MIGRATION PHENOLOGY AND FERTILITY OF IMPERILED ILLINOIS SALAMANDER (*AMBYSTOMA*) SPECIES

BY

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THESIS

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ABSTRACT

Habitat loss is the primary driver of global amphibian declines. Habitat restoration and management of aquatic and terrestrial habitats are underway in Illinois, where over 90% of wetlands have been lost. Demographic and phenologic data are needed to inform land management decisions, such as the timing of controlled burns, to help avoid causing harm to amphibians moving between aquatic and terrestrial habitats (and vice versa). Interfering, stressing, or causing mortality of migrating adults could result in cascading effects on reproduction and recruitment. The Jefferson Salamander (*Ambystoma jeffersonianum*), Silvery Salamander (*A. platineum*), and Blue-spotted Salamander (*A. laterale*) are three species of conservation concern in Illinois that migrate annually from upland habitat to wetlands for reproduction. Juveniles (metamorphs) subsequently emigrate from wetlands to terrestrial habitats after metamorphosis. I conducted a census for each species over three years to understand the environmental factors influencing adult and juvenile movements. Minimum air temperature and 24-hr. precipitation influenced adult *A. jeffersonianum* and *A. platineum* movements, whereas wetland depth (a surrogate for hydroperiod) influenced metamorph emigration. Increases in soil inversion strength promoted *A. laterale* adult movements. To estimate *A. jeffersonianum* population reproductive characteristics, I combined census and fertility data over three years. Fertility estimates for two wetlands ranged from 0.29 to 1.94, possibly due to hydroperiod. Fertility estimates for both wetlands surveyed were larger than previous studies conducted in the same region. A potential reason for the higher fertility is the restoration efforts aimed at wetland creation and increasing the hydroperiod of existing wetlands. Ultimately, my results can inform future restoration efforts on the timing of prescribed burns and illustrate the potential benefits of habitat restoration on population demographics for wetland-breeding amphibians.

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Finally, thank you to my family, especially my mother, who introduced me as a child to Annie Dillard, Pilgrim at Tinker Creek.

"After the one extravagant gesture of creation in the first place, the universe has continued to deal exclusively in extravagances, flinging intricacies and colossi down aeons of emptiness, heaping profusions on profligacies with ever-fresh vigor. The whole show has been on fire from the word go. I come down to the water to cool my eyes. But everywhere I look I see fire; that which isn't flint is tinder, and the whole world sparks and flames."
― Annie Dillard, Pilgrim at Tinker Creek.

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CHAPTER 1: INTRODUCTION AND LITERATURE REVIEW

The current global biodiversity crisis disproportionately affects amphibians, with one in three species threatened with extinction (Baillie et al. 2004; Cushman 2006). Threats attributable to the extinction crisis include invasive species, disease, climate change, and habitat modification (Storfer 2003), whereby habitat modification through fragmentation and loss factor prominently (Cushman 2006). Loss of habitat for amphibians ranges from dredging, draining, and filling of wetlands to removing woodland buffers for roadways (Gibbs 2000; Windmiller et al. 2008). Abrupt habitat losses threaten amphibians due to their limited vagility (Cushman 2006). Limited vagility also exacerbates the negative impacts of habitat fragmentation on amphibian dispersal rates by altering connectivity (Rittenhouse and Semlitsch 2006). Wetland loss disrupts connectivity between terrestrial habitats and breeding sites for amphibians (Cushman 2006).

Illinois has lost ~90% of its wetlands to agricultural development (Suloway and Hubbell 1994; Fretwell et al. 1996), causing declines in many wetland-dependent species. These declines are exacerbated because most loss is of seasonal wetlands that amphibians use for reproduction (Hart and Newman 1995; Dodd and Cade 1998; Semlitsch and Bodie 1998). Compounding the threat of wetland loss is losing the surrounding terrestrial habitat amphibians occupy outside the breeding season (Windmiller et al. 2008). The terrestrial habitat is where foraging, torpor, and migration occur for wetland-breeding amphibians and is where most of their life cycle is spent (Guerry and Hunter 2002). The loss of habitat and connectivity between terrestrial habitat and breeding wetlands is detrimental to the survival of amphibian populations (Rittenhouse and Semlitsch 2006; Crawford et al. 2016). In Illinois, three salamander species of conservation concern (*Ambystoma jeffersonianum*, *A. platineum*, and *A. laterale*) require wetlands for breeding and terrestrial habitat to forage (IDNR 2005; IDNR 2015). The quality of both habitats is vital for population persistence. Land managers employ restoration methods on state-protected land to increase terrestrial and aquatic habitat quality to prevent salamander declines caused by habitat loss and lack of connectivity (IDNR 2015).

One method to maintain suitable upland terrestrial habitat (e.g., woodland habitat) is prescribed burning. Burning is a commonly used management tool to slow the spread of invasive plant species and promote habitat connectivity through native vegetation regeneration (Malanson 1987; DiTomaso et al. 2006). Removing invasive species via burns is beneficial for biodiversity and general ecosystem health (Crooks 2002), and controlled burns can benefit amphibians. Invasive vegetation is detrimental to amphibians via increases in evapotranspiration (Huxman et al. 2005). Invasive vegetation has cascading microclimate shifts for all amphibian life stages (Watling et al. 2011). In addition, promoting native vegetation through burning increases leaf litter and cover for adult and juvenile amphibians traversing the risky terrestrial environment, lessening moisture-related stress (Crooks 2002; Watling et al. 2011). However, the timing of controlled burns could overlap with adult salamander breeding migrations or juvenile salamander emigrations, thus adding a threat (Abrams 1992; Brodman 2010). Predicting when salamanders migrate to and from wetlands will help land managers better plan burns to reduce or eliminate direct management-related mortality or indirect stress-related mortality.

The primary drivers triggering breeding migrations to wetlands in adult ambystomatids include minimum air temperature, precipitation, and shifts in the soil temperature profile (Douglas 1979; Hardy and Raymond 1980; Semlitsch 1985; Sexton et al. 1990; Semlitsch and Anderson 2016). The timing of migration is balanced between adults risking predation or desiccation and providing enough development time for larvae to metamorphose before wetlands dry up in the late summer (Douglas 1979). For juveniles, metamorphosing and emigrating from wetlands at different times can confer fitness advantages at later life stages (Douglas 1979; Semlitsch et al. 1988). The advantage of leaving the wetland earlier is increased foraging time in a more favorable terrestrial environment and reducing the risk of larval mortality from the wetland drying out (Semlitsch 1985; Semlitsch et al. 1988; Rothermal and Semlitsch 2006). However, leaving the wetland early increases vulnerability to terrestrial predators at a smaller body size (Rothermal and Semlitsch 2006). Metamorphosing later results in larger body sizes, protection from gape-limited predators, reduced evaporative water loss, and increased survival to first reproduction (Rothermal and Semlitsch 2006). However, metamorphosing later increases the risk of not completing metamorphosis and traversing a drier terrestrial environment (Rothermal and Semlitsch 2006). Adult breeding can impact a juvenile's strategy depending on when egg deposition occurs, directly influencing the time of year metamorphs disperse from the wetland (Semlitsch and Anderson 2016). Movement strategies for both adults and juveniles impact population stability and future reproductive success (Semlitsch et al. 1998; Biek et al. 2002). Different movement strategies could make adults and juveniles susceptible to prescribed burns depending on when land managers decide to burn forested habitats. Understanding movements through the terrestrial environment, such as migrations, can inform restoration practices.

Maintaining suitable aquatic habitat by improving the quality of existing breeding wetlands or creating new wetlands are other techniques to restore the terrestrial environment (i.e., through prescribed burns). Wetland creation has gained momentum due to a > 53% loss of wetland area from the 1780s to 1980s in the contiguous U.S. (Dahl 1990). National policy changes have attempted to address the unprecedented habitat loss with "no net loss" regulations (Brown and Lant 1999; Mack 2007). This type of wetland restoration creates new wetlands to replace or increase breeding areas amphibians can use. However, replacing high-quality wetlands with high canopy cover and long hydroperiods (Windmiller 1996; Porej et al. 2004) with lower quality open-water wetlands negatively affects amphibian populations (Mack 2007; Harper et al. 2008; Dahl 2011). Adding wetland habitats, regardless of quality, addresses the loss of acreage but does not necessarily address the effects of reduced ecosystem heterogeneity, isolation, and associated synergies on amphibian populations (Mack 2007; Harper et al. 2008; Dahl 2011). Creating poor-quality habitats could potentially harm amphibian populations as these habitats may act as ecological traps (Harper et al. 2008).

Another wetland restoration option includes enlarging the wetland to increase the hydroperiod. Hydroperiods are significant for amphibians because of aquatic fertilization and larvae requiring 2–5 months of development before metamorphosis. Due to climate change, hydroperiods of many ephemeral wetlands are less stable/are decreasing since droughts are increasing in frequency (IPCC 2014). Deepening an existing wetland or improving a wetland's ability to retain water (i.e., repairing berms) combats hydroperiods too short for breeding or larval development. Increasing the hydroperiod of wetlands can also increase larval growth and then increase survival (Pechmann et al. 1989; Ryan 2007). The benefits of longer hydroperiods quickly diminish if wetlands become permanent and fish predators are introduced and persist. Balancing wetland enhancements for amphibians while deterring fish is crucial for wetland restoration. Monitoring amphibian breeding wetlands, both created and natural/altered could provide insight into the impacts of wetland restoration on population dynamics during a shifting climate.

Reproductive success in ambystomatids is highly variable, so "boom-bust" population cycles are common (Pechmann et al. 1991; Harper et al. 2008). However, declines in recruitment for ambystomatids are often due to truncated hydroperiods. For example, in a two-year study of *A. jeffersonianum*, reproductive failure occurred because hydroperiods were too short to afford complete metamorphosis (Mullin and Klueh 2009). Other studies of ambystomatids have also shown frequent reproductive failure due to drought and shorter hydroperiods (Williams 1973; Pechmann et al. 1991; Semlitsch et al. 1996; Taylor et al. 2006; Anderson et al. 2015). Thus, monitoring the reproduction of the three imperiled ambystomatids is essential for accessing their population persistence into the future.

My study examines the relationships between environmental variables and the movement of both adult and juvenile *A. jeffersonianum*, *A. platineum*, and *A. laterale*. Determining variables predicting migrations allows land managers to target management activities during periods of least threat or harm. I also collected reproductive data on *A. jeffersonianum* to calculate demographic variables necessary for constructing egg and larval survival and fertility to complement the migration data. Lastly, I determined what female body size parameter best-predicted clutch size.

Study Species

Of the eight-mole salamander (*Ambystoma*) species in Illinois, my study focuses on three imperiled species (*A. jeffersonianum*, *A. platineum*-unisexual, and *A. laterale*) and the host for the unisexual species (*A. texanum*).

Jefferson Salamander, *Ambystoma jeffersonianum*

The Jefferson Salamander, *A. jeffersonianum*, can have a dark gray to a translucent brownish-gray coloration, with blue or silvery spots along its lower side and limbs (Fig 1.1 A; Green 1827). The range of *A. jeffersonianum* extends from the Northeast (Southwestern New Hampshire, Southern Vermont, Western Massachusetts, Western Connecticut, Southern New

York, Northwestern New Jersey), through the Mid-Atlantic (Pennsylvania, Western Maryland, Northern Virginia, West Virginia), and into the Central U.S. (Ohio, Indiana, and Kentucky) (Petranka 1998). In Illinois, they occur in the deciduous woodlands of the Wabash Border Natural Division in Edgar and Clark counties along the Illinois-Indiana border (Phillips et al. 1999; Crawford et al. 2016). The Illinois population is considered isolated and is state-threatened due to its vulnerable habitat (IDNR 2005; IDNR 2015).

The earliest spring-breeding *Ambystoma* species is *A. jeffersonianum* (Petranka 1998). Before migration, they likely move up the soil column through burrows as soil surface temperature and moisture increase (Brodman 2005a). Breeding occurs in fishless, ephemeral wetlands with high canopy cover (Peterman et al. 2013). Breeding migrations occur when adult movements to wetlands are triggered by warm nocturnal rains (Brodman 1995; Petranka 1998). Males migrate before females (Douglas 1979) and migrate annually, whereas some females exhibit biennial breeding (Downs 1989; Petranka 1998). Both sexes of *A. jeffersonianum* are highly philopatric to breeding wetlands (Crawford et al. 2016). After mating, adults migrate back to terrestrial sites and remain fossorial for the rest of the year (Petranka 1998).

Female *A. jeffersonianum* oviposit on small twigs or emergent vegetation 1–2 days after mating. Egg masses laid by the same female are typically laid close together (Petranka 1998). Clutch size varies from 140–280 eggs, and although embryonic survival is relatively high (71–96%; Rowe and Dunson 1994), it varies with wetland pH (Brodman 1995) and temperature, as well as late-season wetland freezes (Brodman 2005a). The embryonic period ranges from 4–7 weeks and depends on the time of oviposition, temperature, and latitude (Petranka 1998). The larval stage can range from 2–4 months, with much lower survival rates (>1%) than embryonic stages (Williams 1973; Thompson et al. 1980; Downs 1989; Mullin and Klueh 2009). The low survival rate is likely due to predation (Petranka 1998; Brodman 2005a) and competition.

Silvery Salamander, *Ambystoma platineum*

The Silvery Salamander, *A. platineum*, is an all-female polyploid within the unisexual *A. jeffersonianum* complex (Fig. 1 B; Clanton 1934; Uzzell 1964). They are a triploid salamander with two chromosome sets from *A. jeffersonianum* and one from *A. laterale* (JJL). Although *A. platineum* requires spermatophores from males of one parental species to reproduce gynogenetically, the populations in Vermilion County, IL use spermatophores from *A. texanum* because neither parental species occurs at *A. platineum* breeding wetlands (Phillips et al. 1999; Phillips and Mui 2005). Morphologically, *A. platineum* are similar to *A. jeffersonianum* and cannot be reliably distinguished without karyology (Petranka 1998; Phillips and Mui 2005). Known *A. platineum* populations occur in east-central Illinois (Vermilion County; Phillips et al. 1999), Southern Michigan, Northwestern Ohio, Northern New Jersey, with scattered occurrences in New York, Massachusetts, and Connecticut (Petranka 1998; Phillips and Mui 2005). The populations in Vermilion County are considered endangered in Illinois due to their rare status (IDNR 2005; IDNR 2015)

Because *A. platineum* requires spermatophores of other *Ambystoma* species, their breeding migrations coincide with *A. texanum* following a late winter to early spring nocturnal rainfall (Petranka 1998; Phillips and Mui 2005). Preferred breeding wetlands of *A. platineum* are similar to other ambystomatids, vernal wetlands with high canopy cover, and no fish predators (Petranka 1998). However, the JJL unisexual species occupy more "marginal" habitat (drier, warmer, higher elevation) when in the presence of *A. jeffersonianum* (Greenwald et al. 2016).

Reproduction for *A. platineum* in the Illinois population consists of parasitizing spermatophores from *A. texanum* (Phillips and Mui 2005). Unisexuals have smaller clutch sizes (124–200 eggs) than parental species (Uzzell 1969; Downs 1989), and the egg survivorship is much lower because failure to stimulate egg development is common (Petranka 1998). Males of the parental species can discriminate between unisexuals and conspecifics and lay fewer spermatophores in the presence of *A. platineum* (Uzzell and Goldblatt 1967; Dawley and Dawley 1986; Phillips et al. 1997). Stimulated eggs have an embryonic period of ~30 days and complete metamorphosis in ~2 months (Petranka 1998).

Blue-spotted Salamander, *Ambystoma laterale*

The Blue-spotted Salamander, *A. laterale*, is dark gray-black with bluish-white spots covering its relatively small body (Fig. 1.1 C; Petranka 1998). Of the species included in this study, *A. laterale* are the most northerly distributed *Ambystoma* species ranging from southern Canada and the northern United States (from Maine to Minnesota) southward to northern Indiana, Illinois, and Iowa (Petranka 1998). In Illinois, *A. laterale* have no formal protected status but are considered a Species of Greatest Conservation Need due to the threat of urbanization (SGCN, IDNR 2005; IDNR 2015). They are primarily found in Illinois' Northeastern Morainal Natural Division (five counties outside Chicago; Phillips et al. 1999).

As a result of their northerly distribution, *A. laterale* breed later in the season (late March to early April) than Jefferson and Silvery Salamanders in Illinois (Brodman 2005b). This explosive breeding season can last from a few days (Brodman and Kilmurry 1998) to 2–3 weeks (Brodman 2005b) and is triggered by precipitation (Lowcock et al. 1991). Similar to *A. jeffersonianum*, males migrate to the ponds earlier than females (Lowcock et al. 1991). Populations of *A. laterale* typically breed in fishless temporary wetlands, and populations in northern Illinois are usually present in wooded moraines (Brodman 2005b). Once *A. laterale* return to the terrestrial habitat, they can still be found under logs more frequently than other *Ambystoma* species, likely due to a higher tolerance of dry, sandy conditions (Brodman 2005b).

The reproduction of *A. laterale* is aquatic, and females oviposit on emergent aquatic vegetation (Brodman 2005b) and clutch size averages from 196–250 eggs (Minton 2001). After 3–4 weeks, the eggs hatch, and larvae complete metamorphosis in 2–3 months (Brodman 2005b). Little is known about metamorph egress from breeding wetlands.

Small-mouthed Salamander, *Ambystoma texanum*

The Small-mouthed Salamander (*A. texanum*) is dark gray to black salamander with lichen spotting along the sides of its body with a small head (Fig.1.1 D). The distribution of *A. texanum* extends from Texas northward to Michigan and from Ohio westward to Kansas and Oklahoma (Petranka 1998). Compared to other ambystomatids, *A. texanum* often use shallower breeding wetlands but breed in the same wetlands as the *A. jeffersonianum* populations in Clark County and the *A. platineum* populations in Vermilion County (Petranka 1998, Phillips and Mui 2005). In Illinois, this species is considered common and abundant on the landscape (Phillips et al. 1999).

Breeding migrations occur on rainy nights as punctuated explosive breeding events (Kraus and Petranka 1989). Illinois populations breed in late winter or early spring, following snowmelt from warm precipitation (Brodman 2005b). Preferred breeding wetlands are fishless. The interaction between hydroperiod and length of time to metamorphosis drives *A. texanum* juvenile migrations (Semlitsch 1985; Semlitsch et al. 1988), and hydroperiod also affects larval survival (Ryan 2007). Shorter hydroperiods (< 100 days) can cause mortality if larvae are unable to complete metamorphosis before the wetland dries (Paton and Crouch 2001; Ryan 2007).

Longer hydroperiods (> 200 days) allow more larvae to complete metamorphosis (Paton and Crouch 2001; Ryan 2007). Juvenile emigration usually occurs a few weeks after metamorphosis, and dispersal is nocturnal (Petranka 1998).

Study Sites

I conducted my study at Lincoln Trail State Recreation Area (LTSRA), Kickapoo State Recreation Area (KSRA), and Pine Dunes Forest Preserve (PDFP) (Fig. 1.2). All three sites undergo controlled burns and have natural and created breeding wetlands. The Illinois Department of Natural Resources (IDNR) owns Lincoln Trail State Recreation Area and has the only protected population of *A. jeffersonianum* in the state. The metapopulation of *A. jeffersonianum* comprises two wetlands on private property adjacent to the park and ten wetlands within the park (Crawford et al. 2016). One historical wetland and nine created wetlands represent the breeding habitat for the LTSRA metapopulation. I sampled two of the park's wetlands for the study – one smaller created wetland and a larger natural wetland (Fig. 1.3). The larger natural wetland is in the southwestern portion of LTSRA, whereas the smaller created wetland is in the northwestern portion (Fig. 1.3). The smaller created wetland (136 m^2) has a shorter hydroperiod (8–9 months) compared to the larger natural wetland (483 m^2; nearly permanent) due to the difference in sizes (Mullin and Klueth 2009). LTSRA consists of an oak-hickory forest tract with a high overstory canopy cover (~80%). Small-mouth salamanders (*A. texanum*) also breed at surveyed wetlands and generally arrive later than *A. jeffersonianum*. Despite the proximity of the wetlands, *A. jeffersonianum* demes have little genetic connectivity suggesting movement between wetlands is rare (Crawford et al. 2016), although it is more common for other ambystomatids (Shoop 1968; Gamble et al. 2007).

Kickapoo State Recreation Area is owned by the IDNR and supports an *A. platineum* metapopulation. All occupied wetlands occur in the western portion of KSRA and consist of created and natural wetlands. I sampled three wetlands in the western portion of KSRA (Fig. 1.4) – two smaller created wetlands and one larger natural wetland. The larger natural wetland (1810 m^2) has the longest hydroperiod, and the smaller wetlands (113 m^2 and 257 m^2) have shorter hydroperiods and less canopy cover. The four mole salamanders breeding at the site are Silvery, Spotted (*A. maculatum*), Marbled (*A. opacum*), and Small-mouthed (*A. texanum*) salamanders.

The Lake County Forest Preserve District owns Pine Dunes Forest Preserve (PDFR), and I focused sampling at one natural wetland (>1810 m^2) within the preserve (Fig. 1.5). The natural wetland has a long hydroperiod (nearly permanent). Tiger salamanders (*A. tigirum*) also breed at the site. Pine Dunes Forest Reserve has more prairie vegetation than the other sites and lower canopy cover. The sandy soils support a mixed deciduous forest (some conifers) in this area. The wetland crosses private land to the north, so little management has occurred along that edge.

Figures

Figure 1.1. The four species of mole salamanders studied: A) Jefferson salamander (*Ambystoma jeffersonianum*); B) Silvery salamander (*A. platineum*); C) Blue-spotted salamander (*A. laterale*); D) Small-mouthed salamander (*A. texanum*).

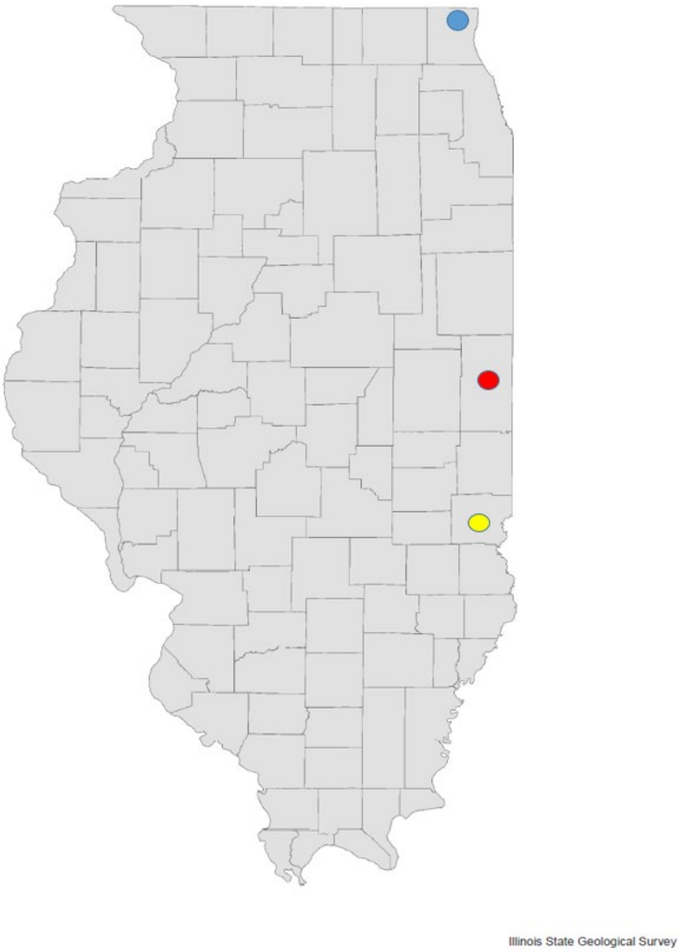

Figure 1.2. Map of Illinois with circles showing the latitudinal gradient among the study sites. Blue circle = Pine Dunes Forest Preserve (Lake County), red circle = Kickapoo State Recreation Area (Vermilion County), and yellow circle = Lincoln Trail State Recreation Area (Clark County).

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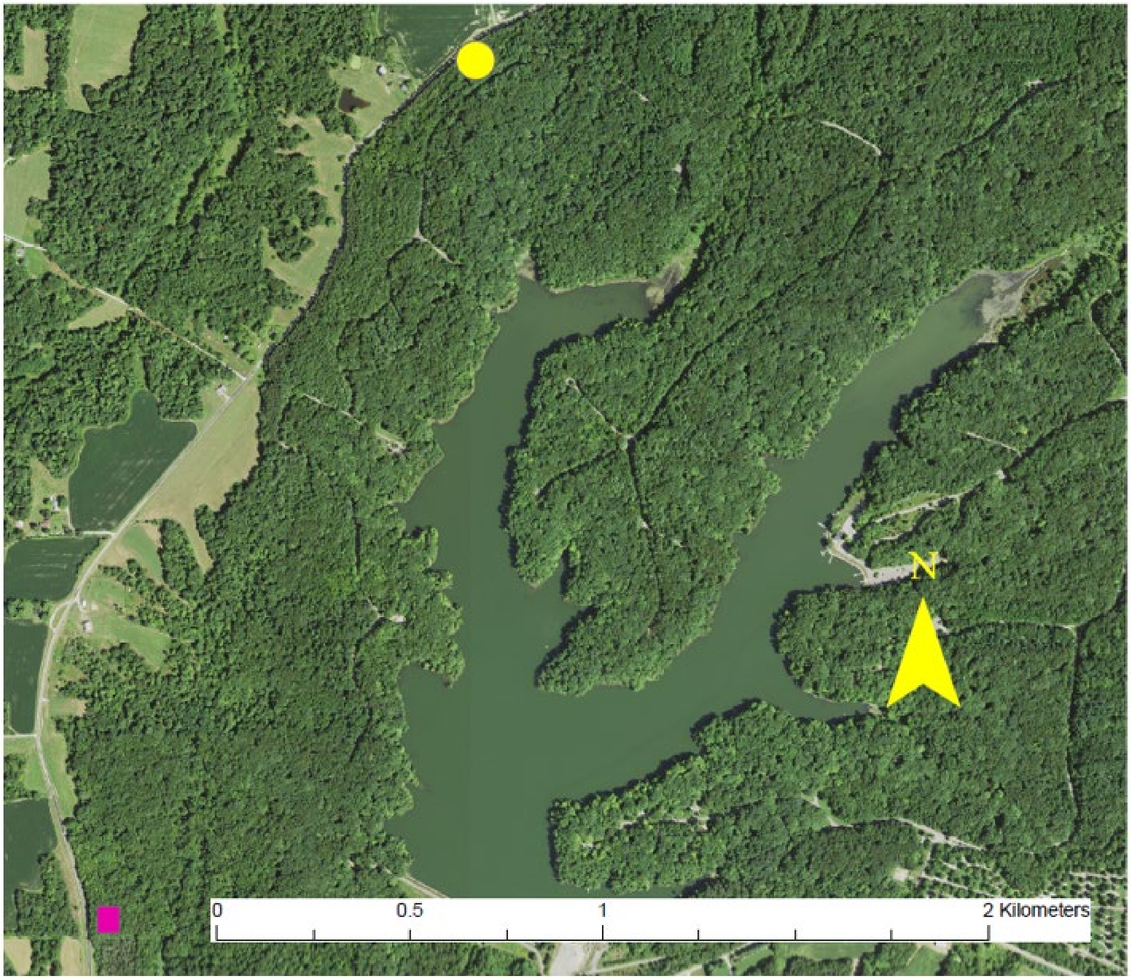

Figure 1.3. Field sites for *Ambystoma jeffersonianum* at Lincoln Trail State Recreation Area (LTSRA). The yellow circle shows the smaller, created wetland, and the pink square shows the larger, natural wetland— the distance in km. The source of this DOQ is the 2015 Illinois NAIP.

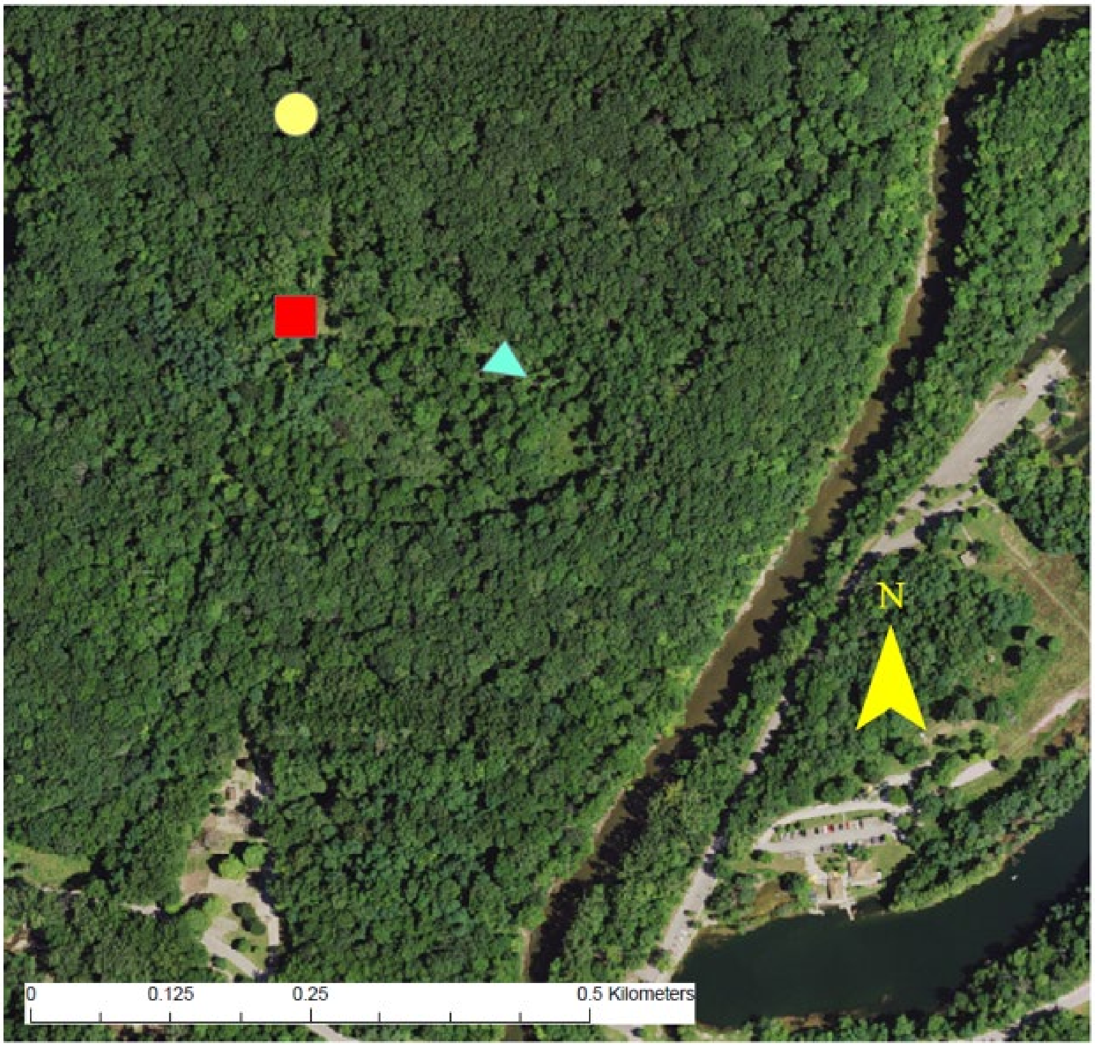

Figure 1.4. Field sites for *Ambystoma platineum* at Kickapoo State Recreation Area (KSRA). The yellow circle shows the largest natural wetland's location, the blue triangle and the red square show the two smaller, created wetlands—the distance in km. The source of this DOQ is the 2015 Illinois NAIP.

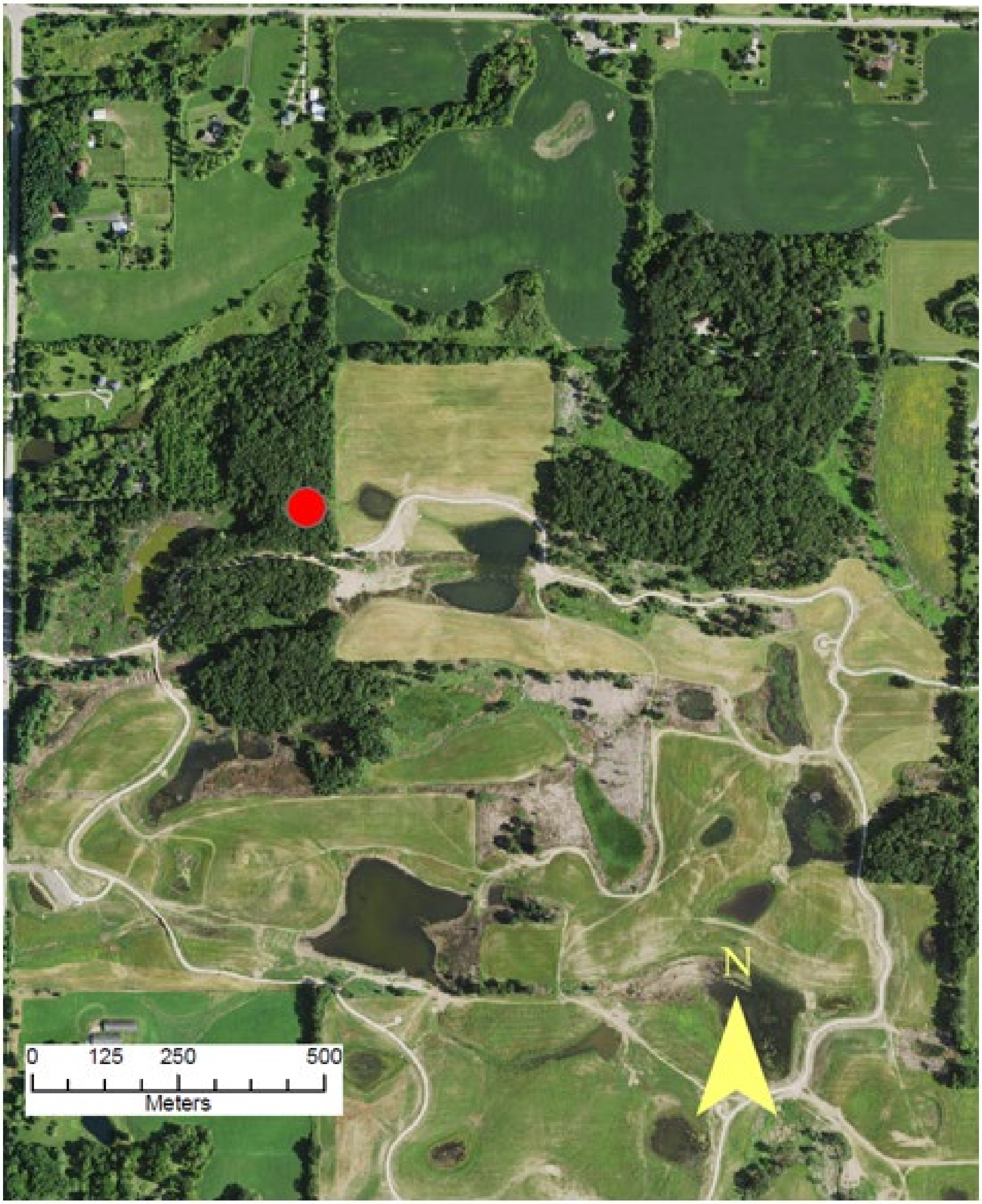

Figure 1.5. Field sites for *Ambystoma laterale* at Pine Dunes Forest Preserve (PDFP). The red circle indicates the location of the wetland sampled— the distance in m. The source of this DOQ is the 2015 Illinois NAIP.

CHAPTER 2: PHENOLOGY OF THREE *AMBYSTOMA* SPECIES

Introduction

Conservation efforts to maintain habitat connectivity are essential to stem the current global extinction crisis for numerous species. Habitat connectivity ensures all parts of a habitat are accessible (Taylor et al. 1993). One of the most pervasive threats to functional habitats is fragmentation, which occurs when parts of the habitat become inaccessible, altered, or eliminated, leading to loss of habitat connectivity (Cushman 2006). Fragmentation threatens species migrating between habitats during breeding and foraging events (Cushman 2006). Species migrating to breeding grounds, feeding grounds, or a particular water source can be impacted, and experience population declines when habitat connectivity is not maintained. Without habitat connectivity, population viability declines, and gene flow diminishes within a metapopulation (Clobert et al. 2012). Thus, maintenance of habitat connectivity is essential to population stability and recovery of isolated populations.

Habitat connectivity is essential to amphibians because their complex life cycle requires aquatic and terrestrial habitats (Semlitsch 2008). Disruption or removal of connectivity between upland terrestrial and breeding wetland habitats has drastic effects on amphibian populations, such as reducing genetic diversity (Cushman 2006; Cosentino et al. 2011; Crawford et al. 2016). Amphibians have increased vulnerability to habitat fragmentation due to limited dispersal abilities. Wetland-breeding amphibians are typically philopatric to a breeding wetland and the surrounding terrestrial habitat because of survival risks and high energetic costs of exploratory behavior and dispersal (Shoop 1968; de Maynadier and Hunter 1995; Gamble et al. 2007; Semlitsch 2008). Therefore, it is critical to conserve and expand extant high-quality amphibian habitats to conserve amphibian populations with high degrees of philopatry as it can be difficult for amphibian populations to persist in highly fragmented landscapes (Semlitsch 2008).

Amphibian populations in the Midwestern U.S. have lost a prolific amount of terrestrial (Windmiller et al. 2008) habitat and thus are experiencing disrupted habitat connectivity. Three mole salamanders, *Ambystoma jeffersonianum*, *A. platineum*, and *A. laterale,* are of conservation concern in Illinois due to habitat loss and the effects of urbanization (IDNR 2005). All three require a terrestrial environment to forage and hibernate and suitable wetland habitat to breed. Terrestrial habitat is where ambystomatids spend most of their life cycle (Guerry and Hunter 2002); however, traversing the terrestrial habitat to reach breeding wetlands increases mortality risk (Semlitsch 2008). Habitats with lower canopy cover and reduced leaf litter have a higher desiccation risk for amphibians and traversing in open areas results in high exposure to predators (Semlitsch 2008). Even when the terrestrial habitats present risks (i.e., clear-cut forest), *Ambystoma* salamanders will still traverse the dangerous habitat to reach breeding wetlands (Todd et al. 2009), but when a higher quality terrestrial route is available (high canopy cover near wetlands), ambystomatids will choose the safer route (Todd et al. 2009). Therefore, restoration aimed at habitat connectivity is an important and effective measure.

Land management methods can help counteract poor habitat connectivity by either expanding habitat or revitalizing older habitat. For example, prescribed burns are a common management tool to help combat invasive species and encourage native species with higher canopy cover and more favorable evapotranspiration regimes (Abrams 1992; Huxman et al. 2005). However, mistiming of management methods such as prescribed burns could introduce anthropogenic harm to migrating ambystomatids. Being able to anticipate ambystomatid migrations would allow land managers to avoid direct fire mortality and limit unfavorable conditions such as bare ground cover and low moisture proximate to breeding wetlands. Some climate factors thought to initiate migrations are overnight precipitation, relative humidity, soil temperature, and cooler air temperatures, all of which lessen desiccation, which is a significant risk for both adults and juveniles (Douglas 1979; Semlitsch 1985; Semlitsch and Wilbur 1989; Semlitsch et al. 1996; Semlitsch 2008; Semlitsch and Anderson 2016). These environmental conditions can influence migration timing through trade-offs between resource availability for larvae, terrestrial migration risks (such as desiccation), and resource availability in the overwintering habitat (Semlitsch 2008).

Given the importance of better understanding *Ambystoma* migrations, the primary objective of my study was to identify important biotic and abiotic factors influencing the timing and magnitude of adult and juvenile *Ambystoma* salamander movements between terrestrial and wetland habitats. I predicted environmental factors influencing moisture, such as overnight precipitation and minimum air temperature, would influence the timing and magnitude of migrations. Soil temperature would influence the timing of migrations more than the magnitude of migrations. A secondary objective was to provide insights into the phenology of adult and juvenile movements of the unisexual species *A. platineum,* parasitizing *A. texanum*. Monitoring migration to breeding wetlands for these species of conservation concern provides critical information to inform best burn practices to conserve these populations.

Materials and Methods

Data Collection

I monitored *Ambystoma* breeding and metamorph migrations at three sites from January 2018 through August 2020. Two wetlands at Lincoln Trail State Recreation Area (LTSRA) in Marshall, IL, three wetlands at Kickapoo State Recreation Area (KSRA), and one wetland at

Pine Dunes Forest Preserve (PDFP) were sampled. I sampled from January through early May for adult migrations and from late May through mid-August for juvenile emigrations. I ceased monitoring in March and April at LTSRA and KSRA, respectively, and did not monitor PDFP for the entirety of 2020 due to the COVID–19 pandemic.

To capture migrating salamanders (adults and juveniles), I used ~50 cm high drift fences constructed of aluminum flashing with pitfall traps (19 L buckets) placed approximately every 5 m inside and outside the fence. Fences completely encircled each wetland at a distance of 5–10 m from the wetland margin (depending on how inundated the basin was) and were buried a few cm into the soil to reduce trespass. Sponges and floating styrofoam were placed in each pitfall trap to prevent desiccation and drowning, respectively. Pitfall traps were checked at least once every 48 hr. I considered individuals captured from outside buckets as immigrating (ingressing) into the wetland, and those from inside buckets as emigrating (egressing) from the wetland — dates when salamanders were captured were converted to the Julian date, hereafter referred to as day-of-year. The day-of-year variable is valuable for parsing male and female movements and providing a possible range of dates during which management could occur (i.e., prescribed burns).

All captured individuals were identified to species and had snout-vent-length (SVL), total length (TL), and mass (grams) measured. I determined sex of adults using secondary sexual characteristics whereby males have a swollen cloaca during the breeding season. All metamorphs were placed into the juvenile category because there is no reliable way to determine sex. Initial captures were marked with a PIT (passive integrated transponder; Biomark Inc.) tag if they were an adult or an alpha-numeric tag (2 mm x 5 mm VI Alpha Tag; Northwest Marine Technology Inc.) if the individual was a metamorph. Count results for adults included new and recapture combined. Once field processed, I released salamanders on the opposite side of the fence they were captured. For KSRA, I included movements of male and female *A. texanum* because the unisexual *A. platineum* females parasitize male *A. texanum* spermatophores. Therefore *A. platineum* could be motivated to move into the wetland before *A. texanum* females due to resource competition, and I wanted to ensure that possibility was included in my analysis.

Environmental Variables

I downloaded minimum air temperature (°C) and precipitation (mm) data from the National Center for Environmental Information (NCEI) website for the weather station nearest each study site with at least 95% temporal data coverage between 2018–2020. The sites chosen were: Chicago Waukegan Regional Airport, IL for PDFP (~12 km away; Lat/Long 42.42, -87.87), Danville, IL for KSRA (~10 km away; Lat/Long 40.14, -87.65), and Casey, IL for LTSRA (~25 km away; Lat/Long 39.29, -87.97). I used precipitation accumulation (mm) from the day before and minimum air temperature (°C) from the day of the survey (minimum air temperature would occur during the period of movement). Because there was no hourly precipitation data available, I used the full 24-hr. (8 am of previous day– 8 am of day when salamanders were counted) precipitation accumulation. Hereafter I refer to previous-day precipitation accumulation as 24-hr. precipitation. I calculated the previous day and three-day average minimum temperatures from the minimum air temperature data.

To measure the thermal profile of the soil at each field site, I buried a pair of HOBO Pendant temperature data loggers at the soil surface beneath detritus and 30 cm deep (level where salamanders hibernate and are influenced by temperature profile; Sexton et al. 1990) ~50 m from the monitored wetlands. The loggers collected hourly data from early January until mid-August or when the last metamorph exited the wetlands. I then averaged all the hourly data per day for the surface and 30 cm loggers. To calculate the soil inversion strength, I subtracted the average 30 cm temperature from the average surface temperature for each day. Positive values indicated warmer surface temperatures, and negative values indicated warmer 30 cm temperatures. I measured depth at the deepest part of the wetland with a 1.5 m staff gauge and recorded data coincident with monitoring days. Because the gauges showed signs of subsidence, I subtracted the amount of subsidence from the recorded measurement. I then scaled wetland depth as the proportion of the maximum depth for that year at each wetland.

Statistical Analysis

I calculated variance inflation factors (VIF) using the vif function in the car R package and removed variables with values > 2 to eliminate potential multicollinearity (Table 2.1). The 24-hr. minimum air temperature and the previous 3-day average minimum temperature had high VIF values (for all three species); thus, I removed them from the analysis. Minimum air temperature on the survey day, 24-hr. precipitation, soil inversion strength, day-of-year, and wetland depth were chosen because there were no collinearity issues, and these variables were relevant in previous studies (Pechmann et al. 1989; Sexton et al. 1990; Ryan 2007; Semlitsch and Anderson 2016). I treated day-of-year and minimum air temperature as 2nd order polynomials because of potential peaks in migration for both adults and metamorphs (Semlitsch 1985; Semlitsch and Anderson 2016; Crawford et al. 2020).

Using the finalized variable set (Table 2.1), I constructed a series of hypothesis-based models, including global and null models, for adults and metamorphs (Table 2.2; Table 2.3). The response variable used for the timing models was binary (1 – move, 0 - no move). The raw number of salamanders moving (when movements occurred) was the response variable for migration magnitude models. I created mixed-effects models using the glmer function in the lme4 R package for timing and magnitude of movement for *A. jeffersonianum* and *A. platineum* models (fitted with maximum likelihood via Laplace Approximation; Bates et al. 2014). The random effect used in each mixed-effects model was the year the data were collected. For *A. laterale*, I only used general linear models (glms) to create timing and magnitude models (Table 2.2; Table 2.3). The different modeling methods stemmed from having too few data points (two years of data for a single wetland) for *A. laterale* to use random effects. I used the optimizer, bobyqa, when models failed to converge (Bates et al. 2014), but some models constructed for the hypothesis-based sets failed to converge even with an optimizer (included in the supplementary table; Table S1). For the adult model sets, I included sex as an interaction term for each variable because males and females of the same species could react differently to environmental variables (Petranka 1998). I collapsed wetlands for each species in the analyses because the populations are considered part of the same metapopulations (*A. jeffersonianum*-Crawford et al. 2016, *A. platineum*-Phillips et al. 1999) and to ensure I had enough observations to avoid convergence issues. I also created *post-hoc* models for movement probability based on the top-ranked *a priori* model variables to ensure I selected the best predictive model from the variables recorded (Table 2.2; Table 2.3; Crawford et al. 2020).

I ranked models either by using the corrected Akaike Information Criterion (AIC_c) or Quasi-Akaike Information Criterion ($QAIC_c$) from the AICcmodavg package to assess which model had the most parsimonious predictive power (AICcmodavg; Akaike 1974; Anderson et al. 2001; Burnham and Anderson 2002). I used QAIC when significant overdispersion ($\hat{c} > 1.5$) occurred in the data (using the dispersion_glmer function in blmeco package; Barry et al. 2003). If overdispersion occurred in the *A. laterale* model sets, I used generalized linear models with a negative binomial distribution (*glm.nb),* and if no overdispersion was evident, then simple glm or glm Poisson models was used.

I calculated pseudo-R^2 values (marginal and conditional) using the piecewiseSEM R package to assess model fit for the glmm models and used nagelkerke R^2 values for the *A. laterale* models (Lefcheck 2016). Beta parameter estimates for each variable in the top-ranking model were calculated and the 85% confidence intervals (CIs) to check for significance (85% CIs do not bound zero). I combined beta parameter tables and confidence intervals with information criteria rankings against literature suggestions (Burnham and Anderson 2002) to assess whether all variables contributed to the rank of the model and were not just "hitchhiking" (poor predicting variables leaning on highly predictive variables). I used 85% confidence intervals to be more compatible with AIC ranking (Arnold 2010). I also used the effects package in R to analyze how each significant variable impacted the predicted fit of the model (assess the direction and effect size of each variable; Fox 2003; Fox and Hong 2009). Prediction intervals were plotted with predicted estimates to check for the spread of the data and display uncertainty associated with the insufficient number of samples for specific ranges of variables.

Results

Probability of Movements for Adult Ingress

For *A. jeffersonianum*, I used 330 observations over three years (2018–2020) to construct ingress models at two wetlands. For *A. platineum* (unisexual) and *A. texanum*, I used 843 observations over three years (2018–2020) from three wetlands to create the models. For *A. laterale*, I used 47 observations over two years (2018–2019) at one wetland. No overdispersion was found in any model (*A. jeffersonianum* – $\hat{c} < 1.02$; *A. platineum* - $\hat{c} < 0.90$; *A. laterale* – $\hat{c} < 0.98$), so I used to rank the model sets. The most parsimonious model for *A. jeffersonianum* and

A. platineum included day-of-year, 24-hr. precipitation, and minimum air temperature, whereas the day-of-year and soil inversion model was the top-ranking for *A. laterale* (Table 2.4).

Phenologically, day-of-year was a strong predictor across species (Table 2.5). For day-of-year, *A. jeffersonianum* males moved earlier than females (Fig 2.1a) and had a 0.45 ingress probability at day 10 (10 January), whereas females had a near 0 probability (Fig. 2.1a). Peak ingress occurred earlier at day 30 (30 January) for males compared to day 60 (1 March) for females. For female *A. platineum* and both sexes of *A. texanum*, the difference in peak ingress for day-of-year was less distinct (Fig. 2.1b). Male *A. texanum* peaked at an ingress probability at 0.3 around day 60 (1 March), whereas female *A. texanum* peaked at 0.4 around day 70 (11 March: Fig. 2.1b). The peak ingress probability for *A. platineum* was 0.75 around day 65 (6 March; Fig. 2.1b). For *A. laterale*, the peak ingress probability was highest for males at 0.65 around day 80 (21 March), whereas females peaked at 0.85 around day 100 (10 April; Fig. 2.1c). The lack of a full unimodal shape with a peak for males may be due to surveys starting too late for *A. laterale*. The *A. laterale* peaks are later in the year than both *A. platineum* and *A. jeffersonianum* (Fig. 2.1a-c).

Twenty-four-hour precipitation was a strong predictor for both *A. platineum* and *A. jeffersonianum* (Table 2.5). Twenty-four-hour precipitation positively correlated with *A. jeffersonianum* ingress probabilities for both sexes (Fig. 2.1d). Males and females showed the same positive trend for 24-hr. precipitation, whereby at no 24-hr. precipitation, males had a 0.10 ingress probability, and females had a 0.30 probability (Fig. 2.1d). At the maximum predicted 24-hr. precipitation (~62 mm), both sexes had nearly a 1.0 probability. The same positive relationship with 24-hr. precipitation was observed for *A. platineum* females and both sexes of *A. texanum* (Fig. 2.1e). However, female *A. platineum* maintained a greater than 0.50 ingress probability on days with no 24-hr. precipitation. The ingress probabilities were lower for *A. texanum* females (0.25) and males (0.15) at 0 mm of 24-hr. precipitation (Fig. 2.1e).

Soil inversion was a strong predictor for *A. laterale*, but only for males (Table 2.5). Soil inversion strength positively correlated with ingress probabilities for male *A. laterale* (Fig.2.1f). The male ingress probability curve was steep and neared 0 around -3 °C (when 30 cm soil is 3.0 °C warmer than surface soil) but increased to 0.9 once the inversion strength reached 5 °C (when the soil surface is 5 °C than the 30 cm soil; Fig. 2.1f). The large 95% prediction intervals for the ingress probabilities may result from the small sample size of the *A. laterale* population.

Minimum air temperature was only informative for *A. jeffersonianum*. The response to minimum air temperature appeared unimodal for male and female *A. jeffersonianum* peaking between 4.0–5.0 °C for males at 0.20 and 7.0–9.0 °C for females at 0.60 (Fig. 2.1g). However, the ingress probability becomes less confident after the minimum air temperature reaches 10 °C as the prediction intervals widen substantially. The larger prediction intervals suggest few females move near or below 10 °C or less frequently sampled conditions, reducing power (Fig. 2.1g).

Probability of Movements for Metamorph Egress

For *A. jeffersonianum*, I used 198 observations over three years to create egress models. For *A. platineum* and *A. texanum*, I used 299 observations over three years. Finally, for *A. laterale*, I used 47 observations over two years. No overdispersion was found for any models (*A. jeffersonianum* – $\hat{c} < 0.98$; *A. platineum* - $\hat{c} < 0.95$; *A. laterale* – $\hat{c} < 1.24$), so AIC_C was used to rank the model sets. The top-performing model for *A. jeffersonianum* included day-of-year, wetland depth, and precipitation, whereas the day-of-year and 24-hr. precipitation model was the top-ranked model for *A. platineum* (Table 2.6). The day-of-year model was the top-ranked model for *A. laterale* (Table 2.6).

The day-of-year variable was informative for *A. jeffersonianum* and *A. platineum* but not *A. laterale*. The *A. jeffersonianum* metamorph day-of-year plot showed a similar peak to *A. jeffersonianum* adults, but later in the year (140 to 235 days, mid-May to August). The lag reflected the time eggs and larvae needed to develop (Fig. 2.2a). The peak *A. jeffersonianum* metamorph egress probability (0.75) occurred around day 200 (19 July), ~4 months post adult female peak ingress (Fig. 2.2a). A similar trend was exhibited for *A. platineum,* whereby peak egress probabilities (0.45) occurred around day 175 (24 June; Fig. 2.2b). For *A. laterale*, day-of-year, while not as impactful (Table 2.7), was still plotted to observe the temporal trend of egress probabilities, which peaked at 0.86 around day 200 (19 July) and decreased to 0.10 by day 250 (7 September; Fig. 2.2c). The non-unimodal relationship could be a function of not surveying early enough in the year to catch the first individuals emigrating from the wetland and is further evidenced by the wide uncertainty around day 240 (28 Aug; Fig. 2.2c).

Wetland depth and 24-hr. precipitation were also informative for *A. jeffersonianum* (Table 2.7). Both wetland depth and 24-hr. precipitation were variables only important to *A. jeffersonianum*. The egress probability for *A. jeffersonianum* with 24-hr. precipitation showed a similar positive trend as the adults; metamorphs egress probabilities increased with 24-hr. precipitation (Fig. 2.2d). However, metamorphs still had a relatively high probability of egressing (0.55) with no 24-hr. precipitation (Fig. 2.2d). As wetland depth decreased (wetland loses water), *A. jeffersonianum* metamorph egress probabilities increased (Fig. 2.2 e). However, there is still a 0.30 probability of metamorphs egressing even when the wetland depth value is close to one (maximum pool for the year) (Fig. 2.2e).

Magnitude of Adult Ingress Movements

I used 79 observations (movement > 0) over 3 years (2018–2020) to create *A. jeffersonianum* ingress magnitude models. The *A. platineum* and *A. texanum* model set used 185 observations over 3 years (2018–2020) and the *A. laterale* model set used 25 observations over 2 years (2018–2019). Overdispersion was evident in the model sets for *A. jeffersonianum* and *A. platineum* ($\hat{c} = 2.00$ and $\hat{c} = 2.89$), so $QAIC_C$ was used to rank the models. I also used generalized linear models with a negative binomial distribution (*glm.nb)* to help address overdispersion ($\hat{c} = 1.77$) in the adult *A. laterale* model set. Due to convergence issues, day-of-year had to be removed from all adult ingress magnitude model sets (Table S1). The top model for *A. jeffersonianum* included minimum air temperature, whereas the top model for *A. platineum* was the global (Table 2.8). The soil inversion strength model was the top model for *A. laterale* (Table 2.8).

Minimum air temperature was informative for the magnitude of *A. jeffersonianum* and *A. platineum* ingressing (Table 2.9). For *A. jeffersonianum*, both males and females showed a similar, overlapping unimodal with a peak for minimum air temperature (Fig. 2.3a). The maximum magnitude value (8 for males and 5 for females) of ingressing salamanders for both sexes peaked around 3.0 °C (Fig. 2.3a). Males and females ingressed at different times, but the minimum air temperature showed a difference in the magnitude between sexes (Fig. 2.3a). For *A. platineum,* the response to minimum air temperature was U-shaped with a trough around 5.0 °C (Fig. 2.3b). Minimum air temperature had a greater impact on *A. texanum* than *A. platineum*. From -4.0–14.0 °C, there was a difference of over 50 salamanders for both *A. texanum* sexes (Fig. 2.3b). The *A. platineum* trend was also a U-shape, with most salamanders moving minimum air temperatures were between -4.0–14.0 °C (Fig 2.3 A PLAT).

Twenty-four-hour precipitation was an important predictor for only *A. platineum*. Twenty-four-hour precipitation had little to no effect on *A. texanum* but positively correlated with *A. platineum* (Fig. 2.3c). As 24-hr. precipitation increased, so did the magnitude of *A. platineum* ingress, but the difference between 0 and 55mm of 24-hr. precipitation is only ~9 salamanders (Fig. 2.3c). Both *A. texanum* sexes followed the same trends (Fig. 2.3c).

Soil inversion strength was an informative variable for *A. platineum* and *A. laterale*. For *A. laterale* females, the difference between the min (-2.0) and max (4.0 °C) soil inversion strengths resulted in an eight-salamander difference in the magnitude (Fig. 2.3d). For males, the difference between the min and max soil inversion strengths resulted in an 18-salamander difference in magnitude (Fig. 2.3d). However, the 85% prediction intervals widened towards the greater soil inversion values (Fig 2.3d). The response to soil inversion strength differed between *A. platineum* and *A. texanum*. As soil inversion strength increased, the magnitude of female and male *A. texanum* ingressing decreased (Fig. 2.3e). The opposite trend was true for *A. platineum*; as the soil inversion strength increased, the magnitude of *A. platineum* ingressing increased (Fig. 2.3e). Soil inversion strength followed the same positive trend for males and females (Fig. 2.3e).

Magnitude of Metamorph Egress Movements

For the metamorph egress magnitude analysis, I used 90 observations over 3 years (2018–2020) to create *A. jeffersonianum* magnitude models, 75 observations over 3 years for *A. platineum*, and 20 observations over 2 years for *A. laterale*. I ranked *A. jeffersonianum* and *A. platineum* models with $QAIC_C$ to address overdispersion (*A. jeffersonianum* – $\hat{c}$ =1.70; *A. platineum* - $\hat{c}$ =3.64). There was no overdispersion in the *A. laterale* model set ($\hat{c}$ = 0.61), so AIC_C was used to rank the models. As in the adult data sets, I omitted the day-of-year as a variable from the juvenile magnitude model sets because of convergence issues (Table S1). The top model for *A. jeffersonianum* and *A. platineum* included 24-hr. precipitation and wetland depth, whereas the top model for *A. laterale* was the minimum air temperature model (Table 2.10).

Twenty-four-hour precipitation was informative for *A. jeffersonianum* and *A. platineum* (Table 2.11). While 24-hr. precipitation was informative for *A. jeffersonianum*, the positive relationship between 24-hr. precipitation and egress magnitude was not substantial; there was only one salamander difference between 0–50mm of 24-hr. precipitation (Table 2.11; Fig. 2.4a). For *A. platineum,* there was a difference of approximately 14 salamander difference between 0-30mm of precipitation and some were predicted to move when there was no rain (Fig. 2.4b).

Wetland depth was also informative for both *A. jeffersonianum* and *A. platineum* (Table 2.11). Wetland depth showed a negative relationship with the magnitude of *A. jeffersonianum* egressing, where more metamorphs egressed when wetland depth decreased (Fig. 2.4c). More *A. platineum* metamorphs egressed when wetlands were deeper; however, there was only a five metamorph difference between a dry and full basin (Fig. 2.4d).

Minimum air temperature informed the magnitude of *A. laterale* egressing metamorphs (Table 2.11). There was a slight increase (approximately five salamanders) from 12.5–22.5 °C minimum air temperature (Fig. 2.4e). Although the minimum air temperature might influence when metamorphs move during the summer, sample sizes are small.

Discussion

My results emphasize the importance of environmental variables, such as minimum air temperature and 24-hr. precipitation, but reveal other variables and their relative significance to the probability and magnitude of *Ambystoma* breeding migrations. Soil inversion strength was only identified as important in Sexton et al. (1990), so its effects on *A. laterale* movement are novel. The importance of some environmental variables varied between *A. platineum* and *A. jeffersonianum*. For instance, both species responded to minimum air temperature but in different ways. While I provide some possible explanations for these dissimilarities, there is also the possibility unisexual movements are more dependent on the species they parasitize. Comparing movement predictors between these species is also unique as most studies usually focus on only one species. I have also provided some variables to monitor before conducting prescribed burns to prevent harm to migrating salamanders. While precipitation deters burning, movements were still possible when there was no 24-hr. precipitation, so land managers should consider other factors such as minimum air temperature.

Effects of Day-of-year

The importance of day-of-year was the only commonality for the probability of adult and metamorph movements between the three *Ambystoma* species. The day-of-year variable was consistently informative for adults and confirmed the often-referenced lag period between male and female arrival at breeding wetlands (e.g., Semlitsch 1985, Petranka 1998). Of the *Ambystoma* species, *A. jeffersonianum* are the earliest winter/spring breeding species (Petranka 1998) and were the earliest of the three species to move. The *A. jeffersonianum* study population is also further south in the latitudinal cline. Hence, a more southerly latitude and early breeding tendencies result in winter breeding events over two months before *A. platineum* and *A. laterale*. While the day-of-year was informative, it can also surrogate other variables such as air temperature and precipitation.

Adult males of the three bisexual study species (*A. jeffersonianum*, *A. texanum*, and *A. laterale*) arrive at wetlands earlier than adult females, corroborated by previous studies (Douglas 1979; Semlitsch 1985; Sexton et al. 1990). Mate choice increases for males if they arrive at the wetland earlier (Semlitsch et al. 1993), while females limit environmental risks (i.e., early freezing and food availability) by ingressing later (Douglas 1979; Sexton et al. 1990).

Unisexual *A. platineum* moved after male *A. texanum,* but they initiated ingress slightly before female *A. texanum*. The disadvantages of arriving early (freeze risk) for *A. platineum* were not as costly as the competition for *A. texanum* spermatophores with female *A. texanum*. Thus other factors such as male *A. texanum* movement might influence *A. platineum* movement more. The competition for limited spermatophores from male *A. texanum* between female *A. texanum* and *A. platineum* may be the primary factor in their movement. The all-female unisexual species *A. platineum* parasitize spermatophores from other male ambystomatids and are endangered in Illinois (Phillips and Mui 2005). The Illinois population is unique because they use spermatophores from *A. texanum* and not from either parental species. Since *A. platineum* requires spermatophores from *A. texanum*, their breeding migration also occurs in late winter to early spring following a nocturnal rainfall (Petranka 1998; Phillips and Mui 2005). Migratory triggers such as mate choice and desiccation risk could also impact a species trying to parasitize a limited resource such as spermatophores (Shoop 1979). An asexual species might try to arrive at a wetland and breed earlier (even if fewer males are available) to capitalize on the lack of competition from the female species (Shoop 1979; Semlitsch 1985). My finding is relatively novel as few studies examine how female *A. platineum* migrations might time differently from females of the species they parasitize.

Effects of Twenty-four-hour Precipitation

Twenty-four-hour precipitation was an informative predictor for the probability and magnitude of adult and metamorph movements, albeit at different levels. The adult populations of *A. jeffersonianum, A. platineum,* and *A. texanum* were more likely to move as 24-hr.

precipitation increased, decreasing desiccation risks during terrestrial breeding migrations (Semlitsch 1985; Anderson and Semlitsch 2016). Desiccation is a significant risk, so the 24-hr. precipitation and the resulting moisture are important factors to consider when making long-distance movements (Cosentino et al. 2011). Some *A. jeffersonianum* have been found to disperse up to 1600 m from their natal wetland (Williams 1973), so more moisture in the environment would lessen the desiccation risk when moving that distance. The distance between terrestrial habitat and aquatic habitat increases as habitat connectivity decreases; thus, variables influencing moisture and desiccation risk such as 24-hr. precipitation may influence movement even more in the future.

My results are similar to other studies, having found 24-hr. precipitation to positively affect *Ambystoma* movements (Semlitsch 1985; Sexton et al. 1990). Precipitation is considered the most important factor for amphibian breeding migrations (Blanchard 1930; Packer 1960; Semlitsch and Anderson 2016), linking directly to desiccation risks and wetland hydroperiods are impacted by overnight precipitation (Sexton et al. 1990; Semlitsch and Anderson 2016). One study suggested overnight precipitation acts as a threshold variable (Sexton et al. 1990), meaning only a certain amount of precipitation is required to stimulate movements. Both *A. jeffersonianum* and *A. platineum* were predicted to move even with no 24-hr. precipitation, indicating it is not the only influential factor and may not be as important a threshold as previously assumed.

Effects of Minimum Air Temperature

Minimum air temperature was an informative variable for the probability of adult *A. jeffersonianum* movement and the magnitude of adult *A. jeffersonianum* and *A. platineum* movements. One difference between the two species, *A. jeffersonianum* and *A. platineum*, was minimum air temperature was informative for adult ingress probability of *A. jeffersonianum* but not for *A. platineum.* For *A. jeffersonianum*, lower movement probabilities were exhibited at lower temperatures and reflected the greater risk of movement to a frozen breeding wetland. The peak minimum temperatures for male and female *A. jeffersonianum* magnitudes likely reflect the temperature balance between the desiccation risk and avoiding freezing temperatures. It is also possible warming temperatures melt snowpack, increasing moisture in the environment. Whereas minimum temperature's role in *A. jeffersonianum* movement is not novel, it is interesting *A. platineum* was not as impacted by minimum temperature.

For *A. platineum*, minimum air temperature showed greater magnitude at the extremes. More *A. platineum* moving at the coldest and warmest minimum temperatures could be explained by size. Larger individuals have a lower risk of freezing and could move earlier, whereas smaller animals may move later due to their surface area:volume ratio (Rothermal and Luhring 2005). Freezing risk was likely a factor influencing movement. Early breeding movements place males at risk of freezing (Brodman 2005a); however, one way to reduce freezing risk is to move when the surface thaws. If males move early, their chances of finding a mate increase, although, as noted above, premature movements increase mortality risk due to freezing (Douglas 1979). Male ambystomatids have a lower metabolic rate than females, so emerging from their hibernacula earlier could reduce energy expenditures (Finkler 2006).

The risk of the wetland freezing and reduced mate choice are possible disadvantages of arriving earlier for females (Douglas 1979). Females also benefit from the later migration with reduced chances of egg mortality from wetland freezing and depositing eggs when water depth levels and food availability are greatest (Douglas 1979; Semlitsch 2008). The benefits of early egg deposition, allowing larvae to have more time to grow in the wetland, appear to be negated by the benefits of later arrival (Wilbur and Collins 1973; Douglas 1979).

Effects of Soil Inversion Strength

For *A. laterale*, the soil inversion was an informative predictor for both the probability of adult movement and the magnitude of adult movement; increased soil surface temperature corresponded to an increased magnitude of salamanders moving. The inversion of soil temperature in the overwintering terrestrial habitat has been hypothesized to influence the initial migration event of salamanders due to the shift in the frostline in the soil profile (Sexton et al. 1990). A strong soil inversion, surface warmer than deeper soil, suggests extreme weather like freezing is less likely to occur since the energy to change (or warm in this case) the soil temperature is substantial (Sexton et al. 1990). Warmer soil surface also causes snowmelt resulting in warmer topsoil and fills vernal wetlands.

However, only the probability of *A. laterale* movements was significantly influenced by the soil inversion strength. One possible explanation for the significance of soil inversion for *A. laterale* and not the other species is the soil types at the different sites. The Illinois *A. laterale* populations typically occupy habitats with sandy, loamy soils, whereas *A. jeffersonium*, *A. platineum*, and *A. texanum* occur in soils with higher organic content. These different soils would have different specific heat values (sand would have lower specific heat) and change at different rates (Marshak 2011). Soil temperature could be conflated with other environmental variables for organic soils since the air temperature would warm faster. However, the sandy soils could be more influential in causing salamanders to emerge because sand warms faster (Marshak 2011). Males also have a lower metabolic rate than females and maintain homeostasis during colder periods with less energy.

Effects of Wetland Depth

Wetland depth influenced *A. jeffersonianum* metamorph egress probability and the magnitude for *A. jeffersonianum* and *A. platineum* movements. For *A. jeffersonianum* metamorphs, wetland depth showed a negative relationship with egress probability and magnitude. The result suggests metamorphs would stay in the wetland as long as possible before the wetland completely dries. The wetland is considered a safer environment and leaving the wetland at a larger size lessens the risk of desiccation and predation (Rothermal and Semlitsch 2006). Once the wetland loses too much water, competition between larvae would likely drive metamorphs to egress (Rothermal and Semlitsch 2006). However, *A. platineum* showed the opposite trend for the magnitude of metamorph movement; more metamorphs emerged as the wetland depth increased. The cautious behavior suggests more metamorphs try to leave the wetland before the threat of desiccation (from no water in the wetland) becomes too great (Rothermal and Semlitsch 2006; Ryan 2007). Ranavirus is also a factor at the *A. platineum* wetlands and the likelihood of contracting the virus increases with exposure time in the wetland (Brunner et al. 2007).

Wetland depth determines how long a larval salamander can reside in the wetland before metamorphosis; metamorphs must disperse before the wetland dries, and the risk of desiccation becomes too great (Pechmann et al. 1989; Ryan 2007). Greater wetland depth means larvae can acquire more resources to grow and emerge larger, decreasing mortality risks from desiccation and predation (Rothermal and Semlitsch 2006). Additionally, the timing of adult breeding migrations can indirectly impact larval growth and initiate juvenile dispersal in late summer when females lay eggs in the wetland (Semlitsch 2008).

Conclusions

Day-of-year, 24-hr. precipitation, and minimum air temperature were important variables for all three species' (*A. jeffersonianum*, *A. platineum*, and *A. laterale)* movement, whereas soil inversion strength was only important for *A. laterale* and wetland depth influenced *A. jeffersonianum* and *A. platineum* metamorph egress. Conditions such as high accumulation of precipitation and relatively warm minimum air temperatures during February and March are likely to be associated with the breeding migrations (Fig. 2.5). For metamorphs, the months of May through August with high 24-hr. precipitation are conditions favorable to egress (Fig. 2.5). Day-of-year was a reliable variable for all three species, but its inclusion in most models suggests my study did not include enough relevant environmental variables. Many models were weighted highly in the set; however, some variation remained unexplained within all model sets across three species. One possible avenue to account for the unexplained variation would be to measure or calculate additional variables such as relative humidity, which accounts for moisture and the air's holding capacity for moisture and is related to temperature. Baldauf (1952) observed relative humidity was important to migrations of Spotted salamanders (*A. maculatum*). Relative humidity may be a simpler indicator of movement because it combines temperature and moisture. New environmental variables should be explored in further movement analyses.

Movement for *A. jeffersonianum*, *A. platineum*, and *A. laterale* was motivated by factors lessening the risks associated with traversing the terrestrial environment. The terrestrial environment has become risky for amphibians as the habitat connectivity decrease between the terrestrial and aquatic habitat. Todd et al. (2009) found ambystomatids (*A. maculatum* and *A. opacum*) still traversed clear-cut areas to reach breeding habitat despite the increased predation and desiccation risk. While clear-cutting the forest and altering the habitat connectivity did not eliminate movement, increasing stress and lower survival would be the trade-off for attempting migration to a hospitable area (Todd et al. 2009). Restoring habitat connectivity is one way to make the migration less risky for both adults and metamorphs, but mistiming restoration could introduce more anthropogenic harm (Brodman 2010).

One restoration technique to improve habitat connectivity and maintain upland habitat is prescribed burning (Clark 1989; Brodman 2010). Prescribed burns are used to eliminate invasive plant species and promote native plant growth (Abrams 1992). While burns primarily eradicate invasive flora species, burns can benefit the amphibian population by restoring habitat connectivity between terrestrial and aquatic habitats. Restoring native plant growth via burns maintains optimal habitat connectivity by producing more leaf litter for amphibians in the terrestrial environment, making the terrestrial environment less of a desiccation risk. However, an unintended consequence of prescribed burns is increased mortality of amphibians traversing terrestrial habitats during breeding season migrations (Schurbon and Fauth 2003; Brodman 2010).

Direct mortality by fire is rare for amphibians (Russell et al. 1999), but indirect effects on soil moisture, soil temperature, and leaf litter depth negatively affect amphibians in the terrestrial environment (Schurbon and Fauth 2003). A burned landscape changes the microhabitat by decreasing the moisture available at the surface by diminishing the leaf litter depth. Depleting leaf litter can stress the respiratory ability of amphibians due to dermal stress (Duellman and Trueb 1994; Ash 1997; Mosely et al. 2003). Bare ground cover can also increase with burns which can stress amphibians. One study found a decrease in the abundance of salamanders with an increase in bare ground cover from burns, likely a decrease in the leaf litter and an increase in soil temperature (Mosely et al. 2003). Burns can also eliminate resources such as coarse woody debris (Mosely et al. 2003). Coarse woody debris, which intense fires eliminate, provides a reliable constant moist refuge during dry periods for amphibians and a source of food (i.e., arthropods; Boddy 1983; Hanula 1993). While beneficial for vegetation structure and composition, burns can be detrimental to amphibians; therefore, timing prescribed burns when amphibians are not moving in the terrestrial environment is important for restoration. Given my results, in terms of planning prescribed burns, early winter burns would be the safest option for the three *Ambystoma* species to create unfavorable conditions in the terrestrial environment (Brodman 2010). Burning should also occur, so some sides of the wetland are untouched and retain their leaf litter layer, so at least one direction is less desiccation risk. Future recommendations for this study include how burning could affect desiccation rates of migrating salamanders.

Tables

Table 2.1. Table of all explanatory parameters used in movement and magnitude models and descriptions. Variance inflation factors (VIF) for continuous variables presented as average to incorporate VIF value for each species. The Sex_spp parameter is only used in the *A. platineum* models. The shaded variables were removed from analysis due to high VIF values.

Parameters	**VIF average**	**Description**
PRCP	1.22	Precipitation accumulation (in mm) on day (24hrs) before survey
TMIN	1.11	Minimum temperature (°C) on day of survey
TMIN_24	>19	Minimum temperature (°C) on before day of survey
TMIN_3day	>39	Minimum temperature (°C) 3 day mean
Inv_Strength	1.18	Soil Inversion Strength (°C) at each site and is the 30cm depth soil temperature subtracted from the surface soil temperature
Gauge_pond	1.4	Proportion of water depth at each wetland relative to year
Year	NA	Year of observation
doy	NA	Day-of-year when survey conducted
Sex and Sex_spp	NA	Sex of individual; Sex of specified species (for *A. platineum* models)

Table 2.2. The candidate model sets used for adult ingress timing and magnitude for each species (*A. jeffersonianum*, *A. platineum, A. platineum*). *Post-hoc* models (shaded) were included for timing model sets. Analyses show which models were used for timing, magnitude, or both sets of models. Each model is sex-specific. The sex by species variable was used in place of the Sex variable for *A. platineum*. The optimizer used for both *A. jeffersonianum* and *A. platineum* was "bobyqa." Year is the random variable used in *A. jeffersonianum* and *A. platineum* models.

Candidate Models for Adults	Candidate Model Formulas	Analyses	Hypotheses
Null model	(1|Year)	Both	*a priori*
Global model	Sex:poly(doy,2) + Sex:poly(TMIN,2) + Sex:PRCP + Sex:Inv_Strength	Both	*a priori*
Precipitation model	Sex:PRCP	Both	*a priori*
Temperature model	Sex:poly(TMIN,2)	Both	*a priori*
Soil Inversion Strength model	Sex:Inv_Strength	Both	*a priori*
Day-of-year model	Sex:poly(doy,2)	Timing	*a priori*
Day-of-year and Min. Temperature model	Sex:poly(doy,2) + Sex: poly(TMIN,2)	Timing	*a priori*
Day-of-year and Precipitation model	Sex:poly(doy,2) + Sex:PRCP	Timing	*a priori*
Min. Temperature and Soil Inversion Strength model	Sex:poly(TMIN,2) + Sex:Inv_Strength	Magnitude	*a priori*
Precipitation and Soil Inversion Strength model	Sex:PRCP + Sex:Inv_Strength	Magnitude	*a priori*
Day-of-year, Precipitation, Min Temperature model	Sex:poly(doy,2) + Sex:PRCP + Sex:poly(TMIN,2)	Timing	*post-hoc* for *A. jeffersonianum* & *A. platineum*
Day-of-year and Soil Inversion Strength model	Sex:poly(doy,2) + Sex:Inv_Strength	Timing	*post-hoc* for *A. laterale*

Table 2.3. The candidate model sets used for metamorph ingress timing and magnitude for each species (*A. jeffersonianum*, *A. platineum, A. platineum*). One *post-hoc* model (shaded) was included for timing model sets. The optimizer used for *A. platineum* was "bobyqa." Year is the random variable used for *A. jeffersonianum*, *A. platineum* models**.**

Candidate Models for Metamorphs	Candidate Model Formulas	Analyse	Hypotheses
Null model	(1|Year)	Both	*a priori*
Global model	Global	Both	*a priori*
Precipitation model	PRCP	Both	*a priori*
Minimum Air Temperature model	poly(TMIN,2)	Both	*a priori*
Wetland Depth model	Gauge_pond	Both	*a priori*
Day-of-year model	poly(doy,2)	Timing	*a priori*
Day-of-year and Wetland Depth model	poly(doy,2) + Gauge_pond	Timing	*a priori*
Min. Temperature and Wetland Depth model	poly(TMIN,2) + Gauge_pond	Both	*a priori*
Precipitation and Wetland Depth model	PRCP + Gauge_pond	Both	*a priori*
Min. Temperature and Precipitation model	poly(TMIN,2) + PRCP	Both	*a priori*
Wetland Depth, Day-of-year, and Precipitation model	Gauge_pond + poly(doy,2) + PRCP	Timing	post-hoc for *A. jeffersonianum*
Precipitation and Day-of-year model	PRCP + poly(doy,2)	Timing	*post-hoc* for *A. platineum* & *A. laterale*

Table 2.4. Candidate models for adult emergence probability for each species ranked by AIC$_C$. Pseudo-R-squared marginal (r^2_m), conditional (r^2_c), and R-squared ($\mathbf{r^2}$) values were calculated to assess fit of each model. The rank is how each model ranked with the complete model set (nine models) for each species. The weights (w_i) of the model within each model set are shown. The top-ranked model, global model, null model, and any models within 2 ΔAIC$_C$ are included. The data used in this table were collected in Clark Co., IL, USA, from 2018 to 2020.

Model Names							
Ambystoma jeffersonianum	**Rank**	K	**-2LL**	**ΔAIC$_C$**	w_i	r^2_m	r^2_c
Day-of-year, Precipitation, Min. Temperature model	1	12	-123.61	0.00	0.95	0.79	0.80
Global	2	15	-123.27	5.87	0.05	0.81	0.82
Null	9	2	-177.47	86.76	0.00	--	--
A. platineum & A. texanum	**Rank**	K	**-2LL**	**ΔAIC$_C$**	w_i	r^2_m	r^2_c
Day-of-year, Precipitation, Min. Temperature by Sex model	1	17	-313.64	0.00	0.98	0.65	0.65
Global	3	22	-313.38	9.98	0.01	0.65	0.65
Null	9	2	-441.05	224.10	0.00	---	--
A. laterale	**Rank**	K	**-2LL**	**ΔAIC$_C$**	w_i	r^2	
Day-of-year and Soil Inversion Strength model	1	7	-19.73	0.00	0.57	0.56	
Day-of-year model	2	5	-23.14	1.42	0.28	0.44	
Null	7	1	-32.48	10.72	0.00	---	
Global	9	16	-15.39	24.57	0.00	0.69	

Table 2.5. Parameters estimate table for top ranking candidate models for adult emergence probability for each species. Confidence Intervals (85%; C.I.s) were calculated for each parameter. Significant 85% C.I.s (do not bound zero) are starred. The data used in this table were collected in Clark Co., Vermilion Co., and Lake Co. IL, USA from 2018 to 2020.

Parameters			
Ambystoma jeffersonianum	**Estimate**	**Lower CI**	**Upper CI**
Female Day-of-year 1st poly	-367.36	-507.14	-227.57***
Male Day-of-year 1st poly	-298.81	-445.16	-152.45***
Female Day-of-year 2nd poly	-138.78	-194.87	-82.70***
Male Day-of-year 2nd poly	-84.72	-139.40	-30.05***
Precipitation, Female	0.89	0.41	1.37***
Precipitation, Male	0.93	0.39	1.47***
Min. Temperature Female 1st poly	-20.10	-82.48	42.27
Min. Temperature Male 1st poly	-69.35	-158.97	20.28
Min. Temperature Female 2nd poly	-29.58	-59.09	-0.06***
Min. Temperature Male 2nd poly	-42.52	-80.53	-4.52***
A. platineum & A. texanum	**Estimate**	**Lower CI**	**Upper CI**
Female *platineum* Day-of-year 1st poly	-349.37	-418.31	-280.42***
Female *texanum* Day-of-year 1st poly	-318.57	-393.85	-243.28***
Male *texanum* Day-of-year 1st poly	-288.30	-359.56	-217.03***
Female *platineum* Day-of-year 2nd poly	-161.09	-195.99	-126.18***
Female *texanum* Day-of-year 2nd poly	-161.00	-204.37	-117.63***
Male *texanum* Day-of-year 2nd poly	-118.92	-153.86	-83.98***
Female *platineum* Precipitation	0.41	0.05	0.77***
Female *texanum* Precipitation	0.45	0.10	0.80***
Male *texanum* Precipitation	0.40	0.05	0.76***
Female *platineum* Min. Temperature 1st poly	6.81	-41.32	54.93
Female *texanum* Min. Temperature 1st poly	28.55	-15.73	72.82
Male *texanum* Min. Temperature 1st poly	7.80	-35.76	51.36
Female *platineum* Min. Temperature 2nd poly	-25.40	-51.65	0.85
Female *texanum* Min. Temperature 2nd poly	-5.44	-31.64	20.76
Male *texanum* Min. Temperature 2nd poly	-10.13	-36.75	16.49
A. laterale	**Estimate**	**Lower CI**	**Upper CI**
Day-of-year Female 1st poly	-343.41	-752.94	-55.59***
Day-of-year Male 1st poly	-319.65	-721.64	-36.12***
Day-of-year Female 2nd poly	-77.60	-176.16	-4.31***
Day-of-year Male 2nd poly	-57.95	-148.35	9.19
Female Soil Inversion Strength	0.72	-0.30	2.04
Male Soil Inversion Strength	1.44	0.15	3.44***

Table 2.6. Candidate models for metamorph egress probability for each species ranked by AIC$_C$. Pseudo-R-squared marginal (r^2_m), conditional (r^2_c), and R-squared (R^2) values were calculated to assess fit of each model. The rank is how each model ranked with the complete model set (eleven models) for each species. The weights (w_i) of the model within each model set are shown. The top-ranked model, global model, null model, and any models within 2 ΔAIC$_C$ are included. The data used in this table were collected in Clark Co., Vermilion Co., and Lake Co. IL, USA from 2018 to 2020.

Model Names							
Ambystoma jeffersonianum	**Rank**	***K***	**-2LL**	**ΔAIC**	w_i	r^2_m	r^2_c
Wetland Depth, Day-of-year, and Precipitation model	1	6	-96.31	0.00	0.59	0.5	0.55
Global	2	8	-94.84	1.38	0.30	0.5	0.55
Null	8	2	-135.12	69.25	0.00	---	---
A. platineum	**Rank**	***K***	**-2LL**	**ΔAIC**	w_i	r^2_m	r^2_c
Precipitation and Day-of-year model	1	5	-136.04	0.00	0.42	0.3	0.38
Day-of-year model	2	4	-137.24	0.34	0.35	0.3	0.38
Wetland Depth and Day-of-year model	3	5	-136.8	1.52	0.20	0.3	0.36
Global	4	8	-135.37	4.96	0.04	0.3	0.36
Null	8	2	-163.58	48.91	0.00	---	---
A. laterale	**Rank**	***K***	**-2LL**	**ΔAIC**	w_i	r^2	
Day-of-year model	1	3	-19.28	0.00	0.46	0.2	
Null	4	1	-23.03	2.84	0.11	---	
Global	9	8	-16.18	8.76	0.01	0.4	

Table 2.7. Parameters estimate table for top ranking candidate models for metamorph emergence probability for each species. Confidence Intervals (85%; C.I.s) were calculated for each parameter. Significant 85% C.I.s (do not bound zero) are starred. The data used in this table were collected in Clark Co., Vermilion Co., and Lake Co. IL, USA from 2018 to 2020.

Parameters			
Ambystoma jeffersonianum	**Estimate**	**Lower CI**	**Upper CI**
Wetland Depth	-0.70	-1.17	-0.24***
Day-of-year 1st poly	428.91	236.97	620.85***
Day-of-year 2nd poly	-134.65	-201.09	-68.21***
Precipitation	0.50	0.05	0.94***
A. platineum	**Estimate**	**Lower CI**	**Upper CI**
Day-of-year 1st poly	707.89	392.81	1022.97***
Day-of-year 2nd poly	-311.96	-446.21	-177.70***
Precipitation	-0.31	-0.77	0.15
A. laterale	**Estimate**	**Lower CI**	**Upper CI**
Day-of-year 1st poly	-38.09	-309.40	271.76
Day-of-year 2nd poly	-0.59	-74.32	58.74

Table 2.8. Candidate models for adult magnitude for each species ranked by QAIC$_c$ and AIC$_C$. QAIC$_c$ used when overdispersion present. Pseudo-R-squared marginal (r^2_m), conditional (r^2_c), and R-squared (R^2) values were calculated to assess fit of each model. The rank is how each model ranked with the complete model set (seven models) for each species. The weights (w_i) of the model within each model set are shown. Included are the top-ranked model, global model, null model, and any models within 2 ΔAIC$_C$ or 2 ΔQAIC$_C$ are included. The data used in this table were collected in Clark Co., Vermilion Co., and Lake Co. IL, USA from 2018 to 2020.

Model Names							
Ambystoma jeffersonianum	**Rank**	***K***	**-2LL**	**ΔQAIC$_C$**	w_i	r^2_m	r^2_c
Min. Temperature model	1	6	-332.82	0.00	0.63	0.46	0.68
Min Temp. and Soil Inversion Strength model	2	8	-326.93	1.93	0.24	0.47	0.72
Global	4	10	-326.85	5.91	0.03	0.47	0.72
Null	5	2	-378.34	7.97	0.01	---	---
A. platineum & A. texanum	**Rank**	***K***	**-2LL**	**ΔQAIC$_C$**	w_i	r^2_m	r^2_c
Global	1	14	-1055.41	0.00	0.49	0.46	0.79
Min Temp. and Soil Inversion Strength model	2	11	-1086.41	0.89	0.31	0.45	0.77
Null	7	2	-1244.34	18.00	0.00	---	---
A. laterale	**Rank**	***K***	**-2LL**	**ΔAIC$_C$**	w_i	r^2	
Soil Inversion Strength model	1	4	-67.83	0.00	0.87	0.56	
Null	2	2	-73.65	6.18	0.04	---	
Global	7	12	-65.26	34.87	0.00	0.71	

Table 2.9. Parameters estimate table of top-ranking candidate models for adult magnitude for each species. Confidence Intervals (85%; C.I.s) were calculated for each parameter. Significant 85% C.I.s (do not bound zero) are starred. The data used in this table were collected in Clark Co., Vermilion Co., and Lake Co. IL, USA from 2018 to 2020.

Parameters			
Ambystoma jeffersonianum	**Estimate**	**Lower CI**	**Upper CI**
Min. Temperature Female 1st poly	-97.61	-125.47	-69.76***
Min. Temperature Male 1st poly	-105.81	-133.59	-78.04***
Min. Temperature Female 2nd poly	-47.19	-60.23	-34.15***
Min. Temperature Male 2nd poly	-47.81	-59.74	-35.87***
A. platineum & A. texanum	**Estimate**	**Lower CI**	**Upper CI**
Female *A. platineum* Min. Temperature 1st poly	18.20	8.05	28.35***
Female *A. texanum* Min. Temperature 1st poly	65.23	50.80	79.66***
Male *A. texanum* Min. Temperature 1st poly	76.77	59.47	94.07***
Female *A. platineum* Min. Temperature 2nd poly	19.82	14.87	24.76***
Female *A. texanum* Min. Temperature 2nd poly	15.38	7.83	22.92***
Male *A. texanum* Min. Temperature 2nd poly	33.60	22.66	44.55***
Female *A. platineum* Precipitation	0.28	0.21	0.35***
Female *A. texanum* Precipitation	-0.13	-0.30	0.03
Male *A. texanum* Precipitation	0.02	-0.19	0.23
Female *A. platineum* Soil Inversion Strength	0.22	0.09	0.35***
Female *A. texanum* Soil Inversion Strength	-0.56	-0.79	-0.34***
Male *A. texanum* Soil Inversion Strength	-0.68	-0.99	-0.37***
A. laterale	**Estimate**	**Lower CI**	**Upper CI**
Female Soil Inversion Strength	0.5144	0.1479	0.9126***
Male Soil Inversion Strength	0.7614	0.2487	1.3623***

Table 2.10. Candidate models for metamorph magnitude for each species ranked by QAIC$_c$ and AIC$_C$. QAIC$_c$ used when overdispersion present. Pseudo-R-squared marginal (r^2_m), conditional (r^2_c), and R-squared (R^2) values were calculated to assess fit of each model. The rank is how each model ranked with the complete model set (eight models) for each species. The weights (w_i) of the model within each model set are shown. Included are the top-ranked, global, null, and any models within 2 ΔAIC$_c$ or 2 ΔQAIC$_c$ are included. The data used in this table were collected in Clark Co., Vermilion Co., and Lake Co. IL, USA from 2018 to 2020.

Model Names							
Ambystoma jeffersonianum	**Rank**	***K***	**-2LL**	**ΔQAIC$_C$**	w_i	r^2_m	r^2_c
Precipitation and Wetland Depth model	1	4	-240.84	0.00	0.43	0.13	0.55
Wetland Depth model	2	3	-243.72	0.44	0.35	0.09	0.56
Global	3	6	-239.36	2.75	0.11	0.13	0.56
Null	5	2	-252.69	6.03	0.02	0.00	0.56
A. platineum	**Rank**	***K***	**-2LL**	**ΔQAIC$_C$**	w_i	r^2_m	r^2_c
Precipitation and Wetland Depth model	1	4	-643.07	0.00	0.39	0.15	0.86
Precipitation model	2	3	-665.81	1.15	0.22	0.06	0.82
Global	3	6	-630.53	2.26	0.13	0.19	0.87
Null	5	2	-696.07	3.35	0.07	0.06	0.82
A. laterale	**Rank**	***K***	**-2LL**	**ΔAIC$_C$**	w_i	r^2	
Min. Temperature model	1	3	-31.49	0.00	0.64	0.87	
Min. Temperature and Wetland Depth model	2	4	-30.98	2.16	0.22	0.89	
Global	4	6	-30.95	9.89	0.00	0.89	
Null	8	1	-44.8	21.35	0.00	0.00	

Table 2.11. Parameters estimate table of top-ranking candidate models for metamorph magnitude for each species. Confidence Intervals (85%: C.I.s) were calculated for each parameter. Significant 85% C.I.s (do not bound zero) are starred. The data used in this table were collected in Clark Co., Vermilion Co., and Lake Co. IL, USA from 2018 to 2020.

Parameters			
Ambystoma jeffersonianum	**Estimate**	**Lower CI**	**Upper CI**
Precipitation	0.1141	0.0241	0.2040***
Wetland Depth	-0.2886	-0.4079	-0.1694***
A. platineum	**Estimate**	**Lower CI**	**Upper CI**
Precipitation	0.4388	0.3408	0.5367***
Wetland Depth	0.3335	0.2368	0.4301***
A. laterale	**Estimate**	**Lower CI**	**Upper CI**
Min. Temperature 1st poly	-41.44	-95.98	17.43
Min. Temperature 2nd poly	21.77	1.24	41.41***

Figures

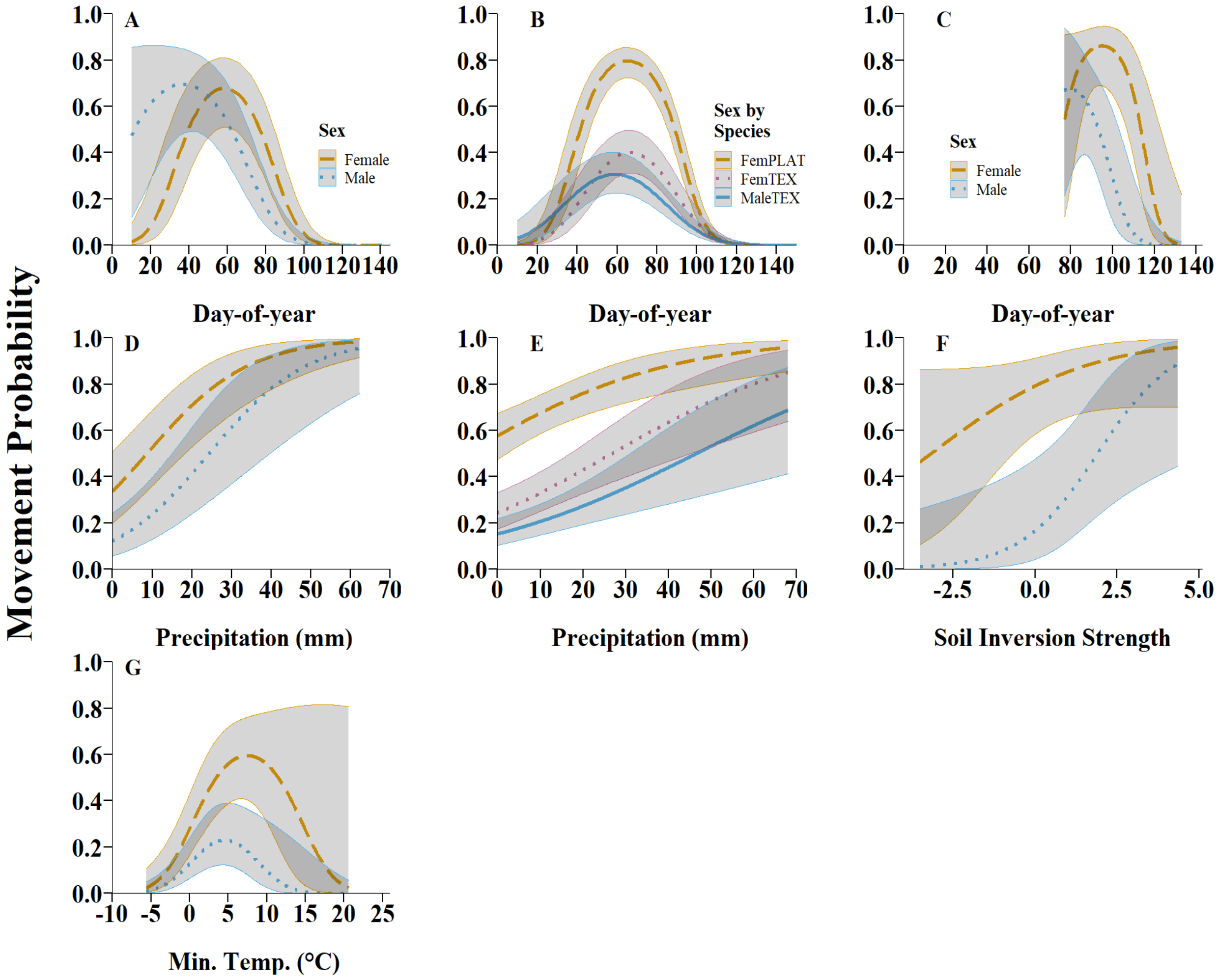

Figure 2.1. Adult ingress movement probabilities based on significant parameters from top candidate model for each species (*Ambystoma jeffersonianum* – 2.1a,d,g, *A. platineum* – 2.1b,e, and *A. laterale* – 2.1c,f). The brown dashed line represents female predicted values, and the blue dotted line represents male show predicted estimates, and the shaded region represents the 85% prediction intervals. The brown dashed lines for female *A. platineum* (FemPLAT), purple, dotted lines for female *A. texanum* (FemTEX), and blue, solid lines for male *A. texanum* (MaleTEX) show estimates as well. The data used in this figure were collected in Clark Co., Vermilion Co., and Lake Co. IL, USA from 2018 to 2020.

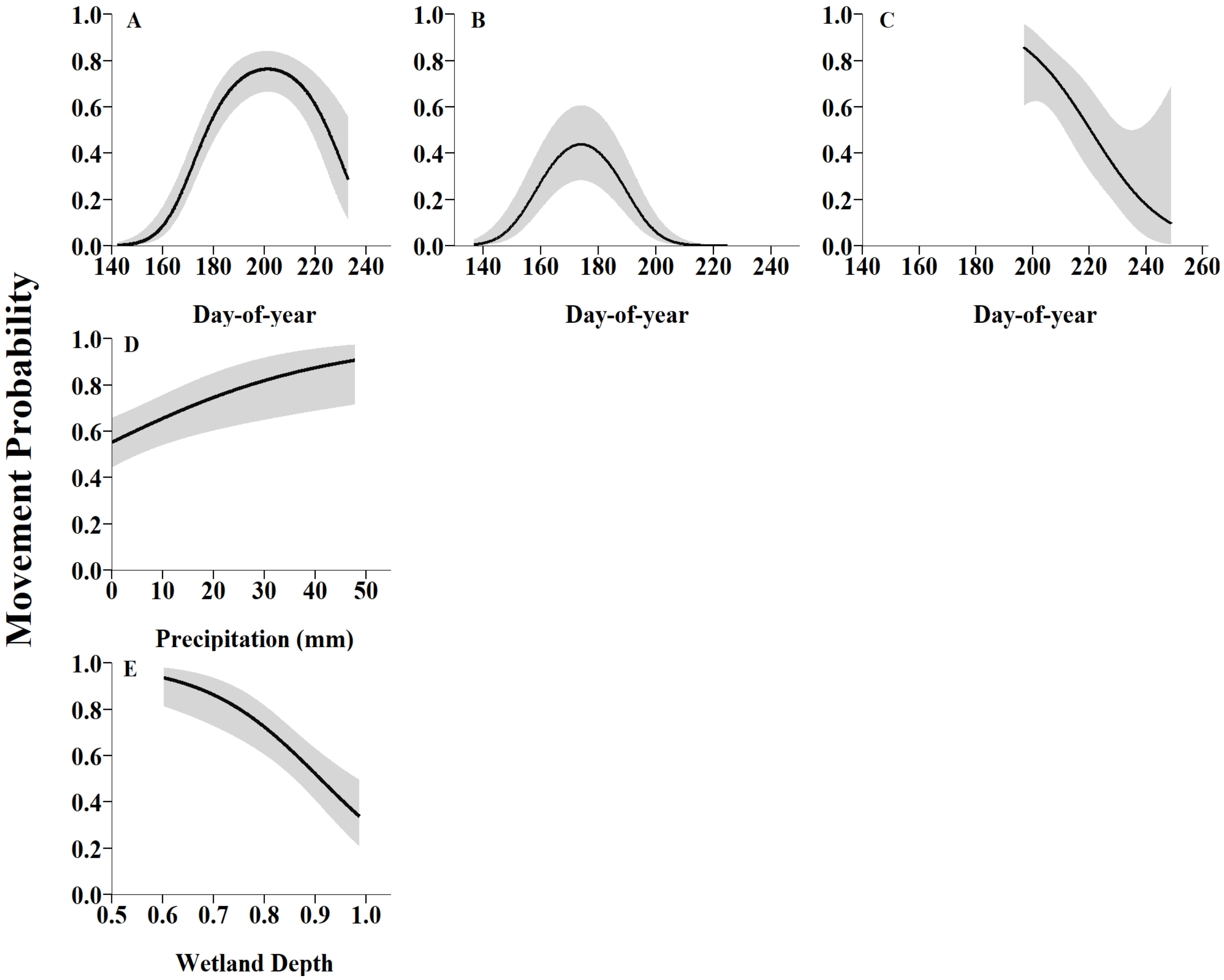

Figure 2.2. Metamorph movement probabilities based on significant parameters from top candidate model for each species (*Ambystoma. jeffersonianum* – 2.2 a,d,e, *A. platineum* –2.2b, and *A. laterale* – 2.2c). The solid lines show the estimates, and the shaded region represents the 85% prediction intervals. The data used in this figure were collected in Clark Co., Vermilion Co., and Lake Co. IL, USA from 2018 to 2020.

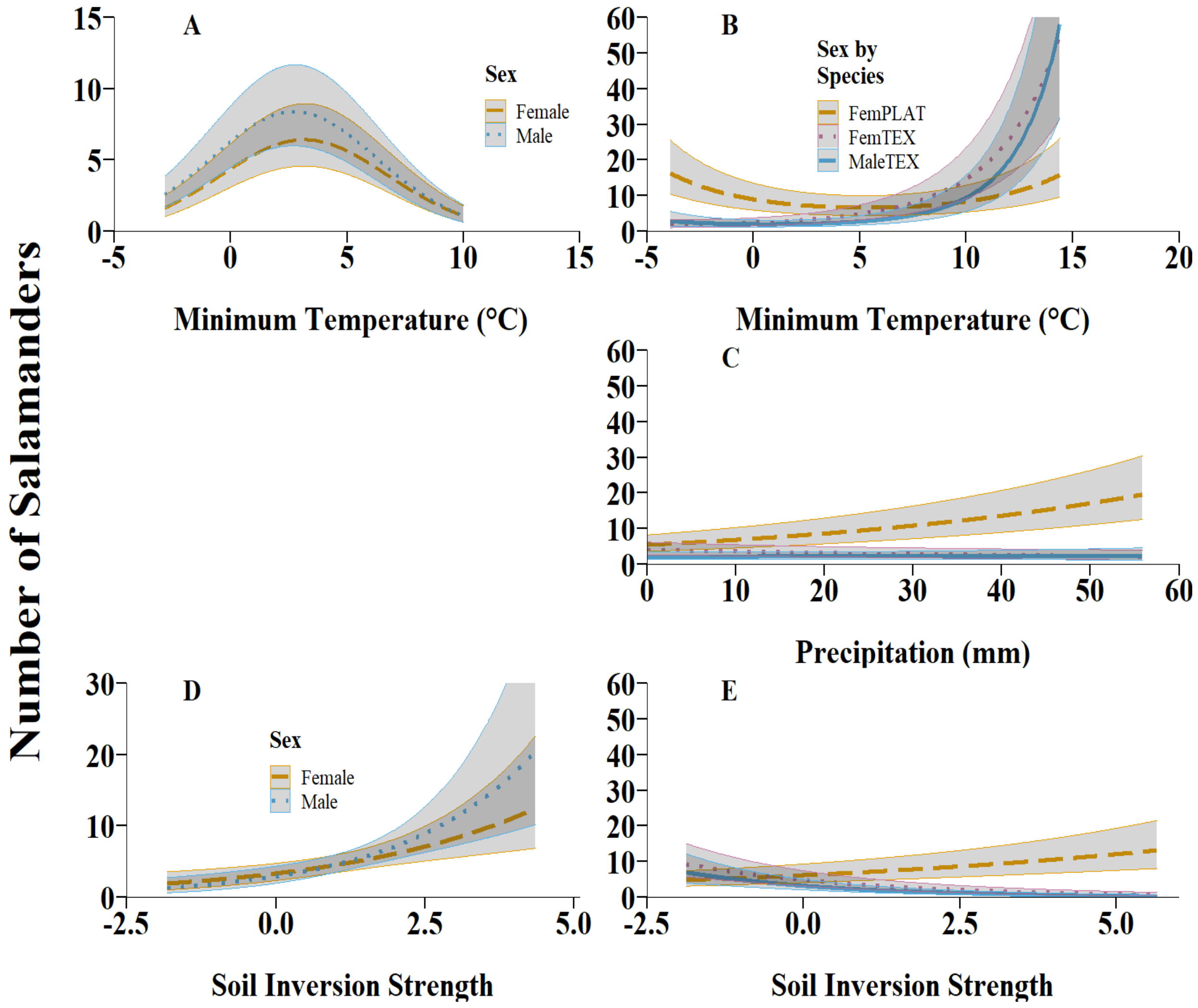

Figure 2.3. Adult magnitude based on the significant parameter from the top candidate model for each species (*Ambystoma jeffersonianum* 2.3a, *A. platineum* 2.3b,c,e, and *A. laterale* 2.3d). The brown dashed line represents female predicted values, the blue dotted line represents male predicted estimates, and the shaded region represents the 85% prediction intervals. The brown dashed lines for female *A. platineum* (FemPLAT), purple, dotted lines for female *A. texanum* (FemTEX), and blue, solid lines for male *A. texanum* (MaleTEX) show estimates as well. The data used in this figure were collected in Clark Co., Vermilion Co., and Lake Co. IL, USA from 2018 to 2020.

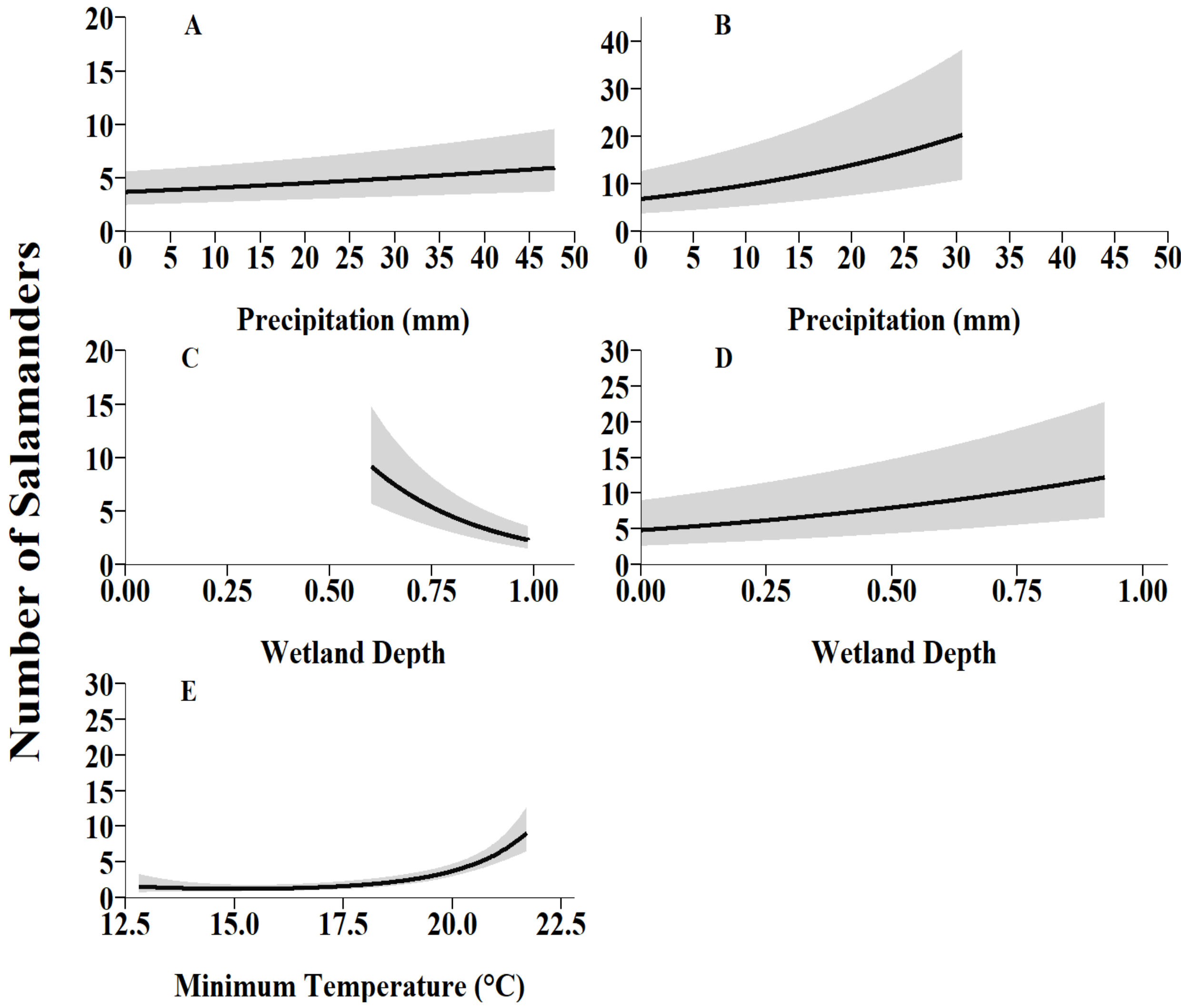

Figure 2.4. Metamorph magnitude based on significant parameters from top candidate model for each species (*Ambystoma jeffersonianum* - 2.4a,c, *A. platineum* – 2.4b,d, *A. laterale* – *2*.4e). The y-axis is the number of salamanders captured. The solid lines show the estimates, and the shaded region represents the 85% prediction intervals. The data used in this figure were collected in Clark Co., Vermilion Co., and Lake Co. IL, USA from 2018 to 2020.

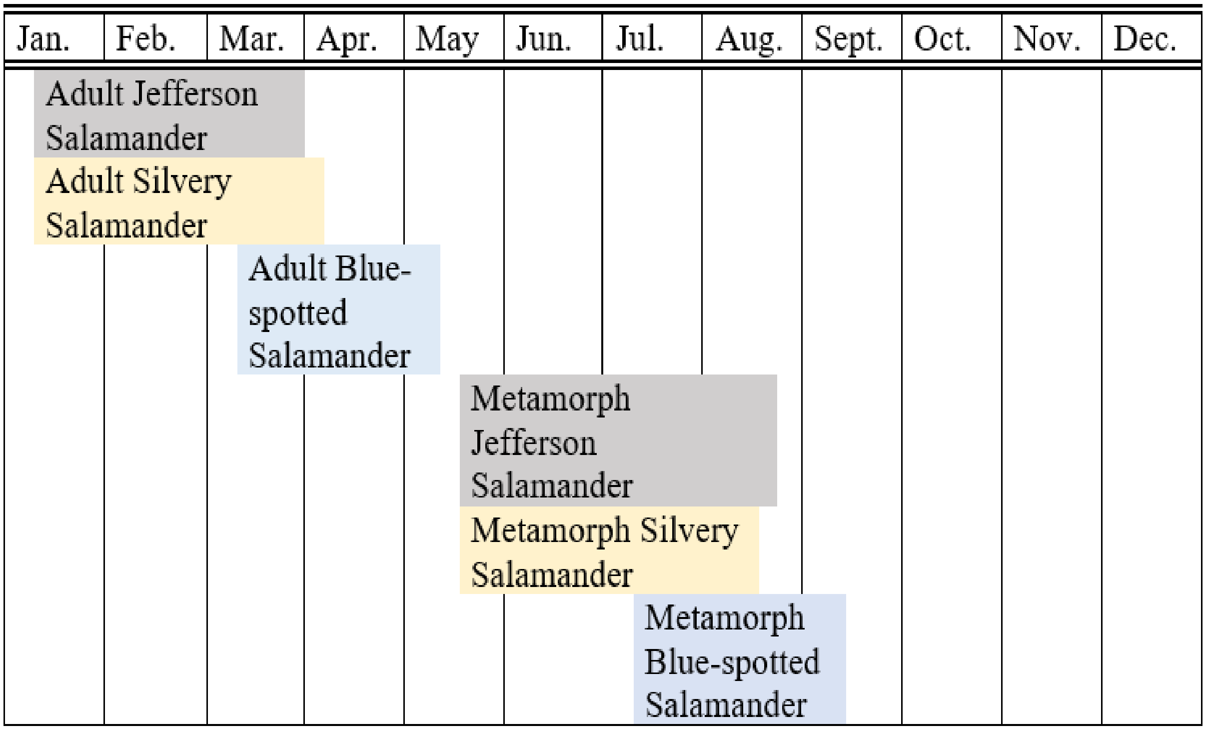

Figure 2.5. Phenology calendar for adult ingress and metamorph egress for the three target species: Jefferson salamander (*Ambystoma jeffersonianum*), Silvery Salamander (*A. platineum*), and Blue-spotted Salamander (*A. laterale*).

CHAPTER 3: FERTILITY OF JEFFERSON SALAMANDER, *AMBYSTOMA JEFFERSONIANUM*

Introduction

Understanding the extent of amphibian declines, causes, and possible solutions requires demographic data to determine population dynamics (Schmidt 2004). Collecting demographic parameters for amphibian populations is critical to assess populations adequately; however, few monitoring studies exist, and fewer include individual census data (Semlitsch et al. 1988; Pechmann et al. 1991; Rothermel and Semlitsch 2006; Anderson et al. 2015). As a result, estimates of demographic vital rates such as fertility and stage-based survival for many amphibian species are scarce and little replication exists (Stenseth & Mysterud 2002; Mills 2006; Rothermel and Semlitsch, 2006). Replication is important for obtaining precise estimates and verifiable results (Open Science Collaboration, 2015). Additionally, variation can exist in demography estimates within species and over time, and it is important to capture both (Mills 2006).

Reproductive estimates are valuable because they can help assess population health (and the intrinsic rate of growth; Semlitsch 1987). Fertility is a crucial variable in determining recruitment and is often defined as the number of offspring produced per individual over time (Mills 2006). For wetland-breeding amphibians, fertility is determined during an annual breeding period (breeding effort) and the number of metamorphs leaving the wetland (population recruitment). Thus, recruitment is a function of how many eggs are laid in the breeding wetland, embryonic/egg survival, and larval survival (Mills 2006). Counting the number of individual gravid females entering and the number of metamorphs exiting the wetland after larval development requires less extrapolation than trying to calculate egg and larval survival.

However, demographic variables are subject to environmental stochasticity. For example, fertility estimates in a population of mole salamanders ranged from 0.16 to 3.38 (Semlitsch and Anderson 2016). The difference in reproductive output stemmed from environmental stochasticity (i.e., drought) in different years (Semlitsch and Anderson 2016).

Environmental stochasticity is a factor that can introduce variation when monitoring demographic variables. The potential impacts of environmental stochasticity are exacerbated in more vulnerable habitats; seasonal and semi-permanent wetlands are highly vulnerable habitats and are declining worldwide. Despite the importance of wetlands for various ecosystem services (Mitsch et al. 2000), more than 53% of U.S. wetland area was lost between 1780 and 1980 (Dahl 1990; Dahl 2011). The Midwestern U.S. has experienced extreme wetland loss; for example, Illinois has lost more than 90% of original wetlands to agriculture and other anthropogenic activities (Suloway and Hubbel 1994). “No net loss" is a somewhat recent national policy mandating created or restored wetlands must be constructed to replace any lost from development and is an attempt to reverse the drastic wetland loss (Brown and Lant 1999; Mack 2007). Despite reclaiming and protecting some habitats, amphibian populations in protected landscapes are still declining (Adams et al. 2013), questioning the efficacy of current practices protecting existing habitats (Collins and Stofer 2003). Creating new, lower-quality wetlands could be less effective than restoring a pre-existing wetland in terms of conservation. These lower-quality wetlands could act as sinks, further threatening populations (Semlitsch and Bodie 1998). Limited vagility and high site fidelity for ambystomatids (de Maynadier and Hunter 1995; Rittenhouse and Semlitsch 2006; Gamble et al. 2007) could impact the effectiveness of restoration, so analyzing restoration techniques (creating new vs. restoring pre-existing) and how they translate to demographic variables such as fertility could be informative for conservation purposes.

Previous demographic work has been conducted on *Ambystoma jeffersonianum* in Illinois at my study site, but the research occurred before wetland restoration. The two-year (2004–2005) demographic study at Lincoln Trail State Recreation Area (LTRSA) used a stage-based matrix model to predict population persistence at one wetland (Mullin and Klueh 2009). The model predicted the population would be extirpated by 2010 without conservation intervention (Mullin and Klueh 2009), yet the salamander population persisted. Restoration efforts at LTRSA in 2010, including berm restoration and wetland creation, could have positively impacted the population's trajectory. Given the level of restoration efforts and the population's persistence well beyond predicted extirpation, it was essential to conduct follow-up monitoring to determine if the trajectory changed or demographic vital rates had improved.

My study seeks to answer four questions relating to the demographics of the isolated *A. jeffersonianum* population: 1) What is the average number of eggs produced by gravid females?; 2) Is there a size-based fertility advantage?; 3) What are egg and larval survival estimates as well as fertility estimates for LTSRA populations?; 4) How do these demographic vital rates compare to previous studies (before and after restoration)? My research provides valuable parameter estimates in population persistence analyses for conserving and managing a state-threatened species and compares a site pre- and post-restoration.

Methods and Materials

Study Site

From 2018–2020, I surveyed a natural wetland and a smaller, created wetland at Lincoln Trail State Recreation Area (LTSRA; see Chapter 1 for site description). The natural wetland at

LTSRA was also the wetland surveyed by Mullin and Klueh in 2004–2005 (2009). Based on 2018–2020 data, the adult breeding season spanned January–April, and juvenile emigration occurred from May–September; however, in 2020, COVID-19 restrictions prevented breeding surveys from late March through April.

Both wetlands are within 30 m of a road on the park's western side, situated in oak-hickory forest (Figure 3.1). LTSRA has the only protected populations of *A. jeffersonianum* in Illinois, and immigration between wetlands (both natural and created) within the park is limited (Crawford et al., 2016). The restoration included rebuilding a berm at the natural wetland and creating smaller wetlands, including one I surveyed. The berm helped increase the wetland's hydroperiod to allow the completion of different life stages of *A. jeffersonianum*, and the newly created wetlands added additional breeding habitat for amphibians.

Data Collection

I installed a drift fence constructed of aluminum flashing and 19 L buckets (pit-fall traps) to capture all adult and metamorphic salamanders moving to and from the wetlands. The drift fence completely encircled the wetlands (ranging 5–10 m from wetland edge), and pitfall traps were buried flush with the ground every 5 m along both sides of the fences. Fences were high enough to prevent salamander trespass (~50 cm) and had a portion buried to deter underground trespass (Fig. 3.1B). I surveyed at least once every 48 hr. when pitfall traps were open with lids removed to capture moving salamanders (January–April for adults and May–September for metamorphs). For each salamander captured, I measured snout-vent-length (SVL, in mm, to one decimal place), total length (TL, in mm, to one decimal place), and mass (in grams, to the tenth decimal place), recorded sex for adults only, and marked them either using Passive Integrated Transponders (PIT) tags (adults) or alpha-numeric tags (juveniles). I determined sex of adults using secondary sexual characteristics; during the breeding season, males have swollen cloaca in which females lack. Once field processed, I released salamanders on the opposite side of the fence or placed them in a breeding cage for reproductive work (described below).

Breeding cages were modified minnow traps (Promar collapsible trap TR-501) with openings sealed using zip ties to prevent adults from escaping (Fig. 3.1C). Fifty-three cages were used for the egg counts between 2018–2020, but only five were used for the hatching success estimates because only five cages were surveyed for sufficient time to allow for egg hatching. The other 48 cages were released before I could confirm the female had laid all their eggs. Cages were subjected to natural environmental and hydrological processes and were 3/4ths submerged to allow adults to reach the surface for oxygen yet provided sufficient area for aquatic egg deposition; I placed sticks in the cages as structure for egg deposition. Thus, cages were constructed to prevent predation while allowing eggs and larvae exposure to natural aquatic chemical and visual cues. I measured the mass and SVL of females before and after being caged and checked cages daily for eggs and adult escapees. Each cage contained one female and two male salamanders to ensure enough spermatophores were available for fertilization (Harris and Lucas 2002; Gopurenko et al. 2006). Salamanders did not have mate choice, and the forced pairings could have affected the number of eggs laid, spermatophores laid, or both. As there is limited courtship and sexual dimorphism between ambystomatids, mate choice ostensibly does not drive mating success, but female ambystomatids are known to frequently mate with multiple male partners (Gopurenko et al. 2006). The number of spermatophores laid by male ambystomatids can also vary based on the number of males in the wetland, the density of spermatophores, or the overall mate competition in the wetland (Harris and Lucas 2002; Gopurenko et al. 2006).

I made final egg counts once the laying of egg masses ceased, usually between 8 and 10 days after the first egg mass was laid, then measured and released adults. Every other day, I checked egg development and monitored egg survival and hatching success/failure (Fig 3.1D) by counting how many eggs were viable (alive) and non-viable (eggs appeared damaged or lysed; Fig. 3.2). Larvae were counted once hatched, but the possibility of trespass (larvae leaving the cage or other larvae entering) and predation was high. Only five of the 53 cages were maintained long enough to calculate egg survival. Similar studies used either impermeable aquaria (Mullin and Klueh 2009) or monitored egg masses *in vivo* (Williams 1973). My cage method had the advantage of pairing maternal metrics to the reproductive metrics (egg masses, egg viability, larvae) in a primarily natural but controlled setting.

Statistical Analysis

I calculated the descriptive statistics of mean, sample size, standard error, and minimum and maximum value for clutch size and number of egg masses to provide a baseline for the population (combined all three years of data 2018–2020). To connect maternal metrics to the number of eggs deposited, I chose SVL, initial mass, mass loss, and the scaled mass index (SMI) variables due to the simplicity of measuring and the body of literature covering body and clutch size (Petranka 1998). I chose SMI because it assesses overall body condition (SVL and mass), not just energy reserves related to fat (Peig and Green 2009). The SVL and initial mass measurements were taken before the female was placed in the cage. Mass loss was calculated by subtracting the release mass from the initial mass for each caged female. The scaled mass index was calculated with the formula:

$$SMI_i = \mathrm{M}_\mathrm{i} \, [\, L_i \, / \, L_0]^{b/\mathrm{r}}$$

where M_i and L_i are the mass and the SVL of the individuals, respectively, and L_0 is the mean SVL for the population (Peig and Green 2009, Kuhns et al. *in prep*). The ratio of slope (b) and Pearson's correlation coefficient (r) calculated via the ordinary least squares linear regression of the natural logarithms of mass and length is also used to calculate SMI (Peig and Green 2009, Kuhns et al. *in prep*.).

I used linear regression to model the relationship between clutch size and SVL, weight loss, initial weight, and SMI. Both the response and dependent variables were scaled and centered with the scale function in R. The estimate, confidence intervals, and adjusted r^2 were calculated for each model to determine which variable best-predicted clutch size of a female.

Once the best predictor for clutch size was found, I used ingress data to extrapolate the number of eggs laid in each wetland. I first counted the number of females ingressing at each wetland each year and then separated females into two groups; females with morphometry measured (i.e., initial mass, SVL, mass loss, or SMI) and females without morphometry measured. For example, if there were only six females with the morphometric variable recorded (decided by which model is best) for the small, created wetland out of 29 females recorded entering the wetland, I would use two different calculations for each group and then sum them. In this case, I would impute egg clutch size for the 23 females without the measured morphometric variable, using the mean estimate of clutch size multiplied by the number of females without the morphometric variable measured (in this case, 23 females). For females with the morphometric variable recorded, I would calculate clutch size by multiplying the morphometric variable model coefficient for each female variable measurement and then summing the intercept coefficient to obtain the predicted number of eggs produced. Finally, to combine the egg counts from females with and without the morphometric variable, I would sum the total egg counts for both methods to obtain the total predicted number of eggs in each wetland. I also calculated 95% confidence intervals as the error estimate for the female group with the morphometric variable measured.

I calculated the egg survival (Hatched in Table 1) by multiplying the number of eggs by three egg survival estimates: 90% survival (Williams 1973), 77% survival (Mullin and Klueh 2009), and the estimate in this study. My egg survival estimate was a simple proportion of viable eggs given the total number of eggs (both viable and non-viable) from the cages. The egg survival estimate assumed all eggs considered viable at the time of the survey survived. Next, I calculated larval survival by dividing the number of metamorphs captured exiting each wetland by the predicted larval hatch rates. Fertility (metamorph/female) was then calculated by dividing the number of egressing metamorphs by the number of breeding females ingressing.

Results

Mean clutch size for both wetlands combined was 136.45 eggs per female with a standard error of ~7 eggs, and the mean number of egg masses per female was approximately nine egg masses with a standard error of less than one (Table 3.1). Unfortunately, mean clutch size estimates for both wetlands in 2018 suffered from low sample sizes; only 6 females were used to calculate the mean clutch size and had initial mass data.

Of the four female body measurements, initial mass was the best predictor for clutch size ($r^2= 0.143$), whereby heavier gravid females had more eggs (Table 3.2; Fig. 3.3A). Increased SVL, SMI, and weight loss were associated with larger clutch size but explained less variance (Fig. 3.3B–D; Table 3.2). Thus, the initial mass model was used to predict clutch size and the total number of eggs deposited in each wetland. Initial weights were recorded for all ingressing females in 2019 and 2020, so only the 2018 data were calculated using females with and without initial mass. More females entered the natural wetland than the small, created wetland in all three years (Table 3.3). Therefore, the natural wetland had more eggs laid/was more productive than the small, created wetland (Table 3.3). The most productive years for each wetland were 2019 (12,422 ± 1433 eggs) for the natural wetland and 2018 (4642 ±1 eggs for the created wetland (Table 3.3). The highest 95% confidence intervals/greatest variation in eggs deposited for each wetland were in 2019 (±1433 eggs) for the natural wetland and 2020 (±309) for the created wetland (Table 3.3).

Mean predicted clutch size per female (eggs/female; Table 3.3) varied minimally between wetland and year, but the smallest estimates for the created wetland was in 2019 (~120 eggs) and for the natural wetland was 2020 (~129 eggs); the largest estimate for the created wetland was 2018 (~132 eggs) and for the natural wetland was 2019 (~138 eggs; Table 3.3). In 2018 and 2020, the mean estimated clutch size per female was similar between wetlands (within 1 egg). In 2019, the natural wetland had a larger estimate for mean clutch size (18 egg difference), possibly due to a larger sample size – 90 females entered the natural wetland and 27 entered the created wetland (Table 3.3).

Due to documented trespass during the study, the mean egg survival/hatching success (~2.3%) calculated from the five cages could not be used because it was biased. Instead, I used the viable to total egg (viable plus non-viable) ratio of the five cages to provide more accurate estimates of egg survival. The new value (78.5%) was similar to other studies (Williams 1973; Mullin and Klueh 2009). As a result, egg survival rates estimated from my five cages at the natural wetland were slightly higher than the Mullin and Klueh (2009) and Williams (1973) estimates.

I captured more metamorphs exiting the larger wetland than the small wetland in 2018 and 2020 (Table 3.3). The predicted number of metamorphs using the Mullin and Klueh (2009) and Williams (1973) rates were substantially lower than the actual number of metamorphs captured exiting both wetlands (Table 3.3). All calculated larval survival rates at both wetlands were greater than the Williams (1973) and Mullin and Klueh (2009) estimates (Table 3.3). The larger natural wetland had a low larval survival rate in 2019, which was also the year a late freeze occurred after egg deposition in March. The smaller, created wetland still had additional breeding adults enter after the freeze and thus showed a greater larval survival rate (Table 3.3).

Fertility estimates calculated from metamorph egress and female ingress captures were high (> 1) for all years at both wetlands except for 2019 at the natural wetland (Table 3.3). Even the lowest estimate calculated for this study (0.29) was higher than the two-year Mullin and Klueh (2009) estimate (0.015) for the natural wetland (Table 3.3).

Discussion

My study summarizes an *A. jeffersonianum* population at LTSRA and a possible body metric to monitor to predict the clutch sizes of females entering wetlands during the breeding season. Initial mass of gravid females was the best predictor of clutch size, with mass loss second in explaining the variation. Survival estimates for eggs in my study were similar to previous studies, but the larval survival and fecundity estimates differed (Williams 1973; Mullin and Klueh 2009). In my study, initial mass measurements of females were used to predict the number of eggs and egg survival for each wetland and differed from the transect and scale to wetland size approach in Mullin and Klueh (2009).

Body Metrics and Clutch Size

Individual mass is an important indicator (Semlitsch et al. 1988) of clutch size, so I included initial mass and mass loss as possible variables. Unfortunately, I did not have many observations for mass loss, which encompasses the variation in initial mass. While small sample size posed a problem, mass loss does not just occur from depositing eggs (water and lipid/tissue loss). One possibility is that during the explosive breeding period, tissue loss occurs in adults because adult salamanders do not feed during the breeding season, thus confounding mass loss as a variable (Hardy and Raymond 1980). The mass loss variable could also be confounded due to greater individual variation in resources allocated per egg (proteins and lipids) and could be a strategy for smaller females to produce fewer higher-quality eggs (Semlitsch 1987). However, mass loss cannot be eliminated as an explanatory variable because my study did not obtain enough samples of mass loss, and I did not weigh each egg mass to account for resources allocated to each egg.

The SVL and SMI showed a positive relationship with clutch size, but SVL and SMI were not as strong as predictors as initial mass. Semlitsch (1987) found SVL had a strong positive relationship with clutch size with *A. talpoideum* (r^2=0.77), but a longer SVL did not always translate to a heavier female. Like my study, Shoop (1974) found SVL was not a good predictor of clutch size for *A. maculatum*. The SMI included both initial mass and SVL of females but explained less variation than either SVL or initial mass individually. The SMI requires enough samples to represent populational variation, so perhaps its lack of predictive ability for clutch size in *A. jeffersonianum* could also stem from insufficient sample size, or SVL is not a strong predictor, as a lone variable or included in a condition index, for this species or population.

The relationship between initial mass and clutch size, albeit weak, is a relatively easy metric to collect. Initial mass measurements require the researcher only to encounter salamanders when first entering wetlands. Applying the method to other *Ambystoma* species could also aid conservation because initial mass measurements allowed for estimating the total eggs laid in each wetland. While there is still more variation to be accounted for ($r^2 = 0.143$), testing the relationship between female initial mass and clutch size by collecting more samples would benefit monitoring efforts. Predicting the number of eggs within a wetland without disturbing the actual wetland saves needed resources and time.

Restoration Effects

The 16-year difference between my study and Mullin and Klueh (2009) is sizeable, but egg survival rates would not be expected to change dramatically unless fish were introduced, or significant hydrological changes occurred. However, my study's estimated larval survival was far greater than previous studies (Williams 1973; Mullin and Klueh 2009). Of the two published estimates used for hatching/egg survival, the Williams (1973) rate was the most optimistic, whereas the Mullin and Klueh (2009) value was the most conservative. The Mullin and Klueh (2009) estimate likely represents the most realistic egg survival rate due to its methodology. The wetlands used in the other studies were similar in size to the created wetland, but both the smaller created wetland and the larger natural wetland had higher estimated larval survival estimates than Williams (1973) and Mullin and Klueh (2009). Unfortunately, my egg survival estimates were derived from only five cages due to unforeseen factors (late season wetland freezes and COVID-19); increased samples are needed to provide more robust conclusions.

The natural wetland had a low larval survival rate in 2019, which could have resulted from a late freeze in early March when eggs had been laid, and most adults had already exited.

Because the created wetland had breeding adults entering the wetland after the freeze, it had higher larval survival rates. One reason for higher larval survival and fertility estimates in my study could be high trespass rates, resulting in underestimating ingressing females and egressing metamorphs. While trespass likely occurred, larval survival, recruitment, and fecundity are substantially higher in my study than in other *A. jeffersonianum* studies (William 1973; Mullin and Klueh 2009). Thus, the increased larval survival at the larger, natural wetland in 2018 and 2020 could be due to the wetland berm restoration and subsequently increased hydroperiod.

The Mullin and Klueh (2009) study conducted at the larger natural wetland 16 years prior predicted the *A. jeffersonianum* population would likely be extirpated by 2010. However, the decline was primarily attributed to the unusually short hydroperiod (due to a damaged berm) and its repercussions for larval survival (Mullin and Klueh 2009). In their model, larval survivorship had the greatest effect on population persistence, so the shorter hydroperiod was likely the causative factor. While some trespass may have occurred, the recruitment rate was too low to support the population. Following their recommendations, the larger natural wetland underwent restoration in 2010, where the berm was restored, wetland surface area was increased (300 m^2 to 483m^2), and more wetlands were created in LTSRA (including the smaller created wetland in this study). Increased larval survival and recruitment due to the restoration at the larger natural wetland would abate the population's decline, especially when population persistence heavily depends on larval survival (Mullin and Klueh 2009).

The survival of the *A. jeffersonianum* population and increase in recruitment at LTSRA is an example of how restoration can work within a short period. By restoring the breeding habitat of *A. jeffersonianum,* historical environmental stochasticity has been muted. Neither wetland, natural or created, dried thoroughly, or forced metamorphs to leave early during my study, likely one reason the number of metamorphs increased at the natural wetland from 2005 to the present. However, late-season freezes pose a threat for the *A. jeffersonianum* population. In 2019, I collected the most females entering the natural wetland but captured the least number of metamorphs egressing resulting in the lowest fertility estimate for females. Because egg masses are deposited on the substrate near the wetland surface, they are prone to freeze kills. Additionally, *A. jeffersonianum* are also early breeding amphibians, thus exacerbating the potential threat (Petranka 1998).

By resampling the *A. jeffersonianum* population, I provided estimates for clutch sizes, the number of egg masses, an estimate of the total number of eggs laid in the wetlands, and female fertility using gravid female migration data. While monitoring wetland-breeding amphibians is time- and labor-intensive, measuring the mass of gravid females entering ponds provides a non-invasive method for estimation. Future directions should include more mating cage studies to test the initial mass relationship, exploring female reproductive-size relationships, reproductive/breeding cycles, and better methods for analyzing larval survival. Nevertheless, calculating these estimates is vital to understanding isolated populations vulnerable to stochastic events, especially as wetland habitats continue to disappear.

Tables

Table 3.1. Descriptive statistics of *Ambystoma jeffersonianum* female reproductive characteristics at two wetlands in Lincoln Trail State Recreation Area. Mean and standard deviation were calculated for total eggs laid per female and egg masses laid per female. The data summarized in this table was collected from mating cages between 2018 and 2020 in Clark County, Illinois.

Trait	***n***	**Min**	**Max**	**Median**	**Mean**	**Std. Error**	**Std. Dev.**
Total Eggs	53	28	223	142	136.45	7.11	51.79
Egg Masses	50	1	32	8	9.02	0.89	6.26

Table 3.2. Summary of β parameter estimates for each linear regression model explaining the total number of eggs laid per *Ambystoma jeffersonianum* female. Initial mass, Scaled Mass Index (SMI), mass loss, and snout-vent-length (SVL) of females were all single variable models used to explain the response variable of total eggs laid. The estimate, 95% confidence intervals (CIs), sample size (n), p-value from t-test, and R^2 values were included for each model. Initial mass of female was the best predictor of the total number of eggs laid per female. The data were collected from mating cages between 2018 and 2020 in Clark County, Illinois.

Model	**Estimate**	**Std. Error**	**Lower CI**	**Upper CI**	***n***	***p***	**r^2**
Initial Mass	0.38	0.13	0.12	0.65	52	0.006	0.143
SMI	0.11	0.15	-0.19	0.41	49	0.457	0.012
Mass Loss	0.31	0.19	-0.08	0.69	28	0.112	0.094
SVL	3.30	1.92	-0.56	7.16	49	0.092	0.059

Table 3.3. Summary of fertility, predicted egg totals, and survival estimates for *Ambystoma jeffersonianum* at two different wetlands over three years. The data is separated by wetland and year (with the number of ingressing females included). Estimation consists of the number of females with initial mass measurements/females with no mass measurement, so different methods of calculating the total number of eggs were used. The predicted number of eggs (Eggs, in bold) is calculated from the female initial mass relationship with the egg range (95% confidence interval). The clutch size per female (Eggs/female) was calculated by dividing the number of eggs by the number of females entering the wetland. The number of larvae hatched (Hatched) is calculated from egg survival values from two different studies and my own calculated egg survival rates for my mating cages. The calculated larval survival is for my wetland data. The number of metamorphs and number of females captured is census data from each wetland, and fecundity is calculated from these capture values. Survival estimates from William[1] (1973), Mullin and Klueh[2] (2009), and this study[3] were used to extrapolate egg and larval survival for the study wetlands. The data summarized in this table was collected between 2018 and 2020 in Clark County, Illinois.

					Hatched				Larval Survival			
Wetland	**Year**	**Females**	**Eggs**	**Eggs/ Female**	**90%[1]**	**77%[2]**	**78.5%[3]**	**Metamorphs**	**0.08%[1]**	**0.02%[2]**	**Calculated Larval Survival**	**Metamorphs/ Female**
Small, created	2018 (n=35)	6/29	**4642**±1	132.63	4178	3575	3644	68	3.34	0.72	1.87%	1.94
	2019 (n=27)	0/27	**3244**±151	120.13	2920	2498	2547	35	2.34	0.50	1.37%	1.30
	2020 (n=36)	0/36	**4635**±309	128.76	4171	3569	3639	31	3.34	0.71	0.85%	0.86
Large, natural	2018 (n=49)	6/43	**6498**±34	132.61	5848	5004	5101	173	4.68	1.00	3.39%	1.53
	2019 (n=90)	0/90	**12422**±1433	138.03	11180	9565	9752	26	8.94	1.91	0.27%	0.29
	2020 (n=57)	0/57	**7402**±532	129.86	6662	5700	5811	236	5.33	1.14	4.06%	4.14

Figures

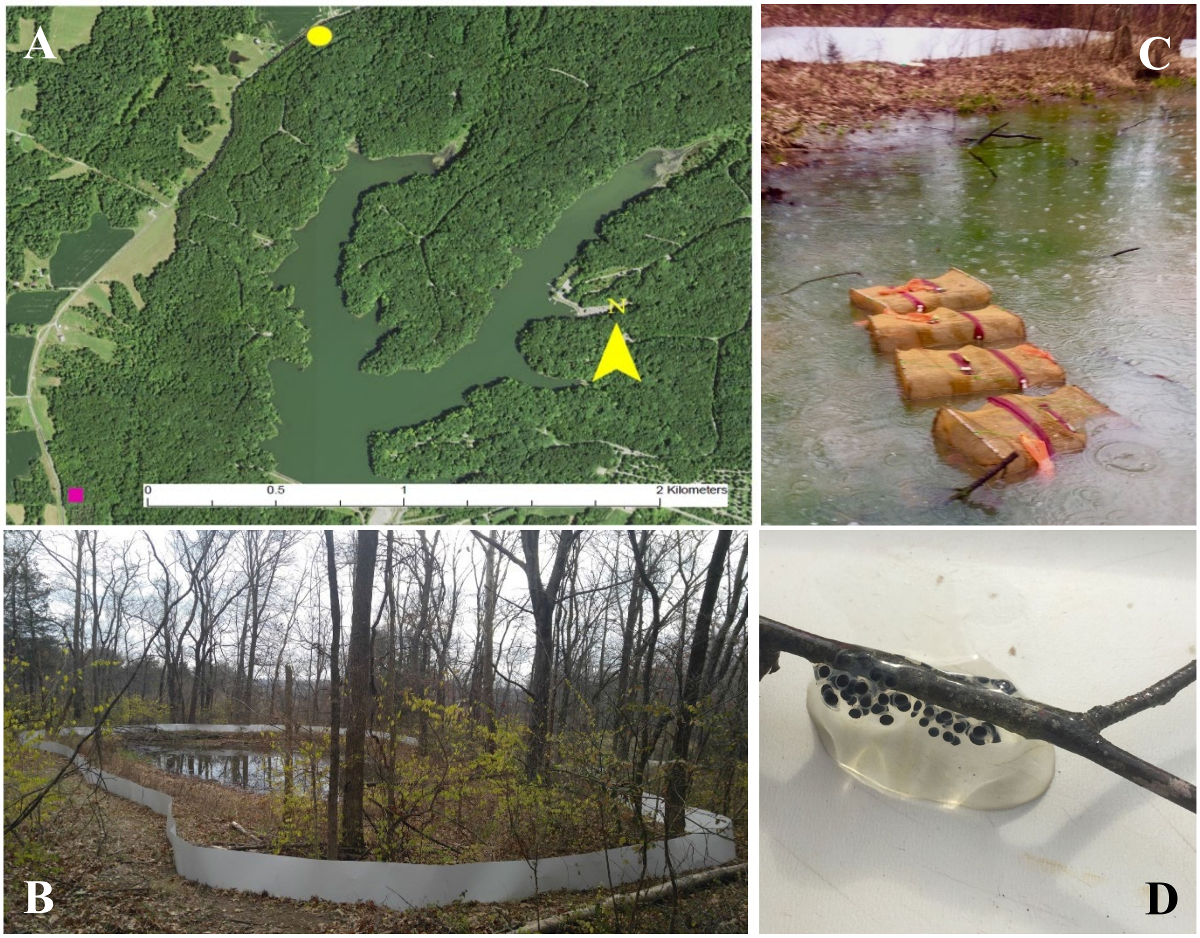

Figure 3.1. Location and method of *Ambystoma jeffersonianum* study. Panel A shows Lincoln Trail State Recreation Area field sites where the yellow circle shows the created, smaller wetland and the pink square shows the larger, natural wetland. The source of this DOQ is the 2015 Illinois NAIP. Panel B shows the drift fencing used for the census data at the natural wetland. Panel C shows some mating cages at the larger, natural wetland where one female and two males were placed in cages until egg masses were laid. Finally, panel D shows egg masses counted for each mating cage once adult pairings were released.

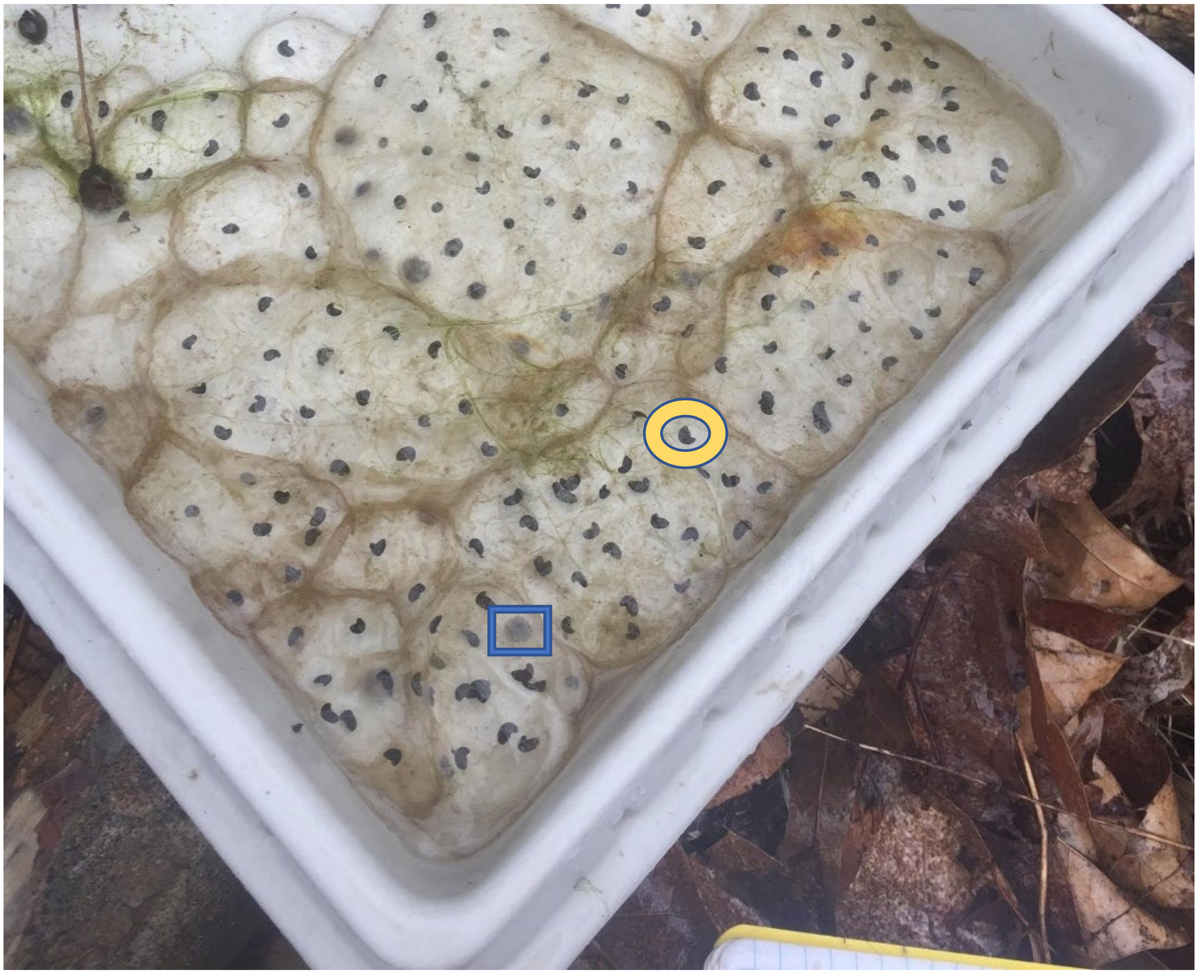

Figure 3.2. Jefferson salamander (*Ambystoma jeffersonianum*) egg masses in counting tray. The yellow circle shows an egg that would be counted as viable, and the blue square shows an egg that would be considered non-viable (in this case, lysed). The viable eggs would continue to develop to larvae, while the non-viable eggs would be stunted in development and usually be milky within the egg mass. This picture was taken in Clark County, Illinois, in 2019.

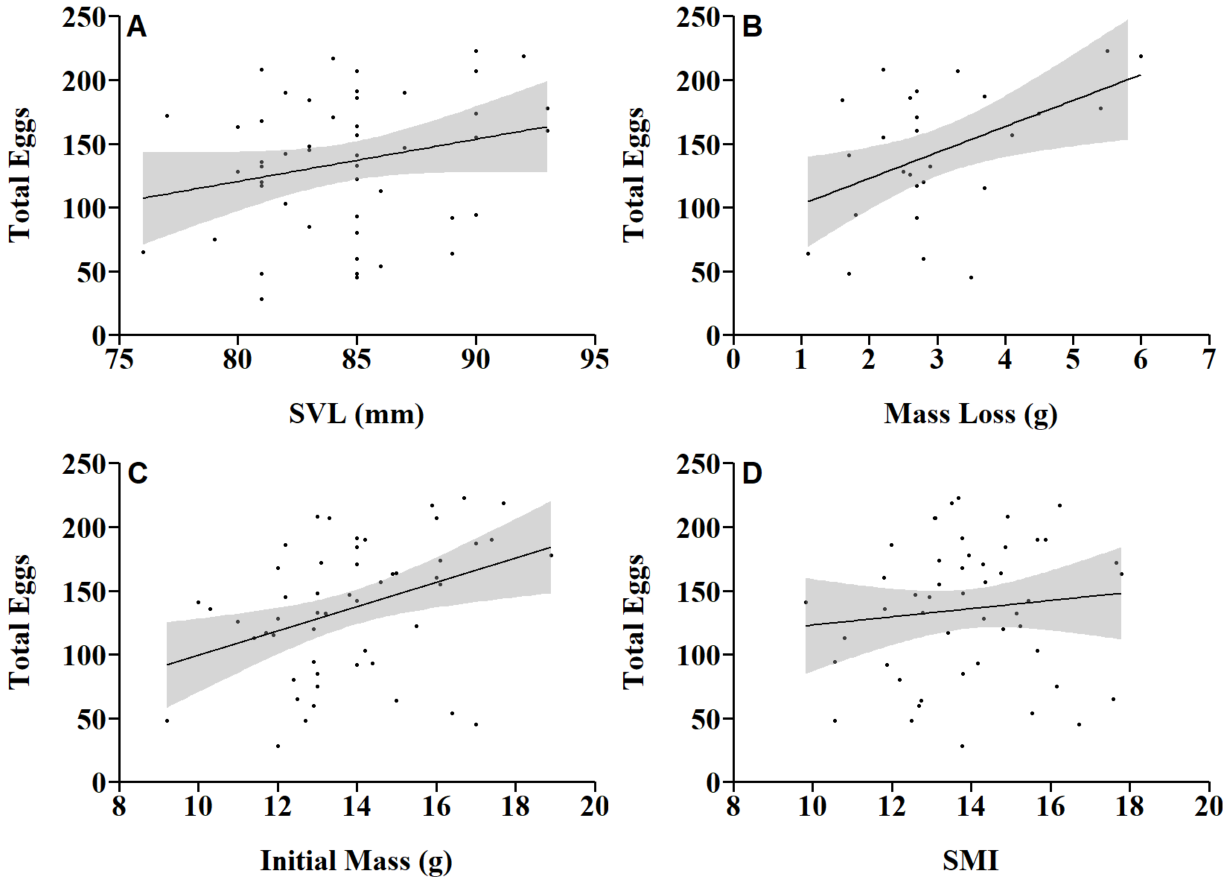

Figure 3.3. Plots of linear regression models of different measurements were used to explain the total number of eggs laid by *Ambystoma jeffersonianum* females in mating cages. The solid line is the mean predicted values, dots represent each cage sample, and the gray shaded areas are the 95% prediction intervals. Snout-vent-length (SVL) (A), mass loss of female (B), initial mass of female (C), and Scaled Mass Index (SMI, D) were all measured from females in mating cages. All four models show a positive relationship with the total number of eggs laid. Initial mass (C) was the best predictor of the response variable. The data summarized in this table was collected between 2018 and 2020 in Clark County, Illinois.

CHAPTER 4: SUMMARY AND CONSERVATION IMPLICATIONS

Amphibian populations are declining dramatically worldwide, primarily due to habitat loss and alteration (Cushman 2006). Amphibians are critical to food webs and for the integrity of forest and wetland ecosystems (Davic and Welch 2004). Further, amphibians are environmental bioindicators due to heightened vulnerability and requiring two types of habitats (aquatic and terrestrial) to complete their life cycle (Semlitsch 2008). Therefore, conservation and restoration of habitat are vital to reverse amphibian population declines (Pechmann et al. 1991). My research has provided predictors for conditions when salamanders would be most vulnerable to harm during terrestrial management and demographic parameters impacting population stability in wetland-breeding *Ambystoma* salamanders.

In Chapter 2, I used weather and census data to understand the phenology of adult and metamorph migrations in *A. jeffersonianum*, *A. laterale, A. texanum*, and *A. platineum*. My data showed salamanders moved to breeding wetlands between late January and April with variations due to species and sex. Metamorph egress occurred between late May and early September. Nighttime air temperature correlated with peaks in movement for both adults and metamorphs for all three species. Increased precipitation increased the probability of movement for adults but did not increase movement likelihood for metamorphs as dramatically. Decreasing wetland depths increased the probability of movements for *A. jeffersonianum* metamorphs. Soil inversion only influenced *A. laterale* adult movements, whereas warmer soil surface would increase movement. The asexual *A. platineum* ingressed earlier than their host species (*A. texanum*) and responded to environmental variables less so than their hosts, perhaps indicating their host's movement is just as important as environmental conditions. My data suggest a small window for prescribed burns or other disturbance-based management in late April and early May. A safer and more effective strategy would be to conduct fall burns in mid to late September, once metamorphs have migrated through the terrestrial habitat. Additionally, restricting a burn to one side of the wetland would ensure leaf litter remains for individuals to use as cover while traversing the terrestrial environment.

In Chapter 3, I used mating cage and census data to predict total reproductive effort and estimated larval survival rates for *A. jeffersonianum* in two wetlands at Lincoln Trail State Recreation Area. Clutch size was positively correlated to the initial mass of ingressing females. Restoration of a larger natural wetland and the creation of smaller wetlands likely prevented the extirpation of the *A. jeffersonianum* population. Current estimates of recruitment at the larger wetland are substantially greater than previous estimates collected over a decade ago, indicating wetland restoration activities in 2010 had a positive impact.

Management Implications

Prescribed Burns

One threat to *Ambystoma* species is habitat loss but prescribed burning used to maintain habitat can also threaten amphibians traversing the terrestrial landscape. My results identified environmental variables impacting adult and juvenile movements to predict optimal times for salamander movement and provide insight into prescribed burn timing to avoid unnecessary mortality. Twenty-four-hour precipitation, minimum air temperature, wetland depth, and the soil temperature profile are all parameters that should be monitored if land managers would like to conduct prescribed burns during low movement probability windows. Periods of high rainfall and warmer winter minimum temperatures for adult movement and droughts or drying wetlands (reaching about 50% water capacity) during the summer would be critical times to avoid prescribed burns. These conditions are not conducive to burns during spring adult movements, but awareness during the summer juvenile movements is beneficial. The *A. platineum* environmental relationships are less intuitive; however, monitoring their sexual dependent *A. texanum* would likely prevent overlap of burns and salamander movements.

Fire can also impact soil moisture and leaf litter cover for migrating adults. Preventing direct fire mortality is important but analyzing the indirect effects of burns should also be considered. Removing leaf litter and decreasing soil moisture could put migrating salamanders at higher mortality risk (Brodman 2010). Longer intervals between burns at sites could limit indirect mortality related to fire or burn during the growing season (Schurbon and Fauth 2003; Brodman 2010), so land managers should balance amphibian populations and native plant species maintenance and regeneration. Varying the spatial cover and fire intensity could also lessen amphibian casualties (Schurbon and Fauth 2003).

For Lincoln Trail State Recreation Area (LTSRA), I recommend burning in late April and early May with a generous-sized buffer around the breeding wetlands. However, if the wetland's depth falls below half, I recommend sampling for metamorphs to ensure the drying is not forcing early metamorphosis. Fall burns after metamorph dispersal would also not harm *A. jeffersonianum* populations and would not require monitoring variables as closely. If winter burning is unavoidable, burns should not be conducted when there is greater than 10 mm of overnight precipitation (they can move in snow) and/or when the minimum air temperature (nighttime low) ranges between 2.5–15.0°C.

For Kickapoo State Recreation Area, I would recommend burning in November and December. Because the site also has fall-breeding Marbled Salamanders (*Ambystoma opacum*) and other species of concern, Wood frogs (*Rana sylvatica*), early winter burns with large buffers around wetlands would cause the least amount of amphibian mortality. Spatial heterogeneity with burning would make terrestrial migration less stressful, especially if at least one side of the wetland maintains its leaf litter.

For Pine Dunes Forest Preserve, I would recommend burn treatments between October and early February to avoid *A. laterale* and Tiger Salamander (*A. tigrinum*) migrations. If spring burns cannot be avoided, spatial heterogeneity with burns and a buffer zone around the wetland would leave some leaf litter for the following *A. laterale* migration.

Restoration Effects

While more than a decade passed between the Mullin and Klueh (2009) study and my study, the fecundity and recruitment results for the larger, natural wetland at LTSRA provided some evidence for the efficacy and importance of wetland restoration. Fecundity and recruitment in *Ambystoma jeffersonianum* were much higher in my assessment, and larval survival rates were estimated to be improved. Extirpation was predicted for the larger natural wetland (Mullin and Klueh 2009); repairing the berm increased the wetland depth and supported a longer hydroperiod. Subsequently, these restoration measures likely aided larval development and likely prevented population collapse (Semlitsch 2002). Even a newly created wetland such as the smaller wetland at LTSRA had higher fertility than the natural wetland between 2004–2005 (Mullin and Klueh 2009). While ambsytomatids require both terrestrial and wetland habitat, in this case, improving only wetland habitat had a significant impact on recruitment.

From my results, I would recommend restoration prioritize wetland quality (via maintenance of appropriate wetland hydroperiods) in areas with high habitat heterogeneity and other breeding wetlands because connectivity of the habitats is another important factor (Harper et al. 2008; Crawford et al. 2016; Kuhns et al. *in prep*). Genetic diversity is necessary for population persistence, and wetland protection must be landscape-level (Cosentino et al. 2011;

Crawford et al. 2016). I would continue to monitor the population at LTSRA because long-term studies (> 5 years) are needed to properly assess amphibian population trends and structure (Sexton et al. 1998; Pechmann et al. 1999).

For Kickapoo State Recreation Area (KSRA), the *A. platineum* wetland and surrounding terrestrial habitat require restoration. At LTSRA, restoring the wetland's hydroperiod helped prevent failed recruitment and restoring the KSRA large wetland could have the same effect. Large swamp oaks need to be removed from the largest KSRA wetland because the root system is beginning to harm the hydrology of the natural wetland. While there are still the created wetlands at KSRA, maintaining the large wetland should be a conservation priority to conserve source-sink dynamics (Semlitsch and Bodie 1998). Autumn olive (*Elaeagnus umbellata*) has also invaded much of the terrestrial habitat between wetlands and should be chemically and mechanically removed to restore habitat connectivity and improve wetland quality.

Another concern at KSRA is the declining *A. texanum* population. Although *A. texanum* populations in Illinois are not a listed species, there has been a steady decline at KSRA, especially in the number of *A. texanum* males. Having migration predictors from my phenology results to understand unisexual phenology helps *A. platineum* conservation, but their phenology, like their survival, depends on *A. texanum*. Conservation is usually abiotic focused, but in the case of *A. platineum*, focusing on the conservation of their hosts could be just as effective. It is likely that without intervention (removal of invasive plants and trees), *A. platineum* and *A. texanum* could be extirpated from the site.

For Pine Dunes Forest Preserve, the large wetland has a relatively permanent hydroperiod. However, the *A. laterale* population could benefit from additional suitable forested wetlands on the landscape. Although there are other wetlands at this site, restoration was focused on open canopy habitats such as marshes and sedge meadows. Few have the canopy cover suitable for *A. laterale* and will most likely only benefit *A. tigrinum* populations. Other wetlands on the landscape or fragmented, require road crossings which represents a threat to *A. laterale*. Adding additional flatwoods wetlands could help sustain and bolster the isolated *A. laterale* population.

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APPENDIX A: SUPPLEMENTAL TABLE

Table A.1. The candidate models not used in analysis due to convergence issues even after using the optimizer "bobyqa".

Candidate Models	Candidate Model Formulas	Analyses
Adult		
Inversion Strength interaction model	Sex*Inv_Strength	Magnitude
Inversion Strength interaction and Precipitation model	Sex*Inv_Strength + PRCP	Timing
Day-of-year interaction model	Sex*poly(doy,2)	Timing
Metamorph		
Day-of-year model	poly(doy,2)	Magnitude
Day-of-year and Wetland Depth model	poly(doy,2) + Gauge_pond	Magnitude
Day-of-year and Precipitation model	Sex:poly(doy,2) + Sex:PRCP	Magnitude
Wetland Depth, Precipitation, and Day-of-year model	Gauge_pond + poly(doy,2) + PRCP	Timing

APPENDIX B: SUPPLEMENTAL FIGURES

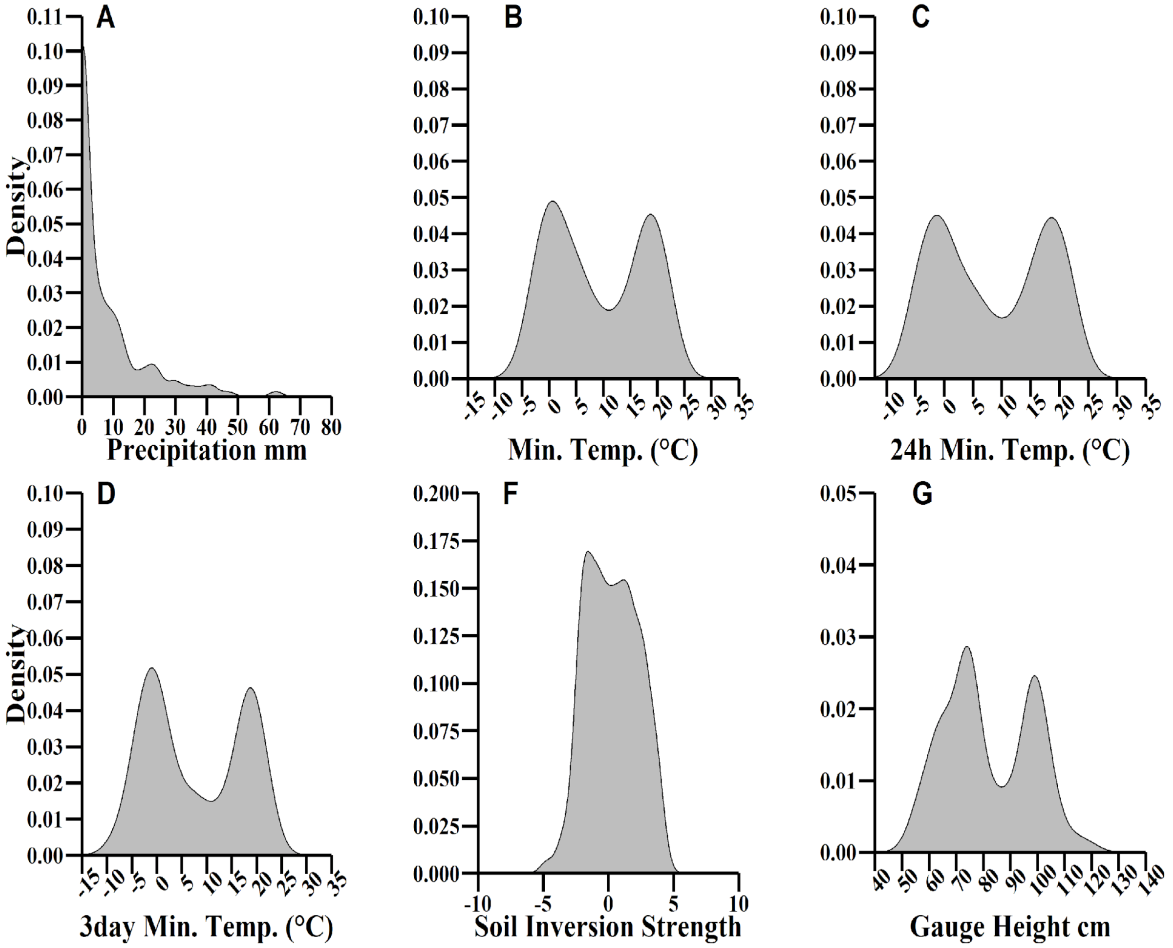

Figure. B.1. *Ambystoma jeffersonianum* density plots for variables calculated in Table 2.1 to show variance of surveyed data.

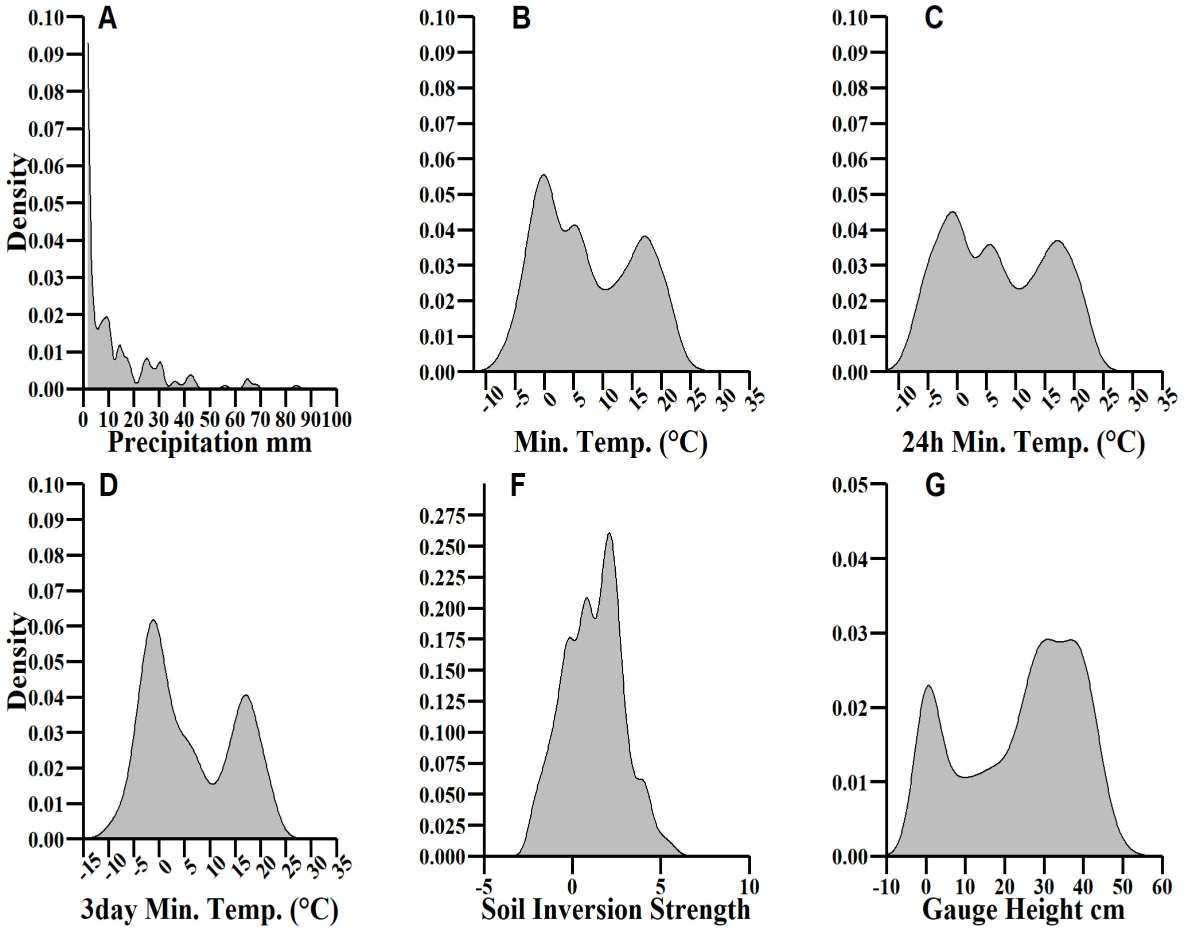

Figure. B.2. *Ambystoma platineum* density plots for variables calculated in Table 2.1 to show variance of surveyed data.

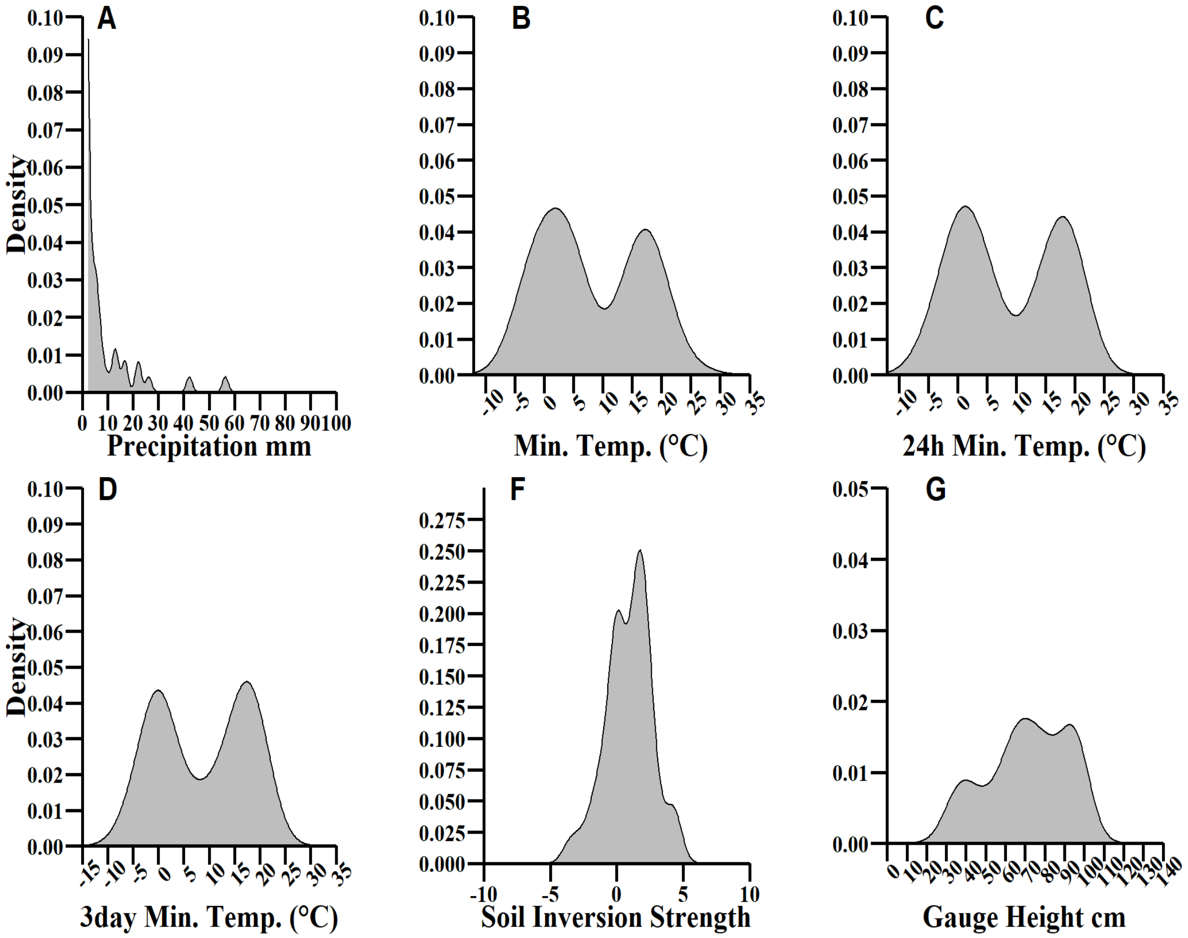

Figure. B.3. *Ambystoma laterale* density plots for variables calculated in Table 2.1 to show variance of surveyed data.