BRILL

Amphibia-Reptilia 42 (2021): 29-41

brill.com/amre

Post-emergence survival and dispersal of juvenile Jefferson salamander (*Ambystoma jeffersonianum*) and their unisexual dependents

Stephen G. Van Drunen[1,*], Jessica E. Linton[2], James P. Bogart[1], D. Ryan Norris[1,3]

Abstract. Understanding population demography and dispersal of species at risk is integral for evaluating population viability, identifying causes of decline, and assessing the effectiveness of recovery actions. In pond-breeding amphibians, juvenile survival and dispersal are key components linked to population and metapopulation stability but little is known about this life stage. We use mark-recapture methods to estimate juvenile daily apparent survival, dispersal distance, and initial dispersal orientation during summer and fall dispersal of endangered *Ambystoma jeffersonianum* and their unisexual dependents (*Ambystoma laterale – jeffersonianum*). Over four years (2015-2018), 1018 juveniles (612 bisexual, 406 unisexual) were marked and 192 (19%) were recaptured at least once. Total captures varied widely between years, with the highest number of captures (88% of all individuals) occurring in 2017. Cormack-Jolly-Seber estimates of daily apparent survival were low in all years (0.76-0.95) but was higher for unisexuals than bisexuals. The majority of juveniles (71%) did not disperse further than 10-40 m after which movement appeared to cease. While most juveniles remained close to their natal pond, at least 2% of juveniles in 2017 travelled further than 100 m. Dispersal orientation varied by year and there was no difference in either dispersal orientation or distance between bisexual and unisexual individuals. This work is the first to estimate and compare juvenile survival and dispersal of sympatric *A. jeffersonianum* and *A. laterale – jeffersonianum* individuals, the results of which help inform population viability assessment and increase our understanding of juvenile dispersal dynamics and habitat use.

Keywords: *Ambystoma laterale – jeffersonianum*, dispersal direction, dispersal distance, mark-recapture, pond-breeding amphibian, Visible Implant Elastomer tags.

Introduction

Information on demographic rates and dispersal dynamics of juvenile amphibians are crucial for effective protection, management, and recovery of species at risk (Schemske et al., 1994; Doak et al., 2015; Walls et al., 2017). Juvenile survival rates are strongly linked to overall population stability (Taylor et al., 2005; Harper et al., 2008; Pittman et al., 2014) and understanding population demography is integral for evaluating population viability, identifying causes of endangerment, setting appropriate recovery criteria, and quantifying the effects of recovery actions (Schemske et al., 1994; Lesbarrères et al., 2014; Doak et al., 2015; Walls et al., 2017). In addition, juvenile dispersal is a critical component of amphibian species' ability to colonise new habitat, increase gene flow, and adapt to changing environmental conditions or habitat fragmentation (Gill, 1978; Berven and Grudzien, 1990; Rothermel, 2004; Cushman, 2006; Gamble et al., 2007; Semlitsch, 2008; Clobert et al., 2009; Griffiths et al., 2010; Osbourn, 2012; Pittman et al., 2014). Despite the importance of juvenile survival and dispersal dynamics to amphibian species persistence, little is known about this key life stage (Ronce, 2007; Harper et al., 2008; Walls et al., 2017). This lack of knowledge has been identified as a significant barrier to conservation of amphibian species (McCune et al., 2013; Lesbarrères et al., 2014; Camaclang et al., 2015; Bird and Hodges, 2017; Walls et al., 2017).

1 - Department of Integrative Biology, University of Guelph, Guelph, ON, N1G 2W1, Canada
2 - Natural Resource Solutions Inc., Waterloo, ON, N2L 3X2, Canada
3 - Nature Conservancy of Canada, Toronto, ON, M4P 3J1, Canada
*Corresponding author;
e-mail: s.vandrunen@gmail.com

DOI:10.1163/15685381-bja10028

Jefferson salamander (*Ambystoma jeffersonianum*) and their unisexual dependents (*A. laterale* – (2) *jeffersonianum*) are examples of endangered species in Canada for which juvenile demographic and dispersal data is limited. Bisexual *A. jeffersonianum* (denoted as JJ) include diploid male and female individuals, while Jefferson-dependent unisexuals are predominately female and can range in ploidy anywhere from diploid to pentaploid, although most are generally triploid (Bogart, 2003; Bogart and Klemens, 2008). Unisexuals possess at least one blue-spotted salamander (*Ambystoma laterale*) chromosome complement (denoted as L) and up to four *A. jeffersonianum* chromosome complements (i.e. LJ – LJJJJ). Unisexual reproduction occurs via kleptogenesis (Bogart et al., 2007) where unisexuals require the sperm from bisexual males to initiate egg development but rarely incorporate the bisexual genetic material, resulting in gynogenetic offspring that are clones of the unisexual mother. Unisexual *A. laterale* – (2) *jeffersonianum* (LJJ) are found in association with all Canadian *A. jeffersonianum* populations and, because they are morphologically similar, can only be reliably differentiated through DNA testing. For the purposes of species at risk assessment and management in Canada, unisexual *Ambystoma* are grouped together based upon their primary sperm donor (COSEWIC, 2016) and therefore considers *A. jeffersonianum* and *A. laterale* – (2) *jeffersonia*num to be distinct entities (COSEWIC, 2016; Linton et al., 2018).

A. jeffersonianum and *A. laterale* – *jeffersonianum* are endemic to areas throughout eastern North America and inhabit areas of upland forest with access to vernal ponds or wetlands for breeding (Klemens, 2000; Bogart and Klemens, 2008). Endangered in Canada, they are listed as Apparently Secure within the U.S., though *A. jeffersonianum* are classified as Vulnerable or Imperilled in 9 of the 14 states where they occur (NatureServe, 2020). They are fossorial in nature, spending much of their life underground, making them difficult to study. In March and April, mature adults move to breeding ponds to reproduce and, after breeding, disperse back into the surrounding terrestrial habitat (Pfingsten et al., 2013). By mid-July, surviving larvae within the breeding pond undergo metamorphosis, emerge, and being to disperse into the surrounding landscape (Pfingsten et al., 2013).

In Ontario, presence/absence data from breeding pond and egg mass surveys suggest that *A. jeffersonianum* and/or *A. laterale* – *jeffersonianum* populations have declined by $>90\%$ over the past 30 years (COSEWIC, 2016; Linton et al., 2018). In addition, Bogart et al. (2017) showed a decline of 50% over six years in a small population consisting purely of unisexual *A. laterale* – *jeffersonianum*, likely due to a lack of sperm-donor species within the breeding pond. Beyond these general trends, there is little information available on population demographics. A small number of studies have attempted to estimate *A. jeffersonianum* adult or juvenile survival (Williams, 1973; Weller, 1980; Mullin and Klueth, 2009; De Lisle and Grayson, 2011). However, juvenile estimates have been confounded by a lack of recaptures (Weller, 1980) or the impact of drought (Mullin and Klueth, 2009), which resulted in no initial captures. Similarly, only a few studies have estimated *A. jeffersonianum* or unisexual juvenile dispersal distance (Williams, 1973) or direction (Weller, 1980; De Lisle and Grayson, 2011; Hoffmann, 2017). Further research to determine juvenile demographic and dispersal dynamics, and any differences between bisexual and unisexual individuals, is required to assess surviving populations' viability, improve assessment of extinction threats, and provide baseline information to measure the effectiveness of management actions.

There is also little information about whether juvenile survival rates and dispersal may differ by genomotype. Difficulties in mitosis and meiosis or epigenetic instability as ploidy level increases (Teltser and Greenwald, 2015) could result in lower unisexual survival. Alternately, unisexual juveniles may have higher survival than bisexual due to increased habitat tolerances, reproductive advantages, or increased aggression resulting from heterosis (Teltser and Greenwald, 2015). For example, *A. laterale* are generally associated with lower temperature and drier habitat sites (Greenwald et al., 2016), which may impart larger environmental tolerances to unisexuals when compared to bisexuals. Higher habitat tolerances would enable colonization of edge habitat unsuitable to co-occurring bisexual individuals and result in differences in juvenile dispersal distances between genomotypes (Teltser and Greenwald, 2015; Greenwald et al., 2016). However, in a radio telemetry study, adult *A. jeffersonianum* travelled three times as far on average than *A. laterale – jeffersonianum* to reach their overwintering locations (Van Drunen et al., 2020), which may indicate greater locomotor endurance in bisexual individuals, similar to that found by Denton et al. (2017). Filling knowledge gaps regarding differences between juvenile bisexual and unisexual salamanders is important for understanding the population demographic and dispersal dynamics of these endangered species.

Using a mark-recapture approach, we address four main questions related to juvenile *A. jeffersonianum* and *A. laterale – jeffersonianum* ecology: (1) What are the rates of juvenile survival during dispersal in summer and fall?; (2) What distances do juveniles disperse away from their natal pond after undergoing metamorphosis?; (3) Does survival or dispersal distance differ between bisexual and unisexual individuals; and (4) Are there patterns between years and/or bisexuals and unisexuals in initial dispersal direction away from their natal pond?

Materials and methods

Study site

Our study pond is located near Dundas, Ontario, Canada (exact location withheld because of the endangered status of the species). This precipitation and groundwater fed vernal pond (approx. 450 m^2) is located within a relatively undisturbed area (>3 km^2) of mature deciduous forest. *A. jeffersonianum* and their unisexual dependents are also supported by a few other small vernal ponds within 300 m of the study pond (J.E.L., J.P.B., pers. obs.). *A. jeffersonianum* make up approximately one-third of breeding adults within the study pond, with the remaining two-thirds consisting primarily of triploid *A. laterale-jeffersonianum* (J.P.B., unpubl. data). No *A. lat*erale co-occur in the area (J.P.B., unpubl. data). In addition to *A. jeffersonianum* and *A. laterale – jeffersonianum*, other amphibian species found in this forest include American toad (*Anaxyrus americanus*), wood frog (*Lithobates sylvaticus*), spring peeper (*Pseudacris crucifer*), green frog (*Lithobates clamitans*), eastern newt (*Notophthalmus viridescens*), eastern red-back salamander (*Plethodon cinereus*), four-toed salamander (*Hemidactylium scutatum*), and spotted salamander (*Ambystoma maculatum*).

Mark-recapture data collection

Juvenile *A. jeffersonianum* and *A. laterale – jeffersonianum* were marked and recaptured in various summer and fall seasons from 2015 to 2019 (table 1) using drift fence and pitfall traps. This project was initiated, and field work primarily conducted by, the environmental consulting firm Natural Resource Solutions Inc. In June 2015, two drift fences were installed that completely encircled the study pond at distances of approximately 1-6 m (inner fence) and 14-27 m (outer fence; fig. 1) from the edge of the water. In addition, a single linear section of fence was installed 65 m from the pond. Then in September 2015, five "star" arrays were added (fig. 1) with the idea that they would better delineate the direction of movement of captured individuals. Finally, in March 2016, nine additional linear sections of drift fence were installed at distances ranging from 50 to 132 m from the study pond (fig. 1). Linear sections of fence ranged in length from 20 to 40 m (mean = 26 m) and the fencing furthest from the study pond encompassed approximately 34% of the outer perimeter (270/790 m). The circular fences consisted of recycled plastic Animex Wildlife Fencing and the array and linear segments consisted of standard construction silt fencing. All drift fencing was buried at least 10 cm into the ground to prevent individuals escaping underneath. Pitfall traps were positioned on both sides of all fencing at approximately 5 m intervals. These traps consisted of metal

Table 1. Pitfall trapping start and end dates per season and year at the study site near Dundas, ON, Canada. Trapping was halted early in the fall of 2016 and at the start of fall 2018 due to drought conditions and funding limitations respectively.

Season	Date	2015	2016	2017	2018	2019
Spring	Start	–	08-Mar	–	27-Mar	28-Mar
	End	–	21-Apr	–	14-Apr	18-Apr
Summer	Start	26-Jun	27-Jun	17-Jul	23-Jul	–
	End	31-Aug	31-Aug	31-Aug	31-Aug	–
Fall	Start	01-Sep	01-Sep	01-Sep	24-Sep	–
	End	30-Oct	09-Sep	27-Oct	25-Oct	–

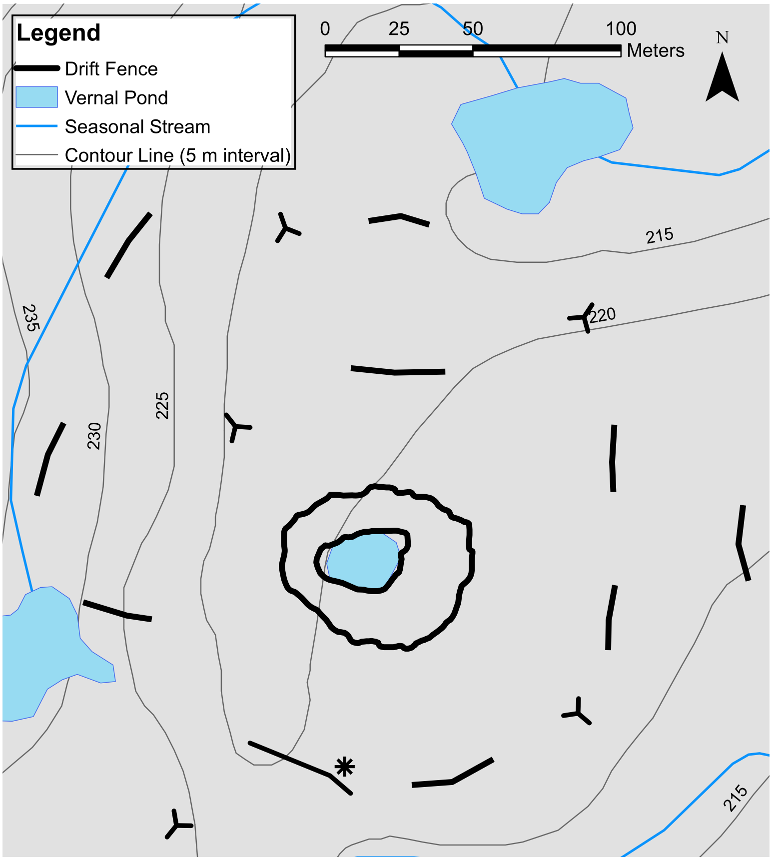

Figure 1. Drift fencing setup at the study site near Dundas, ON, Canada. Study pond is at center surrounded by the inner and outer circular fences. The inner and outer circular fences and one linear fence (marked with an asterisk) were installed in June 2015. The five 'star' arrays (three prong arrays) were installed in September 2015, while the remaining linear fences were installed in March 2016. Pitfall traps were installed on both sides of all fencing at approximately 5 m intervals. This map depicts vernal ponds during spring conditions, actual pond size fluctuates through time depending on weather.

cans (3.7 liters with a diameter of 15 cm and depth of 19 cm) with holes in the bottom covered in fine mesh to facilitate drainage but prevent small individuals from escaping. A wet sponge and leaf litter was placed in each trap to keep captured individuals moist and provide them with cover. In addition, a thin wooden dowel was inserted in the trap to allow small mammals to escape and each trap was partially covered with a rock to deter predation.

During trapping periods, traps were checked twice daily approximately 12 hours apart. Captured *A. jeffersonianum* and *A. laterale – jeffersonianum* were marked with a unique identifying code using visible implant elastomer (VIE) tags. VIE tags are commonly used in amphibian studies and are considered a humane and effective method for identification of individuals (Davis and Ovaska, 2001; Bailey, 2004). VIE tag colors included red, orange, blue, green, yellow, and pink. Blue and green as well as red and pink were never used together on the same individual to avoid problems differentiating between these colors in the field. A total of six unique marking locations were available for use: each upper limb and either side of the base of the tail. Every individual was given three VIE tags where the combination of colors and body locations of these marks were unique to each individual. Individuals were marked in the field without anaesthetization. In addition, a 3 mm tail clip was collected from each marked juvenile and stored in 70% ethanol for later genetic analysis of genomotype, and individuals' snout-to-vent length (SVL) was measured to the nearest mm. Captured individuals were released on the opposite side of the fence from where they were caught. Recaptured individuals were identified by their VIE tag and another SVL measurement recorded. Outside of trapping periods, the pitfall traps were closed, and sections of fencing opened to allow free movement throughout the study area.

Individual genomotype was determined using DNA extracted from the tail tip samples using microsatellite DNA analyses at six polymorphic, tetranucleotide loci (AjeD75, AjeD94, AjeD283, AjeD346, AjeD378, AjeD422) (Julian et al., 2003), which have been used to identify bisexual and unisexual genomotypes in previous studies (Bogart et al., 2007, 2009, 2017). Ploidy was assigned to individuals based on the largest number of microsatellite DNA alleles observed at any locus and the lowest number of chromosomes that could be present based on genome-specific microsatellite DNA alleles.

Mark-recapture model

We used fixed group Cormack-Jolly-Seber models (Cormack, 1964; Jolly, 1965; Seber, 1965) to estimate genotype-specific summer to fall daily apparent survival and detection probabilities per year. Our two groups consisted of bisexual (*A. jeffersonianum*) and unisexual (*A. laterale – jeffersonianum*; LJJ and LJJJ) juveniles. A separate model was run for each year (2015, 2017, 2018) where survival and detection were held constant per group through time. Our models used code adapted from Kéry and Schaub (2012) and were analyzed within a Bayesian framework implemented in JAGS v4.3.0 (Plummer, 2003) using the R package 'R2jags' (Su and Yajima, 2015). Uninformative priors, uniformly distributed between 0 and 1, were used for all parameters. Daily apparent survival was defined as the probability of a juvenile salamander surviving from day t to day $t + 1$ and detection probability was defined as the probability of detection for a juvenile salamander that is alive and present in the study site at day $t + 1$. Three chains were run for 200 000 iterations with a burn-in of 100 000 iterations and every third sample kept. Convergence via standard MCMC diagnostics (Brooks and Gelman, 1998) was reached for all parameters (Rhat $\leqslant$ 1.01).

Morning and evening capture data were combined into single day observations, as the majority (83%) of captures were made in the morning trapping periods. No juvenile individuals were recaptured outside of the summer to fall period they were initially tagged in, making estimates of yearly survival impossible. Variation in the start date of the trapping period between years (table 1) was a result of increasing experience with predicting the timing of juvenile emergence as the project progressed. Since the first capture of individuals occurred on July 30, July 18, and July 24 in 2015, 2017, and 2018 respectively, we truncated our 2015 capture history to July 17 to match the start date of trapping in 2017. So, the capture histories used in our models included data from July 17 to Oct. 30 in 2015, July 17 to Oct. 27 in 2017, and July 23 to Oct. 25 in 2018. Unfortunately, due to funding limitations trapping was halted from Sept. 1 to Sept. 23 in 2018 which was not accounted for in our 2018 model. This likely resulted in biased estimates for this year as actual detection probability would have be higher than estimated.

Variation in the field methods to record the age of captured individuals occurred between years. In 2015, individuals were categorized as either juvenile or adult then, in the years after, further refined to classify metamorphs and juveniles separately. Unfortunately, delineations of metamorphs from juveniles was inconsistently applied by field technicians. For the analyses here, we took the SVL measurements from individuals that were recorded as metamorphs in 2017 (mean = 36 mm, range 26 to 53 mm) and defined juveniles in each year as those individuals with an initial capture SVL $\leqslant$ 54 mm. It is possible this included some smaller first-year juveniles, but most individuals captured were recent metamorphs, often with obvious gill reabsorption sites present (J.E.L., SVL, pers. obs.).

Dispersal distance and orientation

Dispersal distance was estimated as the distance from a juvenile's last capture location to the center of the study pond. Because juveniles were captured from other breeding ponds near to the study pond, only juveniles known to have emerged from the study pond (i.e. their first capture was in any trap located within the area contained by the outer circular fence) were included. We refer to this subset of marked individuals as "dispersing juveniles".

We used a generalized linear model (gamma family with log link) to assess whether body size (SVL) predicted distance travelled by dispersing juveniles. Genotype (bisexual, unisexual) was included in the model to account for differences between bisexuals and unisexuals in distance travelled, and year (2015, 2017, 2018) was included to account for differences in sampling effort.

The first capture of each of the dispersing juveniles was examined to assess uniformity and similarity of initial dispersal orientation. Coordinates of each pitfall trap were recorded with ±1 m accuracy using SXBlue II GNSS GPS (SXBlue GPS, Anjou, QC) and the direction of each trap from the center of the study pond was estimated using ArcGIS v10.5.1 (ESRI, 2017). For years with sufficient sample size, we analyzed captured bisexual (2015: $n = 30$; 2017: $n = 415$) and unisexual (2015: $n = 8$; 2017: $n = 193$) individuals separately. The Rayleigh test was used to assess if the distribution of initial dispersal directions was uniformly distributed per group by year. Finally, we used the Kruskal-Wallis test to assess differences in direction between samples with non-uniform emergence orientation. Because only eight bisexual and no unisexual dispersing juveniles were captured in 2018 and, because of a drought, no juveniles were captured in 2016, these years were excluded from the orientation analyses. Circular analyses were conducted using the R package "circular" (Agostinelli and Lund, 2017) within R v3.5.0 (R Core Team, 2018).

Results

Juvenile survival

We marked 1018 juveniles (612 bisexual, 406 unisexual) over four years of trapping with 192 individuals (19%) recaptured at least once (table 2). An additional four recapture observations of incomplete identification (i.e. a VIE ID missing one or two of its three colored tags) occurred, these observations are excluded from all analyses. Over the course of the study, approximately 0.7% of all target and incidental species

Table 2. The number of captures per individual by genotype and year during summer and fall pitfall trapping at a study site near Dundas, ON, Canada. Bisexual and Unisexual represent *Ambystoma jeffersonianum* and *Ambystoma laterale – jeffersonianum* (LJJ and LJJJ) individuals respectively. No juveniles were captured in 2016 due to a drought which caused the study pond to dry up by July 7.

	2015		2017		2018		
Number of Captures	Bisexual	Unisexual	Bisexual	Unisexual	Bisexual	Unisexual	Total
1	43	18	421	307	30	7	826
2	8	11	85	57	3	1	165
3	2	0	17	5	0	0	24
4	0	0	3	0	0	0	3
Total	53	29	526	369	33	8	1018

captured within our traps were found injured or dead. Juvenile *A. jeffersonianum* and *A. laterale – jeffersonianum* captures were highest in 2017 (88% of all individuals) and relatively low in other years (table 2). No juveniles were captured in any of the spring trapping periods or at all in 2016 when a drought completely dried up the study pond by July 7. Survival of larvae to metamorphosis was assumed to be zero for both bisexuals and unisexuals at the site in 2016. In addition, the small unisexual sample size in 2018 ($n = 8$) was insufficient to estimate survival and detection parameters for these individuals, only bisexual survival and detection were estimated in this year.

Juvenile daily apparent survival from emergence in mid-July to the end of October was higher for unisexuals compared to bisexuals in both 2015 and 2017 (fig. 2a). Bisexual survival was 0.76 (95% credible interval (CI) = 0.64, 0.86) in 2015, 0.78 (95% CI = 0.75, 0.82) in 2017, and 0.83 (95% CI = 0.68, 0.94) in 2018. Unisexual survival was 0.95 (95% CI = 0.90, 0.98) in 2015 and 0.87 (95% CI = 0.84, 0.90) in 2017. Detection probabilities were very low and similar between bisexual and unisexual individuals in 2015 but not in 2017 (fig. 2b). Bisexual detection probability was 0.08 (95% CI = 0.04, 0.15) in 2015, 0.07 (95% CI = 0.05, 0.08) in 2017, and 0.03 (95% CI = 0.01, 0.07) in 2018. Unisexual detection probability was 0.04 (95% CI = 0.02, 0.07) in 2015 and 0.03 (95% CI = 0.02, 0.04) in 2017.

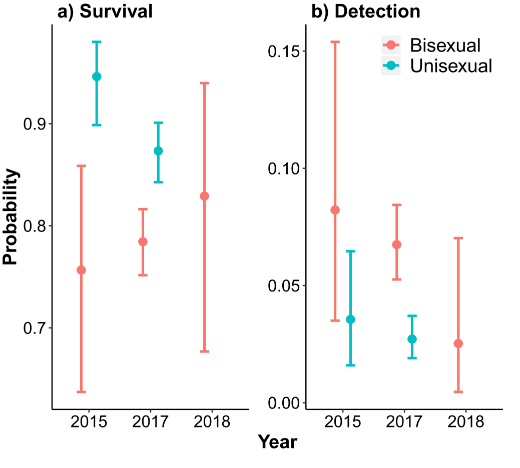

Figure 2. Daily apparent survival (a) and detection (b) estimates from emergence in mid-July to the end of October for juvenile salamanders at a study site near Dundas, ON, Canada. Due to a drought in 2016, no juveniles were captured and survival was assumed to be zero for all individuals in this year. The unisexual sample size ($n = 8$) in 2018 was insufficient to estimate survival and detection parameters. Bisexual are *A. jeffersonianum* and Unisexual are *A. laterale – jeffersonianum* (LJJ and LJJJ) individuals. Points represent mean estimates and error bars are the associated 95% credible intervals.

Dispersal distance and orientation

The vast majority (98%) of dispersing juveniles travelled less than 50 m from their natal pond. Only a small proportion of juveniles (2%) in 2017 travelled greater than 100 m, to the edge of the trapping array (fig. 3). For juveniles whose SVL was recorded, the mean SVL ($\pm$ SE) for bisexuals was 34.6 $\pm$ 0.7 mm in 2015 ($n = 52$), 35.3 $\pm$ 0.2 mm in 2017 ($n = 526$), and 34.8 $\pm$ 0.9 mm in 2018 ($n = 33$). For unisexuals, the mean SVL ($\pm$ SE) was 41.5 $\pm$

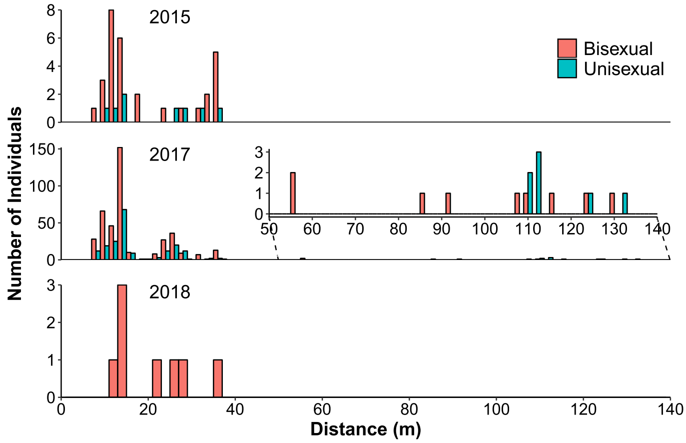

Figure 3. Distance from natal pond to final capture location by year for juvenile salamanders at a study site near Dundas, ON, Canada. Individuals were captured via daily pitfall trapping during June 26 – Oct. 30 in 2015 ($n = 30$ bisexual + 8 unisexual), June 27-Sept. 9 in 2016 (no captures), July 17-Oct. 27 in 2017 ($n = 415$ bisexual + 193 unisexual), and July 23-Aug. 31 and Sept. 24-Oct. 25 in 2018 ($n = 8$ bisexual + 0 unisexual). No unisexual individuals were captured in 2018 and, due to a drought, no juveniles emerged in 2016. Bisexual are *A. jeffersonianum* and Unisexual are *A. laterale – jeffersonianum* (LJJ and LJJJ) individuals. Bars are offset for clarity and the insert is a close-up of the matching section of 2017.

1.2 mm in 2015 ($n = 29$), 36.5 ± 0.2 mm in 2017 ($n = 368$), and 39.5 ± 1.1 mm in 2018 ($n = 8$). There was no effect of genotype ($\beta \pm \mathrm{SE} = 0.05 \pm 0.07$, $t_{612} = 0.66$, $P = 0.51$) or year (2017: $\beta \pm \mathrm{SE} = -0.01 \pm 0.16$, $t_{612} = -0.09$, $P = 0.93$; 2018: $\beta \pm \mathrm{SE} = 0.18 \pm 0.32$, $t_{612} = 0.55$, $P = 0.58$) on distance travelled. Dispersal distance was, however, significantly related to SVL ($\beta \pm \mathrm{SE} = 0.027 \pm 0.009$, $t_{612} = 3.05$, $P < 0.005$), where dispersal distance increased at a multiplicative rate of 1.03 meters per mm increase in SVL. Juvenile dispersal orientation was non-uniform in 2015 and 2017 for both bisexual (2015: $z = 0.53$, $P < 0.001$, $n = 30$; 2017: $z = 0.14$, $P < 0.001$, $n = 415$) and unisexual (2015: $z = 0.66$, $P < 0.05$, $n = 8$; 2017: $z = 0.31$, $P < 0.001$, $n = 193$) individuals. Both bisexual and unisexual orientation differed between years but there was no difference in orientation between genotypes in either 2015 or 2017 (table 3, fig. 4). For both genotypes, initial dispersal direction was predominately westward in 2015, and had major west- and eastward components in 2017 (fig. 4).

Table 3. Kruskal-Wallis test statistic (H), degrees of freedom (df), and P-value for comparisons of groups with non-uniform juvenile salamander emergence direction. Bisexual and Unisexual represent *Ambystoma jeffersonianum* and *Ambystoma laterale – jeffersonianum* (LJJ and LJJJ) individuals respectively.

Comparison	H	df	P-value
2015: Bisexual vs. Unisexual	1.05	1	0.30
2017: Bisexual vs. Unisexual	3.63	1	0.06
Bisexual: 2015 vs. 2017	6.50	1	0.01
Unisexual: 2015 vs. 2017	5.00	1	0.03

Discussion

Daily apparent survival was very low for juvenile *A. jeffersonianum* and *A. laterale – jeffersonianum* in all years of our study. Between mid-July to the end of October, daily survival estimates ranged between years from 0.76 to 0.95 or, calculated as monthly survival (e.g. daily survival$^{30\ \mathrm{days}}$), from 0.0003 to 0.21. Extrapolated over the entire year, this survival rate is effectively zero and much lower than reported for other species of *Ambystoma*. For example, Rothermel and Semlitsch (2006) raised captive marbled (*Ambystoma opacum*) and spotted salamanders (*A. maculatum*) from eggs, releasing newly metamorphosed individuals into forested

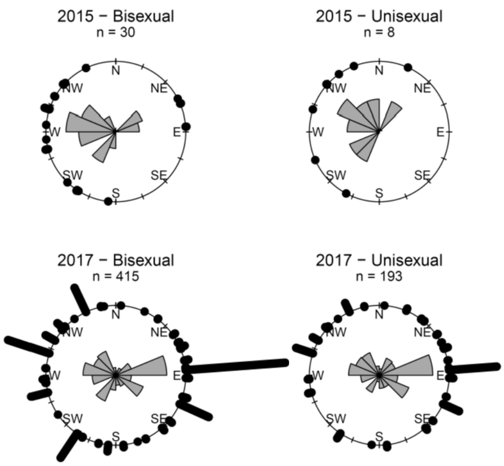

Figure 4. Circular data plots and rose diagrams of pitfall captures of juvenile salamanders per year and genotype. Bisexual are *A. jeffersonianum* and Unisexual are *A. laterale – jeffersonianum* (LJJ and LJJJ) individuals combined. Points are raw counts per direction (points overlap to reduce plot size) and the areas of the sectors in the rose diagram represent the relative frequencies over 16 class intervals. A drought led to no emergence in 2016 and only 8 bisexual juveniles were captured in 2018, so plots for those years have been excluded.

enclosures. Proportion of individuals that survived from summer to fall was 39% for *A. opacum* and 17% for *A. maculatum*. It is unlikely that populations could persist if the low rates of juvenile apparent survival reported in this study were close to actual survival rates.

Expert opinion suggests juvenile *A. jeffersonianum* survival rates are similar to those of adult individuals (Pfingsten et al., 2013). Adult survival estimates are much higher than our juvenile estimates. For example, during mark-recapture studies of *A. jeffersonianum* Williams (1973) found >50% annual adult survival and De Lisle and Grayson (2011) reported annual survival probabilities ranging from approximately 0.45 to 0.65 depending on sex. Pond-breeding juvenile salamanders' elusive nature make accurate estimates very difficult, especially in years with low recruitment. Interestingly, juvenile survival did not appear to be influenced by changes in density as survival rates were similar across years regardless of the large variation in the total number of individuals captured. Further study is required before these juvenile survival estimates can be reliably incorporated into population viability analyses or used to inform conservation management actions, such as reintroduction efforts involving juveniles.

Apparent survival estimates generally underestimate true survival rates because any individuals emigrating out of the study area are indistinguishable from mortality events. Emigration does not seem to be a confounding issue in our estimates because only a small proportion (2%) of individuals in 2017 were captured at the outer limits of the trapping array (>100 m from the study pond). In contrast, the majority of individuals (71%) were only captured within inner fence traps and did not disperse beyond 10-40 m. While gaps between fences likely resulted in some juveniles going undetected at the outer edge of our study area, our results are similar to observations from a study of *A. opacum* where 79% of newly metamorphosed juveniles travelled <90 m and only 8% moved beyond 172 m (Scott et al., 2013). The lack of movement between the inner and outer fences is reflected in our extremely low detection estimates and highlights the difficulty in studying these juvenile salamanders.

The lack of movement observed over the course of our study supports Semlitsch's (2008) theory of interval dispersal for pond-breeding amphibians. He suggested that, due to the high mortality risk encountered upon leaving their natal pond, newly metamorphosed amphibians' first dispersal movement is primarily a short distance into the terrestrial environment. After the first winter or in later years, when they grow larger and are less at risk of predation or desiccation, juveniles then continue to disperse away from their natal pond. As noted, most juveniles in our study did not travel far from the natal pond and we did not recapture any juveniles outside of the year they were initially marked in. If an interval dispersal process is occurring in the study population, then it is possible that we only captured newly metamorphosed individuals during the short initial terrestrial movement phase. These individuals may have continued to disperse out of the study area at a time when trapping did not occur, perhaps during late spring or early summer when weather conditions could be more favorable to extended movements.

Estimating juvenile *A. jeffersonianum* and *A. laterale – jeffersonianum* survival is difficult due to the cryptic nature of these species resulting in low detection of individuals. Weller (1980) found *A. jeffersonianum* juveniles were rarely recaptured reporting only 2 of 181 marked juveniles were encountered as adults. Similarly, in our study no juveniles were recaptured outside of the year they were marked and detection probabilities were low (ranging from 0.03 to 0.08) within each year. Low detection rates of juveniles through time may occur when very few juveniles survive to be captured, if the majority of juvenile movements occur outside of the sampling periods (e.g. during late April to June in our study), or if juveniles remain underground, close to their natal pond, until they reach sexual maturity (Pfingsten et al., 2013).

Another issue could be the short time span of studies in relation to sexual maturity. Juvenile *A. jeffersonianum* require 2-4 years to sexually mature (Pfingsten et al., 2013) before they would be encountered as adults during a period of spring breeding. Williams (1973) suggested a study length of ten years is required to adequately estimate demographic rates of *Ambystoma* populations. In addition, it may be that juveniles are losing their VIE marks or marks are reduced in visibility as individuals mature. Over the course of this study, observations of incomplete VIE IDs comprised only 2% of all recapture observations, compared to 10-30% when recapturing breeding adults as part of a related study (S.G.V., J.E.L., J.P.B, D.R.N, unpubl. data), potentially due to the darker skin of mature individuals reducing tag visibility. These points illustrate some of the challenges associated with estimating demographic rates of ambystomatid salamanders and highlights the importance of carefully considering the study length and marking methods for future work.

Variation in numbers of dispersing juveniles is often directly related to breeding-pond hydrology. Juveniles are highly dependent on their natal pond retaining standing water long enough for metamorphosis to occur, although it is not unusual for ponds to dry early leading to mortality of large proportions of larvae (Semlitsch et al., 1996). In 2016, our study pond dried up in early July and no juveniles were captured across the site. Similarly, the pond studied by Mullin and Klueth (2009) dried up in the spring of both years of their study, making it impossible to estimate juvenile survival. In a long-term study of amphibian populations, Semlitsch et al. (1996) reported pond drying in four of the 16 years of their study. Hydrological variation in vernal ponds has been well documented as a limiting factor in pond-breeding amphibians (Shoop, 1974; Pechmann et al., 1989; Rowe and Dunson, 1995; Semlitsch et al., 1996; Skelly, 1996; Brodman, 2009; Mullin and Klueth, 2009) highlighting the need to protect vernal pond hydrological sources and wetland connections as part of conservation efforts (Rothermel, 2004; Crawford et al., 2016; Linton et al., 2018; Zaffaroni et al., 2019). In addition, further research is needed to understand the potential population impacts of changes in vernal pond hydroperiod due to climate change (Linton et al., 2018).

Even in years when ponds retain sufficient water to support larvae to metamorphosis significant variation in reproductive output can occur. In our study, the number of dispersing juveniles was approximately an order of magnitude larger in 2017 than in either 2015 or 2018. This variation may be due to spring environmental conditions that affect breeding effort or egg viability. In addition, breeding adults are known to skip breeding in years with unfavorable environmental conditions (Williams, 1973; De Lisle and Grayson, 2011; Mills and Ward, 2015) and water temperature has been shown to influence number of egg masses laid and embryo survival

(Brodman et al., 2002). Information is not available from 2016 but in 2018, the vast majority (>80%) of egg masses surveyed in the study pond appeared to be nonviable in April (J.E.L., S.G.V., pers. obs.) suggesting spring conditions were unfavorable to egg development for *A. jeffersonianum*, and/or their unisexuals resulting in the low number of juvenile captures that year. Predation or food abundance during the larval stage may also be key factors in determining the number of larvae surviving to metamorphosis (Searcy et al., 2014).

Differences in the proportion of bisexual to unisexual across different life stages suggests bisexuals are more successful at the egg and/or larval stage than unisexuals. Bisexual adults constituted approximately a third of all breeding adults within our study pond, while bisexual juveniles comprised 59-80% of individuals captured in each year of our study (table 2). One explanation is that egg and/or larval survival rates are lower for unisexuals than bisexuals. Teltser and Greenwald (2015) observed the relative frequency of Blue-spotted dependent unisexuals over the course of their life cycle and found that the proportion of *A.* (3) *laterale – jeffersonianum* (i.e. LLLJ) declined throughout larval development. These differences in survival at the larval stage may be due to difficulties in mitosis and meiosis or epigenetic instability as ploidy level increases (Teltser and Greenwald, 2015). After emergence, the higher survival of unisexuals likely leads to an increase in their relative frequency. Alternately, low numbers of unisexual juveniles may be due to an inverse relationship between unisexual fertilization rates and the proportion of bisexuals within a population, since *A. jeffersonianum* males preferentially breed with female *A. jeffersonianum* over unisexuals (Dawley and Dawley, 1986). Further study is required to understand how varying proportions of bisexual and unisexual individuals influences population dynamics through time.

Differences between bisexual and unisexual juveniles were observed in survival rates but not in dispersal distance or orientation. Higher unisexual survival could be explained by increased environmental tolerance imparted by their *A. laterale* genetic component, which may include reduced susceptibility to lower temperatures and drier habitats (Greenwald et al., 2016). Both bisexuals and unisexuals dispersed similar distances and directions in each year, suggesting either juvenile habitat requirements are identical or, if habitat preferences differ between genomotypes, then these different areas are perhaps equally distributed across the study site. Similar patterns of significant variation in dispersal orientation between years was demonstrated by both bisexuals and unisexuals. Variable juvenile dispersal orientation is a common trait in amphibians (Malmgren, 2002; Jenkins et al., 2006; Patrick et al., 2007; De Lisle and Grayson, 2011). Dispersal orientation may be an inherited trait that increases juvenile likelihood of dispersing to higher quality areas with minimal exploration (Joly, 2019). If inherited in *A. jeffersonianum* or *A. laterale – jeffersonianum*, variation in juvenile orientation could arise from yearly differences in the composition of the adult breeding cohort as individuals skip breeding in some years (Williams, 1973; De Lisle and Grayson, 2011). Unfortunately, our data do not allow us to test for a relationship between adult and juvenile orientation, since we only have data on adult spring breeding migrations from 2016 and 2018, years in which little to no juveniles were captured dispersing from the study pond. Alternately, juvenile dispersal may be related to microhabitat characteristics. For example, juvenile *A. maculatum* prefer areas of high burrow density and high coarse woody debris (Osbourn et al., 2014). Similar to Weller (1980), in our study the highest number of juveniles were captured at traps in low lying areas or near large, decomposing logs (S.G.V., pers. obs.), perhaps because these are areas of high moisture retention. Further research into juvenile microhabitat selection would help to answer uncertainties in habitat use during this key life stage.

This study is the first to estimate and compare juvenile survival and dispersal of sympatric *A. jeffersonianum* and *A. laterale- jeffersonianum* individuals. Our results fill key gaps in basic species biology relating to juvenile salamander demography and increases our understanding of juvenile dispersal dynamics. Future research is required to understand drivers of low detection probability and variability of dispersal dynamics for these cryptic endangered species.

Acknowledgements. Many volunteers assisted with field work, as well as employees from Natural Resource Solutions Inc. Hamilton Conservation Authority provided land access to the study site. A. Sandilands provided input into the initial study design. Funding was provided by Schlegel Urban Developments Inc. and Waterdown Bay Ltd. in support of their Overall Benefit permits under the 2007 *Endangered Species Act* and a Discovery Grant to D.R.N. from the Natural Sciences and Engineering Research Council of Canada. All research was carried out in accordance with the relevant permits and animal care protocols: Wildlife Scientific Collector's Authorizations No. 1079518, 1082343, 1086762, 1088803, 1088920, and 1092124A issued under the *Fish and Wildlife Conservation Act*; Permit No. GU-C-002-14, GU-B-002-17, AND GU-C-003-15 issued under the *Endangered Species Act*, 2007; Animal Care Protocol #145 issued by the Ontario Ministry of Natural Resources and Forestry Wildlife Animal Care Committee; and University of Guelph Animal Utilization Protocol #3673.

References

Agostinelli, C., Lund, U. (2017): R package 'circular': circular statistics (version 0.4-93). URL https://r-forge.r-project.org/projects/circular/.

Bailey, L.L. (2004): Evaluating elastomer marking and photo identification methods for terrestrial salamanders: marking effects and observer bias. Herpetol. Rev. **35** (1): 38-41.

Berven, K.A., Grudzien, T.A. (1990): Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. Evolution **44**: 2047-2056.

Bird, S.C., Hodges, K.E. (2017): Critical habitat designation for Canadian listed species: slow, biased, and incomplete. Environ. Sci. Policy. **71**: 1-8.

Bogart, J.P. (2003): Genetics and systematics of hybrid species. In: Reproductive Biology and Phylogeny of Urodela, vol. 1, p. 109-134. Sever, D.M., Ed., M/s Science, Enfield, New Hampshire, USA.

Bogart, J.P., Klemens, M.W. (2008): Additional distributional records of *Ambystoma laterale*, *A. jeffersonianum* (Amphibia: Caudata) and their unisexual kleptogens in northeastern North America. Am. Mus. Novit. **3627**: 58 pp.

Bogart, J.P., Bi, K., Fu, J., Noble, D.W.A., Niedzwiecki, J. (2007): Unisexual salamanders (genus *Ambystoma*) present a new reproductive mode for eukaryotes. Genome **50**: 119-136.

Bogart, J.P., Bartoszek, J., Noble, D.W.A., Bi, K. (2009): Sex in unisexual salamanders: discovery of a new sperm donor with ancient affinities. Heredity **103**: 483-493.

Bogart, J.P., Linton, J.E., Sandilands, A. (2017): A population in limbo: unisexual salamanders (genus *Ambystoma*) decline without sperm-donating species. Herpetol. Conserv. Bio. **12**: 41-55.

Brodman, R. (2002): Twelve-year study monitoring two species of pond-breeding salamanders in northeast Ohio. Ohio J. Sci. **102** (5): 123-127.

Brodman, R. (2009): A 14-year study of amphibian populations and metacommunities. Herpetol. Conserv. Bio. **4** (1): 106-119.

Brooks, S.P., Gelman, A. (1998): General methods for monitoring convergence of iterative simulations. J. Comput. Graph. Stat. **7**: 434-455.

Camaclang, A.E., Maron, M., Martin, T.G., Possingham, H.P. (2015): Current practices in the identification of critical habitat for threatened species. Conserv. Biol. **29** (2): 482-492.

Clobert, J., Le Galliard, J.F., Cote, J., Meylan, S., Massot, M. (2009): Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecol. Lett. **12**: 197-209.

Cormack, R.M. (1964): Estimates of survival from the sighting of marked animals. Biometrika **51**: 429-438.

COSEWIC. (2016): COSEWIC assessment and status report on the unisexual *Ambystoma*, *Ambystoma laterale*, Small-mouthed Salamander-dependent population, Jefferson Salamander-dependent population and the Blue-spotted Salamander-dependent population, in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xxii + 61 pp.

Crawford, J.A., Peterman, W.E., Kuhns, A.R., Eggert, L.S. (2016): Altered functional connectivity and genetic diversity of a threatened salamander in an agroecosystem. Landscape Ecol. **31**: 2231-2244.

Cushman, S.A. (2006): Effects of habitat loss and fragmentation on amphibians: a review and prospectus. Biol. Conserv. **128**: 231-240.

Davis, T.M., Ovaska, K. (2001): Individual recognition of amphibians: effects of toe-clipping and fluorescent tagging on the salamander *Plethodon vehiculum*. J. Herpetol. **35** (2): 217-225.

Dawley, E.M., Dawley, R.M. (1986): Species discrimination by chemical cues in a unisexual-bisexual complex of salamanders. J. Herptol. **20** (1): 114-116.

De Lisle, S.P., Grayson, K.L. (2011): Survival, breeding frequency, and migratory orientation in the Jefferson salamander, *Ambystoma jeffersonianum*. Herpetol. Conserv. Biol. **6** (2): 215-227.

Denton, R.D., Greenwald, K.R., Gibbs, H.L. (2017): Locomotor endurance predicts differences in realized dispersal between sympatric sexual and unisexual salamanders. Funct. Ecol. **31**: 915-926.

Doak, D.F., Himes Boor, G.K., Bakker, V.J., Morris, W.F., Louthan, A., Morrison, S.A., Stanley, A., Crowder, L.B. (2015): Recommendations for improving recovery criteria under the US Endangered Species Act. Bioscience **65** (2): 189-199.

ESRI. (2017): ArcGIS 10.5.1. Redlands, CA, USA: Environmental Systems Research Institute.

Gamble, L.R., McGarigal, K., Compton, B.W. (2007): Fidelity and dispersal in the pond-breeding amphibian, *Ambystoma opacum*: implications for spatio-temporal population dynamics and conservation. Biol. Conserv. **139**: 247-257.

Gill, D.E. (1978): The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). Ecol. Monogr. **48**: 145-166.

Greenwald, K.R., Denton, R.D., Gibbs, H.L. (2016): Niche partitioning among sexual and unisexual *Ambystoma* salamanders. Ecosphere **7** (11): 17 pp.

Griffiths, R.A., Sewell, D., McCrea, R.S. (2010): Dynamics of a declining amphibian metapopulation: survival, dispersal and the impact of climate. Biol. Conserv. **143**: 485-491.

Harper, E.B., Rittenhouse, T.A.G., Semlitsch, R.D. (2008): Demographic consequences of terrestrial habitat loss for pool-breeding amphibians: predicting extinction risks associated with inadequate size of buffer zones. Conserv. Biol. **22**: 1205-1215.

Hoffmann, K.E. (2017): Breeding ecology and habitat use of unisexual salamanders and their sperm-hosts, Blue-spotted salamanders (*Ambystoma laterale*). Ph.D. Thesis. University of Maine, Orono, ME. xiii + 112 pp.

Jenkins, C.L., McGarigal, K., Timm, B.C. (2006): Orientation of movements and habitat selection in a spatially structured population of Marbled Salamanders (*Ambystoma opacum*). J. Herpetol. **40**: 240-248.

Jolly, G.M. (1965): Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika **52**: 225-247.

Joly, P. (2019): Behaviour in a changing landscape: using movement ecology to inform the conservation of pond-breeding amphibians. Front. Ecol. Evol. **7** (156): 17 pp.

Julian, S.E., King, T.L., Savage, W.K. (2003): Novel Jefferson salamander, *Ambystoma jeffersonianum*, microsatellite DNA markers detect population structure and hybrid complexes. Mol. Ecol. Notes. **3**: 95-97. DOI:10.1046/j.1471-8286.2003.00362.x.

Kéry, M., Schaub, M. (2012): Bayesian Population Analysis Using WinBUGS: a Hierarchical Perspective. Academic Press, Waltham, MA, USA. Xvii + 535 pp.

Klemens, M.W. (2000): Amphibians and reptiles in Connecticut: a checklist with notes on conservation status, identification, and distribution. DEP Bulletin 32: 1-96, Hartford, CT: Connecticut Department of Environmental Protection, Environmental and Geographic Information Center.

Lesbarrères, D., Ashpole, S.L., Bishop, C.A., Blouin-Demers, G., Brooks, R.J., Echaubard, P., Govindarajulu, P., Green, D.M., Hecnar, S.J., Herman, T., Houlahan, J., Litzgus, J.D., Mazerolle, M.J., Paszkowski, C.A., Rutherford, P., Schock, D.M., Storey, K.B., Lougheed, S.C. (2014): Conservation of herpetofauna in northern landscapes: threats and challenges from a Canadian perspective. Biol. Conserv. **170**: 48-55.

Linton, J., McCarter, J., Fotherby, H. (2018): Recovery Strategy for the Jefferson Salamander (*Ambystoma jeffersonianum*) and Unisexual Ambystoma (Jefferson Salamander dependent population) (*Ambystoma laterale* – (2) *jeffersonianum*) in Ontario. Ontario Recovery Strategy Series. Prepared for the Ontario Ministry of Natural Resources and Forestry, Peterborough, Ontario. vii + 58 pp.

Malmgren, J.C. (2002): How does a newt find its way from a pond? Migration patterns after breeding and metamorphosis in Great Crested Newts and Smooth Newts. Herpetol. J. **12**: 29-35.

McCune, J.L., Harrower, W.L., Avery-Gomm, S., Brogan, J.M., Csergő, A., Davidson, L.N.K., Garani, A., Halpin, L.R., Lipsen, L.P.J., Lee, C., Nelson, J.C., Prugh, L.R., Stinson, C.M., Whitney, C.K., Whitton, J. (2013): Threats to Canadian species at risk: an analysis of finalized recovery strategies. Biol. Conserv. **166**: 254-265.

Mills, N.E., Ward, Z.A. (2015): Egg hypoxia decreases posthatching survival and delays metamorphosis in *Ambystoma maculatum* (Spotted Salamander). J. Herpetol. **49** (4): 616-620.

Mullin, S.J., Klueth, S. (2009): Demographics of a geographically isolated population of threatened salamander (Caudata: *Ambystomatidae*) in central Illinois. Herpetol. Conserv. Bio. **4** (2): 261-269.

NatureServe. (2020): NatureServe Explorer 2.0: an online encyclopedia of life. NatureServe, Arlington, Virginia. Web site: https://www.natureserve.org/ [accessed April 2020].

Osbourn, M.S. (2012): Initial juvenile movements of pond-breeding amphibians in altered forest habitat. Ph.D. Thesis. University of Missouri-Columbia, Columbia, MO. Xiii + 155 pp.

Osbourn, M.S., Connette, G.M., Semlitch, R.D. (2014): Effects of fine-scale forest habitat quality on movement and settling decisions in juvenile pond-breeding salamanders. Ecol. Appl. **24** (7): 1719-1729.

Patrick, D.A., Calhoun, A.J.K., Hunter, M.L.J. (2007): Orientation of juvenile Wood Frogs, *Rana sylvatica*, leaving experimental ponds. J. Herpetol. **41**: 158-163.

Pechmann, J.H.K., Scott, D.E., Gibbons, J.W., Semlitsch, R.D. (1989): Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. Wetl. Ecol. Manag. **1**: 3-11.

Pfingsten, R.A., Davis, J.G., Matson, T.O., Lipps, G.J. Jr., Wynn, D., Armitage, B.J., Eds (2013): Amphibians of Ohio. Ohio Biological Survey Bulletin New Series. 17(1): xiv + 899 pp.

Pittman, S.E., Osbourn, M.S., Semlitsch, R.D. (2014): Movement ecology of amphibians: a missing component for understanding population declines. Biol. Conserv. **169**: 44-53.

Plummer, M. (2003): JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: Proceedings of the 3rd International Workshop on Distributed Statistical Computing 124:125. Technische Universitat Wien, Vienna, Austria.

R Core Team (2018): R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ronce, O. (2007): How does it feel to be like a rolling stone? Ten questions about dispersal evolution. Annu. Rev. Ecol. Evol. S. **38**: 231-253.

Rothermel, B.B. (2004): Migratory success of juveniles: a potential constraint on connectivity for pond-breeding amphibians. Ecol. Appl. **14**: 1535-1546.

Rothermel, B.B., Semlitsch, R.D. (2006): Consequences of forest fragmentation for juvenile survival in spotted (*Ambystoma maculatum*) and marbled (*Ambystoma opacum*) salamanders. Can. J. Zool. **84**: 797-807.

Rowe, C.L., Dunson, W.A. (1995): Impacts of hydroperiod on growth and survival of larval amphibians in temporary ponds of central Pennsylvania, USA. Oceologia **102**: 397-403.

Schemske, D.W., Husband, B.C., Ruckelshaus, M.H., Goo, C., Parker, I.M., Bishop, J.G. (1994): Evaluating approaches to the conservation of rare and endangered plants. Ecology **75** (3): 584-606.

Scott, D.E., Komoroski, M.J., Croshaw, D.A., Dixon, P.M. (2013): Terrestrial distribution of pond-breeding salamanders around an isolated wetland. Ecology **94** (11): 2537-2546.

Searcy, C.A., Snaas, H., Shaffer, H.B. (2014): Determinants of size at metamorphosis in an endangered amphibian and their projected effects on population stability. Oikos **124**: 724-731.

Seber, G.A.F. (1965): A note on the multiple recapture census. Biometrika **52**: 249-259.

Semlitsch, R.D. (2008): Differentiating migration and dispersal processes for pond-breeding amphibians. J. Wildlife Manage. **72**: 260-267.

Semlitsch, R.D., Scott, D.E., Pechmann, J.H.K., Gibbons, J.W. (1996): Structure and dynamics of an amphibian community. In: Long-Term Studies of Vertebrate Communities. Cody, M.L., Smallwood, J.A., Eds, Academic Press, San Diego, California, USA, p. 217-248.

Shoop, C.R. (1974): Yearly variation in larval survival of *Ambystoma maculatum*. Ecology **55**: 440-444.

Skelly, D. (1996): Pond drying, predators, and the distribution of *Pseudacris* tadpoles. Copeia **1996**: 599-605.

Su, Y., Yajima, M. (2015): R2jags: using R to run 'JAGS'. R package version 0.5-7. https://CRAN.R-project.org/package=R2jags.

Taylor, M.F.J., Suckling, K.F., Rachlinski, J.J. (2005): The effectiveness of the Endangered Species Act: a quantitative analysis. BioScience **55** (4): 360-367.

Teltser, C., Greenwald, K.R. (2015): Survivorship of ploidy-variable unisexual *Ambystoma* salamanders across developmental stages. Herpetologica **71** (2): 81-87.

Van Drunen, S.G., Linton, J.E., Bogart, J.P., McCarter, J., Fotherby, H., Sandilands, A., Norris, D.R. (2020): Estimating critical habitat based on year-round movements of the endangered Jefferson Salamander (*Ambystoma jeffersonianum*) and their unisexual dependents. Can. J. Zool. **98**: 117-126.

Walls, S.C., Ball, L.C., Barichivich, W.J., Dodd, C.K. Jr., Enge, K.M., Gorman, T.A., O'Donnell, K.M., Palis, J.G., Semlitsch, R.D. (2017): Overcoming challenges to the recovery of declining amphibian populations in the United States. Bioscience **67** (2): 156-165.

Weller, W.F. (1980): Migration of the salamanders *Ambystoma jeffersonianum* (Green) and *A. platineum* Cope to and from a spring breeding pond, and the growth, development and metamorphosis of their young. M.Sc. Thesis. University of Toronto, Toronto, ON. xv + 248 pp.

Williams, P.K. (1973): Seasonal movements and population dynamics of four sympatric mole salamanders, genus *Ambystoma*. Ph.D. thesis. Indiana University, Bloomington, IN. 47 pp.

Zaffaroni, M., Zamberletti, P., Creed, I.F., Accatino, F., De Michele, C., Devries, B. (2019): Safeguarding wetlands and their connections within wetlandscapes to improve conservation outcomes for threatened amphibian species. J. Am. Water Resour. As. **55** (3): 641-656.

Submitted: October 28, 2019. Final revision received: June 25, 2020. Accepted: June 27, 2020.
Associate Editor: Marc Mazerolle.