

# The effects of hydropattern and predator communities on amphibian occupancy

S.M. Amburgey, L.L. Bailey, M. Murphy, E. Muths, and W.C. Funk

**Abstract:** Complex, interactive ecological constraints regulate species distributions, and understanding these factors is crucial for predicting species persistence. We used occupancy analysis, which corrects for imperfect detection, to test the importance of abiotic and biotic habitat and landscape factors on probability of occupancy by Boreal Chorus Frog (*Pseudacris maculata* (Agassiz, 1850)) tadpoles. We hypothesized that hydropattern and predators are primarily important because they affect desiccation and predation risk and can interact in ways difficult to predict. We surveyed 62 wetland sites across an elevational gradient in Colorado, USA, and modeled patterns in *P. maculata* occupancy. Tadpoles were most frequently present in intermediate-length hydropattern systems with lower desiccation risk and no predatory fish because of occasional drying. *Pseudacris maculata* occupancy had a strong negative relationship with fish presence, while tadpoles, odonate larvae, and Barred Tiger Salamanders (*Ambystoma mavortium mavortium* Baird, 1850) frequently co-occurred. Dry seasonal conditions will likely result in fewer intermediate-length hydropattern ponds available for amphibian breeding. We hypothesize that this will force *P. maculata* to breed in habitats with fish. As habitats shrink, predators that co-occur with *P. maculata* are expected to concentrate in the remaining habitat and increase predation risk for developing tadpoles (assuming predators are similarly constricted in their habitat use as amphibians are).

**Key words:** species distributions, fish predation, odonate larvae, habitat suitability, amphibian decline, *Pseudacris maculata*, Boreal Chorus Frog.

**Résumé :** Des contraintes écologiques interactives et complexes régissent la répartition des espèces, et la compréhension de ces facteurs revêt une importance cruciale pour la prédiction de la persistance des espèces. Nous avons utilisé l'analyse de l'occupation, qui corrige d'éventuelles détections imparfaites, pour évaluer l'influence de facteurs abiotiques et biotiques de l'habitat et du paysage sur la probabilité d'occupation de têtards de rainette faux-grillon boréale (*Pseudacris maculata* (Agassiz, 1850)). Nous avons postulé que le schéma hydrologique et les prédateurs sont les facteurs les plus importants parce qu'ils influencent l'assèchement et le risque de prédation et qu'ils peuvent interagir de manière difficilement prévisible. Nous avons étudié 62 sites de milieu humide le long d'un gradient altitudinal au Colorado (États-Unis) et modélisé la répartition de l'occupation de *P. maculata*. Les têtards étaient le plus souvent présents dans les réseaux à schéma hydrologique intermédiaire caractérisés par un risque d'assèchement relativement faible et l'absence de poissons prédateurs en raison de l'assèchement occasionnel. L'occupation de *P. maculata* était fortement négativement corrélée à la présence de poissons, alors que la cooccurrence de têtards, de larves d'odonates et de salamandres tigrées (*Ambystoma mavortium mavortium* Baird, 1850) était fréquente. Des conditions saisonnières sèches se traduiront vraisemblablement par un moins grand nombre d'étangs à schéma hydrologique intermédiaire disponibles pour la reproduction des amphibiens. Nous postulons que cela forcera *P. maculata* à se reproduire dans des habitats renfermant des poissons. La réduction des habitats entraînera une concentration accrue des prédateurs qui coexistent avec *P. maculata* dans les habitats restants et un plus grand risque de prédation pour les têtards (en présumant que, comme pour les amphibiens, l'utilisation de l'habitat par les prédateurs sera restreinte). [Traduit par la Rédaction]

**Mots-clés :** répartition des espèces, prédation par les poissons, larves d'odonates, qualité de l'habitat, déclin des amphibiens, *Pseudacris maculata*, rainette faux-grillon boréale.

## Introduction

Numerous factors control the distribution and persistence of species globally, and better predictions of future distributions can be made if factors most important to habitat suitability are identified. Factors that regulate habitat suitability for a species may include abiotic and biotic habitat characteristics along with landscape features (Pilliod et al. 2002; Scherer et al. 2012), but isolating these factors and understanding their individual and combined roles in determining species distributions is challenging.

We focused on modeling amphibian occurrence due to their sensitivity to environmental conditions (Bartelt and Peterson 2005), their presence in freshwater habitats vulnerable to climatic stochasticity (Matthews et al. 2013), and their already heightened conservation risk (Stuart et al. 2004; Adams et al. 2013). Amphibians play a crucial role in ecosystem food webs and nutrient transfer between terrestrial and aquatic environments (Seale 1980; Ranvestel et al. 2004), highlighting the importance of their conservation. In addition, many amphibians utilize ephemeral ponds

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**Table 1.** Hypotheses of covariate relationships to probability of occupancy of Boreal Chorus Frog (*Pseudacris maculata*) tadpoles.

	Relationship	Ecological justification	
<b>Primary factors</b>			
Hydropattern (HYDRO)			
Very ephemeral (VE)	–		Rapid drying excludes breeding and persistent populations (Matthews et al. 2013)
Ephemeral (E)	+		Favorable temperatures and vegetation, exclusion of fish (Hammerson 1999; Scherer et al. 2012), but rapid drying
Intermediate-length (I)*	+		Moderate vegetation with less desiccation risk and exclusion of fish predators (Hammerson 1999; Scherer et al. 2012)
Permanent (lack of VE, E, I)	–		Cool temperatures, lack of emergent vegetation, and predominance of fish (Newman 1989; Hecnar and M'Closkey 1997; Skelly et al. 2002)
<b>Predators</b>			
Fish (FISH)*	–		Exclusionary predator (Hecnar and M'Closkey 1997; Hero et al. 1998)
Odonate larvae (ODO)	+/-		Co-occur in similar habitats but alter developmental stress and predation (Amburgey et al., submitted and in review <sup>1</sup> )
Salamanders (SAL)	+/-		Moderate predator (Maret and Collins 1994) but similar habitat needs
	Relationship	Source	Ecological justification
<b>Secondary factors</b>			
Conductivity (COND)	–		High conductivity may be detrimental (Hamer and Parris 2011)
Vegetative cover (VC)	+		Used for oviposition (Hamer and Parris 2011; Scherer et al. 2012)
Impervious surface (IMPER)	–	NLCD <sup>†</sup>	Less suitable habitat and dispersal barriers (Murphy et al. 2010b)
Ponds near (PN)	+	NWI, <sup>‡</sup> NAIP <sup>§</sup>	Source of immigrants and metapopulation dynamics (Murphy et al. 2010a)
Heat load index (HLI) <sup>  </sup>	+	SRTM <sup>¶</sup>	Increased vegetation for tadpoles and favorable temperatures for development (Pilliod et al. 2002)
Compound topographic index (CTI) <sup>#</sup>	+	SRTM	Increased moisture, movement facilitated between sites, and seasonal feeding habitats created (Spencer 1964; Pilliod et al. 2002)

\*Intermediate-length hydropattern systems were predicted to have the highest occupancy and fish were expected to exclude *P. maculata* from sites.

<sup>†</sup>National Land Cover Database 2006 (Fry et al. 2011): 30 m resolution, 0%–100% impervious surface measure.

<sup>‡</sup>National Wetlands Inventory 2013 (USFWS 2013): 1 m resolution.

<sup>§</sup>National Agriculture Imagery Program 2011 (USDA 2011): 1 m resolution.

<sup>||</sup>McCune and Keon (2002).

<sup>¶</sup>Shuttle Radar Topography Mission digital elevation model (DEM) (USGS 2004): 30 m resolution.

<sup>#</sup>Moore et al. (1993).

that are most vulnerable to seasonal drying, and these systems are among the most biodiverse and ecologically important (Ormerod et al. 2010).

Hydroperiod, the time water is present in a pond, is tightly linked with seasonal conditions (Corn 2003; Matthews 2010) and shortening of this period may negatively impact organisms that utilize these habitats for breeding and larval development. Even a small reduction in hydroperiod may have a disproportionate effect on larval survival (Matthews et al. 2013), potentially affecting population persistence. Snowmelt is critical for wetland recharge for many amphibian species (Corn 2003), making seasonal conditions an important factor in habitat suitability (Corn 2003; Matthews et al. 2013). Water availability strongly regulates habitat suitability by affecting characteristics like temperature (through depth), habitat vegetation, and desiccation risk directly (Pechmann et al. 1989; Skelly et al. 2002). Changes in the rate of drying and the timing of water cycling within a system also regulate habitat suitability and breeding success of aquatic organisms (Matthews et al. 2013). Hydropattern allows for the characterization of hydroperiod in addition to fluctuations of pond volume and timing that affect habitat suitability (Poff et al. 1997; Jackson 2006), providing a useful variable for assessing the importance of water in freshwater ecosystems (Poff et al. 1997).

In addition to hydropattern, species interactions must also be considered, as altered interactions may be the proximate cause of species' declines (Chapin et al. 2000; Gilman et al. 2010). Pond predators affect amphibian survival (Hecnar and M'Closkey 1997; Hero et al. 1998; Eklöv 2000) and developmental rate (Skelly and Werner 1990), indicating that predator community can strongly

regulate suitability of a site (Chase 2003). Distributions of predators also vary by hydropattern and certain predators such as fish may effectively exclude amphibian species from sites (Skelly 1996; Knapp 2005).

Hydropattern and predators may both impact amphibian occupancy, but little is known about their combined effect. Transition from a long to a short hydropattern system may concentrate predators and their chemical cues in the remaining habitat (Blaustein et al. 2001; Mirza et al. 2006; Amburgey et al., submitted and in review<sup>1</sup>), resulting in increased stress during amphibian larval development and higher levels of mortality (Amburgey et al., submitted and in review<sup>1</sup>). Larvae may accelerate metamorphosis plastically in response to desiccation risk or predation risk (Laurila and Kujasalo 1999; Lardner 2000; Merilä et al. 2000; Amburgey et al., submitted and in review<sup>1</sup>), though this response may be limited when changes to habitats are extreme (DeWitt et al. 1998). By identifying these factors, their current effects on species distributions, and how they vary in occupied habitats, we can better understand species distributions and what impact these factors may have if altered.

To disentangle these factors, we evaluated the impact of pond-level and landscape-level characteristics on site occupancy by Boreal Chorus Frog (*Pseudacris maculata* (Agassiz, 1850)) tadpoles, focusing on current hydropattern and predator occurrence as our primary explanatory factors (Table 1). *Pseudacris maculata* is well-suited to address these questions, as it is distributed across a wide elevational range and a broad spectrum of habitats (Hammerson 1999) that are particularly vulnerable to seasonal variability (Corn

<sup>1</sup>S.M. Amburgey, M. Murphy, and W.C. Funk. Phenotypic plasticity in developmental rate insufficient to offset high tadpole mortality in rapidly drying ponds. Submitted and in review.

2003; Matthews et al. 2013). On average, *P. maculata* take 50–80 days from hatching to metamorphose (S.M. Amburgey, unpublished data) and live a mean of 5 years (Spencer 1964). *Pseudacris maculata* may plastically respond to altered hydroperiod and predation pressure by accelerating metamorphosis, but rapid drying may lead to heightened mortality (Amburgey et al., submitted and in review<sup>3</sup>), thus emphasizing the importance of breeding-habitat selection. We conducted an occupancy study, which allows for modeling of species occurrence using habitat and landscape covariates while accounting for imperfect detection (MacKenzie et al. 2002; Bailey et al. 2004). Few studies have utilized robust occupancy methodology to disentangle the roles of hydroperiod and predator communities on species distributions at such a spatial scale (but see Pearl et al. 2009; Miller et al. 2012).

We hypothesized that *P. maculata* tadpole occupancy would be greatest at ponds with intermediate-length hydroperiods that have a lower desiccation risk but still exclude permanent pond predators due to occasional drying. We also hypothesized that predators would impact the suitability of sites and that fish would exclude *P. maculata* tadpoles entirely. If our hypotheses are supported, the distribution of *P. maculata* may be greatly changed if suitable intermediate-length hydroperiod sites are seasonally unavailable or permanently altered. Adults may be forced to breed at sites that dry too quickly or have predatory fish. In drying habitats, tadpoles may experience higher predation risk. By isolating a suite of factors that are shown to regulate occupancy, we can better identify conservation risks and predict future species persistence and distributions.

## Materials and methods

### Site selection and surveying

We identified sites potentially holding water (e.g., small wetlands to large reservoirs) in Larimer County, Colorado, USA, utilizing historical observations, current survey records, and wetland inventories (National Agriculture Imagery Program (NAIP); USDA 2009; National Wetlands Inventory (NWI); USFWS 2009, 2013; Fig. 1). These sites were stratified by elevation (low, middle, and high; 1480–3132 m; Supplementary Table S1<sup>2</sup>) and expected hydroperiod (short to long, based on historical records and site characteristics). Within each stratum, 25 sites were selected randomly. Inaccessible sites (those without owner permission or those no longer present) were excluded and replaced by the next randomly selected site in that stratum until all potential sites within a stratum were exhausted. Therefore, the number of sites was not even across all strata. Higher concentrations of private property and a dearth of permanent ponds at middle elevation resulted in the smallest sample size in this elevational stratum. Sixty-two sites were surveyed: low = 20, middle = 17, and high = 25 (Supplementary Table S1<sup>2</sup>). We used elevation to stratify a variety of habitats; however, it was excluded from the analysis because we expected to capture variation in elevation via specific ecological characteristics and had no hypotheses specifically pertaining to elevation.

*Pseudacris maculata* breeding was asynchronous across elevations: low-elevation populations began mid-May 2011 and high-elevation populations began early June 2011. We sampled sites on multiple occasions to correct for nondetection of target species (MacKenzie et al. 2002). Sites were sampled biweekly during a period when *P. maculata* tadpoles would be available for detection at occupied sites (4–10 surveys were conducted by site across the larval period). The sampling season was defined based upon first and last observations of individuals at each elevation. Because our goal was to model *P. maculata* breeding occupancy, only tadpole observations were included in the detection history. One or two observers conducted independent surveys during each site visit,

using net sweeps and visual observations to detect and positively identify *P. maculata* tadpoles. Survey time was standardized across all sites regardless of area, focusing on tracts of habitat deemed suitable for *P. maculata* tadpoles (e.g., grassy edges; Hammerson 1999). If *P. maculata* tadpoles were detected, surveys ceased at 15 min. If *P. maculata* tadpoles were not detected within the 15 min window, the survey continued until detection or until a maximum time of 30 min was reached.

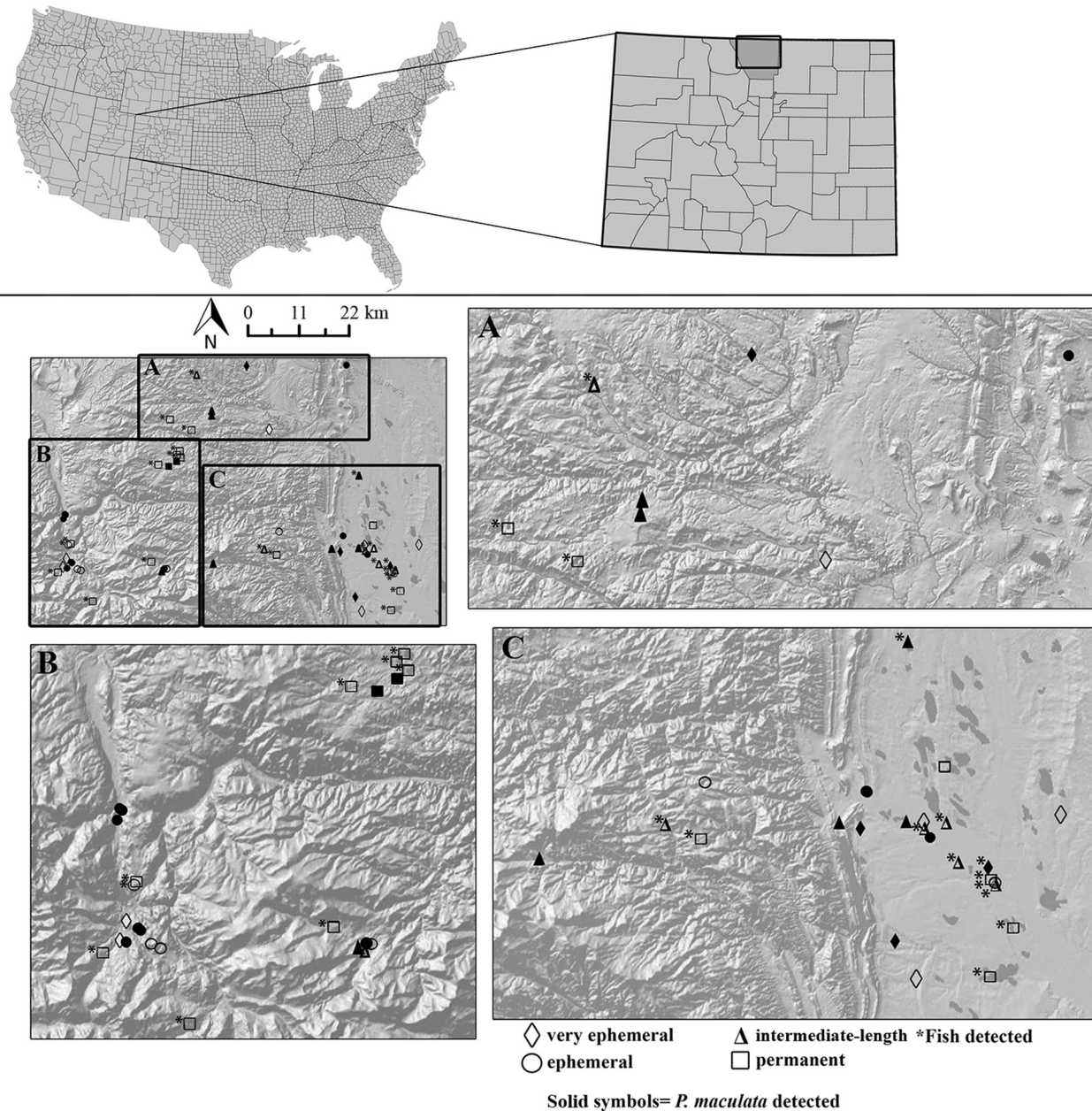
### Primary factors

Hydroperiod and predators were designated primary factors, as they were hypothesized to principally regulate occupancy (Table 1). Hydroperiod was expected to affect occupancy by *P. maculata* directly due to its relationship to desiccation risk for tadpoles (Pechmann et al. 1989) and indirectly due to its relationship to predator occurrence (Babbitt et al. 2003). Though we stratified by expected hydroperiod for our site selection, actual site hydroperiod occasionally did not match our expectations due to seasonal conditions or altered landscape surrounding the site. To improve characterization of hydroperiod, depth was measured at every visit and source of water was categorized (e.g., groundwater, irrigation flow). In addition, maximum and minimum pond areas were measured by either in situ measurement via a handheld GPS device (Garmin® GPSMAP 62s) or by heads-up digitizing the edge of ponds from NAIP (USDA 2011) imagery to estimate pond area (ArcMap version 10; ESRI 2010) for large sites based on seasonal conditions. Minimum and maximum values were based on the lowest and highest observed levels, respectively, during the sampling season. Hydroperiod categories ranged from short to long hydroperiod systems, defined here as very ephemeral (VE; drying within 1–2 weeks of our first survey), ephemeral (E; drying by the end of the sampling season), intermediate-length (I; reducing in volume but not drying completely), and permanent (P; retaining a large volume of water the entire sampling season). These estimates were based upon the conditions of the season surveyed.

Three major predators of *P. maculata* tadpoles were noted during surveys using visual detection and net sweeps: fish (native and introduced; Hecnar and M'Closkey 1997), Barred Tiger Salamanders (*Ambystoma mavortium mavortium* Baird, 1850) (Freda 1983), and odonate larvae (those belonging to the predaceous infraorder Anisoptera; Skelly and Werner 1990). Fish species was not always identifiable; however, we feel confident that this covariate represents potential amphibian predators due to all identifiable, detected fish being carp and trout and that many ponds surveyed had a high likelihood of predatory fish due to stocking and fisherman use. We constructed detection histories for each predator to generate conditional occupancy estimates for each predator at each site (MacKenzie et al. 2006). Differing dramatically from the unconditional estimates, these estimates correspond to the probability the species was present given the survey results; this value will be 1 for sites where the predator was detected. We used the conditional occupancy estimates for each predator as explanatory covariates in our analysis of occupancy for *P. maculata* rather than naïve “presence-absence” information that ignores potential detection differences among predators. To represent the potential link between hydroperiod and predator presence, we considered predator models where the probability of occupancy varied by hydroperiod (HYDRO) and models with  $\psi(\cdot)$  with no variation among sites. Detection probability of predators could be constant, unique for each sampling occasion (VISIT), and vary by complexity of habitat (COMPLEX). Habitat complexity (COMPLEX) was based on a mean value of both observers' at-site rankings of amount of emergent vegetation, water depth, and turbidity to represent difficulty of surveying and was treated as a categorical covariate with four categories. For example, a site ranked as a complexity of one

<sup>2</sup>Supplementary Tables S1–S3 are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2014-0106>.

**Fig. 1.** Map of study sites across Larimer County, Colorado, USA (for site coordinates see Supplementary Table S1<sup>2</sup>). Symbol shapes represent the hydropattern categories, while solid symbols indicate detection of Boreal Chorus Frog (*Pseudacris maculata*) tadpoles. Asterisks next to symbols indicate that fish were detected at the site.



might be shallow with few reeds and clear water. A site ranked as a complexity of four might be deep, have reedy edges, and have cloudy water. Only the top model supported for each predator, determined by Akaike's information criterion (AIC) (MacKenzie et al. 2002; Table 2), was used due to high model weights and little change in conditional occupancy estimates among models.

### Secondary factors

Other pond-level factors that may influence occupancy by *P. maculata* were also investigated (Table 1) and designated as secondary factors. Conductivity and pH were measured via an EC500 ExStik® probe during every visit in the tract of habitat surveyed. Site-specific conductivity remained relatively constant across surveys so a mean value was used for analysis. pH (mean 7.4; range 6.4–9.04) was within the range that *P. maculata* have previously been found (mean 7.14; range 5.36–10.16; M. Murphy, unpublished

data), so it was excluded from subsequent analysis. Percent vegetative cover (VC; percentage of total site with emergent vegetation) was estimated by each observer during surveys and a mean value was included as a continuous covariate because of its importance in oviposition (Hammerson 1999; Scherer et al. 2012).

Landscape factors also potentially influence occupancy by *P. maculata* (Table 1). We calculated heat load index (HLI) (Table 1; Evans et al. 2013) at each site, which is a measure of solar intercept (McCune and Keon 2002). High HLI values are associated with more algae production and warmer water, characteristics important for tadpole development (Newman 1989; Murphy et al. 2010a).

Occupancy by *P. maculata* may be influenced by isolation from other water bodies that could serve as supplementary sources to bolster local populations and allow for recolonization in the case of local extinction (Jiang et al. 2007; Murphy et al. 2010a). Recent

**Table 2.** Top models from each candidate set for occupancy of sites by fish, odonate larvae, and Barred Tiger Salamanders (*Ambystoma mavortium mavortium*).

Predator	Model	AIC	w	K	-2L
Fish	$\psi(\text{HYDRO})p(\text{VISIT}+\text{COMPLEX})$	321.62	0.630	15	291.62
Odonate	$\psi(\text{HYDRO})p(\cdot)$	531.35	0.499	5	521.35
Salamander	$\psi(\cdot)p(\cdot)$	137.30	0.377	2	133.30

**Note:** Our only covariate for occupancy ( $\psi$ ) was hydropattern (HYDRO) because of its importance in regulating predator type. Covariates for detection ( $p$ ) included only survey-specific detection (VISIT) and site complexity (COMPLEX). AIC is Akaike's information criterion,  $w$  is model weight,  $K$  is the number of parameters in a model, and  $-2L$  is twice the negative log-likelihood.

work on this species suggests a maximum dispersal distance of 2400 m (M. Murphy, unpublished data, but note Spencer 1964). Therefore, we buffered all sites by 2400 m (ArcMap version 10; ESRI 2010). Within buffers, we calculated the number of nearby ponds, wetlands, or lakes (PN). We compiled data from two sources (Table 1), as data coverage varied across elevation. A lack of detailed water-body information at middle elevation required a visual check of NAIP 2009 (USDA 2009; Table 1) imagery to count clearly visible additional sites.

Wetness of habitat surrounding a pond may affect the likelihood of dispersal between water bodies (Pilliod et al. 2002; Bartelt and Peterson 2005) and, therefore, occupancy. Mean compound topographic index (CTI) was calculated within buffers (Table 1; Evans et al. 2013), as it represents a measure of the wetness of a site (Moore et al. 1993). *Pseudacris maculata* adults and metamorphosed individuals are also known to use surrounding wetland meadows for summer feeding (Tordoff and Pettus 1977), therefore mean CTI may impact feeding grounds and probability of occupancy.

Finally, anthropogenic disturbance and uninhabitable areas may negatively influence habitat quality and serve as barriers to the movement of individuals (Vos and Chardon 1998; Browne et al. 2009) and were included in the analysis as mean impervious surface within the buffer (IMPER; Table 1; Murphy et al. 2010b).

### Data analysis

We used a likelihood-based method for estimating single-season occupancy probability ( $\psi$ ) and probability of detection ( $p$ ), as outlined by MacKenzie et al. (2002, 2006) and MacKenzie and Bailey (2004), and implemented in program PRESENCE version 5.8 (Hines 2010). Models that included the primary and secondary covariates detailed above were used to test hypotheses regarding  $p_{ij}$  and  $\psi_i$ , the probability of detection at site  $i$  on survey  $j$  and the probability of occupancy at site  $i$ , respectively. Continuous covariate values were scaled between 0 and 10 for analysis by dividing by the largest measurements for each covariate or by a factor of 10.

Before fitting any models, a correlation matrix was generated in R version 2.13.2 (R Development Core Team 2009) to identify and exclude highly correlated covariates ( $r > 0.6$ ). Our correlation matrix indicated that only elevation and conductivity were correlated ( $r = -0.71$ ), providing another reason for elevation to be removed from further analysis.

### Detection probability

We developed and tested models using a sequential approach to model selection (MacKenzie et al. 2006). We began by focusing on detection probability. Using a global model structure for occupancy, we explored the influence of a priori factors on detection probability (MacKenzie et al. 2006; Balas et al. 2012; Table 3). Environmental covariates consisted of complexity (COMPLEX) and hydropattern (HYDRO). Hydropattern may capture variation in detection probability due to site area and variability in depth, allowing animals more or less space to hide (e.g., deep, larger area = permanent hydropattern). Hydropattern was modeled using four categories to allow for a nonlinear effect of hydropattern on occupancy and detection probability. Temporal covariates consisted of survey-specific covariates that allowed detection to vary independently by each sampling occasion (VISIT) or quadratic

function (QUAD). All combinations of these covariates were fit to the detection histories ( $n = 12$ ), excluding combinations of both temporal covariate functions. AIC was used to select the best-supported model for detection probability (MacKenzie et al. 2002). We retained the highest-ranked structure for detection probability while investigating our occupancy hypotheses.

### Occupancy modeling

Following Mattfeldt et al. (2009), we designated our predictor variables as either primary or secondary factors. Hydropattern and predators were designated as primary factors regulating *P. maculata* occupancy because of their central importance in our a priori hypotheses. All other covariates were considered secondary factors because of their potential influence on occupancy, despite not being the focus of this study (Table 1). We developed models based upon combinations of these primary and secondary factors, maintaining a balanced model set such that each covariate within these two categories was included in the same number of models ( $n = 112$  models; Supplementary Table S2<sup>2</sup>). Although models could contain all possible combinations of our primary covariates (Doherty et al. 2012), a maximum of one secondary covariate was included in any given model to limit the number of candidate models and allow for meaningful biological interpretability. Model selection was based on AIC (MacKenzie et al. 2002; MacKenzie and Bailey 2004), and we used AIC weights and  $-2$  log-likelihood values to evaluate the importance of covariates in our top models.

To assess model goodness of fit (GOF), we implemented a parametric bootstrap GOF test in PRESENCE version 5.8 (MacKenzie and Bailey 2004). We tested the GOF of our most parameterized (global) model with the understanding that if the global model adequately fit, then a more parsimonious-supported model would also fit the data (Anderson and Burnham 2002). We used 5000 runs to test GOF and estimate overdispersion (MacKenzie and Bailey 2004).

### A posteriori modeling: conditioning on sites without fish predators

After examining results from our initial model set, we wanted to better understand the effect of hydropattern on occupancy by *P. maculata* in ponds without fish predators. This allowed us to disentangle the direct (i.e., desiccation risk) and indirect (i.e., exclusion of certain predators) effects of hydropattern on probability of occupancy. In the subsequent analysis, we removed sites where fish were detected or had a high probability of containing fish (i.e., all sites with conditional occupancy estimates of 1 were removed). Our conditional occupancy estimates for fish were all close to 0 or 1 because of high detection probability. We retained the best-supported detection structure to investigate the effect of all possible combinations of hydropattern, odonate larvae, and salamanders on occupancy probability by *P. maculata* within our subset of fish-free sites. No secondary factors were included in this analysis.

**Table 3.** Probability of detection while using the global model for occupancy ( $\psi$ (HYDRO+FISH+ODO+SAL+HLI)).

Model	AIC	$\Delta$ AIC	w	K	-2L
$p$ (QUAD+COMPLEX+HYDRO)	177.89	0.00	0.919	15	147.89
$p$ (QUAD+HYDRO)	182.95	5.06	0.073	14	154.95
$p$ (QUAD)	188.24	10.35	0.005	11	166.24
$p$ (QUAD+COMPLEX)	189.36	11.47	0.003	12	165.36
$p$ (HYDRO+COMPLEX)	243.15	65.26	0.00	12	219.15
$p$ (.)	243.57	65.68	0.00	9	225.57
$p$ (HYDRO)	253.85	75.96	0.00	11	231.85
$p$ (COMPLEX)	261.33	83.44	0.00	9	243.33

**Note:** All models containing VISIT were removed because of issues with convergence. AIC is Akaike's information criterion and  $\Delta$ AIC is the difference between a model's AIC score and the top-ranked model.  $w$  is model weight,  $K$  is the number of parameters in a model, and  $-2L$  is twice the negative log-likelihood. For definitions of primary and secondary factors refer to Table 1; QUAD is a quadratic function.

## Results

During our study, we detected *P. maculata* tadpoles at 24 of 62 sites (38.7%). Sites were surveyed between 4 and 10 times during the sampling season. Of sites surveyed, we categorized 13 (21%) as very ephemeral hydropattern systems, 17 (27.4%) as ephemeral hydropattern systems, 14 (22.6%) as intermediate-length hydropattern systems, and 18 (29%) as permanent hydropattern systems. We detected fish at 24 sites (38.7%), odonate larvae at 48 sites (77.4%), and Barred Tiger Salamanders at 6 sites (9.7%). Fish and odonate presence were strongly associated with hydropattern (Table 2). Odonate larvae occurred most frequently at sites with intermediate-length hydropatterns, while fish occurred most frequently at those with permanent hydropatterns. Our global model indicated no lack of fit or signs of overdispersion (GOF,  $P = 0.83$ ).

### Detection probability

The detection-model structure that incorporated a quadratic temporal effect, complexity of habitat, and hydropattern ( $p$ (QUAD+COMPLEX+HYDRO)) was best supported ( $w = 0.918$ ; Table 3). Detection models that included VISIT as a survey-specific detection probability did not converge and were removed from the candidate set. Detection probability estimates approached one during the middle of our sampling period for nearly all occupied sites, but detection probability was highest at occupied permanent hydropattern sites. As expected, complexity had a negative relationship to detection probability.

### Occupancy modeling

#### Primary factors

Eight model structures for  $\psi$  had  $\Delta$ AIC < 2 (Table 4). The top model indicated that occupancy was influenced by fish, odonate larvae, and salamanders, which are three of our four primary factors ( $w = 0.135$ ). Our second-best model included only effects of fish and odonate larvae ( $w = 0.100$ ;  $\Delta$ AIC = 0.61). Fish had a strong negative relationship to *P. maculata* occupancy, while odonate larvae were strongly positively correlated (Table 4). Salamanders were also supported in the top occupancy model with a positive relationship to *P. maculata* occupancy (Fig. 2). Ranking by relative importance as defined by summed AIC weights ( $w_+$ ; Table 4), fish were most important ( $w_+ = 0.999$ ), odonate larvae second ( $w_+ = 0.977$ ), and salamanders third ( $w_+ = 0.588$ ). Salamanders were much rarer in our study area ( $\psi = 0.11$ ; SE = 0.04).

Contrary to our a priori expectations, hydropattern (our other primary factor) was not as important as predators in describing *P. maculata* occurrence among sites ( $w_+ = 0.163$ ; Table 4, Supplementary Table S3<sup>2</sup>). After correcting for detection probability, ponds with intermediate-length hydropatterns had the highest probability of occupancy, while permanent and very ephemeral systems had the lowest (Fig. 2).

#### Secondary factors

The effect of other pond-level characteristics (conductivity, vegetative cover) on occupancy by *P. maculata* received no support. Landscape covariates also received very little support ( $w_+ < 0.14$ ; Table 4). Several of the covariates in the top 10 models can be considered "pretending" covariates; covariates that are included in top models but do not explain much about occupancy (i.e., little change in model fit, as measured by  $-2$  log-likelihood, even with the addition of another parameter; Anderson 2008). These are not discussed due to lack of support (Table 4).

#### A posteriori modeling: conditioning on sites without fish predators

The same detection structure was supported as with the full data set ( $p$ (QUAD+COMPLEX+HYDRO);  $w = 0.63$ ). Occupancy models with the salamander covariate showed issues of convergence and were removed from the candidate model set. The best-supported model contained only odonate larvae (Table 5;  $w = 0.66$ ). Our second-best model contained odonate larvae and hydropattern but had relatively weak support ( $w = 0.32$ ). Intermediate-length hydropattern was positively correlated to occupancy by *P. maculata* in ponds with odonate larvae (Table 5).

## Discussion

Understanding the isolated and combined effects of ecological constraints that lead to patterns in species distributions allows for better predictions of range dynamics and conservation of species. We focused on understanding the role of abiotic and biotic factors in regulating habitat suitability for *P. maculata* across the landscape with a focus on disentangling hydropattern and predator dynamics. Type of predator present was most important to probability of occupancy by *P. maculata*, but hydropattern may still be important due to desiccation risk and regulation of predator presence.

### Detection probability

Habitat complexity negatively affected detectability, highlighting the importance of correcting for imperfect detection because cryptic tadpoles may hide in heterogeneous habitats. Detection probability was highest at permanent sites due to increased consistency of detection (i.e., of the three permanent sites that had *P. maculata* detections, only one ever had a nondetection survey). This may be due to a lack of surface vegetation that may conceal animals.

### Occupancy modeling

#### Primary factors

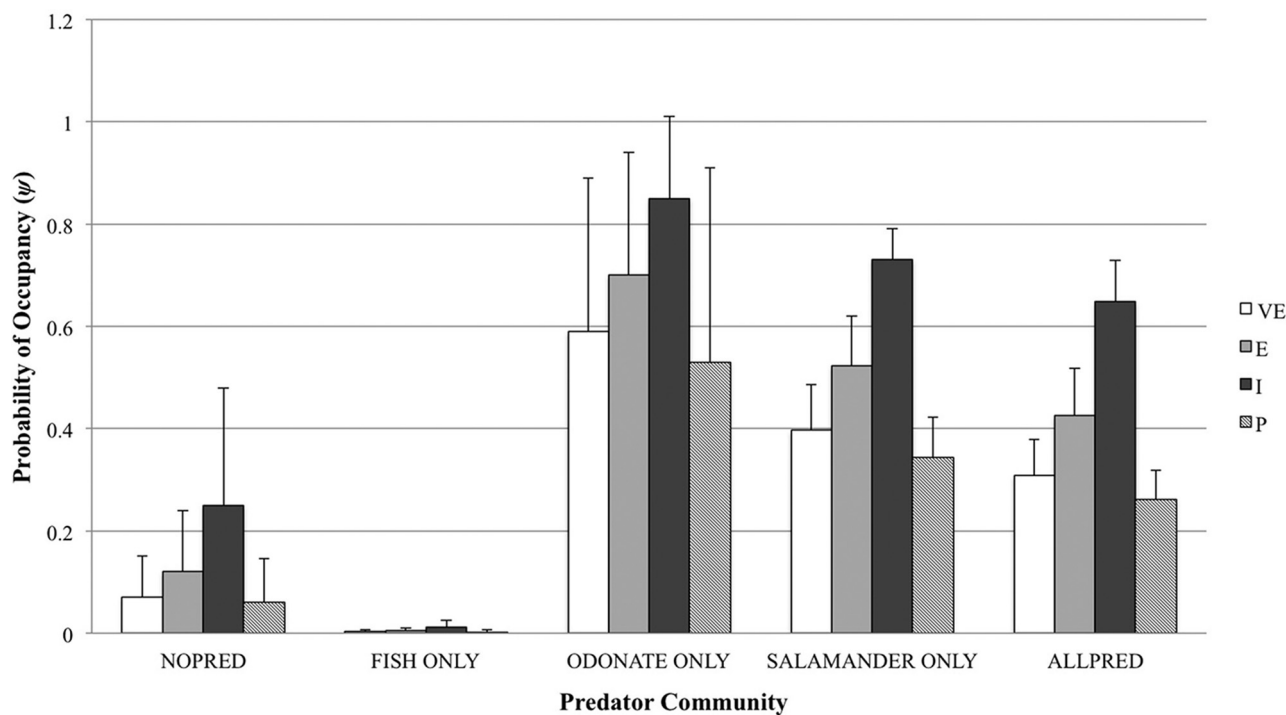
Our models indicated that hydropattern was less supported than other primary factors in predicting probability of *P. maculata*

**Table 4.** Model selection results ( $\Delta AIC < 2$ ) for occupancy by Boreal Chorus Frog (*Pseudacris maculata*) with a detection structure of  $p(\text{QUAD}+\text{COMPLEX}+\text{HYDRO})$ .

	AIC	$\Delta AIC$	$w$	$K$	-2L	FISH	ODO	SAL	CTI	PN	IMPER	VC	COND	HLI
<b>Model</b>														
$\psi(\text{FISH}+\text{ODO}+\text{SAL})$	172.51	0.00	0.135	11	150.51	-3.02	2.92	1.91						
$\psi(\text{FISH}+\text{ODO})$	173.10	0.59	0.101	10	153.10	-3.10	3.18							
$\psi(\text{FISH}+\text{ODO}+\text{SAL}+\text{CTI})$	173.75	1.24	0.073	12	149.75	-3.28	2.86	2.20	0.28					
$\psi(\text{FISH}+\text{ODO}+\text{SAL}+\text{PN})$	173.91	1.40	0.067	12	149.91	-3.24	2.84	2.18		1.38				
$\psi(\text{FISH}+\text{ODO}+\text{SAL}+\text{IMPER})$	174.13	1.62	0.060	12	150.13	-3.23	2.91	2.06			1.07			
$\psi(\text{FISH}+\text{ODO}+\text{SAL}+\text{VC})$	174.45	1.94	0.051	12	150.45	-3.12	2.92	1.87				-0.26		
$\psi(\text{FISH}+\text{ODO}+\text{SAL}+\text{COND})$	174.49	1.98	0.050	12	150.49	-3.04	2.91	1.92					0.04	
$\psi(\text{FISH}+\text{ODO}+\text{SAL}+\text{HLI})$	174.50	1.99	0.050	12	150.50	-3.03	2.91	1.91						-0.47
$w+$														
<b>Covariate</b>														
FISH	0.999													
ODO	0.977													
SAL	0.588													
HYDRO	0.163													
VC	0.0514													
COND	0.108													
PN	0.128													
IMPER	0.119													
HLI	0.107													
CTI	0.141													

**Note:** AIC is Akaike's information criterion and  $\Delta AIC$  is the difference between a model's AIC score and the top-ranked model.  $w$  is model weight,  $K$  is the number of parameters in a model,  $-2L$  is twice the negative log-likelihood, and  $w+$  is the summed AIC weights. Estimated effect sizes (i.e. beta estimates) are provided for primary and secondary factors. For definitions of primary and secondary factors refer to Table 1; QUAD is a quadratic function.

**Fig. 2.** Graph of probability of occupancy by Boreal Chorus Frog (*Pseudacris maculata*) across hydropattern categories and predator communities using back-transformed parameter estimates from our best-supported model containing hydropattern ( $\psi(\text{HYDRO}+\text{FISH}+\text{ODO}+\text{SAL})p(\text{QUAD}+\text{HYDRO}+\text{COMPLEX})$ ;  $w_i = 0.0231$ ). Hydropattern categories are VE (very ephemeral), E (ephemeral), I (intermediate-length), and P (permanent). NOPRED represents ponds lacking fish, odonate larvae, and salamanders. ALLPRED represents ponds with all of the above. Error bars represent standard error.



occupancy but was more important than secondary factors. Hydropattern affected the probability of occupancy by fish directly, thereby indirectly regulating the occurrence of *P. maculata* (Table 2, Fig. 2). Permanent ponds with fish predators excluded *P. maculata* almost entirely (Fig. 2). In ponds with varying communities of predators, intermediate-length hydropattern ponds had the highest prob-

ability of occupancy, even in situations where fish were absent (Fig. 2). This indicates that hydropattern may still have an effect on occupancy in addition to regulating predator presence. Ephemeral systems may be unsuitable due to increased desiccation risk (Table 1). Cool temperatures and a lack of emergent vegetation in permanent systems may also affect suitability, and this pattern may have been

**Table 5.** Model selection results for occupancy of Boreal Chorus Frog (*Pseudacris maculata*) in ponds without fish using only primary factors and with a detection probability structure that was the same as earlier models ( $p(\text{QUAD}+\text{COMPLEX}+\text{HYDRO})$ ).

	AIC	$\Delta\text{AIC}$	w	K	-2L	ODO	VE	E	I	P
<b>Model</b>										
$\psi(\text{ODO})$	142.82	0.00	0.66	9	124.82	3.14				
$\psi(\text{ODO}+\text{HYDRO})$	144.28	1.46	0.32	12	120.28	2.97	-1.27	-0.02	1.50	-1.87
$\psi(\text{HYDRO})$	149.53	6.71	0.02	11	127.53		-2.20	-0.41	0.69	1.10
$\psi(.)$	152.43	9.61	0.00	8	136.43					
w+										
<b>Covariate</b>										
ODO	0.98									
HYDRO	0.34									

**Note:** SAL was excluded from models because of issues with convergence. HYDRO consists of four categories: VE (very ephemeral), E (ephemeral), I (intermediate), and P (permanent). AIC is Akaike's information criterion and  $\Delta\text{AIC}$  is the difference between a model's AIC score and the top ranked model. w is model weight, K is the number of parameters in a model, -2L is twice the negative log-likelihood, and w+ is the summed AIC weights. Estimated effect sizes (i.e. beta estimates) are provided for primary and secondary factors. For definitions of primary and secondary factors refer to Table 1.

stronger if more permanent sites lacking fish were available to survey. Hydropattern has been shown previously to play an important role in habitat selection for species due to desiccation risk (Babbitt et al. 2003; Mattfeldt et al. 2009; Scherer et al. 2012; Matthews et al. 2013) and by regulating predator occurrence (Skelly 1996; Babbitt et al. 2003; Knapp 2005). Hydropattern in concert with predator presence may also have important implications for survival and metamorphosis of developing larvae (Relyea 2007; Amburgey et al., submitted and in review<sup>1</sup>), highlighting the potential importance of both factors in population persistence.

We found that occupancy by *P. maculata* was affected primarily by the presence of predators. Fish excluded *P. maculata* at many permanent hydropattern sites across the landscape and their presence was the most important factor explaining absence of *P. maculata*. This supports previous findings regarding fish (native and nonnative) excluding amphibian species sensitive to fish predation (Hecnar and M'Closkey 1997; Hero et al. 1998; Knapp 2005). In our surveys, we found both fish and *P. maculata* tadpoles at only two sites (Fig. 1). One site had many reeds and was possibly difficult for fish to access the microhabitat being used by tadpoles. The other had only juvenile fish detected immediately following a heavy rain that may have washed animals into the site from nearby sources.

Odonate larvae had a positive relationship to the presence of *P. maculata* tadpoles in our models and were found at every site where *P. maculata* tadpoles were detected. Similar to *P. maculata* tadpoles, odonate larvae were found most often at sites with intermediate-length hydropatterns. Although common predators of amphibian tadpoles (Skelly and Werner 1990; Eklöv 2000), odonate larvae often utilize similar habitats as their amphibian prey (Needham et al. 2000; Babbitt et al. 2003). Odonate larvae have been shown to alter amphibian development (Eklöv 2000; Amburgey et al., submitted and in review<sup>1</sup>), behavior (Skelly and Werner 1990), and body size and shape (McCollum and Leimberger 1997), indicating that tadpoles have other strategies by which to reduce predation risk (Hero et al. 1998) in the presence of these predators. In our system, such strategies may allow them to co-occur with odonate larvae.

Salamanders, much like odonate larvae, may also prey upon other amphibian species (Wilbur et al. 1983; Maret and Collins 1994; Hero et al. 1998) but were much rarer in our study area. They are often found in similar environments as other amphibian larvae (Hero et al. 1998), possibly due to the same habitat requirements for breeding and development (Werner et al. 2007). Salamanders are gape-limited predators, endangering tadpoles only until a certain stage is reached (Wilbur et al. 1983), thus allowing for co-occurrence of predator and prey.

Predators were a factor in all top models, but the direction of the relationship with tadpole occupancy varied by type of predator. Tactics to avoid predation are often specific to habitat type and predator (Hero et al. 1998) and impact the prey species' ability to coexist. Unpalatability may have evolved in amphibian species that coevolved with fish predators, while other tactics may be utilized with ephemeral pond predators (Hero et al. 1998; Relyea 2001). In *P. maculata*, unpalatability has not been reported, potentially explaining their inclusion at sites with only sit-and-wait predators that they can avoid (e.g., odonate larvae). Fish may also exclude other *P. maculata* predators such as odonate larvae, removing them from sites where *P. maculata* are absent (Hero et al. 1998), explaining the positive relationship between odonate larvae and *P. maculata* tadpoles. This highlights the importance and complexity of these community relationships, demonstrating their significance in regulating species distributions. These interactions vary by type of predator, type of habitat, and life stage of each, limiting our ability to predict responses on a broader scale without understanding community-level interactions first.

#### Secondary factors

No other pond-level or landscape-level factors were supported in models of *P. maculata* occupancy. CTI and PN had the most support based on summed model weights and the estimates were consistent with our a priori expectations (positive), suggesting that wetness of the surrounding habitat and metapopulation dynamics may play a small role in explaining occupancy of *P. maculata* (Tordoff and Pettus 1977; Scherer et al. 2012). Previous studies found that these factors were also important for dispersal, probability of recolonization of sites, and production of offspring (Pilliod et al. 2002; Murphy et al. 2010a, 2010b).

#### Conclusions

We determined the relative importance of individual and combined abiotic and biotic landscape-level and pond-level factors on occupancy probability of a pond-breeding amphibian. Determining the relative roles of each factor regulating occupancy allows for higher quality data to be fed into predictive models of future site occupancy. This also provides us with specific characteristics with which to design targeted conservation policies and informs models of climate-change scenarios.

Climate change is predicted to alter temperatures (MacCracken et al. 2003; Matthews 2010), increase evapotranspiration (Matthews 2010), and result in shifts in precipitation form and timing (Magnuson et al. 1997; MacCracken et al. 2003; Barnett et al. 2005; Corn 2005). These changes will impact habitat suitability and alter species' distributions (Matthews et al. 2013). Climate change is



expected to shorten hydroperiods and more long hydropattern systems will shift to short hydropattern systems (Matthews et al. 2013), excluding certain ponds for reproduction. As climate change modifies hydropattern (e.g., through rapid drying (Matthews et al. 2013) and altered water chemistry (Hamer and Parris 2011; Fairman et al. 2013)), it may play a larger direct role in habitat suitability for *P. maculata*. Some amphibian species may be able to respond via developmental plasticity (Skelly 1996; Merilä et al. 2000), but the degree of shortening may be severe and plasticity may not be adequate as a stop-gap measure (DeWitt et al. 1998; Amburgey et al., submitted and in review<sup>1</sup>). Very ephemeral and ephemeral hydropattern systems currently have low probabilities of occupancy by *P. maculata* compared with longer intermediate-length hydropattern systems, indicating that any shortening of hydropattern will likely reduce breeding habitat.

Many permanent ponds, generally reservoirs and man-made lakes, may not seasonally fluctuate as drastically as temporary ponds (Matthews 2010) but may be inadequate habitat for other reasons (e.g., fish presence or cooler temperatures; Hecnar and M'Closkey 1997; Skelly et al. 2002). Fish serve as exclusionary predators to some species of amphibians (Hecnar and M'Closkey 1997; Hero et al. 1998; Knapp 2005) and increased demands for stocking and introduction of fish into historically fishless sites may jeopardize some species of amphibians, including *P. maculata* (Kats and Ferrer 2003; Pilliod et al. 2010). Removal of invasive fish may allow for recolonization of historical amphibian habitats (Funk and Dunlap 1999; Knapp 2005; Walston and Mullin 2007). Some permanent hydropattern systems may shorten in drought years and fish may be excluded by drying, allowing colonization to occur (though seasonal stocking practices may continue).

Altered species interactions can impact habitat suitability and species persistence (Chapin et al. 2000), highlighting the importance of studying the ecology of communities (Gilman et al. 2010). For predators that coexist with amphibian species (e.g., odonate larvae), predator chemical cues may concentrate and actual predation may increase in short hydropattern systems, negatively impacting larval development and survival (Blaustein et al. 2001; Mirza et al. 2006; Amburgey et al., submitted and in review<sup>1</sup>).

Our occupancy analysis shows that several stressors impact this species currently. *Pseudacris maculata* are widespread but have likely already lost breeding sites due to introduction and stocking of non-native trout (Bahls 1992) and habitat destruction (Stuart et al. 2004; Wake and Vredenburg 2008). Other factors, such as seasonal fluctuations and climate change, will serve as an additional stress, potentially exacerbating the negative effects of predators and further limiting potential breeding sites. The factors that we assessed are not unique to this system and may regulate habitat suitability for other types of amphibians, many of which have limited distributions. Our study shows the importance of identifying factors currently regulating species distributions and understanding the way these complex factors interact. This increased understanding allows us to create realistic conservation policies for specific species.

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