

THESIS

EFFECTS OF HYDROPERIODS AND PREDATOR COMMUNITIES ON *PSEUDACRIS*
MACULATA: A MODEL SPECIES FOR CLIMATE CHANGE IMPACTS ON AMPHIBIANS

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ABSTRACT

EFFECTS OF HYDROPERIODS AND PREDATOR COMMUNITIES ON *PSEUDACRIS MACULATA*: A MODEL SPECIES FOR CLIMATE CHANGE IMPACTS ON AMPHIBIANS

The effects of climate change will alter species persistence and distributions globally through shifts in seasonal precipitation, increases in the stochasticity of weather events, and increased temperatures and evapotranspiration rates. Research is needed to predict the effects of these shifts on species worldwide as climate change will likely impact habitat characteristics crucial to maintaining certain species; therefore, identifying the current factors impacting species presence and survival will allow for the focused study of how those variables may change and inform the creation of effective conservation policies.

Amphibian species are of particular conservation concern due to their recent declines and physiological sensitivity, in addition to their basal roles in many food networks and their importance in the transfer of nutrients between aquatic and terrestrial ecosystems. Amphibians are particularly sensitive to environmental conditions due their permeable skin and their reliance on aquatic environments for breeding and larval development, making them highly susceptible to climate change. Climate change has been previously associated with amphibian declines directly by altering habitat suitability or indirectly by changing community interactions within altered habitats.

Hydroperiod, or the amount of time water is present in a pond, is crucial to larval development, and climate change is predicted to reduce ephemeral hydroperiods in some regions, truncating the time available for larval development. Some amphibian species can plastically respond to reduced hydroperiod by accelerating rates of development and potentially

compromising overall growth in order to reach metamorphosis faster. Little is known as to how rapidly organisms may adapt to climate change altered conditions, and plasticity may serve as a buffer to the immediate effects of climate change, allowing for increased survival without rapid adaptation. However, plasticity may not be present in all species and the costs and limits of plasticity are largely unknown. Climate change still may negatively impact populations that can plastically respond through reduced size at metamorphosis resulting from accelerated development, compromised immune system function post metamorphosis, and decreased larval, juvenile, or adult survival. By better understanding the current limits and costs of plasticity, better predictions concerning amphibian persistence and survival can be made.

In addition to hydroperiod, climate change will likely alter community assemblages and interactions, and these altered interactions could also cause declines. Some species of amphibian larvae have been shown to plastically respond to predator presence by altering developmental rate in response to the stress of potential predation. Predator presence, denoted by a released, chemical cue, is also associated with altered behavior such as decreased foraging that affects larval growth and development by altering resource use. Many amphibian predators are also reliant on aquatic environments, suggesting that predator-prey interactions will likely be altered by climate change. Predators may be concentrated in reduced habitats with their prey and may serve as a secondary pressure to accelerate metamorphosis. By better understanding the effect predator cue has on amphibian development in concert with hydroperiod reductions, we can better predict and ameliorate the detrimental effects of climate change.

Specifically, my work has focused on understanding the effects of climate change on amphibians by focusing on the complex interactions in communities in concert with altered habitat conditions. I have focused on the impact of hydroperiod in concert with predator

assemblages in the lab and in nature, utilizing *Pseudacris maculata* (the boreal chorus frog) as a model system. *P. maculata* are distributed nearly statewide in Colorado, USA, across a wide range of elevations and habitat types and across much of the northwestern USA upwards into Canada. Populations exist along an elevational gradient spanning over a 1280 m difference in altitude in Colorado and exist in a range of hydroperiods and predator communities. Common pond-dwelling predators in this system are primarily fish (native and introduced), *Ambystoma tigrinum* (tiger salamanders), and odonate larvae. Due to *P. maculata*'s wide and varied distribution, they are ideal for investigating the effects of various habitat components on persistence and survival. *P. maculata* also have a limited dispersal distance, making them particularly sensitive to fine-scale changes in their local habitats and potentially facilitating local adaptation.

In my first chapter, I analyzed the effects of truncated hydroperiod and odonate larvae predator cues, individually and combined, on metamorphosis of *P. maculata*. In a climate-change scenario where hydroperiod is drastically reduced and predator cue is concentrated within the remaining habitat, tadpoles responded plastically by accelerating development with no difference in size at metamorphosis. However, mortality was much higher in treatments experiencing hydroperiod reductions, indicating that, while plasticity may facilitate escape from suboptimal conditions, populations may still be negatively impacted through heightened mortality.

In the wild, climate change will alter hydroperiod and community interactions in addition to other abiotic and biotic components such as water chemistry, vegetation, and landscape factors that affect dispersal. Without better understanding current factors regulating amphibian occupancy in the wild, predictions made in the laboratory will be limited to only speculative projections. By using variability in current conditions to study what factors shape species

distributions across the landscape, we can isolate factors that may be altered by climate change and may alter habitat suitability in the future. Because amphibians exist in real-world habitats and complex communities, the best climate change conservation strategies will be those considering species of concern as part of a larger community assemblage rather than isolated components.

In my second chapter, I surveyed a broad spectrum of natural conditions to better understand the impact of current habitat and landscape characteristics on occupancy by *P. maculata*. We focused on modeling presence of tadpoles in order to identify likely breeding sites important for population persistence. Using a robust occupancy analysis design that corrects for imperfect detection, I was able to clarify the current factors most important to describing patterns in occupancy. Predator communities strongly impact presence by *P. maculata* tadpoles, with fish excluding tadpoles almost exclusively. Odonate larvae and tadpoles frequently co-occurred, highlighting the relevance of my first chapter and the role predator cue might play in future climate-altered conditions. In addition, intermediate hydroperiod ponds that do not dry rapidly but exclude fish had the highest levels of occupancy probability, though hydroperiod was not well supported in the analyses. This may indicate that future reduced hydroperiods may force pond-dwelling amphibians to utilize sites that dry too rapidly for successful metamorphosis or sites with permanent hydroperiods that put them in contact with fish predators. By using this type of analysis, we were able to isolate a suite of characteristics that may be important for conservation of *P. maculata* and use them to better predict the way climate change may alter populations. Our models agree with other research indicating that predator-prey interactions are important to species occurrence and must be considered in light of climate change.

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LIST OF KEYWORDS

Phenotypic plasticity; Predator cue; Larval growth rate; Metamorphosis; Occupancy analysis; Predator interactions; Hydroperiod; Climate change; Habitat Suitability; Amphibian decline; Pseudacris maculata

PART ONE:

PHENOTYPIC PLASTICITY IN DEVELOPMENTAL RATE INSUFFICIENT TO OFFSET HIGH TADPOLE MORTALITY IN RAPIDLY DRYING PONDS¹

SUMMARY

Two options exist for avoiding local extinction from climate-altered conditions: phenotypic plasticity or adaptive evolution. Evolution may occur too slowly for organisms to adapt to rapid climate change, while phenotypic plasticity may provide an immediate buffer against its effects. We investigated the potential of phenotypic plasticity to offset the negative effects of climate change in a pond-breeding frog, the Boreal Chorus Frog (*Pseudacris maculata*). Truncated hydroperiod (the duration of water in a pond) and altered predator-prey dynamics are predicted results of climate change, limiting time for development and changing predation; we simulated reduced hydroperiod and concentrated predator cue in the lab to understand potential benefits and costs of plasticity. *P. maculata* tadpoles developed faster in response to an interaction between reduced hydroperiod and increased concentration of predator cue. In contrast, there was no effect of reduced hydroperiod or predator cue on size at metamorphosis. Alone, this result suggests that phenotypic plasticity may allow *P. maculata* to escape the negative effects of reduced hydroperiods. However, tadpole survival was significantly lower in hydroperiod treatments than all other treatments, suggesting that even if plasticity acts as a buffer against the effects of climate change and facilitates metamorphosis, heightened mortality may limit the benefits of this rapid response.

¹ Amburgey, S.M., Murphy, M., Funk, W.C. In review. PLOS ONE.

INTRODUCTION

Climate change is impacting habitats and biodiversity across the globe (Parmesan 2006), but our ability to predict its future effects is still in its infancy. To accurately predict species persistence in response to climate change, scientists need a better understanding of potential responses available (Reed et al. 2010). The effects of climate change will span landscapes and habitats, and a limited number of responses will be available to organisms (Fig. 1). Organisms whose habitats have changed beyond their physiological tolerance or ecological needs may disperse, resulting in local extinction (Walther et al. 2002). However, this response will not be possible for all taxa, for example, plants and animals with restricted dispersal abilities (Engler et al. 2009; Schloss et al. 2012). Adaptation and phenotypic plasticity may prevent local extinction in response to climate change (Parmesan 2006; Gienapp et al. 2008; Reed et al. 2010; Anderson et al. 2012), but the roles and costs of these responses are poorly understood (Anderson et al. 2012) and represent a “black box” in our understanding of the effects of climate change on biodiversity (Fig. 1).

Evolution can be rapid when strong directional selection is imposed and there is adequate standing genetic variation in the traits of interest (Ellner et al. 2011 but see Gienapp et al. 2008), but populations experiencing localized effects of rapid climate change may not adapt quickly enough to expand their niche to include new conditions (Gienapp et al. 2008; Reed et al. 2010). In contrast, phenotypic plasticity may allow individuals to respond to altered climate and habitat within a single generation. Plasticity in response to climate change is possible in some species through shifts in breeding, hibernation, and flowering phenology (Charmantier et al. 2008; Blaustein et al. 2010; Anderson et al. 2012; Lane et al. 2012) and can provide more time for adaptation by buffering the immediate effects of altered habitat characteristics (Ghalambor et al.

2007; Gienapp et al. 2008; Anderson et al. 2012). However, plasticity may not be present in all species, as costs of maintaining plasticity may be high (DeWitt et al. 1998; Jannot 2009; Reed et al. 2010) or plasticity may not be selected for in relatively stable environments (Kulkarni et al. 2011). In addition, plasticity may be inadequate to allow organisms to successfully respond to climate change when shifts in phenology or changes in habitat characteristics are extreme (Charmantier et al. 2008; Gienapp et al. 2008; Kelly et al., 2012; Lane et al. 2012).

Understanding the importance of plasticity will allow us to better predict the effects of climate change on population persistence.

Climate change is expected to impact water availability through increased average global temperatures (MacCracken et al. 2003), increased evapotranspiration rates (Matthews 2010), and altered patterns of rainfall, snowfall, snowmelt, and snowpack (MacCracken et al. 2003; IPCC 2007; Barnett et al. 2005; Corn 2005). Hydroperiod, the duration of water in a pond, is expected to shorten in ephemeral ponds due to climate change in many regions (Matthews 2010). This will increase the risk of desiccation for pond organisms and have a cascading effect on habitat characteristics such as temperature and dissolved oxygen levels (Denver 1997; Skoglund et al. 2011). Increased variability of major weather events is also predicted (IPCC 2007) and may favor species with high levels of plasticity that can match conditions as they vary.

For pond-breeding amphibians, developmental plasticity may regulate their ability to respond to altered water availability and allow larvae to successfully metamorphose in situations where climate change has shortened breeding pond hydroperiods (Donnelly and Crump 1998). Most amphibians are tied to water availability for physiological regulation, reproduction, egg deposition, and larval development (Thorson 1955; Bucklet and Jetz 2007), making hydroperiod a key variable in amphibian breeding success. Understanding the impact of climate change on

this group is important as amphibians play an important role in food webs (Ranvestel et al. 2004) and nutrient transfer from aquatic to terrestrial systems (Seale 1980). Desiccation risk directly impacts survival of ephemeral, pond-dwelling amphibian larvae (Pechmann et al. 1989), and larval survival is a particularly important factor in persistence of amphibian populations in some species (Biek et al. 2002).

Some amphibians can plastically adjust larval developmental rates as a means to escape drying ponds and increase survival (Denver et al. 1998; Loman and Claesson 2003; Gervasi and Foufopoulos 2008). While this plasticity may provide a buffer against the potential effects of climate change, accelerated developmental rate has been associated with tradeoffs in size at metamorphosis (Denver et al. 1998; Merilä et al. 2000), which may compromise survival and fitness in juvenile and adult stages (Terentyev 1960; Taylor et al. 1998; Rudolf and Rödel 2007; Márquez-García et al. 2009). In addition, stress due to accelerated development or suboptimal habitat conditions may increase larval mortality (Newman 1992; Relyea and Mills 2001) and therefore make any buffer created by plasticity insufficient at ameliorating the detrimental effects of climate change.

In addition to altering hydroperiod, community interactions in ecosystems will also be impacted due to environmental changes associated with climate change (Gilman et al. 2010), complicating predictions of the effects of reduced hydroperiod on amphibian development. Predator cue, represented by mortality of conspecifics or the presence of a chemical cue from a predator (Petranka et al. 1987), can also elicit a plastic response in tadpole development (Werner 1986). In the presence of predator cue, many models predict and some research has shown accelerated development in amphibian larvae with smaller size at metamorphosis (Skelly and Werner 1990; Wilbur and Fauth 1990). In contrast to this, 95% of experimental studies showed

equivalent or slower developmental rates with predator cue and 86% showed an equal or larger resulting metamorphic size (Relyea 2007). Tadpoles may reduce foraging to decrease detection by predators, thus slowing development by limiting resource acquisition (Altwegg 2002), but providing more time for growth, resulting in a larger size at metamorphosis (Laurila and Kujasalo 1999).

Alone, hydroperiod or predator cue may elicit developmental responses from aquatic larvae; together, they may also interact and alter developmental plasticity. As climate change reduces ephemeral hydroperiods, predator cues may increase in concentration in the remaining habitat, altering prey behavior (Mirza et al. 2006). Reducing hydroperiod and increasing predator cue may additively stress amphibian larvae, resulting in faster development in an attempt to optimize survival by allowing for successful metamorphosis (Werner 1986; Rowe and Ludwig 1991). However, simultaneous exposure to predators and reduced hydroperiod may also result in slowed metamorphosis due to behavioral suppression of foraging (Altwegg 2002). Increased mortality may also result due to the combined effect of multiple stressors (Altwegg 2002). In addition to highlighting the complexity of predicting such interactions, this may mean that plasticity is limited in its ability to respond to multiple stressors, and overall effects of climate change may still be negative. Although several studies have examined plastic responses to reduced water levels, an important remaining question is what is the potential for phenotypic plasticity to buffer organisms from the negative effects of climate change when considering both altered hydroperiod and perceived predation risk.

Here, we examined the role of plasticity as a buffer in a species of pond breeding frog, the Boreal Chorus frog (*Pseudacris maculata*), under likely climate change scenarios. We assessed survival, time to metamorphosis, and size at metamorphosis in *P. maculata* tadpoles

experiencing 1) truncated hydroperiod, 2) predator presence represented by non-lethal predator cue, and 3) truncated hydroperiod in concert with predator cue.

METHODS AND MATERIALS

Ethics Statement

This study was permitted by the Colorado Division of Wildlife (# 10HP957) and approved by the Colorado State University Institutional Animal Care and Use Committee (# 09107A) with Dr. Chris Funk as the principal investigator and strictly followed all committee recommendations. All animals were collected on public lands with permission from the Colorado Division of Wildlife and Fort Collins Natural Areas Program. No endangered species were involved in this experiment, and any necessary euthanasia was performed via topical application of benzocaine (Orajel®) as approved by IACUC in order to minimize animal suffering.

Study Species and Field Sampling

Our study utilized *P. maculata*, a species distributed across the northern and western parts of the United States into Canada (Hammerson 1999). They are a suitable model species for investigating climate change impacts due to their prevalence in ephemeral wetlands (Hammerson 1999), which are threatened by climate change (Matthews et al. 2013). They also exist at higher elevations where changes in temperature and growing season are predicted to be more extreme (IPCC 2007), and breeding pond availability is dependent on snowpack and the timing of snowmelt, such that hydroperiod, breeding, and larval success may be greatly impacted by climate change (Corn 2005). This species also shows limited dispersal ability (Spencer 1964),

suggesting that dispersal will likely be insufficient to track changing climatic conditions and habitats (Fig. 1).

Early stage (Gosner stage 24-25; Gosner 1960) *P. maculata* tadpoles were collected from ponds across mid ($n= 4$; 1923-2432 m) and high-elevations ($n= 5$; 2513-3014 m) from mid to late June 2010 due to asynchronous breeding across elevation. Ponds represented a selection of sites occupied by *P. maculata* that also contained large numbers of early Gosner stages tadpoles. The hydroperiod at each site (“natural hydroperiod”) was estimated by repeat visits tracking depth every other week from the date of collection through August 2010 to characterize the rate of drying. Of the four mid elevation sites, two were categorized as ephemeral (drying or nearly drying by the end of August) and two as permanent (retaining water through the end of August). One of the high elevation sites was classified as ephemeral while all others were permanent (Appendix 1).

Experimental Design and Animal Care

Tadpoles from each pond were randomly assigned to five experimental treatments with three replicates each (5 treatments x 9 ponds x 3 replicates per treatment per pond x 4 animals/container = 540 tadpoles; Fig. 2). The Control treatment had a constant 1.5 L volume of water (approximately 6cm deep) and no predator cue added for the entirety of the experiment. The Hydroperiod-Reduction treatment consisted of a constant hydroperiod reduction, decreasing by 350 mL every water change. The Constant-Pred treatment had a constant 1.45 L of water and a constant 50 mL of predator cue added (for a total 1.5 L volume). The Interaction treatment represented the interaction of predator cue and hydroperiod reduction, involving a reduction of 350 mL of water and the addition of a constant 50 mL of predator cue every change (resulting in

an increased ratio of predator cue to water as the weeks passed, simulating theorized climate change conditions in the wild). The Pred-Ratio treatment remained at a constant 1.5 L volume but received the same proportion of predator cue that the Interaction treatment did (keeping the amount of predator cue the same between the two treatments but not the overall volume of water).

Treatments began within one to two days of collection; all tadpoles were maintained in the lab with food and fresh water until commencement (described below). Water levels were reduced until they reached a final volume of 100 mL (approximately 1cm deep), which was enough water to keep tadpoles submerged. Treatments were maintained until all animals had metamorphosed or died, and dates of metamorphosis and mortality were recorded for every animal.

Tadpoles ($n=4$ per container) were housed in plastic containers measuring 22 cm x 22 cm x 9.5 cm with ventilated lids (Lemmon and Lemmon 2010). De-chlorinated (AmQuel® plus-treated), pH-neutral tap water was used for all treatments (Lemmon and Lemmon 2010). Containers were randomized on 21 shelves, maintained at room temperature (70-76°C) and at a seasonal light cycle (average of 14 hours light, 10 hours dark). Animals were fed daily *ad libitum* rabbit pellets (0.2 g) and chopped, raw organic spinach (0.1 g) (Lemmon and Lemmon 2010). Water changes occurred every five days, consisting of a complete water change, new container, and applicable water reduction and/or fresh predator cue.

Predator cue- Odonate larvae were collected from ponds in Larimer County (Appendix 1) and brought into the lab 48 hours prior to water changes. Larvae came from three sites, two at low elevation (1,496-1,519 m) and one at high elevation. Low elevation odonate larvae were used to make the predator cue during even weeks. A combination of half low elevation and half high

elevation larvae were used during odd weeks. Genera of odonate larvae differ across elevations in Larimer County and to remove the possibility that tadpoles would only respond to odonate larvae found in their native habitats, we used a mixture from different elevations. All odonate larvae were placed in individual containers with mesh lids to prevent intraspecific predation and were soaked in water to be used as predator cue water (Eklöv 2000; Van Buskirk and McCollum 2000). A ratio of one odonate larva to 100 mL water was used to produce predator cue water.

Odonate larvae were not fed while in the laboratory due the limited amount of time wild tadpoles would be available for feeding and in order to limit unnecessary mortality of tadpoles during the study. All sites used were those with wild populations of *P. maculata* and, therefore, the odonate larvae likely fed upon tadpoles prior to collection, allowing for predator “scent” and a slight inclusion of tadpole “death cue”. A pilot study revealed that tadpoles exposed to odonate predator cue suppressed activity immediately and then gradually resumed normal activities after approximately 10 hours (Amburgey, unpublished data; Appendix 2).

Odonate larvae were separated by collection date and site and preserved in 70% ethanol immediately after water changes. Specimens were identified to family and genus (Appendix 3; Needham et al. 2000; Tennessen 2008). Several odonate genera were included to represent a more realistic assemblage of predators. Odonate larvae found at low elevation sites consisted of only four genera of the family Libellulidae. At high elevation, Libellulidae, Aeschnidae, and Cordulidae were collected with only four genera represented. Libellulidae represents one of the largest and most common families of Odonata in Colorado (USGS 2006).

Data Analysis

Correcting for starting stage- Tadpoles were individually photographed to assess starting Gosner stage (Gosner 1960; Appendix 4) and then randomly assigned to experimental treatments. All animals were identified as Gosner stage 23 to 25 at collection. Because starting Gosner stage may influence both time to metamorphosis and size at metamorphosis, a linear regression was used to establish the amount of variation explained by initial Gosner stage for each response variable (JMP 2007). Time to metamorphosis was positively correlated with initial Gosner stage (adjusted $r^2 = 0.288$, $df = 129$, $P = 0.0298$). Therefore, starting stage was included as a covariate in all further models for time to metamorphosis. Size at metamorphosis was not significantly correlated with initial Gosner stage (adjusted $r^2 = -0.00438$, $df = 129$, $P = 0.510$), thus the raw size data were used for further analyses (Appendix 5). Significance was measured at the $\alpha = 0.05$ level for all analyses.

Time to Metamorphosis- Containers were checked daily for newly metamorphosed individuals, defined as any animal with both hind limbs and at least one front limb fully emerged (Lemmon and Lemmon 2010). Time to metamorphosis was calculated for each individual and then averaged by container ($N \leq 4$ individuals/container; 135 containers; Appendix 5). In the full mixed effects ANOVA looking at time to metamorphosis, treatment, natural hydroperiod, stage, pond as a random effect, a pond by treatment interaction as a random effect, and a treatment by natural hydroperiod interaction were included (Zar 1998; JMP 2007). Pond accounted for approximately 30% of total variance, emphasizing the importance of its inclusion as a random effect. However, the random effect of the interaction between pond and treatment explained less than 5% of variance and was removed from the subsequent ANOVA. The reduced mixed effects ANOVA included initial starting stage, treatment, natural hydroperiod, a treatment by natural

hydroperiod interaction, and pond as a random effect. We used Tukey's HSD to assess differences in container means of time to metamorphosis by treatment (Zar 1998).

Size at Metamorphosis- Animals were photographed with a size standard (ruler) upon reaching metamorphosis. We measured snout-vent length (SVL) of all individuals as an index of size at metamorphosis using ImageJ (Rasband 2011) and averaged measurements by container ($N \leq 4$ individuals/container; 135 containers; Appendix 5). The full mixed effects ANOVA looking at size at metamorphosis was analogous to the mixed effects ANOVA used for time to metamorphosis above excluding stage as a covariate (Zar 1998; JMP 2007). Pond accounted for 9.7% of total variance, while the interaction of pond by treatment accounted for <1% of variation and was subsequently excluded (Zar 1998; JMP 2007). The reduced mixed effects ANOVA included treatment, natural hydroperiod, a treatment by natural hydroperiod interaction, and pond as a random effect. As above, we used Tukey's HSD to assess differences in treatment means (Zar 1998).

Survival- Containers were checked daily, and mortalities were recorded to track individual survival. Survival to metamorphosis was designated binomially, with every individual being assigned a one for survival or a zero for mortality (Appendix 5). Mortality was dispersed throughout containers with no specific replicate more affected than others, so the effect of container was excluded in the analysis. We used a random effects logistic regression ($N = 540$) with pond being included as a random effect to examine the response of survival to experimental treatment, natural hydroperiod, and any interaction between the two (R Development Core Team 2009; Zar 1998).

RESULTS

Time to Metamorphosis

Tadpoles in both the Interaction treatment and the Hydroperiod-Reduction treatment took less time on average to reach metamorphosis than all other treatments (Fig. 3). In the reduced mixed model ANOVA, treatment was significantly related to time to metamorphosis ($F = 3.16$, $df = 4$, $P = 0.0169$; Table 1), with the Interaction treatment tadpoles taking the least amount of time to metamorphose ($P = 0.005$). Post hoc comparisons of treatment means using Tukey's HSD verified the above findings (Fig. 3). Pond explained 30.5% of the variation in time to metamorphosis. Natural hydroperiod had no significant effect on time to metamorphosis ($F = 0.0588$, $df = 1$, $P = 0.816$; Table 1), nor did most of the interactions between treatment and natural hydroperiod ($P > 0.1$). However, the interaction between ephemeral natural hydroperiod and the Constant-Pred treatment was marginally significant ($P = 0.035$).

Size at Metamorphosis

Average size at metamorphosis varied little among experimental treatments ($1.10 \text{ cm} \pm 0.053 \text{ cm}$; Fig. 4), although the smallest metamorphosed individuals were found in the Interaction treatment. In the reduced mixed model ANOVA where not all of the interactions were considered, almost all of the variables and interactions had no effect on size at metamorphosis ($P > 0.1$; Table 2). The interaction between ephemeral natural hydroperiod and the Constant-Pred treatment was marginally significant ($P = 0.0445$), although the mean size in the Constant-Pred treatment was only 0.01% larger than the mean size of the Control treatment, so this difference was considered biologically irrelevant. The random effect of pond accounted for only 8.6% of the variation.

Survival

Overall, 73% of the tadpoles survived and metamorphosed. Survival was 50% in the Hydroperiod-Reduction treatment and 55% in the Interaction treatment (Fig. 5), compared to 88.9% in the Control treatment. These two treatments accounted for approximately 74% of total experimental mortality, with all other treatments showing tadpole mortality between 9-20%. In the random effects logistic regression, the Hydroperiod-Reduction treatment had a significant negative effect on survival ($P < 0.001$; Table 3), as did the Interaction treatment ($P < 0.01$). None of the other treatments had a significant effect on survival ($P > 0.1$). Natural hydroperiod was not significantly related to overall survival nor were the interactions between natural hydroperiod and treatment ($P > 0.1$).

DISCUSSION

Tadpoles responded to reduced hydroperiod and increasing predator cue by plastically accelerating development without an observable difference in size at metamorphosis, thus demonstrating no compromise between accelerated development and growth. This result implies that plasticity can buffer organisms against the consequences of climate-altered habitat conditions, allowing them to achieve metamorphosis in stressful conditions without sacrificing size. However, survival was dramatically reduced for *P. maculata* tadpoles in treatments undergoing hydroperiod reductions (tadpole survival declined by 32-38% compared to the control), indicating that even if plasticity allows for metamorphosis under truncated hydroperiods, resulting high mortality is likely to greatly reduce population persistence in the face of climate change.

Time to metamorphosis

On average, tadpoles in treatments with hydroperiod reductions developed faster than those in treatments with stable water levels (Fig. 3). The Interaction treatment, representing a realistic climate-altered habitat with reduced hydroperiod and an increasing concentration of predator cue (Blaustein et al. 2001; Gilman et al. 2010; Matthews 2010), had tadpoles that significantly accelerated development and metamorphosed in 15% less time than tadpoles in any other treatment. In a drying pond, this would translate into individuals being able to escape ponds 2-3 days earlier, a substantial amount of time considering the rapidity of drying in ephemeral ponds (Matthews et al. 2013). Alone, reducing water levels (Hydroperiod-Reduction) and increasing predator cue (Pred-Ratio) did not elicit a plastic response, suggesting that modified development in response to climate-altered conditions may be possible in *P. maculata* and other aquatic larvae only if certain stress thresholds are reached. The concept of a stress threshold for an expensive process such as developmental plasticity is not new (DeWitt et al. 1998; Gervasi and Foufopoulos 2008; Márquez-García et al. 2009) and has been theorized for *P. maculata* previously (Amburgey et al. 2012), implying that cues used to detect and assess the severity of habitat conditions are important.

Hydroperiod reduction did not elicit a plastic response from *P. maculata* tadpoles, which is congruent with previous studies on *P. maculata* (Amburgey et al. 2012) as well as other amphibians (Leips et al. 2000), but was in contrast to other prior studies (Laurila and Kujasalo 1999; Merilä et al. 2000; Rudolf and Rödel 2007). Theoretical models and some research predict that time to metamorphosis should be protracted due to behavioral dampening of foraging to minimize exposure to predators (Skelly and Werner 1990; Hetchel and Juliano 1997; Eklöv 2000). In our experiment, a similar but non-significant pattern was observed in tadpoles

encountering only predator cue (Pred-Constant and Pred-Ratio treatments) compared to the Control (Fig. 3). However, when an additional stressor is present (e.g. a hydroperiod reduction in addition to predator cue), larvae may be forced to overcome behavioral inhibition and develop at a rate consistent with an absence of predators to escape from an increasingly risky habitat (Laurila and Kujasalo 1999; Relyea 2007).

Natural hydroperiod did not have an effect on time to metamorphosis, contrary to previous experiments on *P. maculata* (Amburgey et al. 2012). In our current study, tadpoles were collected at earlier stages (Gosner stages 23-25 in the present study; stages 24-31 in Amburgey et al. 2012) in a shorter period of time, which might have limited behavioral or chemical influences from natal ponds. In light of the results reported by Amburgey et al. (2012), our data suggest an interesting hypothesis. Tadpoles at early Gosner stages may be more responsive to cues affecting development, allowing for introduced experimental cues to have more of an impact than those extant in the natal environment. However, at later Gosner stages, tadpoles may have limited responsiveness, suggesting that plasticity may be elicited only if the cues for altering development are present at certain key stages (Laurila et al 2004).

Size at metamorphosis

There was no significant difference in average size at metamorphosis (as represented by SVL) between the different treatments (Fig. 4). This suggests that, for *P. maculata*, size at metamorphosis may not be impacted when development is accelerated, contrary to previous research focusing on truncated hydroperiod (Denver et al. 1998; Merilä et al. 2000). Conflicting results have previously been reported for size at metamorphosis in the presence of a predator (cue or live). Tadpoles metamorphose at both smaller (Skelly and Werner 1990; Wilbur and

Fauth 1990; Altwegg 2002) and larger (Laurila and Kujasalo 1999; Vonesh and Warkentin 2006; Relyea 2007) sizes, highlighting the complexity of predicting predator-prey interactions in natural communities (Relyea 2007; Gilman et al. 2010). Metamorphosis at a larger size may be possible if development has been slowed behaviorally, allowing for longer growth (Relyea 2007; Higginson and Ruxton 2010). In our study, developmental rate was plastic for surviving individuals, but mortality was also high. It may be that animals that died in response to these treatments may have been the smallest individuals. Predation risk may also be related to size in amphibian larvae, potentially resulting in suppressed foraging behavior and altered size until larvae reach a “safe” size (Eklöv 2000) where growth can once again be maximized. Tadpole body size to tail size ratio and tail shape may also be altered in response to predators (Van Buskirk and McCollum 2000; Relyea 2001) and may be a better metric for understanding and measuring the effect of a predator cue. Reduced size at metamorphosis is associated with lowered immune system function (Terentyev 1960), increased mortality (Rudolf and Rödel 2007), and reduced adult size and fecundity (Day and Rowe 2002; Márquez-García et al. 2009), potentially resulting in negative effects on individuals even if mortality by desiccation is avoided. If size is unaffected in some species, then developmental plasticity may allow for successful metamorphosis and lack the assumed negative impacts on size associated with altered development.

Survival

Survival of tadpoles was unaltered by presence and concentration of predator cue but was dramatically impacted by hydroperiod reduction (Fig. 5). Both treatments experiencing reductions in water level had reduced tadpole survival, with approximately half of all tadpoles in the Hydroperiod-Reduction and Interaction treatments dying. Our result is congruent with

previous studies that showed increased tadpole mortality in response to heightened stress or direct effects of desiccation associated with truncated hydroperiod (Rowe and Dunson 1995; Skelly 1996 but see Ryan and Winne 2001). Amburgey et al. (2012) noted that the severity of the water drawdown might impact survival, with greater drawdowns eliciting more mortality. Survival in treatments involving predator cue was equivalent to the Control treatment, indicating that, in our experiment, pond drying had a greater impact on survival than the presence of predator cue.

The lack of a response to predator cue is contrary to some research, which suggests that treatments with perceived predation risk and hydroperiod reductions should have lower overall survival (Altwegg 2002). In our experiment, the stress from hydroperiod reduction alone had a drastic impact on larval survival, but predator cue only altered developmental rate rather than having a direct impact on survival. In a natural environment, even lower survival and higher stress would be expected due to predator presence, predation, and by heightened cues from consumed conspecifics (Laurila et al. 1997; Altwegg 2002; Relyea 2007), and this may be exacerbated in a climate-altered habitat where pond volume is expected to decrease (i.e., less cover for hiding; Newman 1992; Blaustein et al. 2001).

CONCLUSIONS

Our data show that in the context of climate change, responses to altered habitat and perceived predation risk may differ from theoretical predictions (Werner 1986; Skelly and Werner 1990; Wilbur and Fauth 1990), and the impacts upon organisms may drastically vary. Our experiment shows that a community approach to conservation is central and that organisms

cannot be studied as isolated units in a landscape (Parmesan 2006; Gilman et al. 2010). Models of species distributions and persistence along with management and conservation policies must consider plasticity and community dynamics in order to produce effective and realistic results concerning climate change (Gilman et al. 2010; Bailey et al. 2012; Doney et al. 2012).

Several considerations must be made regarding our experiment and the interpretation of the results. We were not able to explain 91.4% of variation for size at metamorphosis, potentially due to maternal effects (Bernardo 1996) or other variables not included in the analysis. Density can also impact metamorphosis through the effects of crowding or the release from competition for resources (Tejedo and Reques 1994; Relyea 2007). For example, high mortality in treatments may have caused accelerated metamorphosis due to more resources for remaining tadpoles. We are unable to disentangle this in our experiment as all containers had fluctuations in density; however, this experimental design resembles realistic populations that would be altered by the same processes (Tejedo and Reques 1994). Prey responses in the wild will also vary due to actual predation events and conspecific cues (Hetchel and Juliano 1997; Relyea 2007), potentially accentuating the effects on time to metamorphosis and eliciting patterns on size at metamorphosis. The effect of reduced larval survival on population persistence in response to altered conditions may also vary by species (Biek et al. 2002; Vonesh and Warkentin 2006), requiring research to track future population dynamics.

Many amphibian species have experienced severe declines in the last few decades (Stuart et al. 2004; IUCN 2011; Adams et al. 2013), and organisms with complex life cycles, such as amphibians, have life-stages tied to the aquatic environment that may be endangered by climate change (Matthews et al. 2013). Evolution likely occurs too slowly to be a sufficient buffer against the immediate effects of rapid climate change (Gienapp et al. 2008; Reed et al. 2010;

Ellner et al. 2011). Developmental plasticity may ensure that populations survive long enough for the evolution of longer-term adaptations (Gienapp et al. 2008; Nicotra et al. 2010; Anderson et al. 2012), but knowledge of the limits of plasticity (Anderson et al. 2012; Kelly et al. 2012; Lane et al. 2012) and its role in allowing species to overcome suboptimal conditions is currently lacking (DeWitt et al. 1998; Reed et al. 2010). Our study shows that, in climate-altered conditions where hydroperiod is truncated and predator cue is concentrated in the remaining habitat, *P. maculata* tadpoles show plasticity in development with no compromise on size at metamorphosis. However, mortality is heightened in this situation and whenever hydroperiod was reduced, indicating that plasticity may not be a sufficient buffer to mitigate the detrimental effects of climate change.

TABLE 1. – Mixed model ANOVA table of fixed effects tests on time to metamorphosis using the reduced model.

Response: Time			
	Df	F Ratio	P-value
Treatment	4	3.16	0.0169*
NatHydro	1	0.0588	0.816
NatHydro*Trt	4	1.29	0.279
Stage	4	1.06	0.378
Signif. codes: ***p<0.001, **p<0.01, *p<0.05			

TABLE 2. – Mixed model ANOVA table of fixed effects tests on size at metamorphosis using the reduced model.

Response: Size			
	Df	F Ratio	P-value
Treatment	4	0.514	0.726
NatHydro	1	0.436	0.530
NatHydro*Trt	4	1.160	0.330
Signif. codes: ***p<0.001, **p<0.01, *p<0.05			

TABLE 3. - Random effects logistic regression of survival by experimental treatment and natural hydroperiod (NatHydro3= permanent hydroperiod), controlling for the random effect of pond of origin. In the analysis, one level of each of the variables must be held constant for comparison, resulting one less of each variable showing on the table. Interaction represents the Interaction treatment.

Response: Time

	Estimate	SE	z value	P-value
(Intercept)	2.23	0.557	4.00	6.42e-05
Hydroperiod-Reduction	-2.14	0.563	-3.81	1.41e-04 ***
Constant-Pred	-0.702	0.608	-1.15	0.248
Interaction	-1.69	0.567	-2.99	2.80e-03 **
Pred-Ratio	0.997	0.876	1.14	0.255
NatHydro3	-0.0483	0.739	-0.0650	0.948
NatHydro3:HydroRed	-0.109	0.750	-0.146	0.884
NatHydro3:ConstPred	-0.0767	0.803	-0.0960	0.924
NatHydro3:Interact	-0.410	0.753	-0.544	0.586
NatHydro3:PredRatio	-1.16	1.04	-1.11	0.268
Signif. codes: ***p<0.001, **p<0.01, *p<0.05				

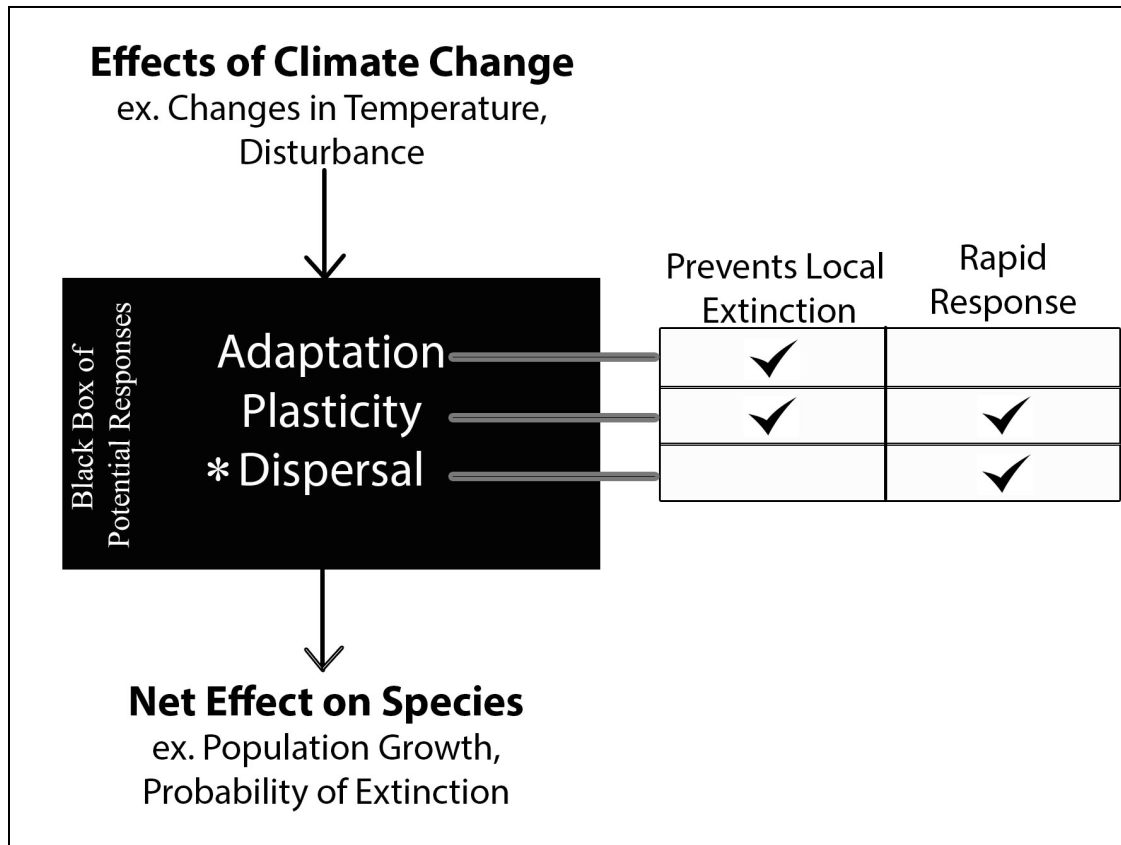


FIGURE 1. Theoretical mechanisms to cope with the effects of climate change. These represent a “black box” in regards to our understanding of why and how species respond. Some of the limitations of the different mechanisms are considered here, and dispersal is highlighted, as our study species—*Pseudacris maculata*—is limited in its dispersal ability and therefore can only respond to climate change via adaptive evolution or phenotypic plasticity.

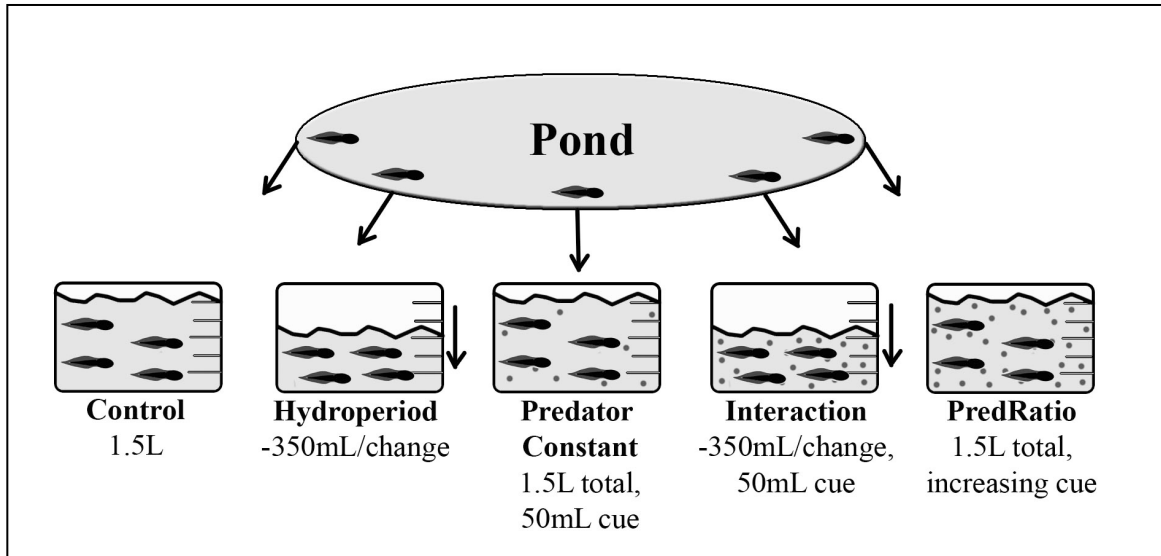


FIGURE 2. – Experimental design. Tadpoles were collected from the natal pond and were randomly assigned to five experimental treatments. Three replicates of each treatment per pond with four tadpoles per replicate container were used (3 replicates per treatment x 9 ponds = 27 replicates of each treatment). Water is gray while predator cue is represented by small particles. Concentrations of predator cue were equivalent in the Interaction and Pred-Ratio treatments, even though water volume decreased in the former yet stayed constant in the latter treatment.

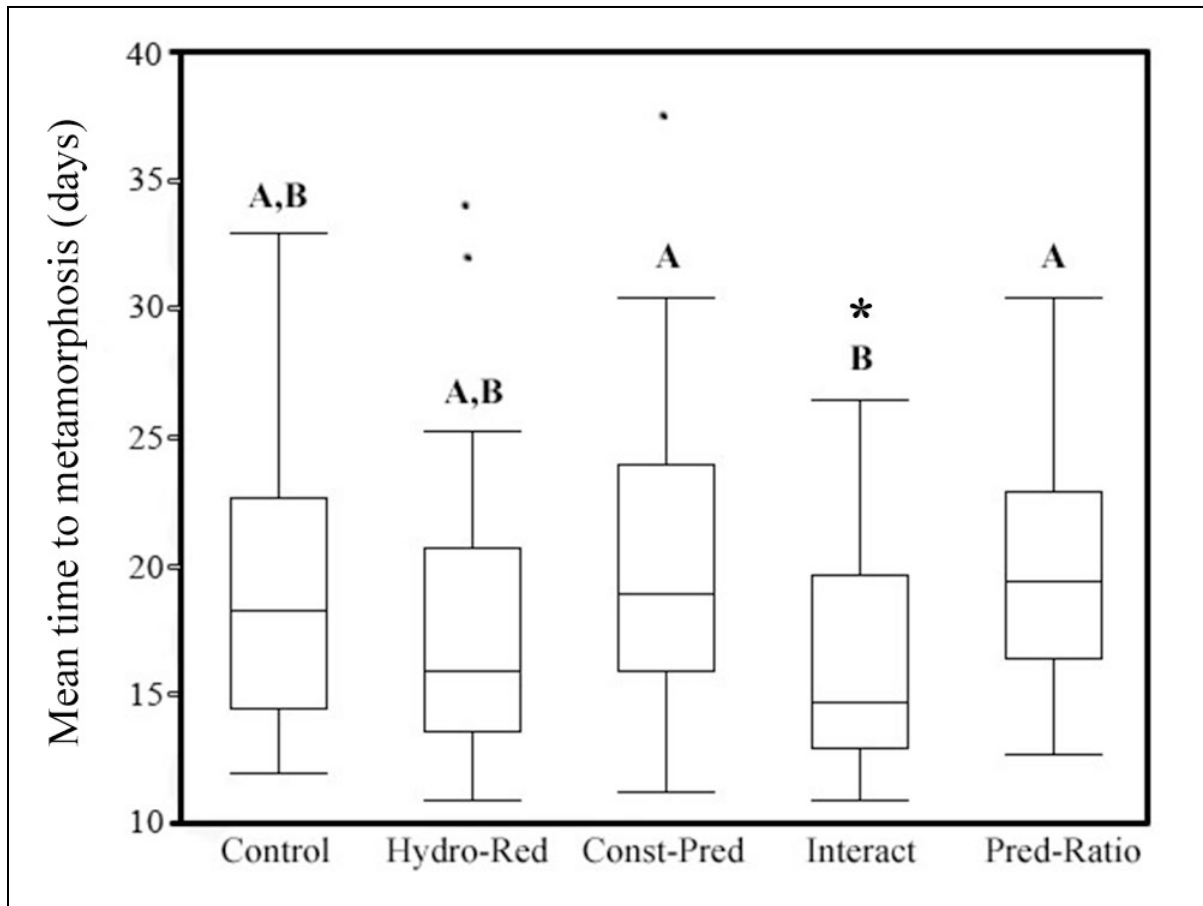


FIGURE 3. – Box plot of average time to metamorphosis by treatment. Boxes represent 25%, 50% (median), and 75% percentiles. Black dots represent outliers, and the error bars represent standard error. Tukey's HSD letters are labeled above treatments. The asterisk indicates a significant difference between time to metamorphosis and the Interaction treatment from the reduced mixed model ANOVA.

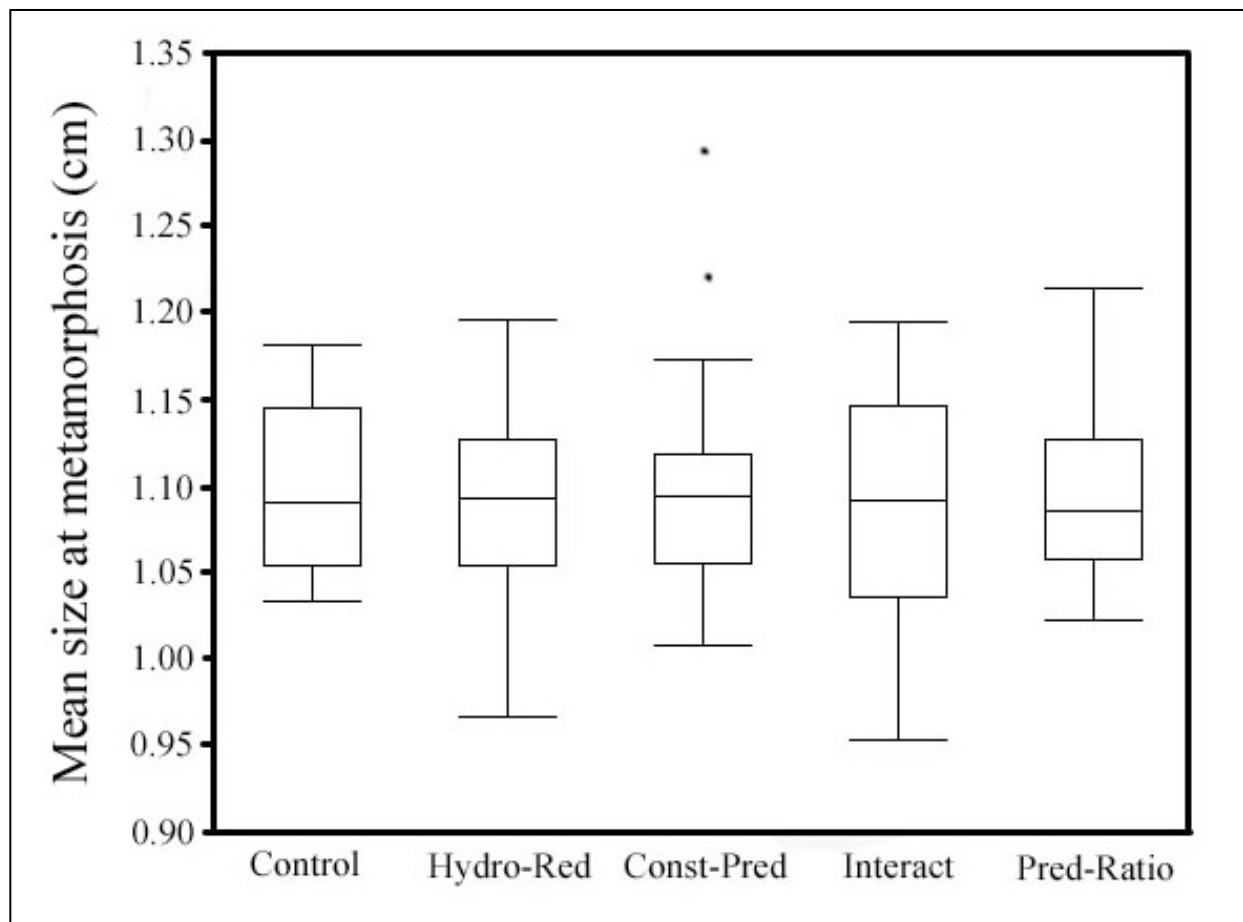


FIGURE 4. – Boxplot of average size at metamorphosis (SVL) per experimental treatment. Boxes represent 25%, 50% (median), and 75% percentiles. Black dots represent outliers, and error bars represent standard error.

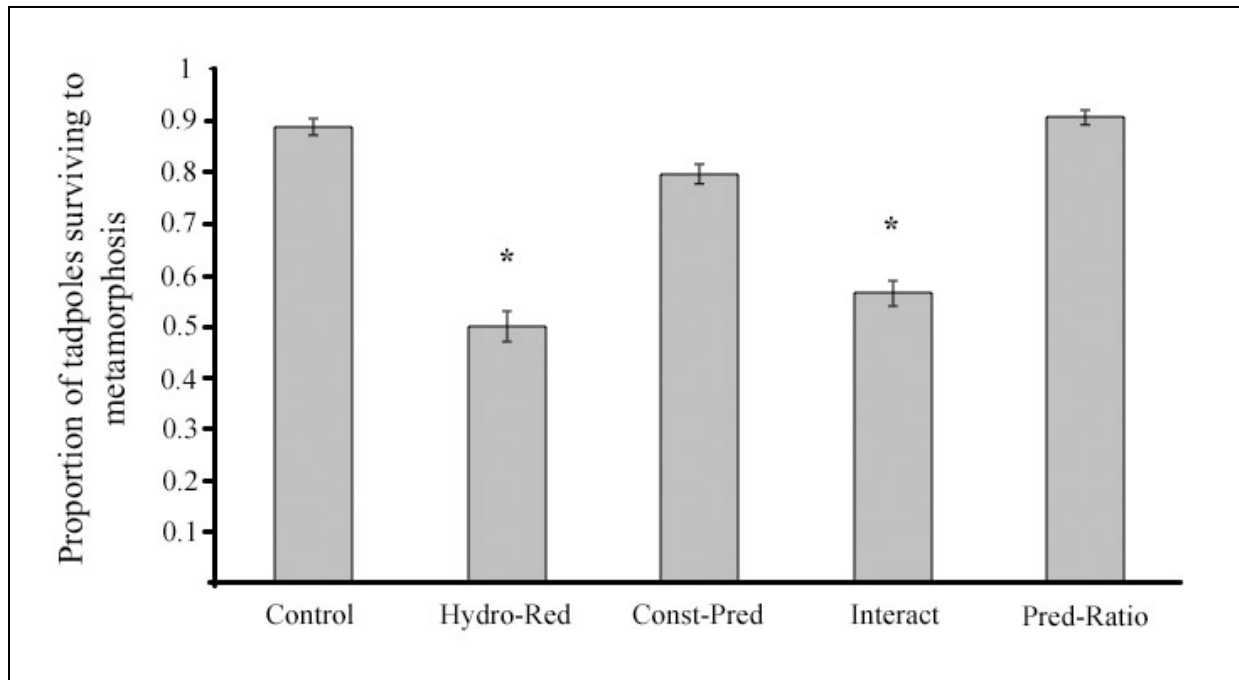


FIGURE 5. – Bar graph of the proportion of tadpoles surviving to metamorphosis by treatment. Error bars are standard error, representing the amount of variation among ponds for each treatment. Asterisks indicate significance of treatment on survival in random effects logistic regression.

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APPENDIX 1. PONDS BY ELEVATIONAL GROUPING AND NATURAL HYDROPERIOD
DESIGNATION WHERE TADPOLES WERE COLLECTED

Site Name	Elevation (meters)	Lat/Long	Natural Hydroperiod
<i>High Elevation Sites</i>			
Phantom Lake	2513	40°46'39.40"N 105°34'17.80" W	Permanent
Molly Lake	2586	40°46'3.76"N 105°35'29.28"W	Permanent
Upper Pingree 1	2858	40°34'6.28"N 105°36'4.49"W	Ephemeral
Surprise Pond	2975	40°33'39.06"N 105°36'41.71" W	Permanent
Sylvatica	3014	40°34'5.00"N 105°50'57.50" W	Permanent
<i>Middle Elevation Sites</i>			
Cherokee B	1923	40°50'28.77"N 105°20'8.71"W	Permanent
Pingree Hill	2388	40°44'35.49"N 105°31'32.08"W	Permanent
Lost Lake	2429	40°50'51.40"N 105°31'33.84"W	Ephemeral
Nairdad	2432	40°50'34.24"N 105°31'35.00"W	Ephemeral
<i>Low Elevation Odonate Larvae Collection Sites</i>			
Riverbend	1496	40°34'24.92"N 105° 1'23.42"W	Ephemeral
Magpie Meander	1519	40°36'15.71"N 105° 5'14.37"W	Permanent

APPENDIX 2. ADDITIONAL METHODOLOGY OF PREDATOR CUE PILOT STUDY

A pilot study was conducted prior to initiation of the experiment to observe the willingness of odonate larvae to consume *P. maculata* tadpoles and the behavioral responses of the tadpoles to predator cues (see METHODS AND MATERIALS- *Predator cue*).

Two odonate larvae and 18 early Gosner stage tadpoles were collected and kept overnight. Odonate larvae were put into their own containers with 1.5L of water. One odonate larva had two tadpoles placed in its container to see if they would be eaten. These were checked hourly and were consumed within 2hrs. The next day, treatments began. Control, Unfed Predator treatment and Fed Predator treatment tadpoles ($N=4$ per container, 2 replicates of each treatment) were randomly placed into containers with 1.45L of water. Sterilized rocks were placed into each container to provide habitat for tadpoles to hide. 50mL of normal, treated water was poured into the Control containers. 50mL of water from the unfed odonate container was added to each Unfed Predator container. 50mL of water from the fed odonate container was added to each Fed Predator container. All tadpoles were fed organic spinach and rabbit pellets and kept in treatments for 8hrs.

I observed tadpole behavior in each of the treatments hourly. Control tadpoles grazed around the container and did not appear to reduce activity for the entire study. Predator treatments tadpoles all reduced activity and hid under the provided rock. Unfed Predator treatment tadpoles minimized activity for approximately 4hrs before returning to activity equivalent to the Control treatment tadpoles. Fed Predator treatment tadpoles minimized activity until nearly the 8hr-mark but also eventually emerged to feed. Both predator treatments continued to be wary and hide quickly if disturbed.

APPENDIX 3. FAMILIES AND GENERA OF ODONATE LARVAE BY ELEVATION USED
FOR THE CREATION OF PREDATOR CUE

<i>Low Elevation- Riverbend and Magpie Meander</i>		
<u>Family</u>	<u>Genus</u>	<u>Number</u>
Libellulidae	<i>Sympetrum</i>	92
Libellulidae	<i>Pachydiplax</i>	2
Libellulidae	<i>Libellula</i>	4
Libellulidae	<i>Erythemis</i>	6
<i>High Elevation- Surprise Pond</i>		
<u>Family</u>	<u>Genus</u>	<u>Number</u>
Libellulidae	<i>Sympetrum</i>	12
Aeschnidae	<i>Aeshna</i>	1
Libellulidae	<i>Leucorrhinia</i>	15
Cordulidae	<i>Somatochlora</i>	3

APPENDIX 4. MODIFIED GOSNER STAGING TABLE

Due to the large number of animals being used for the experiment, tadpoles were not immediately identified by starting Gosner but photographs were taken to allow for later identification. However, the photographs only showed the dorsal and lateral sides of the animals, requiring a modified Gosner staging table to be used as not all characteristics used to stage were evident. Below is the modified table with the defining characteristics and the corresponding Gosner stages they match. No tadpoles were brought into the lab younger than Gosner stage 23.

Gosner Stages	Modified Stage	Characteristics
23-24	1	External gills visible
25	2	External gills not visible, spiracle evident
26-28	3	Limb bud present but no limb emerged
30-34	4	Limb bud emerging from skin, "nub" present off of body
35-36	5	Leg out fully, toes formed and connected together but no distinct knee joint
37-40	6	Leg out, knee joint clear, toes completely separated
41	7	Arms developing, can see under skin around head
42	8	Arms emerged
43-44	9	Face becomes defined and "frog-like"

APPENDIX 5. DATA FOR EXPERIMENT

Container ID is followed by individual ID, starting date for the treatment, date of metamorphosis, initial starting stage, days to metamorphosis, average days to metamorphosis by container, snout-vent length (SVL) at metamorphosis, average SVL by container, and a binomial indicator of survival. Container ID consists of the Site ID_Treatment_Replicate. Keys for Container ID and Site ID are as follows:

Site ID	Site Name	Site ID	Site Name	Trt	Description
2030.2	Cherokee B	3103	Molly	1	Control, 1.5L constant
2050	Pingree Hill	3130	Upper Pingree 1	2	Hydro-Red only, -350mL/change
2101	Lost Lake	3128	Surprise Pond	3	Const-Pred, 1.45L water, 50mL pred cue
2101.2	Nairdad	3112	Sylvatica	4	Interact, -350mL/change, 50mL pred cue
3010	Phantom Lake			5	Pred-Ratio, 1.5L, increasing pred cue

Container	#	Start	Meta	Stage	Days	Days/Cont	SVL	SVL/Cont	Surv=1
2030.2_1_A	1	6/19/10	7/1/10	2	12	16.75	1.223	1.15375	1
2030.2_1_A	2	6/19/10	7/4/10	1	15		1.132		1
2030.2_1_A	3	6/19/10	7/6/10	2	17		1.116		1
2030.2_1_A	4	6/19/10	7/12/10	1	23		1.144		1
2030.2_1_B	1	6/19/10	7/1/10	2	12	20.25	1.137	1.104	1
2030.2_1_B	2	6/19/10	7/10/10	2	21		1.047		1
2030.2_1_B	3	6/19/10	7/11/10	1	22		1.12		1
2030.2_1_B	4	6/19/10	7/15/10	1	26		1.112		1
2030.2_1_C	1	6/19/10	7/2/10	2	13	17.75	1.19	1.05175	1
2030.2_1_C	2	6/19/10	7/4/10	2	15		1.001		1
2030.2_1_C	3	6/19/10	7/6/10	1	17		1.019		1
2030.2_1_C	4	6/19/10	7/15/10	2	26		0.997		1
2030.2_2_A	1	6/19/10	7/4/10	1	15	15	1.186	1.186	1
2030.2_2_A	2	6/19/10	NA	1	-		-		0
2030.2_2_A	3	6/19/10	NA	2	-		-		0
2030.2_2_A	4	6/19/10	NA	2	-		-		0
2030.2_2_B	1	6/19/10	7/4/10	2	15	32	1.095	1.04	1
2030.2_2_B	2	6/19/10	NA	1	-		-		0
2030.2_2_B	3	6/19/10	7/13/10	2	24		1.017		1
2030.2_2_B	4	6/19/10	8/15/10	2	57		1.021		1
2030.2_2_C	1	6/19/10	6/30/10	2	11	13	1.064	1.072	1
2030.2_2_C	2	6/19/10	7/4/10	2	15		1.08		1
2030.2_2_C	3	6/19/10	NA	1	-		-		0
2030.2_2_C	4	6/19/10	NA	1	-		-		0
2030.2_3_A	1	6/19/10	7/1/10	2	12	14.5	1.069	1.085	1
2030.2_3_A	4	6/19/10	7/2/10	2	13		1.049		1
2030.2_3_A	2	6/19/10	7/3/10	2	14		1.029		1
2030.2_3_A	3	6/19/10	7/8/10	2	19		1.193		1
2030.2_3_B	1	6/19/10	7/4/10	1	15	20.5	1.014	1.04675	1
2030.2_3_B	2	6/19/10	7/4/10	2	15		1.021		1
2030.2_3_B	3	6/19/10	7/4/10	1	15		1.06		1
2030.2_3_B	4	6/19/10	7/26/10	2	37		1.092		1
2030.2_3_C	1	6/19/10	6/30/10	2	11	17.66666667	1.72	1.293	1
2030.2_3_C	2	6/19/10	7/6/10	2	17		1.097		1
2030.2_3_C	3	6/19/10	7/14/10	1	25		1.062		1
2030.2_3_C	4	6/19/10	NA	2	-		-		0
2030.2_4_A	1	6/19/10	7/2/10	2	13	15.33333333	0.946	0.9535	1
2030.2_4_A	2	6/19/10	7/5/10	2	16		-		1
2030.2_4_A	3	6/19/10	NA	2	-		-		0

APPENDIX 5. Continued

2030.2_4_A	4	6/19/10	7/6/10	1	17		0.961		1
2030.2_4_B	1	6/19/10	7/2/10	1	13	14.5	1.19	1.1665	1
2030.2_4_B	2	6/19/10	7/5/10	2	16		1.143		1
2030.2_4_B	3	6/19/10	NA	2	-		-		0
2030.2_4_B	4	6/19/10	NA	2	-		-		0
2030.2_4_C	1	6/19/10	NA	2	-	17.33333333	-	1.026	0
2030.2_4_C	2	6/19/10	7/4/10	2	15		1.06		1
2030.2_4_C	3	6/19/10	7/7/10	2	18		0.992		1
2030.2_4_C	4	6/19/10	7/8/10	2	19		1.026		1
2030.2_5_A	1	6/19/10	7/6/10	2	17	22.5	1.146	1.045	1
2030.2_5_A	2	6/19/10	7/7/10	1	18		1.027		1
2030.2_5_A	3	6/19/10	7/14/10	1	25		0.946		1
2030.2_5_A	4	6/19/10	7/19/10	1	30		1.061		1
2030.2_5_B	1	6/19/10	7/2/10	2	13	20.75	1.034	1.04525	1
2030.2_5_B	2	6/19/10	7/3/10	2	14		1.086		1
2030.2_5_B	3	6/19/10	7/11/10	2	22		1.042		1
2030.2_5_B	4	6/19/10	7/23/10	1	34		1.019		1
2030.2_5_C	1	6/19/10	7/6/10	1	17	19.5	1.107	1.048	1
2030.2_5_C	2	6/19/10	7/6/10	2	17		1.004		1
2030.2_5_C	3	6/19/10	7/7/10	2	18		1.033		1
2030.2_5_C	4	6/19/10	7/15/10	1	26		1.048		1
2050_1_A	1	6/19/10	7/1/10	2	12	14.5	1.229	1.15475	1
2050_1_A	2	6/19/10	7/2/10	2	13		1.173		1
2050_1_A	3	6/19/10	7/4/10	2	15		1.034		1
2050_1_A	4	6/19/10	7/7/10	2	18		1.183		1
2050_1_B	1	6/19/10	6/30/10	1	11	14.5	1.094	1.18275	1
2050_1_B	2	6/19/10	7/3/10	1	14		1.18		1
2050_1_B	3	6/19/10	7/5/10	1	16		1.284		1
2050_1_B	4	6/19/10	7/6/10	1	17		1.173		1
2050_1_C	1	6/19/10	7/1/10	1	12	15	1.282	1.15425	1
2050_1_C	2	6/19/10	7/3/10	2	14		1.163		1
2050_1_C	3	6/19/10	7/4/10	1	15		1.147		1
2050_1_C	4	6/19/10	7/8/10	2	19		1.025		1
2050_2_A	1	6/19/10	6/30/10	1	11	12.75	1.321	1.15725	1
2050_2_A	2	6/19/10	7/1/10	2	12		1.039		1
2050_2_A	3	6/19/10	7/1/10	2	12		1.085		1
2050_2_A	4	6/19/10	7/5/10	1	16		1.184		1
2050_2_B	1	6/19/10	6/30/10	2	11	13.66666667	1.126	1.127666667	1
2050_2_B	2	6/19/10	7/3/10	1	14		1.119		1
2050_2_B	3	6/19/10	7/5/10	2	16		1.138		1
2050_2_B	4	6/19/10	NA	2	-		-		0
2050_2_C	1	6/19/10	NA	2	-	14.5	-	1.158	0
2050_2_C	2	6/19/10	7/3/10	2	14		1.161		1
2050_2_C	3	6/19/10	7/4/10	2	15		1.155		1
2050_2_C	4	6/19/10	NA	2	-		-		0
2050_3_A	1	6/19/10	7/1/10	2	12	18.25	-	1.047333333	0
2050_3_A	2	6/19/10	7/4/10	2	15		0.918		1
2050_3_A	3	6/19/10	7/5/10	2	16		1.133		1
2050_3_A	4	6/19/10	7/19/10	2	30		1.091		1
2050_3_B	1	6/19/10	7/2/10	1	13	20.66666667	1.186	1.109666667	1
2050_3_B	2	6/19/10	NA	2	-		-		0
2050_3_B	3	6/19/10	7/10/10	1	21		1.157		1
2050_3_B	4	6/19/10	7/17/10	2	28		0.986		1

APPENDIX 5. Continued

2050_3_C	1	6/19/10	7/1/10	1	12	14.75	1.139	1.098	1
2050_3_C	2	6/19/10	7/4/10	2	15		1.048		1
2050_3_C	3	6/19/10	7/5/10	2	16		1.148		1
2050_3_C	4	6/19/10	7/5/10	2	16		1.057		1
2050_4_A	1	6/19/10	6/30/10	1	11	13	1.082	1.042666667	1
2050_4_A	2	6/19/10	7/2/10	1	13		0.967		1
2050_4_A	3	6/19/10	7/4/10	2	15		1.079		1
2050_4_A	4	6/19/10	NA	1	-		-		0
2050_4_B	1	6/19/10	6/30/10	2	11	13	1.124	1.093333333	1
2050_4_B	2	6/19/10	NA	1	-		-		0
2050_4_B	3	6/19/10	7/2/10	2	13		1.055		1
2050_4_B	4	6/19/10	7/4/10	2	15		1.101		1
2050_4_C	1	6/19/10	6/30/10	2	11	13.25	1.244	1.166	1
2050_4_C	2	6/19/10	7/1/10	2	12		1.069		1
2050_4_C	3	6/19/10	7/2/10	2	13		1.249		1
2050_4_C	4	6/19/10	7/6/10	1	17		1.102		1
2050_5_A	1	6/19/10	7/2/10	2	13	14.75	1.257	1.1435	1
2050_5_A	2	6/19/10	7/2/10	2	13		1.19		1
2050_5_A	3	6/19/10	7/3/10	2	14		1.07		1
2050_5_A	4	6/19/10	7/8/10	2	19		1.057		1
2050_5_B	1	6/19/10	7/3/10	1	14	16.5	1.152	1.08025	1
2050_5_B	2	6/19/10	7/5/10	2	16		0.983		1
2050_5_B	3	6/19/10	7/5/10	2	16		1.116		1
2050_5_B	4	6/19/10	7/9/10	2	20		1.07		1
2050_5_C	1	6/19/10	7/2/10	2	13	15	1.293	1.16625	1
2050_5_C	2	6/19/10	7/2/10	2	13		1.177		1
2050_5_C	3	6/19/10	7/5/10	1	16		1.01		1
2050_5_C	4	6/19/10	7/7/10	2	18		1.185		1
2101_1_A	1	6/19/10	7/6/10	2	17	17.5	1.083	1.0545	1
2101_1_A	2	6/19/10	7/7/10	2	18		1.026		1
2101_1_A	3	6/19/10	NA	1	-		-		0
2101_1_A	4	6/19/10	NA	2	-		-		0
2101_1_B	1	6/19/10	7/3/10	1	14	19	1.171	1.134	1
2101_1_B	2	6/19/10	7/13/10	1	24		1.097		1
2101_1_B	3	6/19/10	NA	1	-		-		0
2101_1_B	4	6/19/10	NA	2	-		-		0
2101_1_C	1	6/19/10	7/4/10	2	15	29.75	1.046	1.077	1
2101_1_C	2	6/19/10	7/6/10	1	17		1.021		1
2101_1_C	3	6/19/10	7/27/10	2	37		1.002		1
2101_1_C	4	6/19/10	8/8/10	2	50		1.239		1
2101_2_A	1	6/19/10	7/1/10	2	12	17.33333333	1.088	1.054333333	1
2101_2_A	2	6/19/10	7/5/10	1	16		1.06		1
2101_2_A	3	6/19/10	7/13/10	2	24		1.015		1
2101_2_A	4	6/19/10	NA	2	-		-		0
2101_2_B	1	6/19/10	NA	2	-	NA	-	NA	0
2101_2_B	2	6/19/10	NA	2	-		-		0
2101_2_B	3	6/19/10	NA	2	-		-		0
2101_2_B	4	6/19/10	NA	2	-		-		0
2101_2_C	1	6/19/10	6/30/10	1	11	11	1.197	1.197	1
2101_2_C	2	6/19/10	NA	1	-		-		0
2101_2_C	3	6/19/10	NA	2	-		-		0
2101_2_C	4	6/19/10	NA	2	-		-		0
2101_3_A	1	6/19/10	NA	2	-	17.33333333	-	1.164	0

APPENDIX 5. Continued

2101_3_A	2	6/19/10	6/30/10	2	11		1.064		1
2101_3_A	3	6/19/10	7/1/10	2	12		1.224		1
2101_3_A	4	6/19/10	7/18/10	1	29		1.204		1
2101_3_B	1	6/19/10	7/5/10	2	16	24	1.037	1.097333333	1
2101_3_B	2	6/19/10	7/5/10	2	15		1.134		1
2101_3_B	3	6/19/10	7/31/10	2	41		1.121		1
2101_3_B	4	6/19/10	NA	2	-		-		0
2101_3_C	1	6/19/10	NA	2	-	24	-	1.118333333	0
2101_3_C	2	6/19/10	7/2/10	2	13		1.229		1
2101_3_C	3	6/19/10	7/3/10	2	14		1.092		1
2101_3_C	4	6/19/10	8/3/10	1	45		1.034		1
2101_4_A	1	6/19/10	6/30/10	2	11	11	1.196	1.196	1
2101_4_A	2	6/19/10	NA	2	-		-		0
2101_4_A	3	6/19/10	NA	2	-		-		0
2101_4_A	4	6/19/10	NA	2	-		-		0
2101_4_B	1	6/19/10	6/30/10	1	11	20.33333333	1.218	1.1	1
2101_4_B	2	6/19/10	7/3/10	2	14		1.026		1
2101_4_B	3	6/19/10	7/26/10	2	36		1.056		1
2101_4_B	4	6/19/10	NA	1	-		-		0
2101_4_C	1	6/19/10	7/4/10	2	15	22.66666667	1.055	1.061333333	1
2101_4_C	2	6/19/10	7/9/10	1	20		1.008		1
2101_4_C	3	6/19/10	7/22/10	1	33		1.121		1
2101_4_C	4	6/19/10	NA	2	-		-		0
2101_5_A	1	6/19/10	7/1/10	2	12	22.5	1.141	1.10025	1
2101_5_A	2	6/19/10	7/2/10	1	13		1.044		1
2101_5_A	3	6/19/10	7/15/10	1	26		1.092		1
2101_5_A	4	6/19/10	7/29/10	2	39		1.124		1
2101_5_B	1	6/19/10	6/30/10	2	11	22.5	1.279	1.127	1
2101_5_B	2	6/19/10	7/8/10	1	19		1.07		1
2101_5_B	3	6/19/10	7/17/10	2	28		0.998		1
2101_5_B	4	6/19/10	7/21/10	2	32		1.161		1
2101_5_C	1	6/19/10	7/2/10	2	13	27.66666667	1.111	1.073666667	1
2101_5_C	2	6/19/10	7/3/10	2	14		1.066		1
2101_5_C	3	6/19/10	NA	2	-		-		0
2101_5_C	4	6/19/10	8/14/10	2	56		1.044		1
2101.2_1_A	1	6/19/10	7/3/10	2	14	19.33333333	1.038	1.043333333	1
2101.2_1_A	2	6/19/10	7/6/10	2	17		1.065		1
2101.2_1_A	3	6/19/10	7/16/10	2	27		1.027		1
2101.2_1_A	4	6/19/10	NA	2	-		-		0
2101.2_1_B	1	6/19/10	7/6/10	1	17	19	1.222	1.1455	1
2101.2_1_B	2	6/19/10	7/7/10	2	18		1.195		1
2101.2_1_B	3	6/19/10	7/7/10	2	18		1.128		1
2101.2_1_B	4	6/19/10	7/12/10	2	23		1.037		1
2101.2_1_C	1	6/19/10	7/3/10	1	14	29	1.027	1.08225	1
2101.2_1_C	2	6/19/10	7/11/10	2	22		1.137		1
2101.2_1_C	3	6/19/10	7/11/10	2	22		1.115		1
2101.2_1_C	4	6/19/10	8/16/10	2	58		1.05		1
2101.2_2_A	1	6/19/10	7/1/10	2	12	18.66666667	1.16	1.092	1
2101.2_2_A	2	6/19/10	NA	2	-		-		0
2101.2_2_A	3	6/19/10	7/6/10	2	17		1.1		1
2101.2_2_A	4	6/19/10	7/16/10	2	27		1.016		1
2101.2_2_B	1	6/19/10	NA	2	-	NA	-	NA	0
2101.2_2_B	2	6/19/10	NA	2	-		-		0

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2101.2_2_B	3	6/19/10	NA	2	-	-	-	0	
2101.2_2_B	4	6/19/10	NA	2	-	-	-	0	
2101.2_2_C	1	6/19/10	7/2/10	1	13	20.75	1.047	1.0405	1
2101.2_2_C	2	6/19/10	7/3/10	2	14		1.048		1
2101.2_2_C	3	6/19/10	7/15/10	2	26		1.038		1
2101.2_2_C	4	6/19/10	7/19/10	2	30		1.029		1
2101.2_3_A	1	6/19/10	7/4/10	2	15	19	1.099	1.097666667	1
2101.2_3_A	2	6/19/10	7/10/10	2	21		1.118		1
2101.2_3_A	3	6/19/10	7/10/10	2	21		1.076		1
2101.2_3_A	4	6/19/10	NA	2	-		-		0
2101.2_3_B	1	6/19/10	7/1/10	2	12	16.75	1.03	1.092	1
2101.2_3_B	2	6/19/10	7/2/10	2	13		1.131		1
2101.2_3_B	3	6/19/10	7/8/10	2	19		0.99		1
2101.2_3_B	4	6/19/10	7/12/10	2	23		1.217		1
2101.2_3_C	1	6/19/10	7/1/10	2	12	22.5	1.138	1.11775	1
2101.2_3_C	2	6/19/10	7/5/10	2	16		1.15		1
2101.2_3_C	3	6/19/10	7/16/10	2	27		1.086		1
2101.2_3_C	4	6/19/10	7/24/10	2	35		1.097		1
2101.2_4_A	1	6/19/10	7/3/10	2	14	15	1.176	1.101	1
2101.2_4_A	2	6/19/10	7/5/10	2	16		1.026		1
2101.2_4_A	3	6/19/10	NA	2	-		-		0
2101.2_4_A	4	6/19/10	NA	2	-		-		0
2101.2_4_B	1	6/19/10	6/30/10	2	11	18	1.129	1.069	1
2101.2_4_B	2	6/19/10	NA	2	-		-		0
2101.2_4_B	3	6/19/10	7/14/10	2	25		1.009		1
2101.2_4_B	4	6/19/10	NA	2	-		-		0
2101.2_4_C	1	6/19/10	7/2/10	2	13	13	1.155	1.155	1
2101.2_4_C	2	6/19/10	NA	2	-		-		0
2101.2_4_C	3	6/19/10	NA	2	-		-		0
2101.2_4_C	4	6/19/10	NA	2	-		-		0
2101.2_5_A	1	6/19/10	7/3/10	1	14	17.75	1.061	1.06525	1
2101.2_5_A	2	6/19/10	7/4/10	2	15		1.052		1
2101.2_5_A	3	6/19/10	7/10/10	2	21		0.993		1
2101.2_5_A	4	6/19/10	7/10/10	1	21		1.155		1
2101.2_5_B	1	6/19/10	7/3/10	1	14	16	1.061	1.14125	1
2101.2_5_B	2	6/19/10	7/3/10	2	14		1.119		1
2101.2_5_B	3	6/19/10	7/4/10	2	15		1.079		1
2101.2_5_B	4	6/19/10	7/10/10	1	21		1.306		1
2101.2_5_C	1	6/19/10	7/6/10	2	17	19.75	1.079	1.09675	1
2101.2_5_C	2	6/19/10	7/9/10	2	20		1.041		1
2101.2_5_C	3	6/19/10	7/9/10	2	20		1.22		1
2101.2_5_C	4	6/19/10	7/11/10	2	22		1.047		1
3010_1_A	1	6/19/10	7/6/10	2	17	18.66666667	1.099	1.080666667	1
3010_1_A	2	6/19/10	7/7/10	2	18		1.089		1
3010_1_A	3	6/19/10	7/10/10	2	21		1.054		1
3010_1_A	4	6/19/10	NA	2	-		-		0
3010_1_B	1	6/19/10	7/6/10	2	17	23	1.092	1.033666667	1
3010_1_B	2	6/19/10	7/13/10	1	24		0.984		1
3010_1_B	3	6/19/10	7/17/10	2	28		1.025		1
3010_1_B	4	6/19/10	NA	1	-		-		0
3010_1_C	1	6/19/10	7/2/10	1	13	13.5	1.13	1.081	1
3010_1_C	2	6/19/10	7/3/10	2	14		1.032		1
3010_1_C	3	6/19/10	NA	1	-		-		0

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3010_1_C	4	6/19/10	NA	2	-		-		0
3010_2_A	1	6/19/10	7/8/10	1	19	19	1.029	1.029	1
3010_2_A	2	6/19/10	NA	2	-		-		0
3010_2_A	3	6/19/10	NA	1	-		-		0
3010_2_A	4	6/19/10	NA	1	-		-		0
3010_2_B	1	6/19/10	7/1/10	2	12	14	0.963	0.9665	1
3010_2_B	2	6/19/10	7/5/10	1	16		0.97		1
3010_2_B	3	6/19/10	NA	2	-		-		0
3010_2_B	4	6/19/10	NA	2	-		-		0
3010_2_C	1	6/19/10	NA	1	-	NA	-	0	0
3010_2_C	2	6/19/10	NA	2	-		-		0
3010_2_C	3	6/19/10	NA	2	-		-		0
3010_2_C	4	6/19/10	NA	2	-		-		0
3010_3_A	1	6/19/10	7/7/10	1	18	18	1.084	1.084	1
3010_3_A	2	6/19/10	-	-	-	-	-	-	-
3010_3_A	3	6/19/10	NA	1	-		-		0
3010_3_A	4	6/19/10	NA	2	-		-		0
3010_3_B	1	6/19/10	7/16/10	1	27	37.5	0.987	1.0085	1
3010_3_B	2	6/19/10	NA	1	-		-		0
3010_3_B	3	6/19/10	NA	1	-		-		0
3010_3_B	4	6/19/10	8/6/10	2	48		1.03		1
3010_3_C	1	6/19/10	7/10/10	1	21	22.33333333	1.129	1.092666667	1
3010_3_C	2	6/19/10	7/12/10	2	23		1.103		1
3010_3_C	3	6/19/10	7/12/10	2	23		1.046		1
3010_3_C	4	6/19/10	NA	1	-		-		0
3010_4_A	1	6/19/10	NA	1	-	13	-	1.039	0
3010_4_A	2	6/19/10	7/2/10	1	13		1.039		1
3010_4_A	3	6/19/10	NA	1	-		-		0
3010_4_A	4	6/19/10	NA	2	-		-		0
3010_4_B	1	6/19/10	6/30/10	1	11	11	1.094	1.094	1
3010_4_B	2	6/19/10	NA	1	-		-		0
3010_4_B	3	6/19/10	NA	1	-		-		0
3010_4_B	4	6/19/10	NA	1	-		-		0
3010_4_C	1	6/19/10	7/2/10	1	13	19.5	1.076	0.997	1
3010_4_C	2	6/19/10	7/15/10	1	26		0.918		1
3010_4_C	3	6/19/10	NA	2	-		-		0
3010_4_C	4	6/19/10	NA	1	-		-		0
3010_5_A	1	6/19/10	7/3/10	1	14	17	1.124	1.11725	1
3010_5_A	2	6/19/10	7/4/10	1	15		1.144		1
3010_5_A	3	6/19/10	7/6/10	2	17		1.021		1
3010_5_A	4	6/19/10	7/11/10	1	22		1.18		1
3010_5_B	1	6/19/10	7/5/10	1	16	18.33333333	1.216	1.127333333	1
3010_5_B	2	6/19/10	7/6/10	2	17		1.126		1
3010_5_B	3	6/19/10	7/11/10	1	22		1.04		1
3010_5_B	4	6/19/10	NA	2	-		-		0
3010_5_C	1	6/19/10	7/2/10	1	13	15	1.142	1.054666667	1
3010_5_C	2	6/19/10	7/5/10	1	16		1.018		1
3010_5_C	3	6/19/10	7/5/10	1	16		1.004		1
3010_5_C	4	6/19/10	NA	2	-		-		0
3103_1_A	1	6/19/10	6/30/10	2	11	14.66666667	1.019	1.039	1
3103_1_A	2	6/19/10	7/1/10	2	12		1.05		1
3103_1_A	3	6/19/10	7/10/10	2	21		1.048		1
3103_1_A	4	6/19/10	NA	1	-		-		0

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3103_1_B	1	6/19/10	6/30/10	1	11	12.75	1.004	1.04775	1
3103_1_B	2	6/19/10	7/2/10	2	13		1.109		1
3103_1_B	3	6/19/10	7/2/10	2	13		0.985		1
3103_1_B	4	6/19/10	7/3/10	1	14		1.093		1
3103_1_C	1	6/19/10	7/3/10	2	14	23.75	1.136	1.08775	1
3103_1_C	2	6/19/10	7/4/10	2	15		1.089		1
3103_1_C	3	6/19/10	7/14/10	2	25		1.128		1
3103_1_C	4	6/19/10	7/30/10	2	41		0.998		1
3103_2_A	1	6/19/10	6/30/10	2	11	12.66666667	1.19	1.093	1
3103_2_A	2	6/19/10	6/30/10	2	11		1.009		1
3103_2_A	3	6/19/10	7/5/10	2	16		1.08		1
3103_2_A	4	6/19/10	NA	2	-		-		0
3103_2_B	1	6/19/10	NA	2	-	NA	-	NA	0
3103_2_B	2	6/19/10	NA	2	-		-		0
3103_2_B	3	6/19/10	NA	2	-		-		0
3103_2_B	4	6/19/10	NA	2	-		-		0
3103_2_C	1	6/19/10	7/4/10	2	15	16	1.089	1.0565	1
3103_2_C	2	6/19/10	7/6/10	2	17		1.024		1
3103_2_C	3	6/19/10	NA	2	-		-		0
3103_2_C	4	6/19/10	NA	2	-		-		0
3103_3_A	1	6/19/10	7/2/10	2	13	17	1.081	1.04025	1
3103_3_A	2	6/19/10	7/4/10	2	15		1.038		1
3103_3_A	3	6/19/10	7/6/10	2	17		1.03		1
3103_3_A	4	6/19/10	7/12/10	2	23		1.012		1
3103_3_B	1	6/19/10	7/2/10	1	13	16	1.122	1.032333333	1
3103_3_B	2	6/19/10	7/5/10	2	16		0.98		1
3103_3_B	3	6/19/10	7/8/10	2	19		0.995		1
3103_3_B	4	6/19/10	NA	2	-		-		0
3103_3_C	1	6/19/10	6/30/10	1	11	13.33333333	1.212	1.095666667	1
3103_3_C	2	6/19/10	7/1/10	1	12		1.006		1
3103_3_C	3	6/19/10	NA	2	-		-		0
3103_3_C	4	6/19/10	7/6/10	1	17		1.069		1
3103_4_A	1	6/19/10	7/2/10	1	13	18.25	1.046	1.00325	1
3103_4_A	2	6/19/10	7/8/10	2	19		1.026		1
3103_4_A	3	6/19/10	7/9/10	1	20		0.995		1
3103_4_A	4	6/19/10	7/10/10	2	21		0.946		1
3103_4_B	1	6/19/10	6/30/10	2	11	12.5	1.121	1.091	1
3103_4_B	2	6/19/10	7/3/10	1	14		1.061		1
3103_4_B	3	6/19/10	NA	2	-		-		0
3103_4_B	4	6/19/10	NA	2	-		-		0
3103_4_C	1	6/19/10	7/3/10	1	14	25.33333333	0.994	1.154	1
3103_4_C	2	6/19/10	7/4/10	1	15		1.221		1
3103_4_C	3	6/19/10	NA	1	-		-		0
3103_4_C	4	6/19/10	8/5/10	2	47		1.247		1
3103_5_A	1	6/19/10	7/1/10	1	12	12.75	1.104	1.10575	1
3103_5_A	2	6/19/10	7/1/10	1	12		1.1		1
3103_5_A	3	6/19/10	7/2/10	2	13		1.15		1
3103_5_A	4	6/19/10	7/3/10	2	14		1.069		1
3103_5_B	1	6/19/10	7/2/10	2	13	18.5	1.102	1.1155	1
3103_5_B	2	6/19/10	7/5/10	2	16		1.142		1
3103_5_B	3	6/19/10	7/10/10	2	21		1.03		1
3103_5_B	4	6/19/10	7/13/10	2	24		1.188		1
3103_5_C	1	6/19/10	6/30/10	2	11	17.75	1.115	1.06825	1

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3103_5_C	2	6/19/10	7/8/10	2	19		1.078		1
3103_5_C	3	6/19/10	7/8/10	2	19		1.018		1
3103_5_C	4	6/19/10	7/11/10	1	22		1.062		1
3130_1_A	1	6/29/10	7/9/10	1	10	12	1.119	1.0915	1
3130_1_A	2	6/29/10	7/11/10	2	12		1.078		1
3130_1_A	3	6/29/10	7/11/10	2	12		1.11		1
3130_1_A	4	6/29/10	7/13/10	2	14		1.059		1
3130_1_B	1	6/29/10	7/8/10	2	9	12.75	1.069	1.05075	1
3130_1_B	2	6/29/10	7/11/10	2	12		1.018		1
3130_1_B	3	6/29/10	7/12/10	2	13		1.1		1
3130_1_B	4	6/29/10	7/16/10	1	17		1.016		1
3130_1_C	1	6/29/10	7/8/10	2	9	14.25	1.199	1.16475	1
3130_1_C	2	6/29/10	7/10/10	2	11		1.149		1
3130_1_C	3	6/29/10	7/14/10	2	15		1.09		1
3130_1_C	4	6/29/10	7/21/10	1	22		1.221		1
3130_2_A	1	6/29/10	7/7/10	2	8	14.5	1.133	1.111	1
3130_2_A	2	6/29/10	7/11/10	2	12		1.104		1
3130_2_A	3	6/29/10	7/17/10	1	18		1.08		1
3130_2_A	4	6/29/10	7/19/10	1	20		1.127		1
3130_2_B	1	6/29/10	7/12/10	2	13	13	1.023	1.023	1
3130_2_B	2	6/29/10	NA	2	-		-		0
3130_2_B	3	6/29/10	NA	2	-		-		0
3130_2_B	4	6/29/10	NA	1	-		-		0
3130_2_C	1	6/29/10	7/10/10	2	11	25.33333333	1.09	1.105	1
3130_2_C	2	6/29/10	7/15/10	2	16		1.143		1
3130_2_C	3	6/29/10	NA	2	-		-		0
3130_2_C	4	6/29/10	8/17/10	2	49		1.082		1
3130_3_A	1	6/29/10	7/12/10	2	13	14.66666667	1.088	1.164666667	1
3130_3_A	2	6/29/10	7/14/10	2	15		1.272		1
3130_3_A	3	6/29/10	7/15/10	2	16		1.134		1
3130_3_A	4	6/29/10	NA	2	-		-		0
3130_3_B	1	6/29/10	7/11/10	1	12	14.5	1.171	1.034	1
3130_3_B	2	6/29/10	7/16/10	2	17		0.897		1
3130_3_B	3	6/29/10	NA	2	-		-		0
3130_3_B	4	6/29/10	NA	2	-		-		0
3130_3_C	1	6/29/10	7/8/10	1	9	11.33333333	1.225	1.219	1
3130_3_C	2	6/29/10	7/10/10	2	11		1.292		1
3130_3_C	3	6/29/10	7/13/10	2	14		1.14		1
3130_3_C	4	6/29/10	NA	2	-		-		0
3130_4_A	1	6/29/10	7/11/10	2	12	12.33333333	1.088	1.029333333	1
3130_4_A	2	6/29/10	7/11/10	2	12		1.08		1
3130_4_A	3	6/29/10	7/12/10	2	13		0.92		1
3130_4_A	4	6/29/10	NA	2	-		-		0
3130_4_B	1	6/29/10	7/11/10	1	12	13.25	1.091	1.07375	1
3130_4_B	2	6/29/10	7/11/10	2	12		1.044		1
3130_4_B	3	6/29/10	7/12/10	2	13		1.108		1
3130_4_B	4	6/29/10	7/15/10	2	16		1.052		1
3130_4_C	1	6/29/10	7/11/10	2	12	20.66666667	1.15	1.164333333	1
3130_4_C	2	6/29/10	7/12/10	1	13		1.044		1
3130_4_C	3	6/29/10	NA	2	-		-		0
3130_4_C	4	6/29/10	8/5/10	2	37		1.299		1
3130_5_A	1	6/29/10	7/10/10	2	11	19	1.307	1.214666667	1
3130_5_A	2	6/29/10	7/12/10	1	13		1.102		1

APPENDIX 5. Continued

3130_5_A	3	6/29/10	8/1/10	1	33		1.235		1
3130_5_A	4	6/29/10	NA	2	-		-		0
3130_5_B	1	6/29/10	7/11/10	2	12	14.25	1.231	1.1375	1
3130_5_B	2	6/29/10	7/11/10	2	12		1.18		1
3130_5_B	3	6/29/10	7/14/10	2	15		1.044		1
3130_5_B	4	6/29/10	7/17/10	2	18		1.095		1
3130_5_C	1	6/29/10	7/14/10	1	15	23.75	1.101	1.02325	1
3130_5_C	2	6/29/10	7/15/10	2	16		1.053		1
3130_5_C	3	6/29/10	7/23/10	2	24		0.942		1
3130_5_C	4	6/29/10	8/8/10	1	40		0.997		1
3128_1_A	1	6/29/10	7/13/10	2	14	17.66666667	1.13	1.149333333	1
3128_1_A	2	6/29/10	7/16/10	2	17		1.091		1
3128_1_A	3	6/29/10	7/21/10	2	22		1.227		1
3128_1_A	4	6/29/10	NA	2	-		-		0
3128_1_B	1	6/29/10	7/11/10	2	12	18.5	1.229	1.11575	1
3128_1_B	2	6/29/10	7/15/10	1	16		1.088		1
3128_1_B	3	6/29/10	7/19/10	2	20		1.085		1
3128_1_B	4	6/29/10	7/25/10	2	26		1.061		1
3128_1_C	1	6/29/10	7/11/10	2	12	18.33333333	1.212	1.142666667	1
3128_1_C	2	6/29/10	7/16/10	2	17		1.112		1
3128_1_C	3	6/29/10	7/25/10	2	26		1.104		1
3128_1_C	4	6/29/10	NA	2	-		-		0
3128_2_A	1	6/29/10	7/16/10	2	17	20	1.072	1.134	1
3128_2_A	2	6/29/10	7/22/10	2	23		1.196		1
3128_2_A	3	6/29/10	NA	2	-		-		0
3128_2_A	4	6/29/10	NA	2	-		-		0
3128_2_B	1	6/29/10	7/15/10	2	16	16	1.127	1.127	1
3128_2_B	2	6/29/10	NA	2	-		-		0
3128_2_B	3	6/29/10	NA	2	-		-		0
3128_2_B	4	6/29/10	NA	2	-		-		0
3128_2_C	1	6/29/10	7/15/10	2	16	16.5	1.156	1.118	1
3128_2_C	2	6/29/10	7/16/10	2	17		1.08		1
3128_2_C	3	6/29/10	NA	2	-		-		0
3128_2_C	4	6/29/10	NA	2	-		-		0
3128_3_A	1	6/29/10	7/18/10	2	19	27.75	1.067	1.05525	1
3128_3_A	2	6/29/10	7/22/10	2	23		0.969		1
3128_3_A	3	6/29/10	7/24/10	2	25		1.094		1
3128_3_A	4	6/29/10	8/12/10	2	44		1.091		1
3128_3_B	1	6/29/10	7/16/10	2	17	30.5	1.173	1.085	1
3128_3_B	2	6/29/10	8/12/10	2	44		0.997		1
3128_3_B	3	6/29/10	NA	2	-		-		0
3128_3_B	4	6/29/10	NA	2	-		-		0
3128_3_C	1	6/29/10	7/16/10	2	17	24.66666667	1.183	1.094666667	1
3128_3_C	2	6/29/10	7/22/10	2	23		1.031		1
3128_3_C	3	6/29/10	8/2/10	2	34		1.07		1
3128_3_C	4	6/29/10	NA	2	-		-		0
3128_4_A	1	6/29/10	7/15/10	2	16	22.5	1.036	1.029	1
3128_4_A	2	6/29/10	7/28/10	2	29		1.022		1
3128_4_A	3	6/29/10	NA	2	-		-		0
3128_4_A	4	6/29/10	NA	2	-		-		0
3128_4_B	1	6/29/10	7/10/10	2	11	13	1.136	1.0885	1
3128_4_B	2	6/29/10	7/14/10	2	15		1.041		1
3128_4_B	3	6/29/10	NA	2	-		-		0

APPENDIX 5. Continued

3128_4_B	4	6/29/10	NA	1	-		-		0
3128_4_C	1	6/29/10	7/12/10	2	13	13	1.144	1.144	1
3128_4_C	2	6/29/10	NA	1	-		-		0
3128_4_C	3	6/29/10	NA	2	-		-		0
3128_4_C	4	6/29/10	NA	1	-		-		0
3128_5_A	1	6/29/10	7/16/10	2	17	20.5	1.061	1.0855	1
3128_5_A	2	6/29/10	7/23/10	2	24		1.11		1
3128_5_A	3	6/29/10	NA	2	-		-		0
3128_5_A	4	6/29/10	NA	1	-		-		0
3128_5_B	1	6/29/10	7/22/10	2	23	28.66666667	1.026	1.038333333	1
3128_5_B	2	6/29/10	7/22/10	2	23		1.115		1
3128_5_B	3	6/29/10	8/8/10	2	40		0.974		1
3128_5_B	4	6/29/10	NA	2	-		-		0
3128_5_C	1	6/29/10	7/14/10	1	15	28	1.053	1.058333333	1
3128_5_C	2	6/29/10	7/29/10	2	30		1.124		1
3128_5_C	3	6/29/10	8/7/10	2	39		0.998		1
3128_5_C	4	6/29/10	NA	1	-		-		0
3112_1_A	1	6/29/10	7/16/10	2	17	22.75	1.027	1.064	1
3112_1_A	2	6/29/10	7/22/10	2	23		1.056		1
3112_1_A	3	6/29/10	7/23/10	2	24		1.061		1
3112_1_A	4	6/29/10	7/26/10	2	27		1.112		1
3112_1_B	1	6/29/10	7/16/10	2	17	25.75	1.122	1.13325	1
3112_1_B	2	6/29/10	7/16/10	2	17		1.216		1
3112_1_B	3	6/29/10	7/24/10	2	25		1.08		1
3112_1_B	4	6/29/10	8/12/10	2	44		1.115		1
3112_1_C	1	6/29/10	7/15/10	2	16	33	1.196	1.1295	1
3112_1_C	2	6/29/10	7/26/10	2	27		1.003		1
3112_1_C	3	6/29/10	8/11/10	2	43		1.075		1
3112_1_C	4	6/29/10	8/14/10	2	46		1.244		1
3112_2_A	1	6/29/10	7/16/10	2	17	21	1.09	1.059	1
3112_2_A	2	6/29/10	7/24/10	2	25		1.028		1
3112_2_A	3	6/29/10	NA	2	-		-		0
3112_2_A	4	6/29/10	NA	2	-		-		0
3112_2_B	1	6/29/10	7/21/10	2	22	34	1.118	1.0715	1
3112_2_B	2	6/29/10	NA	2	-		-		0
3112_2_B	3	6/29/10	NA	2	-		-		0
3112_2_B	4	6/29/10	8/14/10	2	46		1.025		1
3112_2_C	1	6/29/10	7/16/10	2	17	22.66666667	1.198	1.100333333	1
3112_2_C	2	6/29/10	7/18/10	2	19		0.997		1
3112_2_C	3	6/29/10	7/31/10	2	32		1.106		1
3112_2_C	4	6/29/10	NA	2	-		-		0
3112_3_A	1	6/29/10	7/18/10	2	19	24.75	1.125	1.17425	1
3112_3_A	2	6/29/10	7/21/10	2	22		1.089		1
3112_3_A	3	6/29/10	7/22/10	2	23		1.223		1
3112_3_A	4	6/29/10	8/3/10	2	35		1.26		1
3112_3_B	1	6/29/10	7/16/10	2	17	28	1.073	1.07	1
3112_3_B	2	6/29/10	7/21/10	2	22		1.033		1
3112_3_B	3	6/29/10	7/26/10	2	27		1.055		1
3112_3_B	4	6/29/10	8/14/10	2	46		1.119		1
3112_3_C	1	6/29/10	7/16/10	2	17	20.25	1.183	1.13625	1
3112_3_C	2	6/29/10	7/16/10	2	17		1.018		1
3112_3_C	3	6/29/10	7/16/10	2	17		1.174		1
3112_3_C	4	6/29/10	7/29/10	2	30		1.17		1

APPENDIX 5. Continued

3112_4_A	1	6/29/10	NA	2	-	NA	-	NA	0
3112_4_A	2	6/29/10	NA	2	-		-		0
3112_4_A	3	6/29/10	NA	2	-		-		0
3112_4_A	4	6/29/10	NA	2	-		-		0
3112_4_B	1	6/29/10	7/15/10	2	16	26.5	1.131	1.1045	1
3112_4_B	2	6/29/10	8/5/10	2	37		1.078		1
3112_4_B	3	6/29/10	NA	2	-		-		0
3112_4_B	4	6/29/10	NA	2	-		-		0
3112_4_C	1	6/29/10	7/17/10	2	18	18	1.099	1.099	1
3112_4_C	2	6/29/10	NA	2	-		-		0
3112_4_C	3	6/29/10	NA	2	-		-		0
3112_4_C	4	6/29/10	NA	2	-		-		0
3112_5_A	1	6/29/10	7/17/10	2	18	23	1.089	1.0735	1
3112_5_A	2	6/29/10	7/27/10	2	28		1.058		1
3112_5_A	3	6/29/10	NA	2	-		-		0
3112_5_A	4	6/29/10	NA	2	-		-		0
3112_5_B	1	6/29/10	7/16/10	2	17	27.75	1.022	1.08425	1
3112_5_B	2	6/29/10	7/18/10	2	19		1.039		1
3112_5_B	3	6/29/10	8/3/10	2	35		1.082		1
3112_5_B	4	6/29/10	8/8/10	2	40		1.194		1
3112_5_C	1	6/29/10	7/18/10	2	19	30.5	1.103	1.0975	1
3112_5_C	2	6/29/10	7/23/10	2	24		1.083		1
3112_5_C	3	6/29/10	8/1/10	2	33		1.116		1
3112_5_C	4	6/29/10	8/14/10	2	46		1.088		1

PART TWO:

THE EFFECTS OF HYDROPERIOD AND PREDATOR COMMUNITIES ON AMPHIBIAN OCCUPANCY²

SUMMARY

Climate change impacts biodiversity and species distributions by altering factors that regulate habitat suitability. To better predict and potentially ameliorate the impact of climate change, the factors regulating habitat suitability must be identified. We utilize 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*) tadpoles. We hypothesized that hydroperiod and predators are of primary importance as they affect desiccation and predation risk and will be impacted greatly by climate change. We surveyed 62 wetland sites across an elevational gradient in Colorado, USA and modeled patterns in *P. maculata* occupancy. *P. maculata* tadpoles were most frequently present in ponds with intermediate hydroperiod lengths that have lower desiccation risk but exclude predatory fish due to occasional drying. Fish presence had a strong, negative relationship to *P. maculata* occupancy while odonate larvae and tiger salamanders (*Ambystoma tigrinum*) frequently co-occurred with tadpoles. Climate change will likely result in fewer intermediate hydroperiod ponds available as breeding sites for amphibians. Based upon our results, we predict that this reduction in preferred habitat may force *P. maculata* to breed in habitats with fish. In addition, as habitats shrink, predators that co-occur with *P. maculata* may concentrate in the remaining habitat and increase predation risk for developing tadpoles.

² Amburgey, S.M., Bailey, L.L., Murphy, M., Muths, E., Funk, W.C. In review. Biological Conservation

INTRODUCTION

Climate change is expected to affect the distribution and persistence of species globally, and better predictions of risk can be made if factors most important to habitat suitability can be 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). 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). Understanding local dynamics impacting habitat suitability are important as regional predictions of climate change effects may not capture important local processes essential for conservation planning (Pitchford et al. 2011).

We focused on modeling amphibian occurrence due to their sensitivity to environmental conditions (Bartelt and Peterson 2005), their presence in vulnerable freshwater habitats that are expected to alter drastically with climate change (Matthews et al. 2013), and the already heightened level of conservation concern for this group (Stuart et al. 2004; Pounds et al. 2006; 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 that are most vulnerable to climate change (Matthews 2010; Matthews et al. 2013), 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 expected to decrease in some regions in response to climate change (Matthews 2010), negatively impacting organisms that utilize these habitats for breeding and larval development. Snowmelt is critical for wetland recharge for many amphibian species (Corn 2003), making these habitats vulnerable to climate change (Matthews et al. 2013). Hydroperiod strongly regulates habitat suitability by affecting characteristics like temperature, habitat vegetation, and desiccation risk directly (Pechmann et al. 1989; Skelly et al. 2002).

Species interactions must also be considered in concert with the abiotic effects of climate change (Gilman et al. 2010) as alterations in species interactions may be the proximate cause of species' declines (Cahill et al. 2013). 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 hydroperiod, and certain predators such as fish may effectively exclude amphibian species from sites (Skelly 1996; Knapp 2005).

Hydroperiod and predators may both impact amphibian occupancy, but little is known about their combined effect. Truncated hydroperiod may concentrate predators and their chemical cues in the remaining habitat (Blaustein et al. 2001; Mirza et al. 2006; Amburgey et al. in review), resulting in increased stress during amphibian larval development and higher levels of mortality (Amburgey et al. in review). 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. in review), though this response may be limited when changes to habitats are extreme (Gienapp et al. 2008). By identifying these factors, how they affect species

distributions currently, and how they vary in occupied habitats, we can better understand how climate change will alter species persistence and distribution.

To assess the potential effect of climate change on amphibian occurrence, we evaluated the impact of pond-level and landscape-level characteristics on site occupancy by boreal chorus frog (*Pseudacris maculata*) tadpoles, focusing on current hydroperiod and predator interactions as our primary factors. *P. 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). 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).

We hypothesized that *P. maculata* tadpole occupancy would be greatest at ponds with intermediate hydroperiods that have a lower desiccation risk but still exclude permanent pond predators due to occasional drying. We also expected that predators would impact the suitability of sites, and that fish would exclude *P. maculata* tadpoles entirely. If our hypotheses are supported, climate change may alter the distribution of *P. maculata* by shortening the hydroperiod at suitable intermediate sites and excluding breeding. Adults may be forced to breed at sites that dry too quickly or have predatory fish. In shrinking habitats, tadpoles may experience higher predation risk. By isolating a suite of factors that are shown to regulate occupancy, we can better focus on the effect climate change will have on species persistence and distributions.

METHODS AND MATERIALS

Site selection and surveying

We identified potential sites in Larimer County, Colorado, USA utilizing historical observations, current survey records and wetland inventories (NAIP- USDA 2009; NWI-USFWS 2009; Fig. 6). These sites were stratified by elevation (low, mid, and high; 1480-3132m; Appendix 6) and expected hydroperiod (ephemeral to permanent). 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, mid = 17, and high = 25 (Appendix 6).

P. maculata breeding was asynchronous across elevations: low elevation began mid-May 2011 and high elevation began early June 2011. We sampled sites on multiple occasions to correct for non-detection of target species (MacKenzie et al. 2002). Sites were sampled biweekly during a time period when *P. maculata* tadpoles would be available for detection at occupied sites (MacKenzie et al. 2002). 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 *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 minutes. If *P.*

maculata tadpoles were not detected within the 15-minute window, the survey continued until detection or until a maximum time of 30 minutes.

Primary factors

Hydroperiod and predators were designated primary factors as they were hypothesized to principally regulate occupancy (Table 4). Hydroperiod was expected to strongly 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 10; ESRI 2010) for large sites. Hydroperiod categories were defined as very ephemeral (VE = drying within weeks of filling), ephemeral (E = drying by the end of the summer season), intermediate (I = reducing in volume but not drying completely), and permanent (P = retaining a large volume of water the entire season).

Three major predators of *P. maculata* tadpoles were noted during surveys: fish (native and introduced; Hecnar and M'Closkey 1997), tiger salamanders (*Ambystoma tigrinum*; Freda 1983) and odonate larvae (Skelly and Werner 1990). We constructed detection histories for each predator to generate conditional occupancy estimates for each predator at each site (MacKenzie

et al. 2002). These estimates were then used as the covariates in our analysis of occupancy for *P. maculata* to correct for potential non-detection of predators (MacKenzie et al. 2006). In order 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 no variation among sites (.). Detection probability of predators could be constant, unique for each sampling occasion (VISIT), and vary by complexity of habitat (COMPLEX). Only the top model supported for each predator, determined by AIC (Akaike information criterion; MacKenzie et al. 2002; Table 5), 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 4) 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 an average was used for analysis. pH was similar across all sites (average 7.4; range 6.4-9.04) and was within the range that *P. maculata* have previously been found (average 7.14; range 5.36-10.16 ; M. Murphy unpub. data) so it was excluded from subsequent analysis. Percent vegetative cover (VC) was estimated by each observer during surveys and a mean was included as a continuous covariate because of its importance in oviposition (Hammerson 1999; Scherer et al. 2012). Average habitat complexity (COMPLEX) was estimated from at-site observations of vegetative cover, water depth and turbidity to represent difficulty of surveying and was treated as a categorical covariate with four categories. We used elevation to stratify sites surveyed, but it was excluded from the analysis as

we expected to capture variation in elevation via specific ecological characteristics across the landscape.

Landscape factors also potentially influence occupancy by *P. maculata* (Table 4). Recent work on this species suggests a maximum dispersal distance of 2400 m (M. Murphy unpub. data, but note Spencer 1964). Therefore, we buffered all sites by 2400 meters (ArcMap 10, ESRI 2010).

We calculated heat load index (HLI; Table 4; Evans et al. in review) 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). We buffered sites by 2400m and calculated the number of nearby ponds, wetlands or lakes (PN). We compiled data from two sources (Table 4) as data coverage varied across elevation. A lack of detailed water body information at middle elevation required a visual check of NAIP (2009; Table 4) 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. Average compound topographic index (CTI) was calculated within buffers (Table 4; Evans et al. in review) as it represents a measure of the wetness of a site (Moore et al. 1993). *P. maculata* adults and metamorphosed individuals are also known to use surrounding wetland meadows for

summer feeding (Tordoff and Pettus 1977), therefore average 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 average impervious surface within the buffer (IMPER; Table 4).

Data analysis

We used a likelihood-based method for estimating single-season occupancy probability (ψ) and probability of detection (p), as outlined by MacKenzie et al. (2002; 2004; 2006), and implemented in program PRESENCE 5.8 (Hines 2010). Models that included the primary and secondary covariates detailed above were used to test hypotheses regarding p_{ij} and ψ_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 ten.

Before fitting any models, a correlation matrix was generated (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 6). Environmental covariates consisted of complexity (COMPLEX) and hydroperiod (HYDRO). Hydroperiod 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 hydroperiod). Hydroperiod was modeled using four categories to allow for a non-linear effect of hydroperiod 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 this detection structure while investigating our occupancy hypotheses.

Occupancy modeling

Following Mattfeldt et al. (2009), we designated our predictor variables as either primary or secondary factors. Hydroperiod and predators were designated as primary factors regulating *P. maculata* occupancy due to their central importance in our *a priori* hypotheses. All other covariates were considered secondary factors due their potential influence on occupancy, despite not being the focus of this study (Table 4). 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; Appendix 7). While models could contain all possible combinations of our primary covariates (Doherty et al. 2010), 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 -2LogLikelihood 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 5.8 using global models for detection and occupancy (MacKenzie and Bailey 2004). By using the global models for each, we tested the goodness of fit of our most parameterized (global) model with the understanding that if the global model fit adequately then a supported model that is more parsimonious would also fit the data (Anderson and Burnham 2002). We used 5,000 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 hydroperiod 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 hydroperiod 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). We retained the best supported detection structure to investigate the effect of all possible combinations of hydroperiod, 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.

RESULTS

During our study, we detected *P. maculata* tadpoles at 24 of 62 sites (38.7%). Sites were surveyed between four and ten times during the sampling season. Of sites surveyed, we categorized 13 (21%) as having a very ephemeral hydroperiod, 17 (27.4%) as having an ephemeral hydroperiod, 14 (22.6%) as having an intermediate hydroperiod, and 18 (29%) as having a permanent hydroperiod (Appendices 8). We detected fish at 24 sites (38.7%), odonate larvae at 48 sites (77.4%), and *A. tigrinum* at 6 sites (9.7%). Fish and odonate presence were strongly associated with hydroperiod (Table 5). Odonate larvae occurred most frequently at sites with intermediate hydroperiods, while fish occurred most frequently at those with permanent hydroperiods. 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 hydroperiod ($p(\text{QUAD}+\text{COMPLEX}+\text{HYDRO})$) was best supported ($w = 0.918$; Table 6). Detection models that included VISIT as a unique probability for each sampling occasion 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 our occupied permanent hydroperiod sites. As expected, complexity had a negative relationship to detection probability.

Occupancy modeling

Primary factors – Eight model structures for ψ had $\Delta\text{AIC} < 2$ (Table 7). Our top model indicated that occupancy was influenced by fish, odonate larvae, and salamanders, three of our

four primary factors ($w = 0.135$). Our second best model included only fish and odonate larvae effects ($w = 0.100$; $\Delta AIC = 0.61$). Fish had a strong negative relationship to *P. maculata* occupancy while odonate larvae were strongly positively correlated (Table 7). Salamanders were also supported in the top occupancy model with a positive relationship to *P. maculata* occupancy (Fig. 7). Ranking by relative importance as defined by summed AIC weights (w_+ ; Table 7), 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, hydroperiod, our other primary factor, was not as important as predators in describing *P. maculata* occurrence among sites ($w_+ = 0.163$; Table 7; Table S5). After correcting for detection probability, ponds with intermediate hydroperiods had the highest probability of occupancy, and permanent ponds and very ephemeral ponds had the lowest (Fig. 7).

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 7). Several of the covariates in the top ten 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 -2LogLikelihood, even with the addition of another parameter; Anderson, 2008). These are not discussed due to lack of support (Table 7).

A posteriori modeling: conditioning on sites without fish predators

The same detection structure was supported as with the full dataset ($p(\text{QUAD}+\text{COMPLEX}+\text{HYDRO})$; $w = 0.63$). 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 8; $w = 0.66$). Our second best model contained odonate larvae and hydroperiod but had relatively weak support ($w = 0.32$). Intermediate hydroperiod was positively correlated to occupancy by *P. maculata* in ponds with odonate larvae (Table 8).

DISCUSSION

Primary factors

Our models indicated that hydroperiod was less supported than other primary factors in predicting probability of *P. maculata* occupancy but was more important than secondary factors. Hydroperiod affected the probability of occupancy by fish directly, thereby indirectly regulating the occurrence of *P. maculata* (Table 5; Fig. 7). Permanent ponds with fish predators excluded *P. maculata* almost entirely (Fig. 7). In ponds with varying communities of predators, intermediate hydroperiod ponds had the highest probability of occupancy, even in situations where fish were absent (Fig. 7). This indicates that type of hydroperiod may still have an effect on occupancy in addition to regulating predator presence. Hydroperiod 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). As climate change imposes additional constraints on hydroperiod [e.g. rapid drying (Matthews et al. 2013) and altered water chemistry (Hamer and Parris 2011; Fairman et al. in press)], it may play a larger direct role in habitat suitability for *P. maculata*.

We found that occupancy by *P. maculata* was affected primarily by the presence of predators. Fish excluded *P. maculata* at many permanent hydroperiod 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. 6). One site was very reedy and 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 hydroperiods. While 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. in review), 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), 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.

Secondary factors

No other pond level or landscape level factors were supported in models of *P. maculata* occupancy. CTI and ponds nearby (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

By determining factors that currently exclude breeding by a species, we gain a better understanding of how climate change may affect site occupancy in the future. This provides us with specific characteristics with which to design targeted conservation policies.

Climate change is expected to shorten hydroperiods (Matthews et al. 2013), excluding certain ponds for reproduction. Some amphibian species may be able to respond to drying conditions via developmental plasticity (Skelly 1996; Merilä et al. 2000), but little is known about the degree of shortening and whether plasticity will be adequate as a stop-gap measure (Gienapp et al. 2008). Sites with very ephemeral and ephemeral hydroperiods currently have low probabilities of occupancy by *P. maculata* as compared to longer intermediate hydroperiods, indicating that any shortening of hydroperiod through climate change will likely reduce *P. maculata* breeding habitat.

Many permanent ponds, generally reservoirs and man-made lakes, may not fluctuate as drastically as temporary ponds (Matthews 2010), but may be inadequate for amphibians 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 suggests that some species of amphibians, including *P. maculata*, may be jeopardized by this practice (Kats and Ferrer 2003; Pilliod et al. 2010). In certain situations, removal of invasive fish may allow for re-colonization of historical amphibian habitats (Funk and Dunlap 1999; Knapp 2005; Walston and Mullin 2007).

Climate change can cause declines by altering species interactions (Cahill et al. 2013), 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 due to hydroperiod reductions, negatively impacting larval development and survival (Blaustein et al. 2001; Mirza et al. 2006; Amburgey et al. in review).

Our occupancy analysis shows that several different stressors impact this species currently. *P. 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). Climate change will serve as an additional stress, potentially exacerbating the negative effects of predators and further limiting potential breeding sites available to this amphibian. The factors we assessed are not unique to *P. maculata* 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 as a way to test hypotheses regarding climate change and create realistic conservation policies for specific species.

TABLE 4. Hypotheses of covariate relationships to probability of occupancy of *P. maculata* tadpoles. Intermediate hydroperiod ponds were predicted to have the highest occupancy, and fish were expected to exclude *P. maculata* from sites.

Primary Factors	Relationship	Ecological Justification	
<i>Hydroperiod</i>			
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 (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 (Hecnar and M’Closkey 1997; Newman 1989; Skelly et al. 2002)	
<i>Predators</i>			
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. in review)	
Salamanders (SAL)	+/-	Moderate predator (Maret and Collins 1994) but similar habitat needs	
Secondary Factors	Relationship	Source	Ecological Justification
Conductivity (COND)	–	NLCD ^a	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)	–		Less suitable habitat and dispersal barriers (Murphy et al. 2010b)
Ponds Near (PN)	+	NWI ^b , NAIP ^c	Source of immigrants and metapopulation dynamics (Murphy et al. 2010a)
Heat Load Index (HLI) ^d	+	SRTM ^e	Increased vegetation for tadpoles and favorable temperatures for development (Pilliod et al. 2002)
Compound Topographic Index (CTI) ^f	+	SRTM	Increased moisture, movement facilitated between sites and seasonal feeding habitats created (Pilliod et al. 2002; Spencer 1964)

^a National Land Cover Database, 2006, 30m resolution; 0-100% impervious surface measure; Fry et al. (2011)

^b National Wetlands Inventory (2013), 1m resolution

^c National Agriculture Imagery Program (2011), 1m resolution

^d McCune and Keon (2002)

^e Shuttle Radar Topography Mission digital elevation model (DEM), 30m resolution; USGS (2004)

^f Moore et al. (1993)

TABLE 5. Top models from each candidate set for occupancy of sites by fish, odonate larvae, and salamanders. Our only covariate for occupancy (ψ) was hydroperiod due to importance in regulating predator type. Covariates for detection (p) included only survey-specific detection (VISIT) and site complexity (COMPLEX). ΔAIC 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.

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

TABLE 6. Probability of detection while using the global model for occupancy ($\psi(\text{HYDRO}+\text{FISH}+\text{ODO}+\text{SAL}+\text{HLI})$). All models containing VISIT were removed due to issues with convergence. w is model weight, K is the number of parameters in a model, and $-2L$ is twice the negative log-likelihood.

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

TABLE 7. Model selection results ($\Delta AIC < 2$) for occupancy by *P. maculata* with a detection structure of $p(\text{QUAD}+\text{COMPLEX}+\text{HYDRO})$. ΔAIC 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. Estimated effect size (i.e. beta estimates) is provided for primary and secondary factors.

Model	AIC	ΔAIC	w	K	$-2L$	FISH	ODO	SAL	CTI	PN	IMPER	VC	COND	HLI
C														
$\psi(\text{FISH}+\text{ODO}+\text{SAL})$	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
<i>Summed AIC weights by covariate</i>														
FISH	0.999	SAL	0.588	VC	0.0514	PN	0.128	HLI	0.107					
ODO	0.977	HYDRO	0.163	COND	0.108	IMPER	0.119	CTI	0.141					

TABLE 8. Model selection results for occupancy of *P. maculata* in ponds without fish using only primary factors. SAL was excluded from models due to issues with convergence. HYDRO consists of four categories representing VE (very ephemeral), E (ephemeral), I (intermediate), and P (permanent) hydroperiod lengths. Covariates for detection (p) included only survey-specific detection (VISIT) and site complexity (COMPLEX). w is model weight, K is the number of parameters in a model, and $-2L$ is twice the negative log-likelihood. Estimated effect size (i.e. beta estimates) is provided for primary and secondary factors.

Model	AIC	Δ AIC	w	K	-2L	ODO	VE	E	I	P
ψ (ODO)	142.82	0.00	0.66	9	124.82	3.14				
ψ (ODO+HYDRO)	144.28	1.46	0.32	12	120.28	2.97	-1.27	-0.02	1.50	-1.87
ψ (HYDRO)	149.53	6.71	0.02	11	127.53		-2.20	-0.41	0.69	1.10
ψ (.)	152.43	9.61	0.00	8	136.43					
<i>Summed AIC weights by covariate</i>										
ODO	0.98									
		HYDRO	0.34							

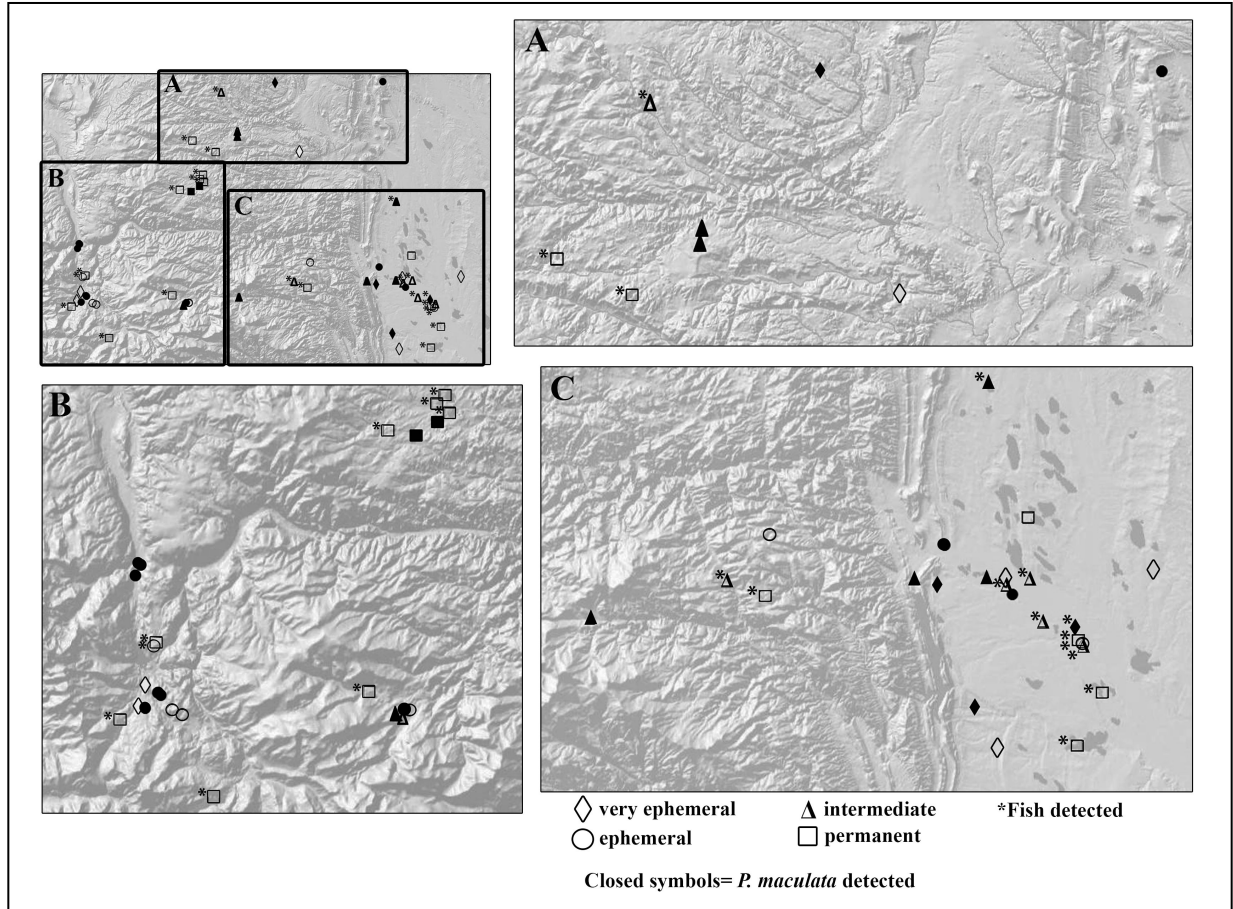


FIGURE 6. Map of study sites across Larimer County, Colorado, USA. Symbol shape represents hydroperiod type while closed symbols indicated detection of *P. maculata* tadpoles. Asterisks next to symbols indicate fish were detected at the site.

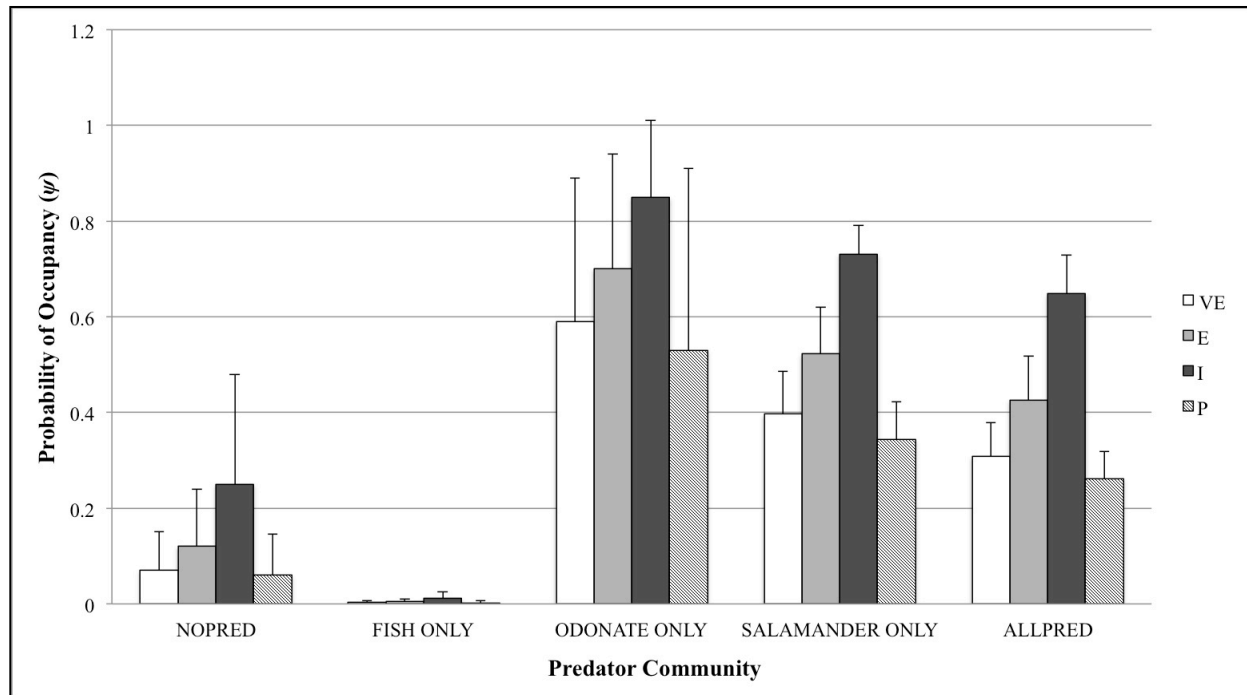


FIGURE 7. Graph of probability of occupancy by *P. maculata* across hydroperiod categories and predator communities using back-transformed parameter estimates from our best supported model containing hydroperiod ($\psi(\text{HYDRO}+\text{FISH}+\text{ODO}+\text{SAL})p(\text{QUAD}+\text{HYDRO}+\text{COMPLEX}); w_i = 0.0231$) Hydroperiod lengths are VE = very ephemeral, E = ephemeral, I = intermediate, and P = permanent. NOPRED represents ponds lacking fish, odonate larvae, and salamanders. ALLPRED represents ponds with all of the above.

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APPENDIX 6. COORDINATES OF SITES SURVEYED BY ELEVATIONAL STRATIFICATION.

Location	Elevation (m)	Latitude	Longitude
<i>Low Elevation Stratification</i>			
Arapaho Bend	1480	40°31'36.33"N	104°59'52.11"W
Fossil Creek	1485	40°29'20.52"N	105° 1'18.78"W
Running Deer 1	1490	40°33'47.56"N	105° 0'58.21"W
Running Deer 2	1490	40°33'45.11"N	105° 0'57.29"W
Arwen	1492	40°33'54.11"N	105° 1'14.44"W
Riverbend	1495	40°34'24.92"N	105° 1'23.42"W
Springer 2	1504	40°34'42.12"N	105° 3'10.27"W
Sayler	1514	40°35'53.43"N	105° 4'55.10"W
Redwing	1517	40°36'32.71"N	105° 3'56.07"W
Magpie	1518	40°36'15.95"N	105° 5'14.48"W
Magpie Dogpark	1520	40°36'23.81"N	105° 5'14.50"W
Sterling	1526	40°36'36.14"N	105° 6'18.60"W
Mariposa	1539	40°29'13.53"N	105° 5'44.80"W
Fromme Prairie	1541	40°30'57.90"N	105° 6'57.65"W
Seidel	1552	40°38'2.70"N	105° 8'42.67"W
Prairie Dog	1554	40°36'59.83"N	104°56'59.29"W
Reservoir Ridge 2	1562	40°36'16.60"N	105° 9'8.44"W
Trilakes	1572	40°39'13.98"N	105° 4'1.15"W
Hansen	1605	40°36'31.36"N	105°10'26.78"W
Frisinger	1626	40°45'5.09"N	105° 6'13.60"W

APPENDIX 6. Continued

<i>Middle Elevation Stratification</i>			
Cherokee A	1932	40°50'27.61"N	105°19'59.11"W
Soapstone 2	2041	40°58'1.85"N	105° 8'9.60"W
Soapstone 1	2042	40°58'1.75"N	105° 8'11.73"W
Colard 3	2155	40°36'26.28"N	105°20'56.21"W
Moen 1	2179	40°58'0.34"N	105°23'36.95"W
Moen 2	2180	40°57'58.50"N	105°23'33.06"W
Moen 3	2181	40°57'56.57"N	105°23'27.60"W
Blue House 2	2195	40°38'30.01"N	105°18'32.87"W
Bryant	2286	40°56'48.46"N	105°31'17.59"W
Church Camp	2329	40°35'47.80"N	105°18'47.93"W
Bull Garden	2367	40°52'34.54"N	105°28'55.41"W
Morgan's	2385	40°52'5.06"N	105°29'0.40"W
Lost Lake 1	2446	40°50'21.32"N	105°32'1.90"W
Parvin Lake	2482	40°47'3.91"N	105°33'33.00"W
Phantom	2513	40°46'39.40"N	105°34'17.80"W
Buckhorn	2531	40°34'44.76"N	105°28'38.36"W
Molly	2586	40°46'3.76"N	105°35'29.28"W
<i>High Elevation Stratification</i>			
Dowdy Lake	2484	40°47'50.83"N	105°33'46.50"W
West Lake	2513	40°47'27.53"N	105°34'18.85"W
Creedmore Lake 1	2519	40°51'33.35"N	105°35'24.56"W

APPENDIX 6. Continued

Lily Pond Lake	2600	40°43'49.20"N	105°51'59.87"W
Tunnel B	2619	40°40'22.42"N	105°51'22.74"W
Tunnel Campground	2623	40°40'19.49"N	105°51'19.44"W
Bellaire Lake	2634	40°46'16.63"N	105°37'4.92"W
Pot Hole	2637	40°39'51.01"N	105°51'35.50"W
Pingree Meadow	2767	40°34'6.42"N	105°35'45.32"W
Meadow	2767	40°34'6.20"N	105°35'45.58"W
Laramie Lake S	2847	40°36'54.73"N	105°50'24.87"W
Laramie Lake N	2848	40°36'57.09"N	105°50'20.99"W
Upper Pingree 1	2858	40°34'6.28"N	105°36'4.49"W
Hourglass Reservoir	2862	40°34'53.51"N	105°38'4.43"W
Old Highway 14	2866	40°35'3.11"N	105°51'1.21"W
Intermediate 2	2912	40°33'51.66"N	105°36'17.43"W
Intermediate 1	2937	40°33'47.74"N	105°36'25.71"W
Three Story	2978	40°34'11.64"N	105°51'20.18"W
Mosquitoes	3009	40°34'45.94"N	105°50'17.39"W
Sylvatica	3012	40°34'5.00"N	105°50'57.50"W
Spencer 10	3013	40°34'43.45"N	105°50'12.54"W
Joe Wright Res.	3036	40°33'34.71"N	105°52'21.78"W
Long Draw Res.	3084	40°30'13.20"N	105°46'59.77"W
Spencer 15	3094	40°33'47.76"N	105°48'52.12"W
Spencer 14	3132	40°34'0.64"N	105°49'26.83"W

**APPENDIX 7. ALL CANDIDATE MODELS ($N = 112$) ASSESSED TO DETERMINE
OCCUPANCY BY *P. MACULATA*.**

Primary factors are covariates that were considered to have the greatest importance, followed by secondary factors. The model in the first row represents $\psi(.)p(.)$ (constant probability of occupancy and detection). Hydro represents hydroperiod type (VE = very ephemeral, E = ephemeral, I = intermediate). Both hydroperiod and predators are pond-level factors in addition to conductivity (COND) and vegetative cover (VC). For a detailed description of factors, please see Methods.

Primary Factors				Secondary Factors					
<i>Hydro</i>		<i>Predators</i>		<i>Pond Level</i>			<i>Landscape Level</i>		
VE+E+I	FISH	ODO	SAL	COND	VC	IMPER	PN	HLI	CTI
				X					
					X				
						X			
							X		
								X	
									X
X	X	X	X	X					
X	X	X	X		X				
X	X	X	X			X			
X	X	X	X				X		
X	X	X	X					X	
X	X	X	X						X
X				X					
X					X				
X						X			
X							X		
X								X	

APPENDIX 7. Continued

VE+E+I	FISH	ODO	SAL	COND	VC	IMPER	PN	HLI	CTI
X									X
	X			X					
	X				X				
	X					X			
	X						X		
	X							X	
	X								X
		X		X					
		X			X				
		X				X			
		X					X		
		X						X	
		X							X
			X	X					
			X		X				
			X			X			
			X				X		
			X					X	
			X						X
X	X			X					
X	X				X				
X	X					X			
X	X						X		

APPENDIX 7. Continued

VE+E+I	FISH	ODO	SAL	COND	VC	IMPER	PN	HLI	CTI
X	X							X	
X	X								X
X		X		X					
X		X			X				
X		X				X			
X		X					X		
X		X						X	
X		X							X
X			X	X					
X			X		X				
X			X			X			
X			X				X		
X			X					X	
X			X						X
	X	X		X					
	X	X			X				
	X	X				X			
	X	X					X		
	X	X						X	
	X	X							X
	X		X	X					
	X		X		X				
	X		X			X			

APPENDIX 7. Continued

VE+E+I	FISH	ODO	SAL	COND	VC	IMPER	PN	HLI	CTI
	X		X				X		
	X		X					X	
	X		X						X
		X	X	X					
		X	X		X				
		X	X			X			
		X	X					X	
		X	X						X
X	X	X		X					
X	X	X			X				
X	X	X				X			
X	X	X					X		
X	X	X						X	
X	X	X							X
X		X	X	X					
X		X	X		X				
X		X	X			X			
X		X	X				X		
X		X	X					X	
X		X	X						X
X	X		X	X					
X	X		X		X				

APPENDIX 7. Continued

VE+E+I	FISH	ODO	SAL	COND	VC	IMPER	PN	HLI	CTI
X	X		X			X			
X	X		X				X		
X	X		X					X	
X	X		X						X
	X	X	X	X					
	X	X	X		X				
	X	X	X			X			
	X	X	X				X		
	X	X	X					X	
	X	X	X						X
X	X	X	X						
X									
	X								
		X							
			X						
X	X								
X		X							
X			X						
	X	X							
	X		X						
		X	X						
X	X	X							
X		X	X						

APPENDIX 7. Continued

VE+E+I	FISH	ODO	SAL	COND	VC	IMPER	PN	HLI	CTI
X	X		X						
	X	X	X						

APPENDIX 8. INPUT DATA FOR OCCUPANCY ANALYSIS OF *P. MACULATA* (SEE METHODS FOR NAMES).

Site Name	VE	E	I	P	COND	COMPLEX	FISH	ODO	SAL	PN	HLI	CTI	VC	IMPER
PrairieDog	1	0	0	0	3.219	2	0.0001	1.0000	0.0002	0.226	3.296	8.7	0.99	0.010
ReservoirRidge2	1	0	0	0	0.842	1	0.0001	1.0000	0.0009	0.505	3.281	8.3	0.99	0.089
MagpieDogPark	1	0	0	0	1.715	1	0.0013	0.0009	0.0044	0.570	3.269	9.8	0.90	0.559
Trilakes	0	0	0	1	1.400	3	0.0001	1.0000	0.0011	0.366	3.265	9.2	0.53	0.076
Seidel	0	1	0	0	1.037	1	1.0000	1.0000	0.0015	0.516	3.362	8.7	0.53	0.102
Sterling	0	0	1	0	0.565	3	0.0001	1.0000	0.0003	0.828	3.264	9.7	0.93	0.353
Saylor	0	1	0	0	0.574	2	0.0001	1.0000	0.0003	0.473	3.261	9.8	0.77	0.756
Hansen	0	0	1	0	0.173	2	0.0003	1.0000	0.0043	0.290	3.340	7.6	0.26	0.042
Fromme	1	0	0	0	4.980	1	0.0001	1.0000	0.0009	0.290	3.264	8.1	0.81	0.314
Mariposa	1	0	0	0	2.344	1	0.0001	1.0000	0.0009	0.172	3.279	8.4	0.99	0.258
Moen1	1	0	0	0	0.139	1	0.0001	1.0000	0.0009	0.022	3.267	6.8	0.28	0.015
Soapstone1	0	1	0	0	0.342	1	1.0000	1.0000	0.0026	0.011	3.325	6.9	0.86	0.000
BlueHouse2	0	1	0	0	0.250	1	0.0003	1.0000	0.0026	0.043	3.490	6.3	0.18	0.018
Morgan	0	0	1	0	0.093	2	1.0000	1.0000	0.0022	0.022	3.401	6.9	0.18	0.011
BullGarden	0	0	1	0	0.460	3	1.0000	1.0000	0.0003	0.022	3.273	6.7	0.73	0.010
Soapstone2	1	0	0	0	0.336	1	0.0003	0.0001	0.0016	0.011	3.351	6.9	0.48	0.000
Moen3	1	0	0	0	0.128	1	0.0003	0.0000	0.0016	0.022	3.437	6.8	1.00	0.016
Moen2	1	0	0	0	0.163	1	0.0001	0.0000	0.0009	0.022	3.380	6.8	0.99	0.015
CherokeeA	1	0	0	0	0.739	1	0.0006	0.0003	0.0027	0.022	3.367	6.5	0.98	0.004
Buckhorn	0	0	1	0	0.063	3	1.0000	1.0000	0.0009	0.022	3.532	6.5	0.38	0.009
Molly	0	0	0	1	0.436	3	1.0000	1.0000	0.0011	0.075	3.287	7.2	0.32	0.006
Phantom	0	0	0	1	0.206	3	0.0006	1.0000	0.0081	0.129	3.375	7.5	0.43	0.022
PingreeMeadow	0	1	0	0	0.093	2	0.0013	1.0000	0.0027	0.247	3.301	7.0	0.62	0.005
Spencer14	0	1	0	0	0.008	1	0.0013	1.0000	0.0074	0.129	3.428	6.6	0.00	0.002
Sylvatica	0	1	0	0	0.021	2	0.0013	1.0000	0.0027	0.172	3.443	6.8	0.80	0.006
Mosquitoes	0	1	0	0	0.015	1	0.0013	1.0000	0.0074	0.215	3.277	6.8	0.43	0.007
TunnelB	0	1	0	0	0.092	2	0.0060	1.0000	0.0218	0.086	3.320	7.0	0.20	0.003
TunnelCamp	0	1	0	0	0.080	2	0.0060	1.0000	0.0218	0.075	3.304	7.0	0.35	0.003
Spencer10	0	1	0	0	0.021	1	0.0013	1.0000	0.0074	0.215	3.322	6.8	0.74	0.006
Meadow	0	1	0	0	0.065	1	0.0013	0.0059	0.0074	0.247	3.301	7.0	0.96	0.004
ThreeStory	1	0	0	0	0.027	1	0.0060	1.0000	0.0044	0.247	3.280	6.9	1.00	0.006
Intermediate2	0	0	1	0	0.033	3	0.0013	0.0100	0.0057	0.290	3.336	7.0	0.75	0.003
Pothole	0	1	0	0	0.057	2	0.0060	0.0612	0.0218	0.108	3.498	6.9	0.01	0.003
Spencer15	0	1	0	0	0.020	1	0.0013	1.0000	0.0074	0.108	3.368	6.6	0.96	0.003
OldHighway14	1	0	0	0	0.030	1	0.0013	0.0009	0.0044	0.172	3.370	7.0	0.00	0.009

APPENDIX 8. Continued

Intermediate1	0	0	1	0	0.027	3	0.0060	1.0000	0.0758	0.290	3.429	7.0	0.75	0.002
LilyLake	0	0	0	1	0.058	4	0.0060	1.0000	0.1135	0.161	3.258	7.2	0.70	0.010
UpperPingree1	0	1	0	0	0.067	1	0.0013	1.0000	0.0074	0.290	3.433	7.1	0.85	0.004

APPENDIX 9. DETECTION HISTORIES FOR *P. MACULATA*, FISH, ODONATE LARVAE,
AND SALAMANDERS

<i>Pseudacris maculata:</i>										
Site Name	Sampling Occasion									
	1	2	3	4	5	6	7	8	9	10
PrairieDog	0	0	0	0	0	0	0	0	0	0
Frisinger	0	0	1	1	1	1	0	0	0	0
Arwen	0	0	0	0	0	0	0	0	0	0
Springer2	0	0	0	0	0	0	0	0	0	0
Riverbend	1	1	1	1	1	1	1	1	0	0
ReservoirRidge2	1	0	1	1	1	1	1	1	0	0
MagpieDogPark	0	0	0	0	0	0	-	-	-	-
RunningDeer2	0	0	0	0	0	0	0	0	0	0
MagpieMeander	0	0	0	0	0	0	0	0	0	0
Trilakes	0	0	0	0	0	0	0	0	0	0
Seidel	1	1	1	1	1	1	1	1	1	1
Sterling	1	1	1	1	1	1	1	1	0	0
Sayler	0	0	0	1	1	1	1	1	0	0
Hansen	-	-	1	1	1	1	1	1	1	1
Fromme	0	0	1	1	1	1	1	1	0	0
RunningDeer1	0	0	0	0	0	0	0	0	0	0
ArapahoBend	0	0	0	0	0	0	0	0	0	0
Redwing	0	0	0	0	0	0	-	-	0	0
Mariposa	0	0	0	0	0	0	0	0	0	0
FossilCreek	0	0	0	0	0	0	0	0	0	0
Moen1	1	1	1	1	1	1	1	1	0	0
Soapstone1	1	1	1	1	1	1	1	1	-	-
BlueHouse2	0	0	0	0	0	0	0	0	-	-
Morgan	0	0	1	1	1	1	1	1	0	0
BullGarden	1	1	1	1	1	1	0	0	0	0
Soapstone2	0	0	0	0	0	0	0	0	-	-
Moen3	0	0	0	0	0	0	0	0	-	-
Moen2	0	0	0	0	0	0	0	0	0	0
Colard3	0	0	0	0	0	0	0	0	-	-
CherokeeA	0	0	0	0	0	-	0	0	-	-
ChurchCamp	0	0	0	0	0	0	0	0	-	-
Buckhorn	1	1	1	1	1	1	1	1	-	-
Molly	1	1	1	1	1	1	1	1	0	0
Bryant	0	0	0	0	0	0	0	0	0	0
PhantomLake	1	1	1	1	1	-	1	1	1	1
LostLake	0	0	0	0	-	-	0	0	0	0
ParvinLake	0	0	0	0	0	0	0	0	-	-
PingreeMeadow	0	0	0	0	0	0	-	-	-	-
Spencer14	0	0	0	0	0	0	-	-	-	-
Sylvatica	1	1	1	1	1	1	-	-	-	-

APPENDIX 9. Continued

Mosquitoes	1	1	1	1	1	1	-	-	-	-
TunnelB	1	1	1	1	-	-	-	-	-	-
TunnelCamp	1	1	1	1	-	-	-	-	-	-
Spencer10	1	1	1	1	1	1	-	-	-	-
Meadow	0	0	0	0	0	0	-	-	-	-
ThreeStory	0	0	0	0	0	0	-	-	-	-
Intermediate2	0	0	0	0	0	0	-	-	-	-
LaramieLakeN	0	0	0	0	-	-	-	-	-	-
Pothole	1	1	1	1	-	-	-	-	-	-
Spencer15	0	0	0	0	0	0	-	-	-	-
OldHighway14	0	0	0	0	0	0	-	-	-	-
Intermediate1	-	-	1	1	1	1	-	-	-	-
LilyLake	1	1	1	1	-	-	-	-	-	-
JoeWright	0	0	0	0	0	0	-	-	-	-
LongDraw	0	0	0	0	0	0	-	-	-	-
WestLake	0	0	0	0	0	0	-	-	-	-
CreedmoreLake1	0	0	0	0	0	0	-	-	-	-
DowdyLake	0	0	0	0	0	0	-	-	-	-
HourglassLake	0	0	0	0	-	-	-	-	-	-
BellaireLake	0	0	0	0	0	0	-	-	-	-
UpperPingree1	1	1	1	1	1	1	-	-	-	-
LaramieLakeS	0	0	0	0	-	-	-	-	-	-
<i>Fish:</i>										
Site Name	Sampling Occasion									
	1	2	3	4	5	6	7	8	9	10
PrairieDog	0	0	0	0	0	0	0	0	0	0
Frisinger	0	0	1	1	1	0	1	0	1	1
Arwen	1	1	1	1	1	1	1	1	1	0
Springer2	0	0	0	0	0	0	1	1	0	1
Riverbend	0	0	0	0	1	1	0	0	0	0
ReservoirRidge2	0	0	0	0	0	0	0	0	0	0
MagpieDogPark	0	0	0	0	0	0	-	-	-	-
RunningDeer2	0	0	1	0	1	1	0	0	1	0
MagpieMeander	1	1	1	1	1	1	0	0	0	0
Trilakes	0	0	0	0	0	0	0	0	0	0
Seidel	0	0	0	0	0	0	0	0	0	0
Sterling	0	0	0	0	0	0	0	0	0	0
Sayler	0	0	0	0	0	0	0	0	0	0
Hansen	-	-	0	0	0	0	0	0	0	0
Fromme	0	0	0	0	0	0	0	0	0	0
RunningDeer1	0	0	0	0	0	1	0	0	0	0
ArapahoBend	1	0	1	1	1	0	1	0	1	1
Redwing	1	0	1	0	1	1	-	-	0	0
Mariposa	0	0	0	0	0	0	0	0	0	0

APPENDIX 9. Continued

FossilCreek	1	0	1	1	1	1	0	1	1	0
Moen1	0	0	0	0	0	0	0	0	0	0
Soapstone1	0	0	0	0	0	0	0	0	-	-
BlueHouse2	0	0	0	0	0	0	0	0	-	-
Morgan	0	0	0	0	0	0	0	0	0	0
BullGarden	0	0	0	0	0	0	0	0	0	0
Soapstone2	0	0	0	0	0	0	0	0	-	-
Moen3	0	0	0	0	0	0	0	0	-	-
Moen2	0	0	0	0	0	0	0	0	0	0
Colard3	1	0	1	0	1	1	1	1	-	-
CherokeeA	0	0	0	0	0	-	0	0	-	-
ChurchCamp	1	0	1	1	1	1	1	1	-	-
Buckhorn	0	0	0	0	0	0	0	0	-	-
Molly	0	0	0	0	0	0	0	0	0	0
Bryant	0	0	0	0	0	0	1	1	1	0
PhantomLake	0	0	0	0	0	-	0	0	-	-
LostLake	1	0	0	0	1	-	1	0	0	0
ParvinLake	0	0	0	0	-	-	1	1	-	-
PingreeMeadow	0	0	0	0	0	0	-	-	-	-
Spencer14	0	0	0	0	0	0	-	-	-	-
Sylvatica	0	0	0	0	0	0	-	-	-	-
Mosquitoes	0	0	0	0	0	0	-	-	-	-
TunnelB	0	0	0	0	-	-	-	-	-	-
TunnelCamp	0	0	0	0	-	-	-	-	-	-
Spencer10	0	0	0	0	0	0	-	-	-	-
Meadow	0	0	0	0	0	0	-	-	-	-
ThreeStory	0	0	0	0	0	0	-	-	-	-
Intermediate2	0	0	0	0	0	0	-	-	-	-
LaramieLakeN	1	0	0	0	0	0	-	-	-	-
Pothole	0	0	0	0	-	-	-	-	-	-
Spencer15	0	0	0	0	0	0	-	-	-	-
OldHighway14	0	0	0	0	0	0	-	-	-	-
Intermediate1	0	0	0	0	-	-	-	-	-	-
LilyLake	0	0	0	0	-	-	-	-	-	-
JoeWright	0	0	1	0	1	1	-	-	-	-
LongDraw	0	1	0	1	1	1	-	-	-	-
WestLake	0	0	1	1	1	0	-	-	-	-
CreedmoreLake1	1	1	1	1	1	0	-	-	-	-
DowdyLake	0	0	1	1	1	0	-	-	-	-
HourglassLake	0	0	1	1	-	-	-	-	-	-
BellaireLake	1	1	0	0	1	1	-	-	-	-
UpperPingree1	0	0	0	0	0	0	-	-	-	-
LaramieLakeS	1	0	1	0	-	-	-	-	-	-

APPENDIX 9. Continued

<i>Odonate Larvae:</i>										
Site Name	Sampling Occasion									
	1	2	3	4	5	6	7	8	9	10
PrairieDog	0	0	0	0	1	0	1	1	1	1
Frisinger	0	0	0	0	1	1	0	1	1	1
Arwen	0	0	1	0	1	1	1	0	0	1
Springer2	1	1	0	1	1	1	1	1	1	1
Riverbend	1	1	1	1	1	0	1	1	1	1
ReservoirRidge2	1	1	1	1	1	1	1	1	0	0
MagpieDogPark	0	0	0	0	0	0	-	-	-	-
RunningDeer2	1	1	1	0	1	1	0	0	1	1
MagpieMeander	1	1	1	1	1	0	1	1	0	0
Trilakes	0	0	0	0	0	0	0	0	1	0
Seidel	0	0	0	0	0	0	1	1	1	1
Sterling	0	0	1	1	1	1	1	1	1	1
Sayler	0	0	1	1	1	1	1	1	1	1
Hansen	-	-	0	1	1	1	1	0	1	1
Fromme	0	0	0	0	1	1	0	0	0	1
RunningDeer1	0	1	1	1	1	1	0	0	1	1
ArapahoBend	0	1	1	0	1	1	0	0	0	0
Redwing	1	1	1	1	1	1	-	-	1	1
Mariposa	0	0	0	0	0	0	1	1	1	1
FossilCreek	0	0	0	0	0	0	0	0	0	0
Moen1	0	0	1	1	1	1	1	1	0	0
Soapstone1	0	0	1	0	1	1	1	1	-	-
BlueHouse2	1	1	1	1	1	1	1	1	-	-
Morgan	1	1	0	1	1	1	1	1	1	1
BullGarden	1	1	1	1	1	1	1	1	1	1
Soapstone2	0	0	0	0	0	0	0	0	-	-
Moen3	0	0	0	0	0	0	0	0	0	0
Moen2	0	0	0	0	0	0	0	0	0	0
Colard3	1	1	1	1	1	1	1	1	-	-
CherokeeA	0	0	0	0	0	-	0	0	-	-
ChurchCamp	0	0	1	1	0	1	0	0	-	-
Buckhorn	1	1	1	1	1	1	1	1	-	-
Molly	0	1	1	1	1	1	1	1	1	1
Bryant	0	0	1	1	1	0	1	1	1	1
PhantomLake	1	1	1	1	1	-	1	1	-	-
LostLake	1	1	1	1	1	-	1	1	1	1
ParvinLake	0	0	0	0	-	-	1	1	-	-
PingreeMeadow	1	1	0	1	1	1	-	-	-	-
Spencer14	1	1	0	0	0	0	-	-	-	-
Sylvatica	1	1	1	1	1	1	-	-	-	-
Mosquitoes	1	1	1	1	1	1	-	-	-	-

APPENDIX 9. Continued

TunnelB	0	0	1	0	-	-	-	-	-	-
TunnelCamp	1	1	1	1	-	-	-	-	-	-
Spencer10	0	1	1	1	1	1	-	-	-	-
Meadow	0	0	0	0	0	0	-	-	-	-
ThreeStory	1	1	1	1	0	0	-	-	-	-
Intermediate2	0	0	0	0	0	0	-	-	-	-
LaramieLakeN	1	1	1	1	-	-	-	-	-	-
Pothole	0	0	0	0	-	-	-	-	-	-
Spencer15	1	1	1	0	1	0	-	-	-	-
OldHighway14	0	0	0	0	0	0	-	-	-	-
Intermediate1	0	0	0	1	-	-	-	-	-	-
LilyLake	1	1	1	1	-	-	-	-	-	-
JoeWright	0	0	0	0	0	0	-	-	-	-
LongDraw	0	0	0	0	0	0	-	-	-	-
WestLake	0	0	0	0	0	0	-	-	-	-
CreedmoreLake1	1	1	1	1	1	1	-	-	-	-
DowdyLake	0	0	1	0	0	0	-	-	-	-
HourglassLake	0	0	0	0	-	-	-	-	-	-
BellaireLake	0	0	1	1	1	0	-	-	-	-
UpperPingree1	0	1	1	1	1	1	-	-	-	-
LaramieLakeS	1	1	1	1	-	-	-	-	-	-
<i>Salamander:</i>										
Site Name	Sampling Occasion									
	1	2	3	4	5	6	7	8	9	10
PrairieDog	0	0	0	0	0	0	0	0	0	0
Frisinger	0	0	0	0	0	0	0	0	0	0
Arwen	0	0	0	0	0	0	0	0	0	0
Springer2	0	0	0	0	0	0	0	0	0	0
Riverbend	0	0	0	0	0	0	0	0	0	0
ReservoirRidge2	0	0	0	0	0	0	0	0	0	0
MagpieDogPark	0	0	0	0	0	0	-	-	-	-
RunningDeer2	0	0	0	0	0	0	0	0	0	0
MagpieMeander	0	0	0	0	0	0	0	0	0	0
Trilakes	0	0	0	0	0	0	0	0	0	0
Seidel	0	0	1	1	1	0	0	0	0	0
Sterling	0	0	0	0	0	0	0	0	0	0
Sayler	0	0	0	0	0	0	0	0	0	0
Hansen	-	-	0	0	0	0	0	0	0	0
Fromme	0	0	0	0	0	0	0	0	0	0
RunningDeer1	0	0	0	0	0	0	0	0	0	0
ArapahoBend	0	0	0	0	0	0	-	-	0	0
Redwing	0	0	0	0	0	0	0	0	0	0
Mariposa	0	0	0	0	0	0	0	0	0	0
FossilCreek	0	0	0	0	0	0	0	0	0	0

APPENDIX 9. Continued

Moen1	0	0	0	0	0	0	0	0	0	0
Soapstone1	1	1	1	1	1	1	1	1	-	-
BlueHouse2	0	0	0	0	0	0	0	0	0	0
Morgan	1	1	1	1	1	1	0	0	1	1
BullGarden	1	0	0	0	0	0	1	0	0	0
Soapstone2	0	0	0	0	0	0	0	0	-	-
Moen3	0	0	0	0	0	0	0	0	-	-
Moen2	0	0	0	0	0	0	0	0	0	0
Colard3	0	0	0	0	0	0	0	0	-	-
CherokeeA	0	0	0	0	0	-	0	0	-	-
ChurchCamp	0	0	0	0	0	0	0	0	-	-
Buckhorn	0	1	1	1	0	0	0	0	-	-
Molly	1	0	0	0	0	0	1	0	0	0
Bryant	0	0	0	0	0	0	0	0	0	0
PhantomLake	0	0	0	0	0	-	0	0	-	-
LostLake	1	1	1	1	1	-	1	1	1	1
ParvinLake	0	0	0	0	0	0	0	0	-	-
PingreeMeadow	0	0	0	0	0	0	-	-	-	-
Spencer14	0	0	0	0	0	0	-	-	-	-
Sylvatica	0	0	0	0	0	0	-	-	-	-
Mosquitoes	0	0	0	0	0	0	-	-	-	-
TunnelB	0	0	0	0	-	-	-	-	-	-
TunnelCamp	0	0	0	0	-	-	-	-	-	-
Spencer10	0	0	0	0	0	0	-	-	-	-
Meadow	0	0	0	0	0	0	-	-	-	-
ThreeStory	0	0	0	0	0	0	-	-	-	-
Intermediate2	0	0	0	0	0	0	-	-	-	-
LaramieLakeN	0	0	0	0	0	0	-	-	-	-
Pothole	0	0	0	0	-	-	-	-	-	-
Spencer15	0	0	0	0	0	0	-	-	-	-
OldHighway14	0	0	0	0	0	0	-	-	-	-
Intermediate1	0	0	0	0	-	-	-	-	-	-
LilyLake	0	0	0	0	-	-	-	-	-	-
JoeWright	0	0	0	0	0	0	-	-	-	-
LongDraw	0	0	0	0	0	0	-	-	-	-
WestLake	0	0	0	0	0	0	-	-	-	-
CreedmoreLake1	0	0	0	0	0	0	-	-	-	-
DowdyLake	0	0	0	0	0	0	-	-	-	-
HourglassLake	0	0	0	0	-	-	-	-	-	-
BellaireLake	0	0	0	0	0	0	-	-	-	-
UpperPingree1	0	0	0	0	0	0	-	-	-	-
LaramieLakeS	0	0	0	0	-	-	-	-	-	-

APPENDIX 10. ALL OCCUPANCY MODELS WITH $W \geq 0.01$

w is model weight, K is the number of parameters in a model, and $-2L$ is twice the negative log-likelihood.

Model	AIC	Δ AIC	w	K	$-2L$
$\psi(\text{FISH+ODO+SAL})$	172.51	0.00	0.135	11	150.51
$\psi(\text{FISH+ODO})$	173.10	0.59	0.101	10	153.10
$\psi(\text{FISH+ODO+SAL+CTI})$	173.75	1.24	0.073	12	149.75
$\psi(\text{FISH+ODO+SAL+PN})$	173.91	1.40	0.067	12	149.91
$\psi(\text{FISH+ODO+SAL+IMPER})$	174.13	1.62	0.060	12	150.13
$\psi(\text{FISH+ODO+SAL+VC})$	174.45	1.94	0.051	12	150.45
$\psi(\text{FISH+ODO+SAL+COND})$	174.49	1.98	0.050	12	150.49
$\psi(\text{FISH+ODO+SAL+HLI})$	174.50	1.99	0.050	12	150.50
$\psi(\text{FISH+ODO+CTI})$	174.82	2.31	0.043	11	152.82
$\psi(\text{FISH+ODO+VC})$	174.88	2.37	0.041	11	152.88
$\psi(\text{FISH+ODO+IMPER})$	174.98	2.47	0.039	11	152.98
$\psi(\text{FISH+ODO+PN})$	174.99	2.48	0.039	11	152.99
$\psi(\text{FISH+ODO+COND})$	175.10	2.59	0.037	11	153.10
$\psi(\text{FISH+ODO+HLI})$	175.10	2.59	0.037	11	153.10
$\psi(\text{HYDRO +FISH+ODO+SAL})$	176.06	3.55	0.023	14	148.06
$\psi(\text{HYDRO +FISH+ODO})$	176.20	3.69	0.021	13	150.20
$\psi(\text{HYDRO +FISH+ODO+SAL+CTI})$	177.40	4.89	0.012	15	147.40
$\psi(\text{HYDRO +FISH+ODO+SAL+PN})$	177.68	5.17	0.010	15	147.68