Performance and Movement in Relation to Postmetamorphic Body Size in a Pond-Breeding Amphibian

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Abstract.—We examined the effect of body size on locomotor performance and movement behavior in early postmetamorphic toadlets of Fowler's Toad (*Anaxyrus fowleri*). Dispersal, if strictly density dependent, should be favored among the relatively small toadlets that emerge from crowded growth conditions, but not among the relatively large toadlets that result from low-density conditions; however, smaller toadlets may have less physical capability to disperse than larger toadlets. The net result may thus be that actual dispersal probability is greatest among intermediate-sized toadlets. Using toadlets of various sizes purposefully raised by manipulating their densities as tadpoles, we tested toadlet locomotor jumping endurance in relation to body size. We also compared the animals' initial body size against their overall movements in the wild, determined using capture–recapture methods, over 2 yr as they grew from toadlets to adults. We calculated movement rate and dispersal probability for each individual recaptured more than twice and determined whether successful movement strategies were correlated or uncorrelated. Our results show that toadlets of intermediate size are most likely to disperse farthest, even though they do not necessarily exhibit the highest levels of endurance. Therefore, knowledge of individual life experience across multiple life stages may be necessary to understand dispersal tendencies in amphibians and may be required in future studies aiming to predict dispersal and population dynamics.

Dispersal, a key process that profoundly affects the structure and dynamics of populations (Bowler and Benton, 2005; Barton et al., 2009), can be defined as the displacement of an individual during its lifetime from its birthplace to a breeding site somewhere else (Clobert et al., 2009). Both decreasing habitat quality and increasing population density have increased the probability for active dispersal in animals (Travis et al., 2009; Innocent et al., 2010; Mathieu et al., 2010). In contrast to their potential for dispersal, realized dispersal (i.e., actual dispersal) may decrease with density (Ims and Andreassen, 2005; Meylan et al., 2007) and be influenced by habitat quality (Travis and Dytham, 1999; Matthysen, 2005).

The probability of dispersal may have a genetic component stemming from the inheritance of certain physical traits (Clobert et al., 2001; Bowler and Benton, 2005; Ronce, 2007) or behaviors (Clobert et al., 2009; Cote et al., 2010). It can also be dependent on an individual's physical condition (Bonte and de la Peña, 2009; Clobert et al., 2009; Gyllenberg et al., 2011), because dispersal itself is a costly process (Bonte et al., 2012) that may be influenced by maternal effects (Williams, 1994; Sakai and Harada, 2001; Sinervo et al., 2006), habitat quality (Maceda-Veiga et al., 2014; Meillère et al., 2015), competition (Lorenzen and Enberg, 2002; Browne et al., 2003; Yagi and Green, 2016), and carry-over effects (Pechenick et al., 1998; Benard and McCauley, 2008; O'Connor et al., 2014). Realized and probability of dispersal are related terms, in that both can refer to a measure of dispersal for individuals or populations, but the probability to disperse is mediated by individual traits that, in turn, ultimately influence the success of their realized dispersal.

Animal movement falls into two basic patterns: correlated movements and uncorrelated movements. Correlated movements are those for which the animal moves in a directed manner and the direction of a movement step is dependent on the immediately previous step (Byers, 2001; Conradt et al., 2003; Bartumeus and Levin, 2008; Barton et al., 2009). The initiation of correlated movement may often be caused by external triggers, such as predation, competition, or change in habitat quality (Bowler and Benton, 2005). There also is some evidence of correlated movement based on an individual's internal condition (Bonte and de la Peña, 2009) and the genetic predisposition for dispersal (Clobert et al., 2001). Uncorrelated movements, however, follow a random-walk pattern, as may be typical of searching behavior in a homogenous landscape (Turchin, 1998; Mårell et al., 2002; Codling et al., 2008). Both movement patterns can occur throughout an individual's lifetime and at various spatial scales (Nathan, 2008). Such common animal movement patterns can result in dispersal as an end product, even though it may not be the initial intention of the movements (Van Dyck and Baguette, 2005; Conradt and Roper, 2006). Movement behavior with both correlated and uncorrelated patterns has been associated with "fat-tailed" probability distance curves similar to a power distribution (Nathan, 2008), also called a Lévy walk (Viswanathan et al., 2000). This pattern includes random walks, with occasional long-distance directed movements, and it has been used to classify searching behavior in animals living within a patchy resource landscape (Bartumeus et al., 2005; Benhamou, 2007).

Amphibians, on the whole, are not typically long-distance dispersers compared to many other vertebrates (Cushman, 2006, but see Smith and Green, 2005) in that they typically show high fidelity to breeding sites (Gamble et al., 2007; Pittman et al., 2014), have specific habitat tolerances (Gibbs, 1998), and can be susceptible to desiccation when moving across open landscapes (Rittenhouse et al., 2008; Mitchell and Bergmann, 2016). Consequently, the ability of amphibians to move across the landscape may depend on body condition (Pittman et al., 2014) or body size (Álvarez and Nicieza, 2002; Tejedo et al., 2010; Cabrera-Guzmán et al., 2013) to a considerable degree. Body condition, or the relative level of fat stores, is strongly correlated with body size, particularly in amphibian metamorphs (Scott et al., 2007). Large body size has been linked to good locomotor performance in newly metamorphosed frogs (Álvarez and Nicieza, 2002) and to large dispersal distances in various taxa

(Jenkins et al., 2007; Shurin et al., 2009), although there are exceptions (Gordon and Hellman, 2015).

If the body size of a young-of-the-year toad (i.e., a "toadlet") is related to its dispersal ability, then there is likely to be a significant relationship between the individual's snout–vent length (SVL) and its relative locomotor performance. This may be a linear relationship; however, dispersal also should depend on movement directionality, not just movement ability, and the favorability of dispersal as a survival strategy. Smaller individuals, such those stemming from crowded growing conditions, low-quality growing conditions, or both (Wilbur, 1977; Altwegg, 2003) as tadpoles, may be incapable of dispersing effectively because of their small size and poor endurance, even though dispersal may be favored. Conversely, larger individuals, which may be the products of uncrowded conditions, high-quality conditions, or both as tadpoles, might be able to disperse with ease, but they do not because dispersal away from optimal conditions would not be favored. As such, and if dispersal probabilities are thus reduced among both the largest and the smallest individuals, then the largest overall movements should be characteristic of intermediate-sized individuals, resulting in a hump-shaped curve when comparing movement distance against body size for animals of equal age. To test these hypotheses, we used both wild-caught toadlets and toadlets that had been purposely grown to be of varying sizes by manipulating larval density (Yagi and Green, 2016), and we compared body size against 1) relative locomotor performance, assessed as endurance when jumping; and 2) movement patterns in the wild, assessed using mark–recapture over time until, in some cases, adulthood.

MATERIALS AND METHODS

Study Site and Species.—This study was conducted in the Thoroughfare Point Unit of the Long Point National Wildlife Area (NWA; between 42°34′33″N–42°35′3″N and 80°22′15″–80°28′24″W). Fowler's Toad (*Anaxyrus fowleri*) is a relatively small and widespread toad in eastern North America and Canada, where it is adapted for living in sand dune–shoreline ecosystems (Greenberg and Green, 2013). In Canada, this species is classified as endangered because of its genetic isolation from the main populations in the United States and the continuing habitat loss from invasive species and shoreline development (Greenberg and Green, 2013). Therefore, adult Fowler's Toads in Long Point, Ontario, use primarily the natural beaches as their main foraging habitat and dispersal corridor (Greenberg and Green, 2013), most of which are assumed to be continuous, unaltered habitat. Natural adult toad densities have fluctuated annually, ranging from 4 to 93 toads per kilometer, and natural tadpole densities have not been estimated in Long Point because of the nature of their ephemeral and dynamic beach habitat (Yagi and Green, 2016). Mean female clutch size in Long Point Fowler's Toads was measured to be 4,443 eggs per clutch, from a sample of 34 individuals (Green, 2015), and tadpole survival to metamorphosis ranged from 5 to 43% as experimental density decreased from 5 to 0.1 tadpoles/L (Yagi and Green, 2016).

We produced toadlets of various sizes in 2014 by manipulating tadpole density within enclosures placed in three nearly identical ponds (Yagi and Green, 2016). Densities were maintained at six levels—0.08, 0.13, 0.25, 0.5, 1.0 and 1.67 tadpoles/L—replicated in each pond. We took three measurements from all toadlets, whether performance tested or not: snout–vent length (SVL; in millimeters), leg length (in millime-

ters), and mass (in grams). We measured leg length from the urostyle to the tip of the longest toe and calculated relative leg length by dividing leg length by SVL. Body condition was calculated using residuals from the regression of SVL vs. mass; positive values indicated a good condition (i.e., heavier than average given their length), and negative values indicated a poor condition (i.e., lighter than average given their length). We made all length measures with a 15-mm dial calipers. Mass was measured using a model SP202 portable weight scale (0.01 g; Ohaus Corp., Parsippany, New Jersey USA). We digitally photographed all toadlets for identification (Schoen et al., 2015) and released them at night into the adult habitat from the same point along the beach.

Locomotor Performance.—We estimated jumping endurance for 29 toadlets by quantifying its jumping fatigue, by measuring the change in length of 60 consecutive series of hops. To do this, we placed toadlets individually into a plastic circular arena (diameter of 91 cm), with the bottom filled with 2 cm of moist sand. The test was initiated after a 60-min acclimation period, during which the toadlets were left undisturbed and generally moved very little. We instigated movement by gently prodding each toadlet on the urostyle, up to a maximum of 60 times. We called this variable "jump no.," or the number identifying the jump from the first to the 60th. All jumping endurance tests were recorded using an infrared camera (model CMC-3MP-OD-I) and DVR unit (VIGIL, DRX-50-16-500; CAMACC Systems Inc., Saanichton, British Columbia, Canada). Because toads tend to not move in singular jumps, like frogs, but in a series of short hops (Reilly et al., 2015), we called the length of a series of hops a "movement segment." All jumping tests were recorded at a rate of 7.5 frames per sec, and the footage was analyzed afterward by taking a freeze-frame image after each movement segment and measuring its length by using the image processing software Fiji ImageJ v1.51g (Schindelin et al., 2012).

To calculate toadlet endurance levels ($N = 29$), we standardized the length of each measured movement segment against the toadlets' SVL, by taking the residuals from a regression of movement segment vs. SVL. Using these new values, we used the slope of the regression of standardized movement segment vs. jump no., or acceleration (millimeters per jump^2), to calculate endurance level per toadlet (EN) according to the formula $EN = \log_e(\text{slope} + 1)$. Neutral or positive EN values indicated good endurance; negative EN values indicated poor endurance. A natural log transformation was used to attain normality.

Movement Strategies.—We monitored the postrelease movement of density-treated toadlets, along with any wild-caught toadlets for the remainder of the toads' 2014 active season, and their movements as juveniles for the 2015 and 2016 seasons from 1 May to 20 August. We used capture–recapture surveys and conducted them along known dispersal corridors (i.e., beaches and sand dunes) of the study area. We noted the sex if secondary sex traits were visible and recorded location coordinates by using a hand-held global positioning system unit for all individuals encountered.

To quantify an individual's movement strategy (i.e., correlated vs. uncorrelated), we used the toadlet encounter data to determine the distance between each consecutive recapture event, and the Euclidean distance, i.e., the distance between their initial point of release and last capture location, per individual by using Excel (Microsoft Office 365; Microsoft Corp., Redmond, Washington USA). We calculated a dispersal ratio (DR) by dividing the straight-line (Euclidean) displacement between the very first and very last capture points

TABLE 1. Summary of endurance-tested Fowler's Toad (*A. fowleri*) toadlets; mean ± SE toadlet SVL, body condition, relative leg length, and EN calculated per density treatment. EN values are shown as $\log_e$-transformed values.

Rearing density (tadpoles/L)	n	Toadlet SVL (mm)	Body condition	Relative leg length (mm)	EN
0.08	7	16.94 ± 0.47	−0.04 ± 0.29	1.07 ± 0.02	−0.12 ± 0.03
0.13	7	16.10 ± 0.45	0.13 ± 0.19	1.03 ± 0.02	−0.13 ± 0.05
0.25	7	17.40 ± 0.87	0.52 ± 0.25	0.99 ± 0.01	−0.10 ± 0.09
0.50	5	14.18 ± 0.33	−0.18 ± 0.26	1.08 ± 0.02	−0.27 ± 0.04
1.00	3	15.97 ± 0.48	0.08 ± 0.24	1.10 ± 0.02	−0.13 ± 0.06

($Dist_{AtoB}$), by the sum of the distances between consecutive recaptures ($Dist_{total}$). For each toadlet DR, values close to 1 indicated correlated movement, whereas values close to 0 indicated uncorrelated movement. DRs were calculated for any toadlet with two or more recapture events. Mean distance moved per day ($Dist_{day}$), or movement rate, was calculated per individual by using $Dist_{total}$ divided by number of active days between the first and last capture, removing the number of days between 15 October and 15 April each year to account for winter dormancy. Adult, or realized, dispersal events were determined only for toads that had reached sexual maturity (in 2016). We considered those toads with $Dist_{AtoB} \geq 1,000$ m to have a positive dispersal trajectory, and they were given a binary response of "yes," and a "no" was given for anything otherwise. Movement data from wild-caught and density-treated toadlets were examined separately, and again when combined, to observe a complete range of body sizes and its effect on movement and dispersal probability.

Analysis.—All statistical analyses were conducted using R v3.3.2 (R Core Team, 2015). The normality assumptions of linear regression were tested using the Shapiro-Wilk normality test. To achieve normal distributions for the analysis, we used a $\log_e$ transformation on $Dist_{AtoB}$ and $Dist_{day}$. Using only the density-treated toadlet data, we used model selection (Akaike, 1987) to examine the explanatory power of the predictors density, SVL, relative leg length, and body condition, on EN, by using the *lmer* function from the 'lme4' package in R. Two additional variables were included in these models: mean air temperature as a fixed predictor and pond origin as a random effect term. The model with the highest small sample size–corrected Akaike information criterion (AIC_c) weight was analyzed using R's summary function. We also examined linear regressions using EN as the predictor variable and tested $Dist_{AtoB}$ and $Dist_{day}$ as responses.

Using the movement data of both density-treated and wild-caught toadlets, we used separate linear regressions to assess the movement response variables $Dist_{AtoB}$ and $Dist_{day}$ as a function of toadlet SVL. We also used the same analysis on the combined data of density-treated and wild-caught toadlets. To determine whether the relationships between toadlet SVL and

TABLE 2. Model selection output for the top six explanatory models, assessing how Fowler's Toad (*A. fowleri*) toadlet size (SVL), body condition, relative leg length, tadpole rearing density (density) and air temperature (temp) explain toadlet EN. Pond origin was set as a random effect term for all models (i.e., 1|pond).

Model	AIC_c	ΔAIC_c	df	ω
SVL + (1|pond)	−30.60	0.00	4	0.97
SVL + density + (1|pond)	−22.20	8.40	5	0.02
SVL + temp + (1|pond)	−21.90	8.70	5	0.01
Body condition + (1|pond)	−17.00	13.60	4	<0.001
(1|pond)	−16.50	14.10	3	<0.001
Relative leg length + (1|pond)	−16.4	14.2	4	<0.001

$Dist_{AtoB}$ and between SVL and $Dist_{day}$ differed among wild-caught and density-treated toads, we used two separate analyses of covariance, with the two movement variables as separate responses, with toadlet SVL and data 'type' (i.e., wild caught or density treated) as interacting predictors. In addition, we used a Kruskal-Wallis nonparametric comparison of means to assess differences in these movement variables between males, females, and juveniles. Toads were categorized as juveniles if they were 45–55 mm SVL and did not exhibit secondary sex characteristics.

Because the DR data was bounded between 0 and 1, we conducted beta regressions to determine whether DR can be predicted by SVL, including SVL as a polynomial term. We examined this relationship for density-treated and wild-caught toadlets separately, and again using the combined dataset. Using only the density-treated toadlets, we also looked at a beta regression with EN as the predictor and DR as the response. We performed all beta regressions using the betareg command, with a *logit* link function in the R package 'betareg' and analyzed using the *Anova* function from the 'car' package in R.

Dispersal probability (D_p) was calculated by using a logistic regression on the binary dispersal data by using R's *glm* function under the binomial family and *logit* link function. We used toadlet SVL as the primary predictor and included it as a polynomial term to assess whether the relationship is quadratic, as predicted. Finally, D_p was calculated for toads identified as adults in 2016 and analyzed using a logistic regression on their binary dispersal data with adult SVL as the primary predictor, again using R's *glm* function. The *Anova* function from R's 'car' package was used to assess the significance of both models.

RESULTS

Toadlet Locomotor Performance.—Toadlets used in the performance trials ranged from 13.3 to 20.2 mm SVL. Relative leg length ranged from 0.93 to 1.10 ± 0.02 SE. The highest mean EN value, −0.10 ± 0.09, came from density level 0.25 tadpoles/L, whereas the lowest mean EN value, −0.27 ± 0.04, came from density level 0.50 tadpoles/L (Table 1). EN was most strongly predicted by SVL ($R^2 = 0.58$, $P < 0.001$) rather than density ($R^2 = 0.02$, $P = 0.46$; Table 2) per the linear equation EN = 0.06 × SVL − 1.19 (Fig. 1).

Displacement and Movement Rate.—Toad movement data included recaptures of 74 individuals between 2014 and 2016, 13 of which were released as density-treated toadlets, and 61 were originally wild-caught toadlets in 2014 (Appendices 1 and 2). Our monitoring showed secondary sex characteristics for most individuals by 2016, revealing 34 toads to be female and 35 to be male. Five individuals not recaptured in 2016 were categorized as juveniles. Mean juvenile $Dist_{AtoB}$ was 232.67 m ± 115.4 SE and $Dist_{day}$ was 2.24 ± 0.9 m/d. For females, mean $Dist_{AtoB}$ was 1,039.77 ± 134.4 m and mean $Dist_{day}$ was 15.77 ± 3.6 m/d. For
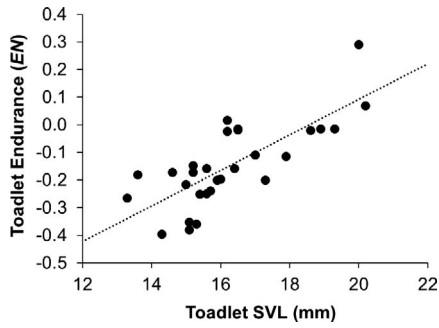
FIG. 1. Results of the locomotor performance tests in Fowler's Toad (*A. fowleri*) toadlets showing that endurance, EN ($\log_e$[endurance + 1]), is positively correlated with toadlet body SVL; $N = 29$.
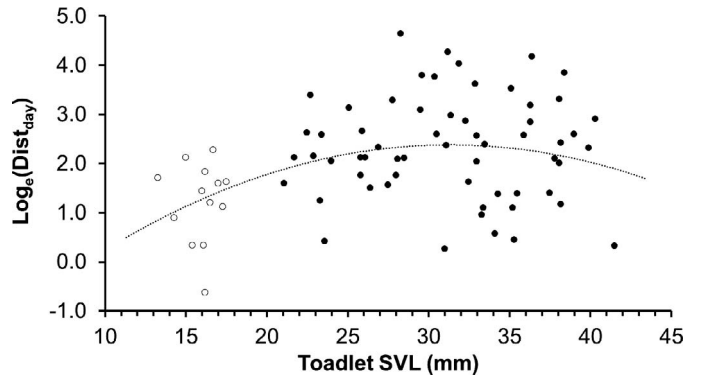

FIG. 2. Fowler's Toad (*A. fowleri*) movement rate, or $Dist_{day}$, from the combined dataset of density-treated (open points) and wild-caught (filled points) toadlets, plotted against toadlet SVL (mm), showing a significant quadratic relationship for the full toadlet SVL range, where intermediate-sized toadlets displayed the greatest distance traveled per day. Density-treated and wild-caught toadlet data did not reveal significant relationships with SVL separately.

males, mean $Dist_{AtoB}$ was 1,473.26 $\pm$ 364.0 m and mean $Dist_{day}$ was 15.03 $\pm$ 2.8 m/d (Table 3).

With *EN* as the predictor, we did not find a significant relationship in density-treated toadlets with $Dist_{day}$ ($R^2 = 0.01$; $F_{1,6} = 0.04$; $P = 0.85$) nor with $Dist_{AtoB}$ ($R^2 = 0.17$; $F_{1,6} = 2.40$; $P = 0.17$), although the trend was negative. Toadlet SVL was not a significant predictor for $Dist_{day}$ in density-treated toadlets ($F_{2,10} = 0.55$; $P = 0.59$) nor in wild-caught toadlets ($F_{2,58} = 0.26$; $P = 0.77$). Similarly, SVL was not a significant predictor for $Dist_{AtoB}$ in density-treated toadlets ($F_{2,10} = 1.59$; $P = 0.25$) or for wild-caught toadlets ($F_{2,58} = 0.62$; $P = 0.54$). When using the combined movement data, however (i.e., both density-treated and wild-caught toadlets), toadlet SVL was a significant quadratic predictor for $Dist_{day}$ ($R^2 = 0.12$; $F_{2,71} = 4.94$; $P < 0.01$; Fig. 2) and for $Dist_{AtoB}$ ($R^2 = 0.10$; $F_{2,71} = 3.49$; $P = 0.04$).

There was no interaction between wild-caught and density-treated toadlets in the relationship between $Dist_{day}$ and toadlet SVL ($F_{1,69} = 0.09$; $P = 0.77$). Similarly, there was no interaction between these two groups in the relationship between $Dist_{AtoB}$ and toadlet SVL ($F_{1,69} = 0.19$; $P = 0.67$). For the density-treated toadlets, there was no significant difference between males, females and juveniles for $Dist_{day}$ ($\chi^2 = 0.56$, df = 2, $P = 0.75$) or for $Dist_{AtoB}$ ($\chi^2 = 1.42$, df = 2, $P = 0.49$). For the wild-caught toadlets, there was a significant difference in $Dist_{day}$ among males, females, and juveniles, where juveniles had a much lower movement rate at 1.59 m/d compared to the adults ($\chi^2 = 6.97$, df = 2, $P = 0.03$; Table 3), but there was no difference in $Dist_{AtoB}$ ($\chi^2 = 4.27$, df = 2, $P = 0.12$).

Movement Strategies.—Mean DR was highest in juveniles for both density-treated (0.44 $\pm$ 0.20 SE) and wild-caught toadlets (0.48 $\pm$ 0.21) and lowest for density-treated males (0.18 $\pm$ 0.07) and wild-caught females (0.38 $\pm$ 0.05). For the density-treated

toadlets, there was no relationship between DR and toadlet SVL by using the mean model (pseudo-$R^2 = 0.002$, SVL: $Z = 0.92 \pm 0.11$, $P = 0.36$; SVL^2: $Z = -0.71 \pm 0.002$, $P = 0.48$). For the wild-caught toadlets, the mean model did show a significant quadratic relationship between DR and toadlet SVL (pseudo-$R^2 = 0.09$, SVL: $Z = -2.23 \pm 0.32$, $P = 0.03$; SVL^2: $Z = 2.21 \pm 0.01$, $P = 0.03$); however, the precision model was not significant (phi SVL: $Z = -0.08 \pm 0.33$, $P = 0.93$; phi SVL^2: $Z = 0.18 \pm 0.01$, $P = 0.86$).

For the combined dataset, the mean model resulting from the beta regression analysis did not reveal a significant quadratic relationship between DR and toadlet SVL (pseudo-$R^2 = 0.04$, SVL: $Z = 0.84 \pm 0.12$, $P = 0.40$; SVL^2: $Z = -0.60 \pm 0.002$, $P = 0.55$); however, the precision model did reveal significant coefficients (phi SVL: $Z = -3.09 \pm 0.15$, $P < 0.01$; phi SVL^2: $Z = 2.98 \pm 0.003$, $P < 0.01$). With EN as the predictor, there was a significant quadratic relationship with DR in both the mean model (EN: $Z = -2.15 \pm 7.28$, $P = 0.03$; EN^2: $Z = -2.06 \pm 22.32$, $P = 0.04$) and the precision model (phi EN: $Z = 2.69 \pm 16.55$, $P = 0.007$; phi EN^2: $Z = 3.95 \pm 60.54$, $P < 0.001$). There was no difference between sexes ($\chi^2 = 0.80$, df = 2, $P = 0.67$).

Probability of Dispersal.—Of the 13 density-treated toadlets recaptured over the 2014–2016 active seasons, only seven were recaptured as adults in 2016. All seven individuals were males, and they did not move farther than 500 m in $Dist_{AtoB}$. Of the 61 wild-caught toadlets that were recaptured over the 2014–2016 seasons, 55 individuals were recaptured as adults in 2016, 27 of which were females and 28 were males.

TABLE 3. Summary of means $\pm$ SE for density-treated and wild-caught Fowler's Toad (*A. fowleri*) toadlets: SVL at initial release in 2014 and at last capture; number of growth days in between initial and final SVL measures; total distance traveled; absolute linear displacement ($Dist_{AtoB}$); dispersal ratio ($Dist_{AtoB}$/total distance); and $Dist_{day}$ for males, females, and juveniles. Only toadlets recaptured more than twice were used in these calculations.

|	Density-treated toadlets			Wild-caught toadlets		
	Males	Females	Juveniles	Males	Females	Juveniles
Sample size (*N*)	6	5	2	29	29	3
Toadlet SVL (mm)	15.62 $\pm$ 0.60	16.04 $\pm$ 0.41	16.80 $\pm$ 0.70	31.54 $\pm$ 1.04	31.23 $\pm$ 1.05	29.53 $\pm$ 3.01
Final SVL (mm)	60.87 $\pm$ 1.81	59.34 $\pm$ 2.46	39.60 $\pm$ 0.00	63.09 $\pm$ 0.83	69.37 $\pm$ 0.95	46.23 $\pm$ 3.01
No. growth days	313.17 $\pm$ 13.18	209.20 $\pm$ 20.17	145.00 $\pm$ 13.50	276.48 $\pm$ 13.89	290.90 $\pm$ 9.49	308.67 $\pm$ 24.25
Total distance (m)	1,550.20 $\pm$ 448.24	933.44 $\pm$ 375.95	483.91 $\pm$ 293.94	5,107.68 $\pm$ 968.01	5,577.74 $\pm$ 1,263.85	492.38 $\pm$ 228.82
$Dist_{AtoB}$ (m)	155.15 $\pm$ 45.50	321.22 $\pm$ 114.61	271.20 $\pm$ 225.20	1,745.97 $\pm$ 384.65	1,163.66 $\pm$ 133.57	206.99 $\pm$ 133.45
DR	0.18 $\pm$ 0.07	0.36 $\pm$ 0.06	0.44 $\pm$ 0.20	0.45 $\pm$ 0.06	0.37 $\pm$ 0.05	0.48 $\pm$ 0.21
$Dist_{day}$ (m)	4.87 $\pm$ 1.29	4.05 $\pm$ 1.15	3.22 $\pm$ 1.77	17.14 $\pm$ 2.93	17.79 $\pm$ 3.74	1.59 $\pm$ 0.79
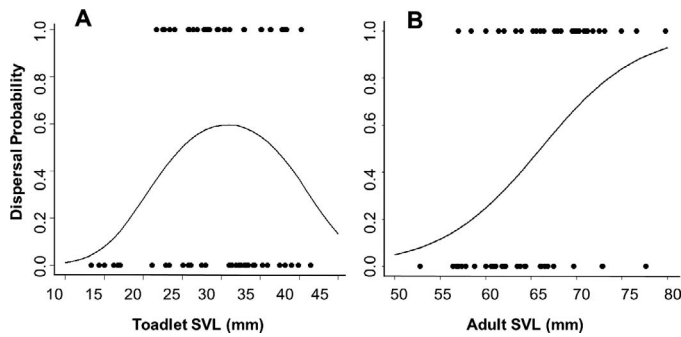
FIG. 3. Dispersal probability of Fowler's Toad (*A. fowleri*) from Long Point, Ontario, Canada, plotted against toadlet SVL (A) and probability of dispersal plotted against adult SVL (B), whereby a positive binary dispersal response (1) came from a $Dist_{AtoB} \geq 1,000$ m and a negative binary response (0) was given when $Dist_{AtoB} < 1,000$ m, per individual. We found a significant quadratic relationship between dispersal probability and toadlet SVL, where the intermediate-sized toadlets were predicted to have the highest probability of dispersal (A). Using the same dataset, we found a positive logistic relationship (B), where the largest adult toads showed the highest dispersal probability.

Looking at only wild-caught toadlets, there was no relationship between dispersal probability and their SVL. There was also no difference in dispersal probability between wild-caught males and females ($Z = -1.08 \pm 0.56$, $P = 0.28$); however, when we combine both density-treated and wild-caught dispersal data, there was a significant quadratic, relationship between toadlet SVL and dispersal probability ($\chi^2 = 4.60$, df = 1, $P = 0.03$; Fig. 3), resulting in the fitted model $D_p = 1 / (1 + \exp(-(0.697 \times SVL - 0.0113 \times SVL^2 - 10.354)))$. In addition, dispersal probability revealed a significant positive relationship with adult SVL ($\chi^2 = 14.04$, df = 1, $P < 0.01$; Fig. 3), with the fitted model $D_p = 1 / (1 + \exp(-(0.185 \times SVL - 12.18)))$.

DISCUSSION

Our results are consistent with the hypothesis that toadlet endurance is best predicted by body size, as seen in laboratory studies (Beck and Congdon, 2000; Cabrera-Guzmán et al., 2013). Because the size range for this analysis was relatively narrow compared to the range of sizes observed in the combined movement dataset, however, we might be able to see only one part of a potentially complex relationship. Also, because toadlet body size is, in turn, strongly dependent on tadpole density (Yagi and Green, 2016), these results are also consistent with other studies showing that amphibian larval density conditions have an impact on post-metamorphic performance (John-Alder and Morin, 1990; Álvarez and Nicieza, 2002; Tejedo et al., 2010).

We did not observe a significant relationship between toadlet size and movement rate when the density-treated and wild-caught datasets were kept separate. We did observe a significant relationship between SVL and movement strategy (i.e., dispersal ratio) for the wild-caught toadlets under the mean model from the beta regression, but not for the density-treated group. When looking at the data separately, the number of data points and the breadth of sizes likely made a difference statistically when trying to see such a trend, where there were only 13 points for the density-treated group and 61 points for the wild-caught. Yet, we did find a significant quadratic relationship between toadlet size and movement rate (Fig. 2), toadlet size and Euclidean displacement, and between toadlet size and dispersal probability (Fig. 3) when looking at the combined dataset with toadlets from a broad size range. These results are consistent

with the hypothesis that toadlets of intermediate size will have the fastest terrestrial movement and probability of dispersal in the wild.

Endurance was found to be a significant quadratic predictor for movement strategy, where intermediately-abled individuals showed a more correlated movement behavior. Because endurance is closely linked to body size (Fig. 1), our results further support the idea that those individuals with the highest endurance level or largest body size do not necessarily choose a movement strategy that will reflect dispersal behavior. This part of the study was similar to that of Llewelyn et al. (2010), which compared laboratory-tested endurance levels of invasive Cane toads (*Rhinella marina*) against dispersal behavior observed from other individuals from the same populations in Australia. Our results were different, however, because the individuals that showed highest endurances in the lab did not reveal the same, dispersal-like behavior in the field. The difference in our results likely is a tribute to the clear differences in the ecology of the two species, and that Cane toads are invasive and resilient in the Australian populations, whereas Fowler's toads exist on the periphery of their native range in Long Point (Greenberg and Green, 2013).

Positive correlation between successive movements, or directional movement, is understood to reflect dispersal behavior (Byers, 2001; Codling and Hill, 2005). In contrast, juvenile amphibian dispersal is considered a more diffusive process (Codling et al., 2008), indicative of uncorrelated movement, that might explain our lack of correlated movement results in our study population. An uncorrelated movement strategy has been associated with searching behavior (Smouse et al., 2010), a potentially costly process if resources are limiting, and may influence the animal's decision to disperse (Morris, 1992; Stamps et al., 2005). Therefore, our measures of uncorrelated movement in many individuals may not necessarily mean they will remain local and breed in their natal pond. Rather, their movement pattern might gradually lead them away from their natal site until they reach adulthood, and breed at a new, distant pond. Consequently, there is evidence of poor agreement between field assessments of amphibian dispersal, and estimates of gene flow using molecular techniques (Sinsch, 2014). In addition, we did not find any differences between sexes in our measures of movement; somewhat surprising because many studies have shown a strong sex-biased dispersal trait in various taxa (Perrin and Mazlov, 2000; Lawson Handley and Perrin, 2007; Trochet et al., 2016).

Unlike the toadlets, adult-sized toads exhibited a positive, logistic relationship between SVL and realized dispersal probability (Fig. 3). This positive trend between body size and dispersal agrees with some past studies (Jenkins et al., 2007; Shurin et al., 2009), although both trends have been detected under different circumstances (Bonte and de la Peña, 2009; Cote and Clobert, 2010). Because our measure for dispersal is the displacement of the animal between 2014 and 2016, and we are using the same individuals in both regressions, we may interpret these results as the toads having different growth rates once released into the terrestrial habitat. Based on Figure 3, the intermediate sized toadlets were more likely to disperse, and as adults these toads became the largest in their cohort. Based on this observation, one would have to consider that adult size might be the response to their dispersal behavior, rather than the cause. This idea agrees with our finding that most toads exhibited uncorrelated movement (dispersal ratio < 0.5), analogous to foraging behavior (Mårell et al., 2002), and

amphibian diffusive dispersal (Codling et al., 2008; Semlitsch, 2008). If those intermediate-sized individuals were acquiring food resources efficiently over their adolescence, then they would reach larger adult sizes by the end of the study, and giving us our positive size *vs.* dispersal probability relationship.

Our results show that small size, that can result from crowded larval growth conditions, is associated with lower movement and performance levels in toads, which may result in lower dispersal probability. We also were able to demonstrate that an intermediate size might be favored for dispersal in toadlets due to a combination of early life density-dependent conditions, and their subsequent vagility. Although we see no clear trend concerning correlated movement strategy in relation to body size, final displacement distances were quite large in some individuals. Therefore, an uncorrelated movement strategy may eventually lead to actual dispersal. These factors all add a level of complexity to dispersal models wherein high population density typically are thought to yield higher dispersal rates. Because dispersal is a key component in sustaining populations, especially those that are small and peripheral, a clear understanding of density-dependent vs. size-dependent dispersal propensities is critical in the management of such vulnerable populations.

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APPENDIX 1. Density-treated Fowler's Toad (*A. fowleri*) toadlets that were recaptured ($N = 13$) between their release date in 2014 and their last recorded capture up to 20 August 2016, where final SVL and the individuals sex also were recorded. Growth days refer to the number of days in between the release and final capture date, excluding the winter months (i.e., excluding the number of days from 15 October 2014 to 15 April 2015 and from 15 October 2015 to 15 April 2016). $Dist_{AtoB}$ refers to the distance between the release location and the location of the last recorded capture, whereas total distance refers to the cumulative sum of distances between each recapture location. Movement rate refers to the total distance moved per growth day, and EN measures were collected for $N = 8$ of these recaptures.

Rearing density (tadpoles/L)	Sex[a]	Toadlet SVL (mm)	Final SVL (mm)	Date of release in 2014	Date of last capture	No. recaptures	No. growth days	EN	Total distance (m)	$Dist_{AtoB}$ (m)	Movement rate (m/d)	DR
0.08	J	16.1	39.6	22 Jul	5 Jun 2015	5	136	—	189.97	46.00	1.40	0.24
0.08	M	16.7	59.4	1 Aug	21 Jul 2016	28	353	−0.11	3,417.26	55.15	9.68	0.02
0.08	M	17	61.8	30 Jul	21 May 2016	3	295	−0.11	1,442.42	199.09	4.89	0.14
0.08	F	16.5	50.8	1 Aug	13 Aug 2015	7	195	—	645.13	360.94	3.31	0.56
0.08	F	15.4	63.8	1 Aug	6 Aug 2015	6	188	−0.25	262.08	56.64	1.39	0.22
0.08	F	17.3	62.4	1 Aug	28 Jul 2015	9	179	−0.20	545.46	258.44	3.05	0.47
0.13	F	16	62.9	1 Aug	13 Aug 2015	9	195	−0.20	821.67	195.01	4.21	0.24
0.13	M	16.2	57.8	1 Aug	20 May 2016	5	291	0.02	1749.01	60.41	6.07	0.03
0.13	M	16.2	56.4	1 Aug	20 May 2016	2	292	−0.02	155.48	72.01	0.53	0.46
0.25	J	17.5	48.2	4 Aug	6 Jul 2015	4	154	—	777.85	496.40	5.05	0.64
0.25	F	15	56.8	15 Aug	31 May 2016	3	289	—	2,402.85	735.07	8.31	0.31
0.25	M	14.3	56.9	7 Aug	27 Jul 2016	9	353	—	860.72	190.04	2.44	0.22
0.5	M	13.3	57.4	15 Aug	24 May 2016	4	281	−0.27	1,544.40	342.58	5.50	0.22

[a] J, juvenile; M, male; and F, female.

APPENDIX 2. Summary of all 171 density-treated Fowler's Toad (*A. fowleri*) toadlets, showing the final number released from each density group in 2014 ($N_{released}$), their mean ± SE SVL at release, body condition, relative leg length, and the number of individuals recaptured more than once (N_{recap}).

Rearing density (tadpoles/L)	$N_{released}$	SVL (mm)	Body condition	Relative leg length (mm)	N_{recap}
0.08	33	14.72 ± 0.34	0.02 ± 0.02	1.05 ± 0.01	6
0.13	24	14.02 ± 0.44	0.00 ± 0.03	1.01 ± 0.01	3
0.25	37	14.10 ± 0.47	−0.01 ± 0.02	1.03 ± 0.01	3
0.50	26	12.13 ± 0.30	−0.08 ± 0.02	1.04 ± 0.01	1
1.00	30	12.10 ± 0.30	0.02 ± 0.02	1.03 ± 0.04	—
1.67	21	10.72 ± 0.28	0.06 ± 0.02	1.07 ± 0.01	—