


# Environmental drivers of juvenile dispersal and adult non-breeding movements in *Ambystoma* salamanders

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## Abstract

Understanding the environmental drivers of species' dispersal and migration patterns is needed to accurately predict climate change impacts on populations. For pond-breeding amphibians, adult movements associated with the breeding period are well studied but major gaps exist in our knowledge of the drivers of adult and juvenile non-breeding movements. Here, we assess environmental drivers of adult and juvenile *Ambystoma maculatum* (Shaw, 1802), *Ambystoma jeffersonianum* (Green, 1827), and their unisexual dependants' (*Ambystoma laterale-jeffersonianum* (Uzzell, 1964)) summer and fall non-breeding movements using data from pitfall trapping and radio telemetry tracking. We used generalized linear models to assess the influence of precipitation, minimum temperature, day of year, and days since last precipitation on salamander movements. Juvenile summer dispersal movements were related to days since last precipitation in Jefferson Salamander complex individuals and 24 h precipitation in Spotted Salamanders. Adult and juvenile fall movements were driven by minimum temperature, 24 h precipitation, and days since last precipitation, and the effect of these environmental factors varied slightly between species and between Jefferson bisexuals and unisexuals. Our work indicates that changes in both temperature and precipitation will likely impact non-breeding dispersal and migration in these species and, overall, improves our understanding of ecological patterns throughout their entire life cycle.

**Key words:** Spotted Salamander, *Ambystoma maculatum* (Shaw, 1802), Jefferson Salamander, *Ambystoma jeffersonianum* (Green, 1827), *Ambystoma laterale-jeffersonianum* (Uzzell, 1964) unisexual polyploids, migration

## Introduction

Climate change is driving notable shifts in the timing of amphibian migration patterns and breeding activity. Warmer autumn or spring temperatures, for example, have been shown to result in later or earlier breeding migrations and breeding activity (e.g., vocalization, egg deposition, etc.) in a variety of frog, toad, and salamander species (Todd et al. 2011; Walpole et al. 2012; Benard 2014; Green 2017; Homan 2019; Kirk et al. 2019), though not all species or populations follow this trend (Blaustein et al. 2001; Walls et al. 2013; Homan 2019). Even changes in environmental variables outside of the breeding season can still impact amphibian breeding. For example, Spotted Salamander (*Ambystoma maculatum* (Shaw, 1802)) body condition has been shown to decrease with increases in summer and autumn temperatures, with implications for breeding in the following spring (Moldowan et al. 2022). Variability in species responses to changing weather conditions indicates a need to further understand how species and populations will respond to climatic change (Brooks et al. 2019; Kirk et al. 2019).

While the impact of climate change on amphibian spring breeding activity has been the principal focus of ecological research, there is less information on how changes will impact

non-breeding movements and behaviours, such as impacts on the timing of migration to overwintering habitat, feeding behaviour, juvenile development, or duration of winter dormancy (Blaustein et al. 2010; Lefebvre et al. 2018; Brooks et al. 2019; Kirk et al. 2019; Moldowan et al. 2022). This lack of knowledge likely results from a combination of an emphasis put on breeding population dynamics (Williams 1973; Blaustein et al. 2001; De Lisle and Grayson 2011; Van Drunen et al. 2021) and the fact that individuals outside the breeding period are generally more dispersed across the landscape (Williams 1973; Faccio 2003; Bériault 2005; Van Drunen et al. 2020), making them difficult to study. However, understanding environmental drivers during non-breeding periods of the life cycle is important to identify climate change impacts on juvenile and adult survival rates, migration and dispersal patterns, food availability, and non-breeding (e.g., overwintering) habitat suitability. Information about the environmental drivers of amphibian movement during the non-breeding season is needed to understand the full impact of climate change on the entire amphibian life cycle (Brooks et al. 2019).

Understanding environmental drivers that underpin amphibian movement also informs conservation management

actions that mitigate anthropogenic impacts on populations. Road mortality is a large threat to many amphibian populations (Beebee 2013) and one mitigation measure is to temporarily close sections of roadways during peak movement periods (OMNRF 2016). For example, in various locations in southern Ontario, roads are closed to protect salamander spring breeding migrations (OMNRF 2016). Effective timing of road closures to target the period when amphibians are moving requires information on the environmental drivers of this movement (Timm et al. 2007b). Similarly, this information could guide conservation mitigation related to the timing of forestry or construction operations that threaten impacts within amphibian habitats. While relationships between amphibian breeding movements and environmental variables have been well studied, a lack of information during other parts of these species' life cycle may limit the ability to effectively manage anthropomorphic threats and impacts.

Over their Canadian range, unisexual *Ambystoma* share nuclear genomes (chromosomes) with three distinctly different bisexual species of *Ambystoma* (*Ambystoma jeffersonianum* (Green, 1827); *Ambystoma laterale* Hallowell, 1856; and *Ambystoma texanum* (Matthes, 1855)) for which basic species biology information is limited (COSEWIC 2016). Jefferson Salamander and their unisexual dependents (*A. laterale-jeffersonianum* (Uzzell, 1964)), together referred to as the Jefferson Salamander complex, are endangered species in Canada (Government of Canada 2022). Due to data deficiencies in our knowledge about Jefferson Salamander and their unisexual dependents, ecological information about the more widespread and abundant Spotted Salamanders is often used to inform their conservation management (Linton et al. 2018). In addition, research into both Spotted and Jefferson Salamander population dynamics and habitat use has primarily focused on movements related to the breeding season (Baldauf 1952; Williams 1973; Douglas and Monroe 1981; Sexton et al. 1990; Brodman 2002; De Lisle and Grayson 2011; Semlitsch and Anderson 2016; Homan 2019), when individuals are easiest to capture and monitor. Once individuals disperse after breeding, the fossorial nature of these ambystomatids makes information about non-breeding activities difficult to obtain, even for abundant species like Spotted Salamander.

Jefferson Salamander, their unisexual dependants, and Spotted Salamanders follow an annual migration pattern in their movements. Spring movements of Jefferson Salamander and unisexuals from overwintering locations to the ephemeral ponds where they breed usually occur during rainy periods when temperatures are consistently above freezing, with Spotted Salamander breeding movements starting a number of weeks later (Williams 1973; St. Andre 2012; Pfungsten et al. 2013). Adult post-breeding movements away from breeding ponds in the late spring are usually related solely to precipitation, since temperatures are generally no longer a limiting factor to survival later in the year (Weller 1980; Bériault 2005). Once Jefferson Salamander, their unisexual dependants, and Spotted Salamander complete their post-breeding movement away from the breeding area, they tend to remain within a relatively small area of habitat during the summer (Bériault 2005; Ledford 2011; Hoffmann et al.

2018) and then in the fall migrate to overwintering locations that can be further away from the breeding pond, where they remain until spring (Faccio 2003; Van Drunen et al. 2020). Transformation of larvae and dispersal of metamorphs into the terrestrial environment occur approximately 120 days after the adults began breeding in the spring (Pfungsten et al. 2013) and larval survival is dependent on the hydroperiod of the ephemeral natal pond, which can be highly variable between years (Semlitsch et al. 1996; Mullin and Klueh 2009; Van Drunen et al. 2021). Environmental drivers of juvenile movements after they have left their natal pond and adult movements to overwintering locations are unclear.

Studies have identified a number of different drivers influencing the initial dispersal of metamorphs from their natal pond. *Ambystoma jeffersonianum*, *A. maculatum*, and *A. laterale* juvenile dispersal has been associated with increased precipitation (Vasconcelos and Calhoun 2004; Timm et al. 2007a; Gravel et al. 2012; Osbourne 2012; St. Andre 2012). Increases in minimum air temperature or number of degree days since 1 May has been found to positively influence initial juvenile dispersal (Vasconcelos and Calhoun 2004; Timm et al. 2007a; Gravel et al. 2012). Hydroperiod of the natal pond was a key factor in *A. jeffersonianum* and associated unisexual juvenile emigration (Callahan 2021), while results from Timm et al. (2007b) suggest that, in addition to hydroperiod, food abundance and water temperature may also be key drivers of juvenile dispersal, with weather factors being secondary drivers. Improving our understanding of the drivers of salamander movement is important to identify potential conservation threats imposed by a changing climate throughout the entire life cycle of these species.

Here, we aim to assess and compare the environmental drivers of summer and fall movements of sympatric adult and juvenile Spotted Salamander (*A. maculatum*), Jefferson Salamander (*A. jeffersonianum*), and Jefferson-dependant unisexual salamanders (*A. laterale-jeffersonianum*) using data from mark-recapture pitfall trapping and radio telemetry tracking. Our three objectives were to (1) identify the key environmental drivers of adult and juvenile fall movement in these species; (2) identify the environmental conditions that influence post-metamorphic juvenile dispersal away from their natal pond; and (3) compare environmental drivers of adult or juvenile movement between species, and between Jefferson bisexuals and unisexuals. This study addresses key gaps in our knowledge of these species' dispersal and migration mechanics that are intrinsic to accurately predicting climate change impacts on these species.

## Materials and methods

### Pitfall trapping data

To assess the relationship of environmental variables to juvenile and adult movement during summer and fall periods, we used pitfall capture data from Van Drunen et al. (2021). Trapping was conducted during various spring, summer, and fall periods from 2015 to 2019 (Table 1) at a site in southern Ontario, Canada, using a combination of drift fence with pitfall traps. Fencing was arrayed in complete and broken circle

**Table 1.** Start and end dates per season of pitfall trapping conducted by Van Drunen et al. (2021).

	Spring		Summer		Fall	
	Start	End	Start	End	Start	End
2015	–	–	26 June	31 August	1 September	30 October
2016	8 March	21 April	27 June	9 September	–	–
2017	–	–	17 July	31 August	1 September	27 October
2018	27 March	14 April	23 July	31 August	24 September	25 October
2019	28 March	18 April	–	–	–	–

patterns around the study breeding pond at distances ranging from 1 to 132 m from the edge of the study pond. Pitfall traps ( $n = 190$ ) were placed flush with the ground on both sides of each fence at approximately 5 m intervals and checked twice daily during trapping periods. Many adult and juvenile *A. jeffersonianum* and *A. laterale-jeffersonianum* individuals were identified using microsatellite DNA analysis. See Van Drunen et al. (2021) for a detailed description of trapping and DNA testing methods.

Raw pitfall capture data from the summer and fall trapping periods of 2015, 2017, and 2018 were extracted and summarized into daily juvenile and adult capture counts per species. Salamanders referred to as “juvenile” in this study are all assumed to be first-year post-metamorphosis individuals, since Van Drunen et al. (2021) report no juvenile individuals were recaptured outside of the year they were first captured. Daily count information of Jefferson Salamander complex individuals was also summarized into three groups: the “bisexual” group contained all *A. jeffersonianum* individuals, the “unisexual” group contained all triploids and tetraploids *A. laterale*–(2–3) *jeffersonianum* unisexual individuals combined, and an “unknown” group contained *A. jeffersonianum* complex individuals of unknown (i.e., untested) genetic makeup. Daily counts of adult and juvenile *A. maculatum* were also summarized. These count data are assumed to be a proxy for salamander movement since individuals are only captured in the pitfall traps when they are moving through the landscape. We did not use data from 2016 because a drought in that year caused the study pond to dry prematurely and no captures were recorded during the summer period. And as a result of the lack of summer captures, trapping was not conducted in the fall of 2016.

Daily climatic variables were calculated from publicly available hourly precipitation amounts and minimum temperature observations from the Environment and Climate Change Canada Hamilton RBG CS Ontario (Station ID: 27529; Climate ID: CA006153301) weather station. Due to the nocturnal nature of the study species, most movement typically occurs at night (Pfungsten et al. 2013). To align the weather data with this nocturnal movement period, we used the minimum temperature and summed the total precipitation that occurred over the 24 h period (0800 to 0700) prior to each morning pitfall trap check.

### Pitfall trapping statistical methods

The relationship between daily environmental factors and capture counts was assessed using generalized linear

mixed-effect models. Preliminary analyses indicated that the negative-binomial distribution outperformed Poisson, zero-inflated Poisson, and zero-inflated negative-binomial distributions for all but two analyses. The analysis of adult unisexual counts required a zero-inflated Poisson distribution and the summer juvenile bisexual analysis required a zero-inflated negative-binomial model.

The dependant variable of daily capture counts from summer and fall periods was used to assess Jefferson and Spotted Salamander groups separately. For the summer analyses of juvenile movement, we used the period of 17 July to 31 August for Jefferson juveniles and 1 August to 13 September for Spotted juveniles. A later summer period for the Spotted salamander was used because Spotted Salamanders typically begin their breeding season later in the spring than Jefferson Salamanders (Pfungsten et al. 2013), leading to delayed Spotted juvenile emergence compared to Jefferson juveniles (Wacasey 1961). We also excluded 2018 from the Spotted juvenile summer analysis because only a single individual was captured in that summer. The fall analyses of juvenile and adult movements used capture counts from 23 September to 31 October. Analyses used total counts of all captured individuals, which in the case of the Jefferson analyses included bisexual, unisexual, and unknown individuals combined together. In addition, the subset of Jefferson unisexual and bisexual groups was assessed separately. In each case, analyses were also separated by age class (juvenile, adult). Likelihood ratio tests ( $\chi^2$ ) of full and reduced models were used to assess the influence of each predictor for each of the analyses.

Fixed effects included year, minimum temperature, total precipitation, day of year (DOY), and days since last precipitation event. Minimum temperature was included in our models for two reasons. First, *Ambystoma* salamander activity is primarily nocturnal and minimum temperatures generally represent the nighttime conditions. Secondly, ambystomatid salamanders cannot survive freezing and must seek shelter underground during freezing temperatures (Weller 1980; Brodman 1995; Madison 1997), suggesting that low minimum temperatures are likely a limiting factor of fall movements. Total precipitation 24 h prior to capture was included because precipitation is a key component of spring breeding movements (Weller 1980; Faccio 2003) and avoiding desiccation may be a limiting factor to movement in the summer or fall. DOY was included to account for temporal drivers of movement not accounted for by the environmental variables (e.g., length of day, seasonal variations in the magnetic field, etc.) and has been shown to be a factor in some *Ambystoma* species'

movements (Brooks et al. 2019; Benard and Greenwald 2023). Finally, the number of days since the last precipitation event was included to account for conditions without precipitation that may still be moist enough to deter desiccation. An interaction term between minimum temperature and total precipitation was also included, since movement may only occur in warm and wet conditions. Finally, we included year as a fixed effect to account for annual differences between trapping periods.

## Radio telemetry tracking data

To examine fall movement patterns beyond the end of October, we used radio telemetry tracking data of 19 bisexual (JJ: *A. jeffersonianum*) and 14 unisexual (13 LJ: *A. laterale*–(2) *jeffersonianum* + 1 LJJ: *A. laterale*–(3) *jeffersonianum*) adult individuals reported in Van Drunen et al. (2020). These individuals were also identified as bisexual or unisexual using microsatellite DNA analysis (Van Drunen et al. 2020). Two separate groups of individuals were located once per week from 13 October to 22 December in 2017 and from 25 September to 21 December in 2018. If an individual had moved from their previous week's location, their new location was flagged, movement of a metre or less was measured with a metre stick, and UTM coordinates were recorded using a SXBlue II GNSS GPS (SXblue GPS, Anjou, QC) with  $\pm 1$  m accuracy. See Van Drunen et al. (2020) for more details about the radio telemetry monitoring methods. Following Van Drunen et al. (2020), individuals' weekly movements were classified as either "moved" when an individual was 5 m or more from their previous week's location or "not moved" if movement was less than 5 m.

Since weather data were not available from the Hamilton RBG weather station during November and December of 2017 when radio tracking occurred, we used daily observations from the Hamilton A station (Station ID: 49908; Climate ID: CA006153193) for the telemetry analysis. To match with the weekly time period of the radio tracking, daily total precipitation and minimum temperatures were averaged over the week prior to the day of each weekly tracking observation.

## Radio telemetry statistical methods

The relationship between telemetry movement and environmental variables was assessed using a generalized (binomial family) mixed-effect model with presence or absence of movement in a given week as the response variable. The environmental variables of weekly average daily total precipitation and weekly average daily minimum temperature, as well as their interaction, were included as fixed effects. We also included the fixed effects of snout-to-vent length (SVL; mm) to account for possible variation in movement due to body size (Faccio 2003; Benard and Greenwald 2023), and salamander type (bisexual, unisexual) because unisexuals have been shown to move less than bisexual individuals (Van Drunen et al. 2020). In addition to the fixed effects, we included the random variable of individual ID to account for repeated observations of individuals. The influence of each predictor was assessed with likelihood ratio tests ( $\chi^2$ ). We

were unable to repeat this telemetry analysis for *A. maculatum* as Van Drunen et al. (2020) did not track individuals of this species.

All analyses were conducted in R version 4.2.0 (R Core Team 2022). Models were specified using the "glmmTMB" package (Brooks et al. 2017), model diagnostics were assessed using the package "DHARMA" (Hartig 2022), and predictor effects plots were created using the "effects" package (Fox and Weisberg 2019). Results are reported as mean  $\pm$  standard error (SE) unless otherwise indicated. This work was carried out in accordance with all applicable animal care and species-at-risk collection permits and protocols.

## Results

### Pitfall analysis

We used data from 768 adult (237 *A. maculatum* + 161 *A. jeffersonianum* + 76 *A. laterale*–(2–3) *jeffersonianum* + 294 unknown Jefferson complex individuals) and 1814 juvenile (484 *A. maculatum* + 738 *A. jeffersonianum* + 445 *A. laterale*–(2–3) *jeffersonianum* + 147 unknown Jefferson complex individuals) salamanders captured across 3 years of trapping (Table 2). Adult Spotted and Jefferson complex individuals were captured on 33 and 47 days, respectively, out of the 103 total days of fall trapping. Similarly, juvenile Spotted and Jefferson complex individuals were captured on 39 and 46 days, respectively, out of the total 103 days of fall trapping. Summer captures of juvenile Spotted Salamander occurred on 37 out of 88 days of trapping, while Jefferson complex individuals were captured on 88 days out of 138 total trapping days.

Weather was similar between all summer and fall periods of this study. During the fall period (23 September to 31 October), minimum temperature ranged from  $-3.3$  to  $18.5$  °C (mean  $\pm$  SE =  $7.9 \pm 0.9$ ) in 2015, from  $0.6$  to  $19.6$  °C ( $10.0 \pm 0.9$ ) in 2017, and from  $-0.9$  to  $20.6$  °C ( $7.9 \pm 1.0$ ) in 2018. Fall total precipitation was 97.7, 79.1, and 72.8 mm in 2015, 2017, and 2018, respectively. During the summer juvenile Jefferson dispersal period (17 July to 31 August), minimum temperature ranged from  $9.6$  to  $22.1$  °C ( $15.7 \pm 0.5$ ) in 2015, from  $7.5$  to  $20.7$  °C ( $15.8 \pm 0.5$ ) in 2017, and from  $10.8$  to  $22.8$  °C ( $16.8 \pm 0.5$ ) in 2018, while precipitation totals were 63.9, 95.0, and 88.5 mm in 2015, 2017, and 2018, respectively. Finally, during the juvenile Spotted Salamander summer period (1 August to 13 September), minimum temperature ranged from  $9.6$  to  $23.0$  °C ( $15.9 \pm 0.6$ ) in 2015 and from  $5.4$  to  $20.7$  °C ( $13.1 \pm 0.6$ ) in 2017, with precipitation totals of 97.0 and 91.1 mm, respectively.

### Summer movement—juveniles

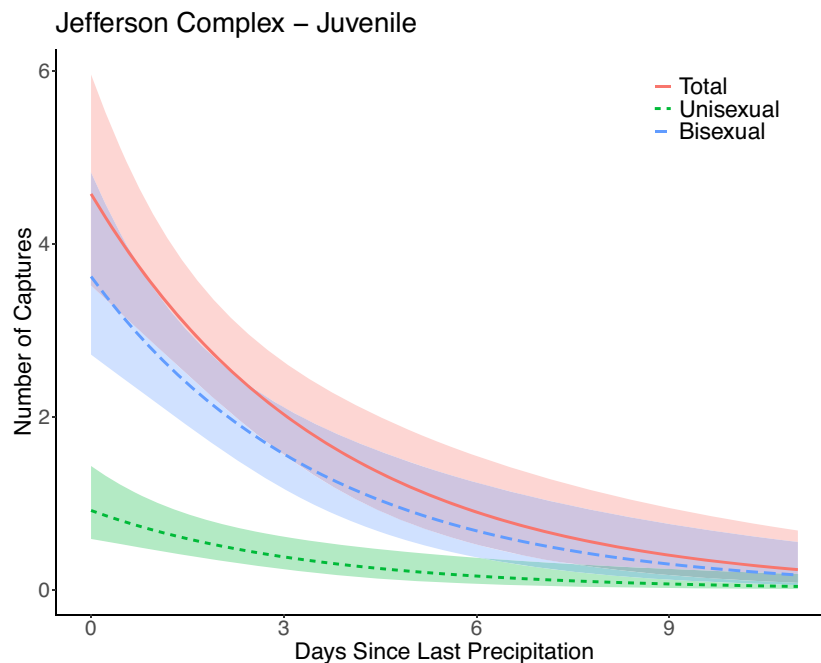
Juvenile Jefferson Salamander total, unisexual, and bisexual summer captures were negatively related to days since last precipitation (all  $p < 0.0005$ ; Fig. 1) with 77% of captures occurring within 0–2 days since last precipitation. Capture counts were also significantly different between years (all  $p < 0.0001$ ) with the highest capture totals occurring in 2017. There was no significant effect of DOY, min-

**Table 2.** Total seasonal pitfall captures by genotype (Jefferson Salamander bisexual = *Ambystoma jeffersonianum*, unisexual = *Ambystoma laterale*–(2–3) *jeffersonianum*, unknown = unknown/untested genotype, Spotted Salamander = *Ambystoma maculatum*) and life stage per species in each year of trapping.

Year	Jefferson Salamander complex							Spotted Salamander		
	Adult			Juvenile				Adult	Juvenile	
	Bisexual	Unisexual		Unknown	Bisexual	Unisexual		Unknown		
		LJJ	LJJJ			LJJ	LJJJ			
Fall captures										
2015	2	3	0	141	13	19	2	52	79	21
2017	119	40	5	72	11	46	2	4	119	174
2018	40	27	1	81	5	4	0	18	39	33
Summer captures										
2015	–	–	–	–	49	9	0	2	–	15
2017	–	–	–	–	629	347	11	70	–	240
2018	–	–	–	–	31	5	0	1	–	1

**Note:** The year 2016 is excluded because trapping did not occur in the fall and the study pond dried up early due to a drought resulting in no captures. Fall period was from 23 September to 31 October for all groups, Jefferson complex summer period was from 17 July to 31 August, and Spotted Salamander summer period was from 1 August to 13 September.

**Fig. 1.** Predictor effect plots showing the relationship between summer movement (i.e., number of individuals captured) and days since last precipitation for juvenile Jefferson Salamander (*Ambystoma jeffersonianum*) and their unisexual dependents (*Ambystoma laterale*–(2–3) *jeffersonianum*). Shaded areas represent the 95% confidence interval.



imum temperature, precipitation, or the interaction term (see Table 3) on Jefferson Salamander juvenile summer movement. Juvenile Spotted Salamander captures were significantly related to 24 h precipitation ( $p = 0.04$ ), where captures increased with increasing precipitation (Fig. 2). Precipitation 24 h prior to days when Spotted juvenile captures occurred ranged from 0 to 19.5 mm ( $3.1 \pm 0.9$ ). There was no significant effect of DOY, days since last precipitation, year, minimum temperature, or the interaction term on juvenile Spotted Salamander summer movement (Table 3).

### Fall movement—juveniles

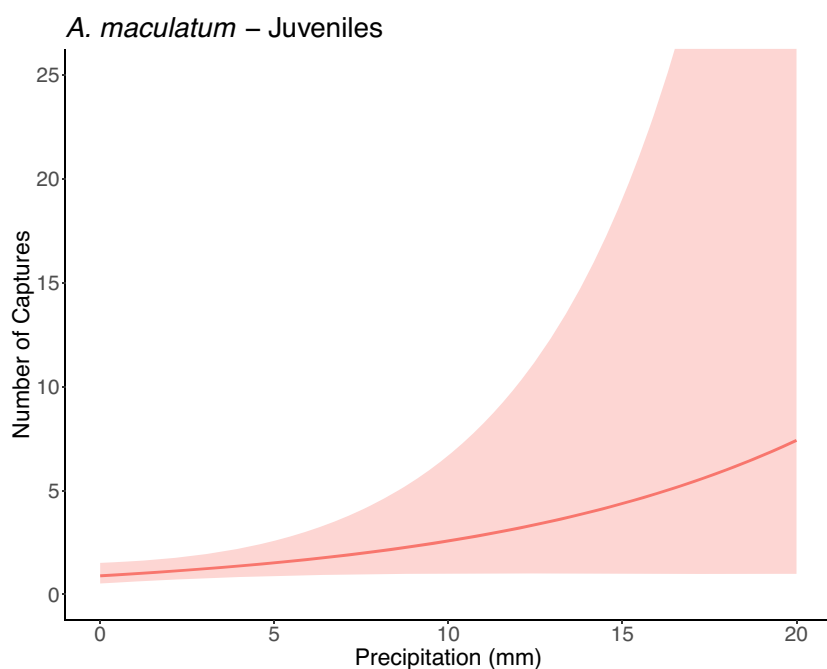
Total captures of Jefferson Salamander juveniles in the fall were related to minimum temperature, 24 h precipitation, and days since last precipitation (all  $p \leq 0.001$ ; see Table 4), whereby captures increased with higher minimum temperatures (Fig. 3A) and precipitation (Fig. 4A) and decreased with more days since last precipitation (Fig. 5A). Bisexual captures were similarly related to minimum temperature and days since last precipitation (all  $p \leq 0.03$ ), but not precipitation. Finally, the only discernible effect on unisexual cap-

**Table 3.** Summer movement likelihood ratio and model results based on pitfall trapping for juvenile Jefferson Salamander complex (bisexual = *Ambystoma jeffersonianum*, unisexual = *Ambystoma laterale*-(2-3) *jeffersonianum*, unknown = unknown/untested genotype) and Spotted Salamander (*Ambystoma maculatum*).

		Jefferson Salamander complex			Spotted Salamander
		Total	Unisexual	Bisexual	Total
Precipitation × temperature	Estimate ± SE	-0.004 ± 0.010	0.003 ± 0.015	-0.008 ± 0.011	0.005 ± 0.011
	$\chi^2_{[1]}$	0.16	0.03	0.51	0.22
	p value	0.69	0.86	0.48	0.64
Temperature	Estimate ± SE	0.02 ± 0.04	-0.015 ± 0.059	0.042 ± 0.045	0.05 ± 0.07
	$\chi^2_{[1]}$	0.20	0.04	0.46	1.00
	p value	0.65	0.84	0.50	0.32
Precipitation	Estimate ± SE	0.10 ± 0.19	-0.02 ± 0.28	0.17 ± 0.19	<b>0.02 ± 0.19</b>
	$\chi^2_{[1]}$	1.74	1.08	1.61	<b>4.09</b>
	p value	0.19	0.30	0.20	<b>0.04</b>
DOY	Estimate ± SE	0.0009 ± 0.009	0.012 ± 0.013	-0.005 ± 0.010	0.007 ± 0.02
	$\chi^2_{[1]}$	0.0005	0.92	0.51	0.05
	p value	0.98	0.34	0.48	0.83
DLP	Estimate ± SE	<b>-0.27 ± 0.06</b>	<b>-0.30 ± 0.08</b>	<b>-0.27 ± 0.06</b>	-0.019 ± 0.11
	$\chi^2_{[1]}$	<b>24.05</b>	<b>13.39</b>	<b>21.66</b>	0.02
	p value	<b>&lt;0.0001</b>	<b>0.0003</b>	<b>&lt;0.0001</b>	0.88
Year	2017: estimate ± SE	<b>2.67 ± 0.22</b>	<b>3.55 ± 0.40</b>	<b>2.24 ± 0.24</b>	3.15 ± 0.54
	2018: estimate ± SE	<b>-0.55 ± 0.29</b>	<b>-0.67 ± 0.60</b>	<b>-0.57 ± 0.31</b>	-
	$\chi^2_{[1]}$	<b>128.89</b>	<b>116.08</b>	<b>96.68</b>	0
	p value	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	1

Note: Significant results are bolded. Precipitation represents total precipitation in the 24 h prior to capture, temperature is minimum air temperature, DOY is day of year, and DLP represents days since last precipitation. SE, standard error.

**Fig. 2.** Predictor effect plots showing the relationship between summer movement (i.e., number of individuals captured) and 24 h total precipitation (mm) for juvenile Spotted Salamander (*Ambystoma maculatum*). Shaded areas represent the 95% confidence interval.

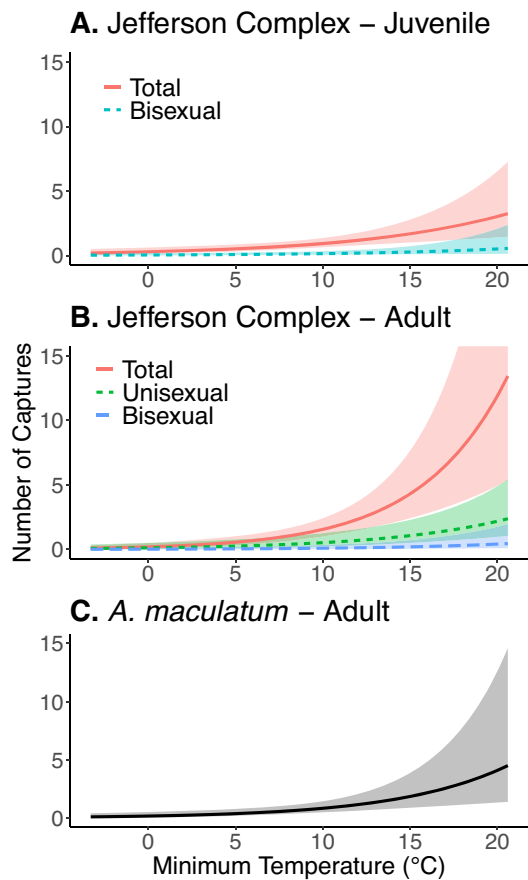


**Table 4.** Fall movement likelihood ratio and model results based on pitfall trapping of Jefferson Salamander complex (bisexual = *Ambystoma jeffersonianum*, unisexual = *Ambystoma laterale*-(2-3) *jeffersonianum*, unknown = unknown/untested genotype) and Spotted Salamander (*Ambystoma maculatum*).

		Adult				Juvenile			
		Jefferson Salamander complex			Spotted Salamander	Jefferson Salamander complex			Spotted Salamander
		Total	Unisexual	Bisexual	Total	Total	Unisexual	Bisexual	Total
Precipitation × temperature	Estimate ± SE	-0.01 ± 0.01	-0.003 ± 0.006	-0.010 ± 0.008	-0.008 ± 0.013	-0.009 ± 0.007	-0.008 ± 0.008	-0.006 ± 0.009	<b>-0.02 ± 0.009</b>
	$\chi^2_{[1]}$	1.90	0.25	1.21	0.36	1.49	1.13	0.47	<b>4.49</b>
	p value	0.17	0.61	0.27	0.55	0.22	0.29	0.49	<b>0.03</b>
Temperature	Estimate ± SE	<b>0.23 ± 0.04</b>	<b>0.16 ± 0.05</b>	<b>0.17 ± 0.05</b>	<b>0.18 ± 0.06</b>	<b>0.14 ± 0.04</b>	0.08 ± 0.04	<b>0.14 ± 0.07</b>	-
	$\chi^2_{[1]}$	<b>24.06</b>	<b>16.05</b>	<b>11.07</b>	<b>9.35</b>	<b>10.79</b>	2.44	<b>4.51</b>	-
	p value	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	<b>&lt;0.001</b>	<b>0.002</b>	<b>0.001</b>	0.12	<b>0.03</b>	-
Precipitation	Estimate ± SE	<b>0.30 ± 0.12</b>	0.07 ± 0.08	<b>0.18 ± 0.10</b>	<b>0.26 ± 0.15</b>	<b>0.18 ± 0.07</b>	0.13 ± 0.08	0.11 ± 0.09	-
	$\chi^2_{[1]}$	<b>17.18</b>	2.61	<b>6.76</b>	<b>16.14</b>	<b>19.14</b>	3.29	2.84	-
	p value	<b>&lt;0.0001</b>	0.11	<b>0.009</b>	<b>&lt;0.0001</b>	<b>&lt;0.0001</b>	0.07	0.09	-
DOY	Estimate ± SE	0.02 ± 0.02	<b>0.08 ± 0.02</b>	-0.004 ± 0.02	0.05 ± 0.03	0.004 ± 0.018	-0.0003 ± 0.03	-0.005 ± 0.03	<b>-0.09 ± 0.02</b>
	$\chi^2_{[1]}$	0.85	<b>15.40</b>	0.02	2.51	0.18	0.035	0.004	<b>15.87</b>
	p value	0.36	<b>&lt;0.0001</b>	0.89	0.11	0.67	0.85	0.95	<b>&lt;0.0001</b>
DLP	Estimate ± SE	<b>-0.44 ± 0.11</b>	<b>-0.36 ± 0.15</b>	<b>-0.87 ± 0.27</b>	<b>-0.26 ± 0.12</b>	<b>-0.26 ± 0.09</b>	<b>-0.16 ± 0.07</b>	<b>-0.41 ± 0.19</b>	<b>-0.31 ± 0.06</b>
	$\chi^2_{[1]}$	<b>23.23</b>	<b>10.17</b>	<b>27.46</b>	<b>6.93</b>	<b>13.53</b>	<b>6.83</b>	<b>8.46</b>	<b>28.16</b>
	p value	<b>&lt;0.0001</b>	<b>0.001</b>	<b>&lt;0.0001</b>	<b>0.008</b>	<b>0.0002</b>	<b>0.009</b>	<b>0.004</b>	<b>&lt;0.0001</b>
Year	2017: estimate ± SE	-0.11 ± 0.42	<b>2.06 ± 0.90</b>	<b>3.73 ± 0.93</b>	-0.07 ± 0.51	<b>-0.22 ± 0.33</b>	<b>0.85 ± 0.38</b>	-0.37 ± 0.57	<b>1.84 ± 0.41</b>
	2018: estimate ± SE	0.18 ± 0.43	<b>1.88 ± 0.86</b>	<b>3.27 ± 0.97</b>	-0.12 ± 0.52	<b>-1.00 ± 0.40</b>	<b>-1.47 ± 0.63</b>	-0.89 ± 0.70	<b>-0.38 ± 0.51</b>
	$\chi^2_{[1]}$	0	<b>4.77</b>	<b>23.19</b>	0	<b>4.82</b>	<b>16.80</b>	1.18	<b>29.60</b>
	p value	1	<b>0.03</b>	<b>&lt;0.0001</b>	1	<b>0.03</b>	<b>&lt;0.0001</b>	0.28	<b>&lt;0.0001</b>

**Note:** Significant results are bolded. Precipitation represents the 24 h total precipitation prior to capture, temperature is minimum air temperature, DOY is day of year, and DLP represent days since last precipitation. SE, standard error.

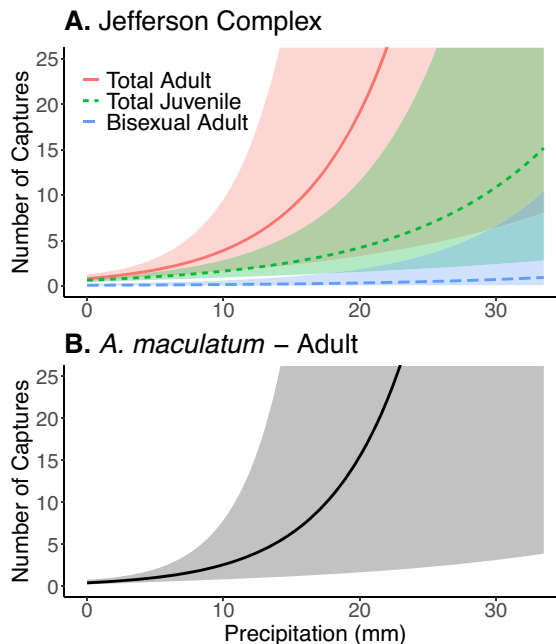
**Fig. 3.** Predictor effect plots showing the relationship between fall movement (i.e., number of individuals captured) and minimum temperature ( $^{\circ}\text{C}$ ) for juvenile and adult Spotted Salamander (*Ambystoma maculatum*), Jefferson Salamander (*Ambystoma jeffersonianum*), and their unisexual dependents (*Ambystoma laterale*–(2–3) *jeffersonianum*). Shaded areas represent the 95% confidence interval.



tures was days since last precipitation ( $p = 0.01$ ) with decreasing captures as days since last precipitation increased. Approximately 90% of Jefferson and Spotted Salamander captures occurred within 0–2 days since last precipitation. On days when juveniles were captured, minimum temperature ranged from 1.0 to 18.5  $^{\circ}\text{C}$  ( $9.7 \pm 0.6$ ) for total Jefferson captures and from 2.5 to 18.5  $^{\circ}\text{C}$  ( $10.6 \pm 1.1$ ) for bisexuals. Precipitation 24 h prior to days when juvenile captures occurred ranged from 0 to 33.5 mm ( $5.3 \pm 1.1$ ) for total Jefferson juvenile captures. There was no significant effect of the interaction between temperature and precipitation or of DOY on Jefferson Salamander juvenile total, unisexual, or bisexual captures (Table 4). Total and unisexual capture counts significantly varied by year ( $p \leq 0.03$ ) but not captures of bisexual juveniles.

Juvenile Spotted Salamander fall captures showed a significant relationship to the interaction between temperature and precipitation, DOY, and days since last precipitation (all  $p \leq 0.03$ ). Captures decreased with increasing DOY (Fig. 6A) or days since last precipitation (Fig. 5B), and increasing precipitation increased captures at lower temperatures (below 10  $^{\circ}\text{C}$ )

**Fig. 4.** Predictor effect plots showing the relationship between fall movement (i.e., number of individuals captured) and 24 h total precipitation (mm) for juvenile or adult Spotted Salamander (*Ambystoma maculatum*), Jefferson Salamander (*Ambystoma jeffersonianum*), and their unisexual dependents (*Ambystoma laterale*–(2–3) *jeffersonianum*). Shaded areas represent the 95% confidence interval.



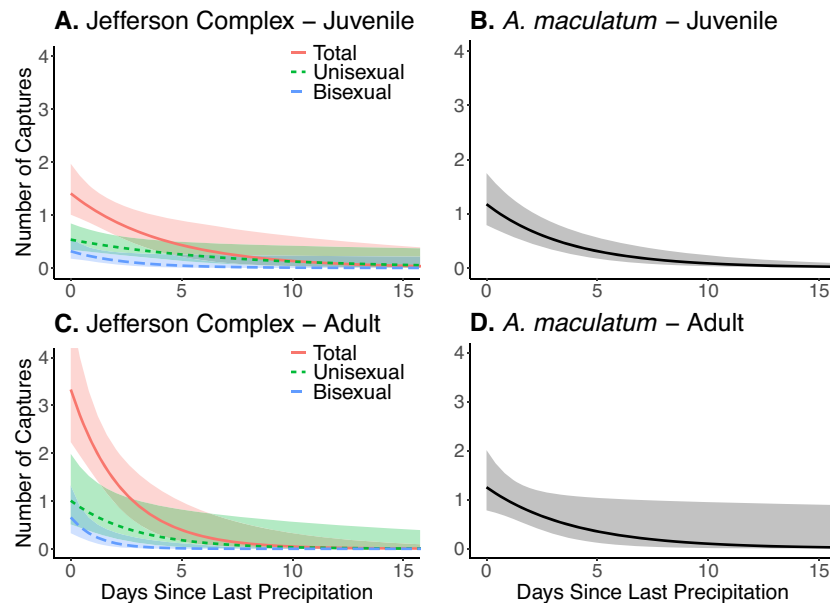
but had little to no effect at higher temperatures (e.g., 20  $^{\circ}\text{C}$ ; Fig. 7A). Juvenile Spotted Salamander capture counts significantly varied by year ( $p < 0.0001$ ).

### Fall movements—adults

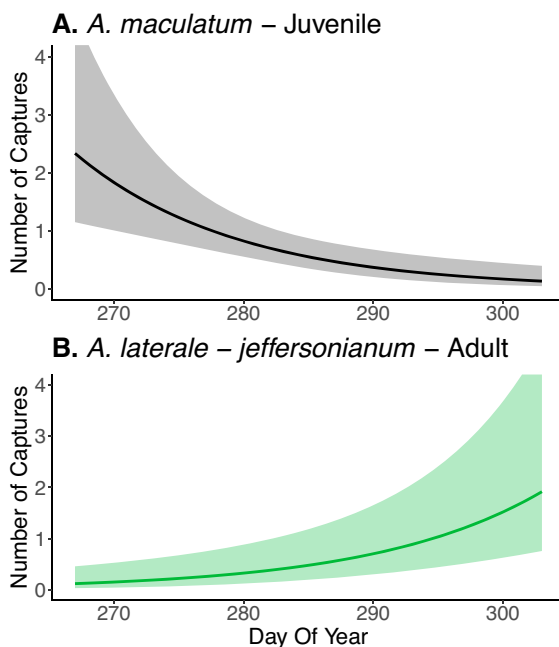
Fall daily captures of adult Spotted and Jefferson Salamanders, as well as the subset of unisexual and bisexual captures, were related to minimum temperature (all  $p \leq 0.002$ ) and days since last precipitation (all  $p < 0.01$ ; see Table 4). In general, captures tended to increase at higher minimum temperatures (Figs. 3B and 3C) and decreased as days since last precipitation increased, with 85% and 94% of Jefferson and Spotted Salamanders captures occurring within 0–2 days since the last precipitation event (Figs. 5C and 5D). On days when adults were captured, minimum temperature ranged from 0.9 to 20.6  $^{\circ}\text{C}$  ( $10.3 \pm 0.7$ ) for total Jefferson captures, from 0.9 to 18.3  $^{\circ}\text{C}$  ( $10.3 \pm 0.8$ ) for bisexuals, from 1.4 to 20.6  $^{\circ}\text{C}$  ( $11.2 \pm 0.8$ ) for unisexuals, and from 1.0 to 18.5  $^{\circ}\text{C}$  ( $10.2 \pm 0.8$ ) for Spotted Salamanders.

Total captures of both species and the bisexual subset were also positively related to total precipitation 24 h prior to capture (all  $p < 0.01$ ; Fig. 4), while unisexual captures were not. Precipitation 24 h prior to days when adult captures occurred ranged from 0 to 33.5 mm ( $5.2 \pm 1.1$ ) for total Jefferson captures, from 0 to 27.0 mm ( $5.0 \pm 1.2$ ) for bisexuals, and from 0 to 33.5 mm ( $6.6 \pm 1.4$ ) for Spotted Salamander. There was no significant effect of the interaction between temperature and precipitation variables for any of the adult groups (Table 4).

**Fig. 5.** Predictor effect plots showing the relationship between fall movement (i.e., number of individuals captured) and days since last precipitation for juvenile and adult Spotted Salamander (*Ambystoma maculatum*), Jefferson Salamander (*Ambystoma jeffersonianum*), and their unisexual dependents (*Ambystoma laterale*–(2–3) *jeffersonianum*). Shaded areas represent the 95% confidence interval.



**Fig. 6.** Predictor effect plots showing the relationship between fall movement (i.e., number of individuals captured) and day of year for juvenile Spotted Salamander (*Ambystoma maculatum*) and adult Jefferson complex unisexuals (*Ambystoma laterale*–(2–3) *jeffersonianum*). Shaded areas represent the 95% confidence interval.



Unisexuals were the only group to have a relationship with DOY ( $p < 0.0001$ ), where captures were more likely later in the year (Fig. 6B). Unisexual and bisexual captures significantly varied between years ( $p \leq 0.03$ ), while total Jefferson and Spotted Salamander captures were not related to year.

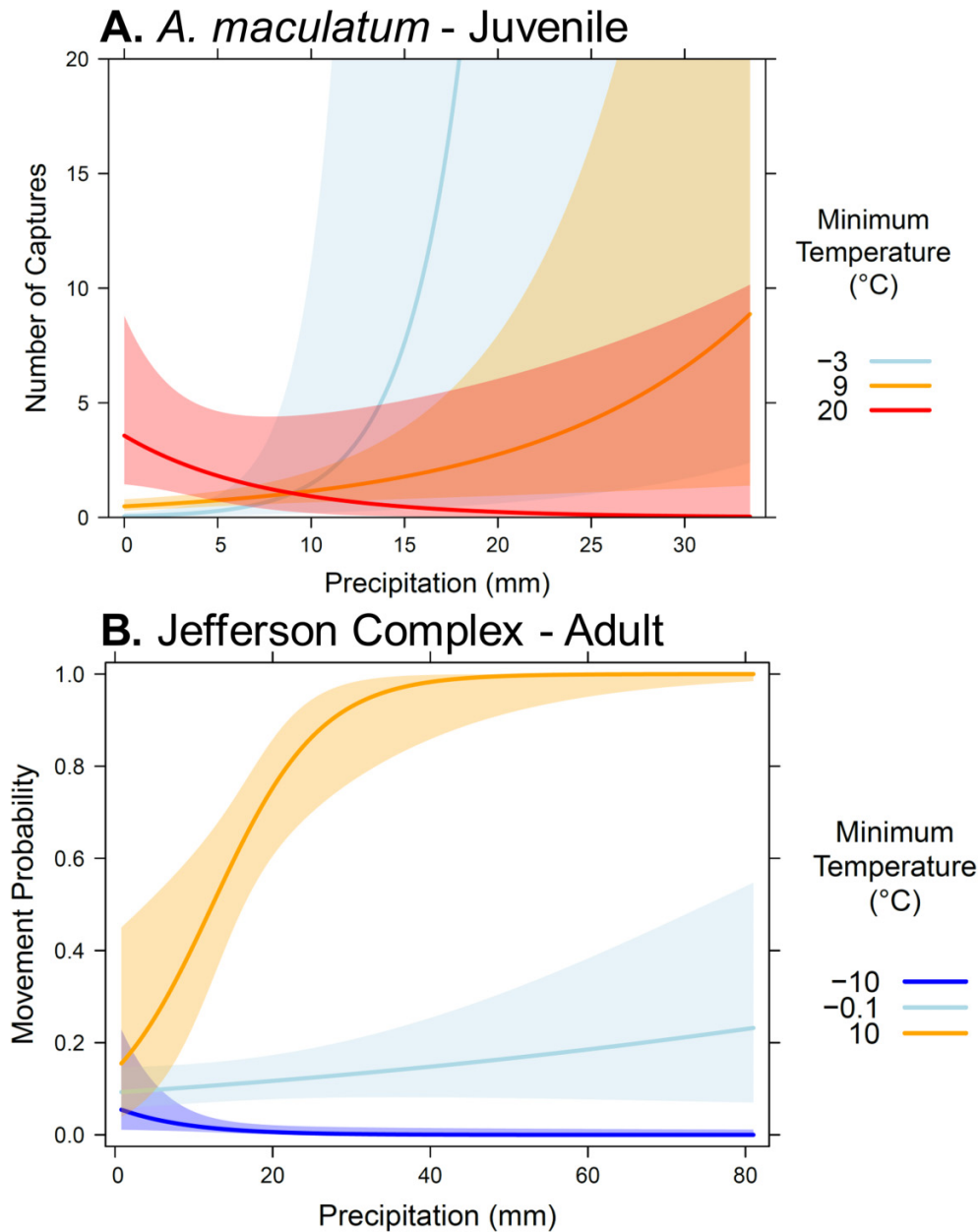
### Telemetry analysis

During radio tracking, individuals made movements of 5 m or more during 16 of the 24 weeks of monitoring. The interaction between minimum temperature and precipitation was significant ( $\beta \pm SE = 0.013 \pm 0.005$ ,  $X^2_{[1]} = 6.55$ ,  $p = 0.01$ ). In general, movement was positively related to precipitation at temperatures above  $0^\circ\text{C}$  and negatively related to precipitation at temperatures below  $0^\circ\text{C}$  (Fig. 7B). Body size (SVL;  $\beta \pm SE = -0.006 \pm 0.022$ ,  $X^2_{[1]} = 0.08$ ,  $p = 0.77$ ) and salamander type (unisexual;  $\beta \pm SE = -0.59 \pm 0.34$ ,  $X^2_{[1]} = 3.03$ ,  $p = 0.08$ ) were not significant predictors of movement.

### Discussion

Our results demonstrate that summer dispersal movements of juveniles in the Jefferson Salamander complex were related to days since last precipitation and that juvenile summer movements in Spotted Salamanders was related to 24 h precipitation. Adult and juvenile fall movements in both species were driven by minimum temperature, 24 h precipitation, and days since last precipitation, and the effect of these environmental factors varied somewhat between species and bisexual and unisexual individuals. Below, we discuss how these findings fill key knowledge gaps and provide important guidance for conservation management activities.

**Fig. 7.** Predictor effect plots showing the relationship between fall movement and the interaction between minimum temperature ( $^{\circ}\text{C}$ ) and precipitation (mm) for (A) juvenile Spotted Salamander (*Ambystoma maculatum*) fall movements based on pitfall trapping and (B) adult Jefferson Salamander complex (*Ambystoma jeffersonianum* and *Ambystoma laterale-jeffersonianum*) fall radio telemetry movements. Shaded areas represent the 95% confidence interval.



### Summer juvenile dispersal

Summer juvenile dispersal showed some association with precipitation metrics (Fig. S1). Jefferson bisexual and unisexual juvenile movement was related to days since last precipitation, but not 24 h precipitation. This lack of direct connection between movement and total precipitation suggests that beyond meeting some soil moisture or humidity threshold required to prevent desiccation, precipitation had little direct influence on juvenile Jefferson Salamander dispersal movements. Alternatively, Spotted Salamander juvenile movements were positively related to 24 h precipitation, which is similar to past findings. In three Maine vernal

pools, Spotted Salamander juvenile emergence and dispersal activity were correlated with precipitation (Vasconcelos and Calhoun 2004), while New Brunswick juvenile Blue-spotted Salamander and Spotted Salamander pitfall captures were positively related to total precipitation (Gravel et al. 2012). Osbourne (2012) reports that increased weekly total rainfall amounts increased movement activity by Spotted Salamander juveniles in Missouri. Similarly, Timm et al. (2007b) found that 24 h precipitation was a significant driver of Spotted Salamander juvenile movement across 14 seasonal ponds in Massachusetts. These findings may indicate that juvenile Spotted Salamander are less resilient to desiccation and more

dependent on precipitation than Jefferson Salamander bisexuals or unisexuals.

Minimum temperature was not a factor in summer dispersal for Jefferson Salamander individuals or Spotted Salamander. This result differs from other studies that show a positive relationship between movement and minimum temperatures in juvenile Spotted Salamander or Blue-spotted Salamander (Vasconcelos and Calhoun 2004; Gravel et al. 2012). Timm et al. (2007b) reports a positive relationship between degree days since 1 May and Spotted Salamander juvenile dispersal, indicating warmer conditions increased movements. There may exist a threshold at which increasing temperature becomes an obstacle to movement, as seen in the Spotted Salamander fall movements in this study. St. Andre (2012) also reported a negative relationship with mean daily temperature and Spotted and Jefferson Salamander juvenile emergence, where movement was limited during precipitation events at hotter ( $\geq 26^\circ\text{C}$ ) temperatures. Temperature's lack of influence on juvenile summer dispersal in our results could be due to minimum temperatures within the years analyzed in this study that generally fell within a range suitable for juvenile dispersal movements. Alternately, it may be that environmental factors are of secondary importance to juvenile dispersal, and other factors, such as timing of larval development, pond hydroperiod, or food availability, have a larger influence on the timing of movements (Timm et al. 2007a).

### Juvenile fall movement

Total captures of juvenile Jefferson individuals were similar to adult salamanders with comparable relationships to minimum temperature, 24 h precipitation, and days since last precipitation. Spotted Salamander juvenile fall movements were similarly related to days since last precipitation but also negatively related to DOY, where most movements occurred earlier in the fall season than later. This DOY pattern was not evident in juvenile Jefferson Salamander movements (Fig. S2) that may indicate they have a greater tolerance than Spotted Salamander to environmental conditions later in the year. Spotted Salamander juvenile movements showed an interaction relationship between temperature and precipitation, where increased precipitation led to increased movements at temperature below  $20^\circ\text{C}$ , but at  $\geq 20^\circ\text{C}$ , movements decreased with increasing precipitation. In this study, 92% and 84%, respectively, of total Jefferson and Spotted fall juvenile captures occurred below a minimum temperature of  $16^\circ\text{C}$ . These findings suggest that an upper limit exists where hotter temperatures become detrimental to *Ambystoma* juvenile fall movements, perhaps due to an increased risk of desiccation or heat stress.

Juvenile movements appear to be part of overall dispersal away from the natal pond. Van Drunen et al. (2021) suggest the juvenile Jefferson Salamander movement could be dispersal because they did not capture any of these juveniles in years following their initial capture. These summer and fall movements may be part of the interval dispersal pattern theorised for pond-breeding amphibians by Semlitsch (2008), where, due to the high risk of mortality, newly meta-

morphosed juveniles' first dispersal movements are primarily over a short distance. Only after juveniles grow larger and are at less risk of predation or desiccation would individuals continue to disperse further afield. In our study, both Spotted and Jefferson Salamander juvenile pitfall captures generally followed a bimodal distribution through time, with peak captures occurring in August and October and little to no activity in early to mid-September (data not shown). If the fall movement is part of dispersal (and not part of some unknown seasonal juvenile migration between summer and overwintering habitat), the differences in environmental drivers between juvenile summer and fall movements suggest that these are separate phases. This is consistent with Semlitsch's (2008) theory. The summer movements could be the initial short dispersal phase out of the natal pond to the nearest suitable habitat. Then, in the fall, after juveniles have grown a little, additional dispersal movement occurs when individuals need to find appropriate overwintering habitat. Overall, information on these species' juvenile movements is scarce and discerning when and where juveniles are moving after leaving their natal pond requires further study.

### Adult fall movements

Fall movements to overwintering habitat by adult Spotted Salamander, Jefferson Salamander, and their unisexual dependants tended to occur during days of precipitation, on days shortly after precipitation events, or on days with high minimum temperatures (Fig. S3). Adult *A. laterale*-(2-3) *jeffersonianum* movement had only a marginally significant relationship with precipitation during the fall period, though this may have been due to a small sample size. Given adult unisexual movement was negatively related to days since last precipitation and significantly related to the interaction between precipitation and temperature during fall telemetry tracking suggests some relationship with precipitation exists. Alternately, the Blue-spotted Salamander component of unisexuals' genetic makeup has been suggested to provide an increased tolerance to drier conditions and lower temperatures compared to bisexual individuals (Greenwald et al. 2016), which could allow for unisexual movement during drier periods when bisexual movement does not occur. Further research to clarify differences between Jefferson Salamander and their unisexual dependants in environmental tolerances and habitat preference is needed.

An interaction between minimum temperature and precipitation only becomes a factor influencing adult salamander movements later in the year. This is likely due to the fact that minimum temperatures during September and October did not reach low enough levels to significantly threaten salamanders with freezing (Fig. S3). Later in the year, however, precipitation events only enable salamander movement at temperatures above freezing when rain prevents desiccation, while below freezing precipitation falls as snow, impeding movement and increasing the risk of individuals freezing.

There was no relationship between body size (SVL) and movement frequency in individuals tracked by radio teleme-

try. Other research has found associations with body size and movement. For example, in a radio telemetry tracking study, [Faccio \(2003\)](#) found a positive relationship between adult salamander mass and distance moved for *A. maculatum* but not *A. jeffersonianum*. In their mark-recapture study, [Van Drunen et al. \(2021\)](#) found that dispersal distance of post-metamorphic *A. jeffersonianum* and *A. laterale*–(2–3) *jeffersonianum* was positively related to SVL. The lack of relationship between movement and body size in our study could be due to bias in the data collected by [Van Drunen et al. \(2020\)](#), since animal care guidelines required a minimum mass for individuals to be eligible for implantation with a radio transponder, excluding small individuals from our analysis.

## Climate change impacts

Climate change predictions for Ontario's Great Lakes Basin (where data from this study were collected) predict a 1.5–7.0 °C increase in mean temperature by the 2080s from 1971 to 2000 baseline levels, with winter warming likely to exceed summer warming ([McDermid et al. 2015](#)). In addition, greater warming of night temperatures compared to day temperatures has been observed ([Zhang et al. 2019](#)), which could lead to a disproportionate increase of impacts on nocturnal species. Precipitation is expected to be more variable with a potential annual increase of up to 240 mm from historic levels ([McDermid et al. 2015](#)). While total precipitation is predicted to increase, this increase is disproportionate in the winter with summer conditions predicted to be drier by up to 60 mm than historic levels by the 2080s ([McDermid et al. 2015](#)).

Increase in summer temperature could directly affect juvenile dispersal through increased heat stress or threat of desiccation or indirectly through impacts on changes to natal pond hydroperiod ([Rowe and Dunson 1995](#); [Brooks 2009](#); [Lesbarrères et al. 2014](#); [Messerman et al. 2022](#)). Drought can also result in severe declines in juvenile recruitment in a given year ([Semlitsch et al. 1996](#); [Mullin and Klueh 2009](#); [Van Drunen et al. 2021](#)) and predicted increases in temperature combined with reduced summer precipitation could pose a serious threat to the persistence of populations ([Walls et al. 2013](#); [Lesbarrères et al. 2014](#)). Warming temperatures and increased precipitation later in the year may extend the length of time salamanders have to reach overwintering habitat but this could come with energetic costs. For example, [Moldowan et al. \(2022\)](#) found that warming summer and fall temperatures had a negative effect on *A. maculatum* breeding body condition the following spring, which they hypothesized was caused by elevated metabolism or thermal stress associated with higher temperatures.

This study fills key gaps in our knowledge of *A. jeffersonianum*, *A. laterale*–*jeffersonianum*, and *A. maculatum* non-breeding dispersal and migration mechanics that are intrinsic to accurately predicting climate change impacts on these species and guiding conservation actions such as informing the timing of road closures to protect migrating individuals. Understanding environmental drivers of behaviour, habitat use, and migration patterns throughout the entire life cycle of these species is important to ensure that conservation

management encompasses all ecological components necessary to sustain populations.

## Acknowledgements

We thank the project staff at Natural Resource Solutions Inc. and all those who volunteered their time to collect the data used in this study, as well as Dr. Wendy Van Drunen for her support throughout this work. This study was funded by the Ontario Ministry of Natural Resources and Forestry Species at Risk Stewardship Program with in-kind contributions from Natural Resource Solutions Inc.

## Article information

### History dates

Received: 30 March 2023

Accepted: 7 July 2023

Accepted manuscript online: 31 July 2023

Version of record online: 7 September 2023

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### Data availability

Data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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### Competing interests

The authors declare there are no competing interests.

## Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjz-2023-0066>.

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