reasonably attributed to extended fasting in years of late ice-off. Similarly, later spring capture dates resulted in reduced body condition of females and males, a result corroborated in similar salamander field studies (Homan et al., 2018; Strickland et al., 2015), and likely related to their non-feeding status and energy expenditure throughout winter (Figure 6b) and during early spring migration and breeding. Although we did not forecast how changes in ice-on duration may affect body condition (largely due to the lack of any projection available), it seems likely that warmer fall temperatures will be associated with decreases in winter duration in future climates, and hence relatively warm temperatures in the over-wintering environment (Figure 6a), which may partly offset the energetic benefit of a shortened winter duration. Furthermore, based on parameter estimates (Figure 1a), a change in ice-on duration of approximately 20 days is associated with the same change in body condition as a 1°C change in summer temperature, suggesting that temperature effects during the active season would overwhelm any benefit associated with shorter winter (fasting) duration.

Our forecast of salamander body condition assumed that salamanders do not demonstrate a compensatory response to warmer temperatures, although behavioral thermoregulation in response to elevated temperatures is a reasonable expectation (Huey & Buckley, 2018; Kearney et al., 2009). Spotted Salamanders often reside in shallow horizontal burrows during the active season (Faccio, 2003;

Madison, 1997) but could become more reliant on vertical small mammal burrows that offer cooler refuge. Although a shift from horizontal to vertical habitat use during the active season may relieve salamanders from high temperatures and elevated metabolism, sheltering deeper underground may further complicate energy acquisition and/or retention by stymieing near-surface foraging opportunities (Gordon, 1968).

Mean autumn temperature was positively correlated with egg mass abundance (Figure 1; Figure S2). A positive association between autumn temperature and egg mass counts suggests energetic gain at the individual level during autumn, but this is contradictory to our analyses incorporating individual-level information, which suggest that autumn temperature was negatively correlated with female body condition. We suspect, for several reasons, that the positive association between autumn temperature and egg mass counts is spurious. First, the frequency of female reproduction in our population is likely not annual (as with Homan et al., 2018; Husting, 1965) and this may confound interpretation of temperature and population-level reproductive output because individuals are amassing energy over multiple years. Second, philopatry at the breeding site may be low, but interpretation of egg mass abundance implies that Bat Lake is the only breeding site used by salamanders within this population. Although pond-breeding amphibians are reputed for their philopatry to breeding sites (e.g., Gamble et al., 2007; Gill, 1978; Semlitsch, 2008; Vasconcelos & Calhoun, 2004), it is also evident that breeding individuals use alternative sites (e.g., colonization of created ponds; Denoël et al., 2017; Patrick et al., 2008; Petranka et al., 2003). Also, temperature may influence reproduction at a finer scale, such as egg size and clutch size (e.g., Fraser, 1980) or clutch partitioning (female Spotted Salamanders are reported to lay two to four egg masses per reproductive bout; Petranka, 2010), rather than at population-level through breeding turnout. In sum, it seems unlikely that autumn temperature is positively associated with egg mass counts, and that more detailed, individual-level data on reproduction may be needed to estimate associations between climate and reproductive output.

We did not find evidence to suggest that salamander breeding phenology was advancing concurrent with climatic warming. Although Algonquin Park and surrounding regions have experienced a warming trend of approximately 1°C in the past half-century (Lemieux et al., 2007; Ridgway et al., 2018), much of the warming has been concentrated in the summer and autumn (Favot et al., 2019; Waite & Strickland, 2006). Given that salamander breeding phenology is closely associated with spring conditions, primarily ice-off, and that there has been little to no significant advancement of spring thaw conditions in Algonquin Park, salamander breeding phenology remains unchanged over the past several decades in the higher elevation uplands of western Algonquin Park. Over our period of continuous monitoring (2008–2019), Spotted Salamanders demonstrated phenological delay in reproductive timing. Arietta et al. (2020) also reported delayed breeding (2000–2020) in another early-spring breeding amphibian, the Wood Frog, in the northeastern United States. These authors cite seasonally heterogeneous warming temperatures, later snow accumulation, and longer spring

snow and ice persistence for delayed breeding, analogous to that observed in Algonquin Park (Favot et al. 2019). Signals of delayed breeding in shorter term datasets of amphibians from northeastern North America (Arietta et al., 2020; this study) are in contrast to longer datasets, which tend to show mixed responses of amphibian breeding phenology to climate change: no change (North America: Blaustein et al., 2001; Green, 2017; Kirk et al., 2019; Klaus & Lougheed, 2013; Todd et al., 2011) or advancement (eastern north America: Gibbs & Breisch, 2001; Todd et al., 2011; Walpole et al., 2012; Klaus & Lougheed, 2013; northern Europe: Terhivuo, 1988; Beebee, 1995a, 1995b; Tryjanowski et al., 2006; Japan: Kusano & Inoue, 2008). Amphibians clearly demonstrate a range of species, regional, and temporal phenological responses to climate change (e.g., Muths et al., 2017; Okamiya et al., 2021).

Fossorial species are difficult to study and are underrepresented in research at the interface of organismal biology and climate change. Our findings show that fossorial species can be susceptible to rapid warming. Subterranean microhabitats, such as burrows, are buffered from surface conditions, but these environments are not completely insulated from aboveground climate. Large numbers of species live in subterranean microhabitats, especially where already extreme ambient environmental conditions prevail. Many fossorial species are ecosystem engineers, creating thermal refugia on the landscape upon which whole ecological communities are dependent (Doody et al., 2021; Pike & Mitchell, 2013), emphasizing the importance of protecting burrowing biota. Landscape-scale changes in species distributions, such as latitudinal and altitudinal shifts, in response to climate change are increasingly recognized. In contrast, comparatively little is known about thermal habitat structure and species responses to environmental change on the microhabitat scale (Scheffers et al., 2013; Scheffers, Edwards, et al., 2014; Scheffers, Evans, et al., 2014), particularly for subterranean environments (Lara-Reséndiz et al., 2021; Moore et al., 2018). Fossorial ectotherms and amphibians in particular may be at elevated risk as their thermal microhabitat warms. Our study draws attention to the vulnerability of subterranean environments and their inhabitants amid global climatic change.

AUTHOR CONTRIBUTION

Patrick D. Moldowan, Glenn J. Tattersall, and Njal Rollinson conceived of the study; Patrick D. Moldowan and Glenn J. Tattersall conducted field data collection; Patrick D. Moldowan and Glenn J. Tattersall curated the dataset; Patrick D. Moldowan, Glenn J. Tattersall, and Njal Rollinson analyzed the data; Patrick D. Moldowan, Glenn J. Tattersall, and Njal Rollinson funded the study; Patrick D. Moldowan and Njal Rollinson wrote the manuscript; Patrick D. Moldowan, Glenn J. Tattersall, and Njal Rollinson edited and approved the final version of the manuscript.

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