



The influence of land cover and within-pool characteristics on larval, froglet, and adult wood frogs along a rural to suburban gradient

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Abstract

Urbanization is known to extirpate many species, but far less is known about how suburbanization may affect amphibian populations. We studied wood frogs (*Lithobates sylvaticus*) to test the effects of site characteristics (within-pool conditions and land cover indicative of suburbanization within 1000 m) and larval morphology on newly emerged froglets and post-breeding males across a suburbanization gradient in 15 pools in greater Bangor, Maine, USA. We raised field-captured larvae in microcosms and examined froglet morphology and locomotor performance at emergence and one month post-emergence. Larval mass was positively correlated with 50% of froglet responses (survival, size, and locomotor performance) but was negatively associated with adult size. Among site characteristics, egg density had the most salient influence with negative effects on larval survival and morphology as well as on 11 of 14 froglet responses. Vegetation, hydrology, and suburban-associated cover near pools also influenced froglet performance, and hydrology and suburban-associated cover was associated with larger and smaller adult morphology. However the influence of suburban-associated cover on froglet performance and adult morphology was small compared to that of within-pool characteristics. Specifically, our findings support the idea that within-pool conditions experienced by larvae can influence terrestrial stages with potentially life-long consequences. Nevertheless, in suburban landscapes where there is evidence of population declines, it is likely that suburbanization has the greatest impact on populations via direct effects on terrestrial stages. We encourage planners to maintain high-quality habitat for aquatic and terrestrial stage wood frogs in suburbanizing landscapes to avoid extirpation.

Keywords Vernal pool · Suburbanization · Latent effects · Locomotor performance · Morphology · Conspecific competition

Introduction

It is well established that intense urbanization and the associated habitat loss can result in the extirpation of many species (Wilcove et al. 1998; McKinney 2008) but the impacts of lower intensities of residential and commercial development are far

from clear. For example, high intensity urban development has clear negative impacts on wood frog (*Lithobates sylvaticus*) populations through the removal of pools necessary for breeding and larval development and large contiguous areas of forest used as non-breeding adult habitat (Gibbs 1998; Homan et al. 2004; Rubbo and Kiesecker 2005; Clark et al. 2008; Windmiller et al. 2008; Nicholls et al. 2017) but suburban development may also harm wood frog populations. In particular, replacement of upland forest by suburban development near breeding pools is correlated with reduced wood frog breeding pool occupancy (Homan et al. 2004; Clark et al. 2008) and breeding population size (Windmiller et al. 2008; Veysey et al. 2011).

The most wide-reaching effects of urbanization on wood frogs may be at the lowest development intensities, where forest is converted to suburban development, typically consisting of light commercial and single-unit residential development. Between 1990 and 2005, suburban expansion at the fringes of core urban areas was the development type primarily responsible for replacing forested areas in New England (Jeon et al. 2014), and by 2000, exurban development – often at the leading

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edge of suburban development and similarly characterized by low density single-unit residential development – within the US had a land area over seven times greater than that of urban and suburban areas (Theobald 2005). This trend is anticipated to continue, with exurban areas expected to cover 14.3% of the US by 2020 (Theobald 2005), with notable increases predicted in undeveloped areas adjacent to core protected natural areas until 2030 (Wade and Theobald 2010). Rapid rural development driven by the expansion of low-density residential development is projected to increase developed areas in the US by 51% between 2003 and 2030 (39% in the Northeast; White et al. 2009).

Suburban landscapes, characterized by relatively small buildings interspersed with lawn, forest fragments, and relatively narrow roads, are structurally different from industrial and agricultural landscapes and also differ in how they affect aquatic ecosystems. Recent work has demonstrated that pollutants affecting amphibians in suburban pools differ from those in agricultural landscapes. Specifically, suburban pools lack the pesticide contamination associated with agriculture, and suburban land cover (landscaping vegetation and impervious cover) is a substantial source of estrogenic compounds (Lambert et al. 2015; Lambert and Skelly 2016). Roadways in suburban landscapes also contribute road salt contamination to breeding pools and can reduce wood frog larval condition and survival (Sanzo and Hecnar 2006), embryo survival (Brady 2013), and post-metamorphic survival (Dananay et al. 2015; Green and Bailey 2015) as well as increase physiological stress of breeding adults (Hall et al. 2017).

Despite negative associations of suburbanization with wood frog population size, breeding occupancy, and negative responses to road salt contamination, wood frog larvae do not necessarily exhibit negative responses to terrestrial disturbances. For example, wood frog larvae have equal if not greater survival, condition, and size in suburban landscapes (Shepack et al. 2017; Eakin CJ (2018) Wildlife use of vernal pools in an urbanizing landscape, in review) and stormwater wetlands (Scheffers and Paszkowski 2016) compared to rural or natural landscapes and pools. Increases in impervious cover within 300 m of pools have been positively associated with wood frog larval responses across a rural-suburban gradient, with faster and larger development in suburban than rural pools (Eakin CJ (2018) Wildlife use of vernal pools in an urbanizing landscape, in review). Increases in wood frog tadpole size across a forest-suburban gradient have also been associated with wastewater intrusion and alterations to aquatic food webs (Holgerson et al. 2017).

For a variety of taxa, including amphibians, environmental conditions experienced during early life stages may have latent effects that influence later life stages (Pechenik 2004). Thus, the influence of suburban land conversion on amphibian aquatic stages may continue to affect individuals after metamorphosis, potentially with lifelong consequences. Several studies have demonstrated that natural differences in pool

conditions during wood frog larval development influence post-metamorphic responses (canopy cover, Boes and Benard 2013; accelerated drying, Gervasi and Foufopoulos 2008; water level and food availability, Crespi and Warne 2013; predator presence, Relyea 2001; Barbasch and Benard 2011; and conspecific density, Goater and Vandenbos 1997). Thus these effects may have life-long consequences, potentially influencing adult physiology and behavior (Denver 2009), and fitness (Semlitsch et al. 1988; Berven 1990; Relyea and Hoverman 2003). Additionally, because larval phenotype may not accurately indicate fitness, responses at later life stages (e.g., post-metamorphic) may be better indicators of fitness (Earl and Whiteman 2015).

Although some research has addressed the response of wood frogs at terrestrial stages to suburban land conversion (breeding population size, Veysey et al. 2011; Clark et al. 2008; Windmiller et al. 2008; adult age and morphology, Jennette 2010; movement patterns, Hoffmann and Hastings unpublished data; movement ability, Cline and Hunter 2014; Cline and Hunter 2016), little work has focused on how suburban land conversion near pools may affect the larval stage. Jennette (2010) suggested that habitat quality at larval or froglet stages may be responsible for size differences in adult wood frogs of the same age in suburban and rural landscapes (smaller in suburban). Furthermore, two studies that examined the effect of road salt contamination during the larval stage showed negative responses at the post-metamorphic stage (Dananay et al. 2015; Green and Bailey 2015). Because suburban land development near pools can alter pool conditions in multiple ways, (e.g., introducing heavy metals [Pb and Zn], Callender and Rice 2000; increasing water temperature, Holgerson et al. 2017; increasing endocrine disrupting compounds, Lambert and Skelly 2016; shifting vegetation composition, Azous and Horner 2000; and altering predator community composition, Rubbo and Kiesecker 2005; Gibbs 1998) examining the latent effects of conditions experienced during larval development across a rural-suburban gradient may integrate the influence of multiple factors associated with suburban land conversion. Additionally, understanding the latent effects of suburban land conversion on terrestrial stages is particularly relevant for vernal pool conservation which often involves conserving habitat some distance from a pool (Calhoun et al. 2005).

In this study we examined how suburban land conversion within 1000 m of pools influences conditions experienced during larval development and produces lasting effects to post-metamorphic stages. We concurrently examined within-pool vegetation, hydrology, and conspecific density because these pool characteristics can result in latent effects in wood frogs (Goater and Vandenbos 1997; Gervasi and Foufopoulos 2008; Crespi and Warne 2013; Boes and Benard 2013). Additionally, because conditions experienced during terrestrial stages can override effects of larval conditions (Boone

2005; Dananay et al. 2015), we also examined how the pool-wide responses of breeding adults were related to conditions experienced by larvae and pool-wide larval responses. Specifically, our objectives were to examine the relative influences of landscape-scale and pool characteristics across a rural-suburban gradient on (1) larval morphology and survival to emergence, (2) newly metamorphosed froglet morphology and locomotor performance, and (3) adult male morphology.

Methods

Study area

The greater Bangor, Maine area is located in the glaciated northeastern US and covers 200 km² encompassing four towns: Bangor, Orono, Hampden, and Old Town (populations of approximately 7000–33,000; U.S. Census Bureau 2011). Within this area there are urbanization intensity extremes of nearly 100% impervious surface in downtown areas to <1% impervious surface in conserved or lightly developed areas (e.g., Bangor City Forest; Fry et al. 2011). However, overall the study area is suburban in character with 42.4–90.4% of the households in Bangor, Orono, Hampden, and Old Town living in detached single-family homes (U.S. Census Bureau 2016), and human land conversion within 1 km of study sites dominated by single-family homes, commercial development interspersed with green spaces, transportation networks, golf courses, cemeteries, and suburban parks (Figs. 1 and 2). We have observed wood frogs breeding within the greater Bangor area in pools with up to 38% impervious cover and as little as 16% tree cover within 1000 m.

Site characteristics

We selected site characteristics to measure in 15 pools that were likely to influence froglet responses based on a concurrent study of larval morphology and development in 30 pools (Eakin CJ, Hunter MLJ, Calhoun AJK (2018) Indicators of wood frog (*Lithobates sylvaticus*) condition in an urbanizing landscape, in review). We used ArcView GIS10.2 to examine the Maine Land Cover Dataset (2004 all land use; 2011 impervious surface; 5 m resolution) and to edit cover types to correct misclassifications and to reflect more recent aerial photographs (World Imagery; 10 July 2015). We then quantified the percent impervious surface within 300 m and forest cover within 100 and 1000 m from pool spring high-water marks (impervious within 300 m: 0–37%, median = 6%; forest within 100 m: 6–100%, median = 74%; forest within 1000 m: 16–78%, median = 55%). We selected 1000 m based on previous evidence that wood frogs respond to conditions within 1000 m (Homan et al. 2004; Rubbo and Kiesecker 2005; Skidds et al. 2007). We used impervious surface to represent urban development

intensity because it includes buildings and pavement and is thus linked to traffic and chemical, light, and noise pollution. We measured spring-high-water depth using a pole marked in centimeter increments. Hydroperiod was determined by the Julian day that standing water was no longer present. Pools that dried to within 10 cm and ≥ 10 cm at the deepest point were assigned Julian day 280 and 300, respectively. We measured summer vegetation within pool basins 19 July–21 August 2014–2016 at late summer dry down by visually estimating percent cover of shrub, emergent vegetation, and submerged vegetation. Woody vegetation canopy density over pools was measured ~1 m above the ground using a spherical convex densitometer (2014 lab-reared larvae pool measurements: 6–100%, median = 68%; 2014–2016 mean adult pool measurements: 39–98%, median = 94%). We used water probes (Hach ©, Loveland, Colorado) to measure water temperature 2 May–16 June 2014–2016. On each date a pool was sampled, we collected and measured 1 L of surface water ~1 m from the water edge at each of three equidistant points around the perimeter. Only one sample was taken at pools that were almost dry and < 2 m². All temperature measurements were conducted at the pool edge within minutes of sample collection. Pool temperature was averaged by day and then year for analyses.

We used wood frog egg mass density (the number of wood frog egg masses counted in a pool divided by pool area; egg masses/m²) to indicate conspecific competition at the larval stage. We counted egg masses after spring breeding (3–8 May 2015), following the apparent peak of breeding using a dependent double-observer method to increase detection (Grant et al. 2005). Observers walked through the pool and wore polarized sunglasses to increase egg mass detection. If eggs had been recently deposited (within approximately 2 days) we revisited pools and counted new masses. The maximum number of egg masses was used to calculate egg mass density.

Site characteristics from 2015 were used in analysis of froglet responses, and mean values from 2014 to 2016 were used in analysis of adult responses because adults were likely from multiple tadpole cohorts (years). We reduced the number of variables in both the 2015 and the 2014–2016 datasets using the ‘Vegan’ library (Oksanen et al. 2017). We conducted separate PCAs for all pool vegetation, land cover type, and hydrology variables and extracted axes values to represent these categories in the two datasets (6 PCAs, total). We also included wood frog egg density as a predictor of larval and froglet responses. Site characteristics variables were not highly correlated (Pearson’s correlation coefficient < |0.36| for 2015 and 2014–2016 site characteristics).

Larval to post-metamorphic latent effects: Morphology and performance measures

In 2015, we conducted a microcosm experiment to assess the effects of environmental conditions experienced during early

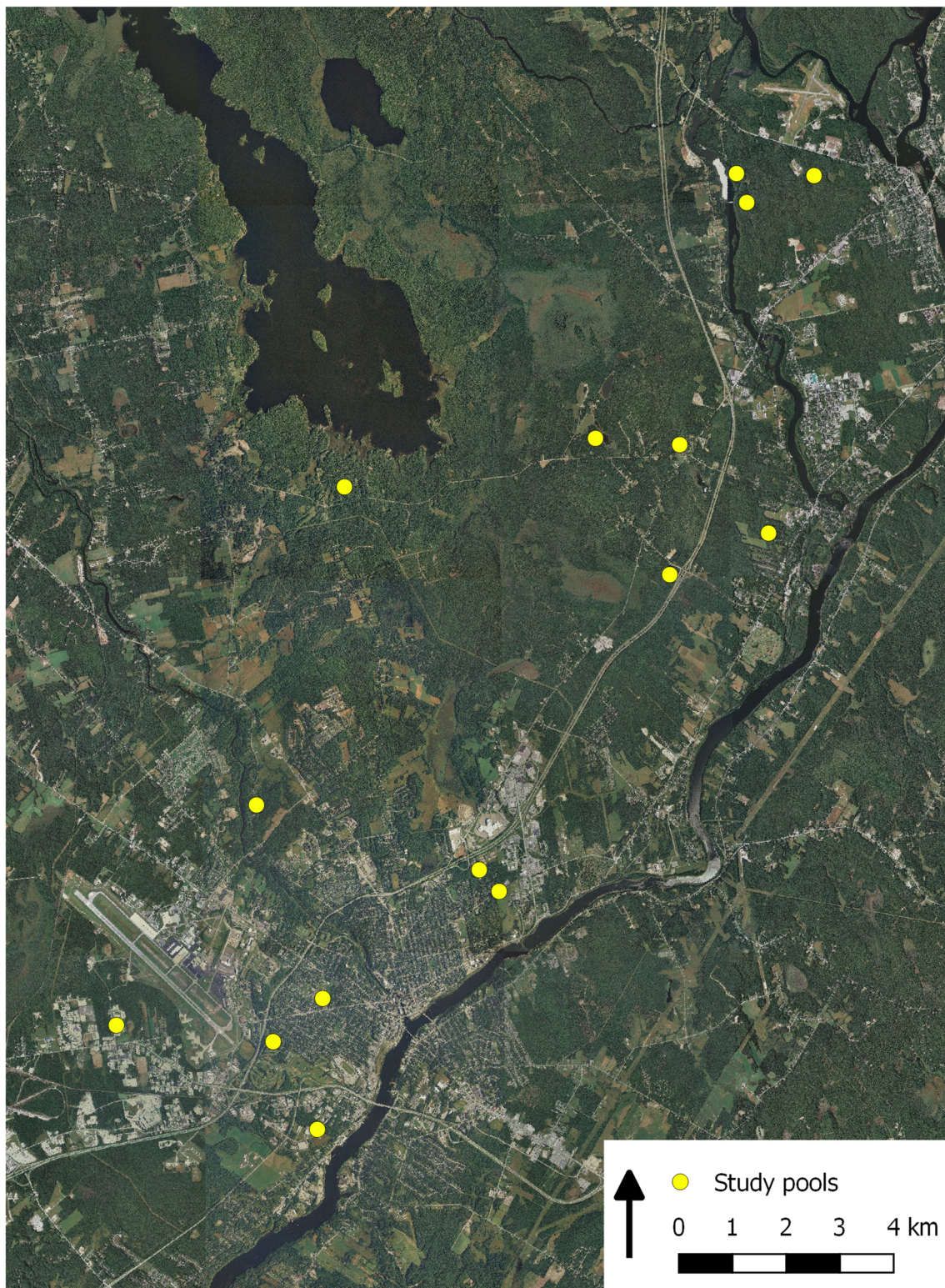


Fig. 1 Aerial photo and study pool locations within the study areas in greater Bangor, Maine. Study pools were located in suburban to rural areas, with single-family homes, commercial development interspersed

with green spaces, transportation networks, golf courses, and suburban parks as the dominant forms of human land use change. Map shows 2015 World Imagery provided by Esri (Redlands, California, USA)

larval development on post-metamorphic morphology, survival, and locomotor performance in wood frogs. Post-metamorphic performance may reflect physiological condition and

movement ability of a froglet, and thus can be useful to indicate aspects of individual condition not represented by morphology that are relevant to dispersal, migration, and resource

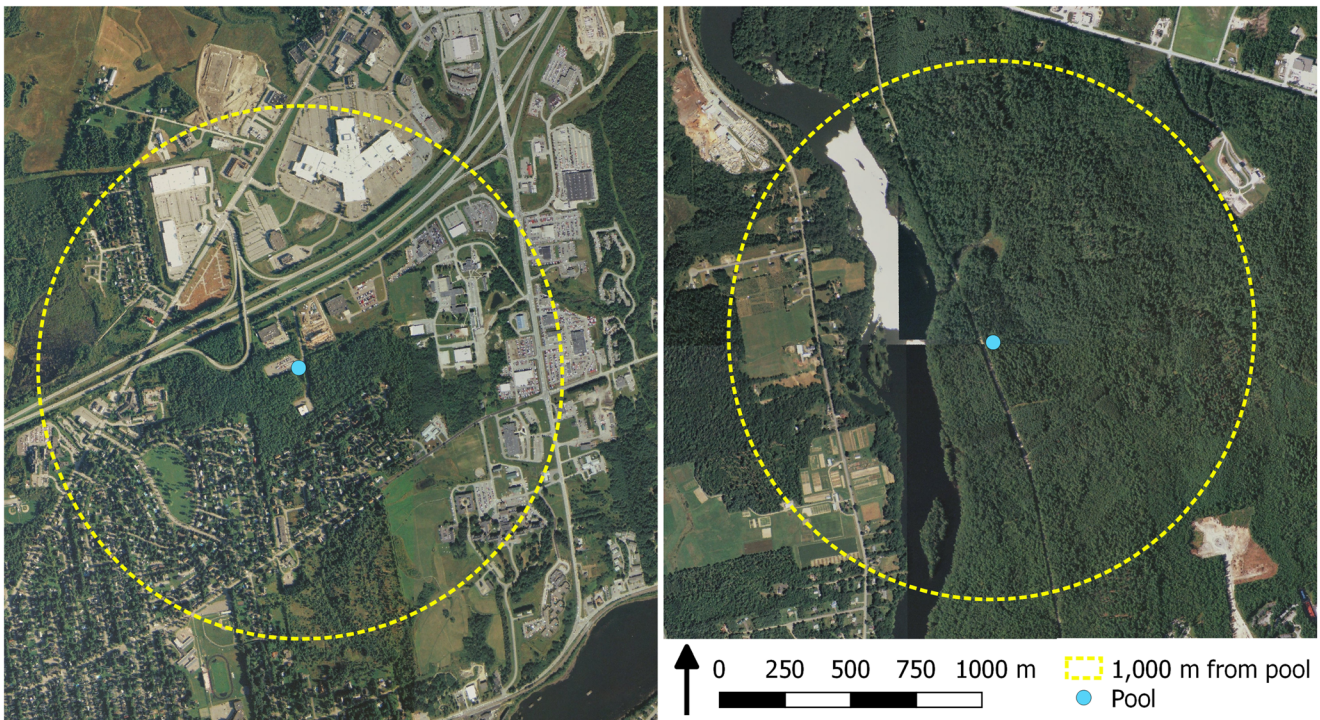


Fig. 2 Study sites with the least and most impervious cover within 1000 m. Maps show 2015 World Imagery provided by Esri (Redlands, California, USA)

selection ability. We captured 10 tadpoles per pool for 10 pools representing the available gradient of impervious surface cover within 1000 m of the pools that had tadpoles surviving to Gosner (1960) stage 36–42 (median = 40). We captured larvae (Gosner stage 36–42) from each pool between June 16–July 22 and transferred individuals from the field in 1 L plastic containers of pool water to a lab at the University of Maine. In the lab, we placed each larvae in 1 L of aged tap water in individual plastic containers that also had 200 cm² of terrestrial area. Small ramps allowed newly emerged froglets to leave the water at will. Each day, we checked microcosms for emerged froglets and for these individuals removed water containers to provide a larger (275 cm²) terrestrial area and to prevent drowning. We changed water every 72 h to prevent fouling. Animals were kept under ambient light conditions. Each terrestrial microcosm contained leaf litter (primarily oak, *Quercus* spp.) approximately 2 cm deep and was misted with water daily. We fed larvae rabbit pellets and boiled romaine lettuce and fed froglets live flightless fruit flies, following Greenspan et al. (2012). Each microcosm was covered with a window-screen lid to prevent froglet escape.

We measured snout-vent length (SVL) and mass of each individual to assess individual morphology at time of capture. After emergence we conducted two “rounds” of post-metamorphic locomotor performance trials and morphology measurements representing early and late froglet responses: first on days 1 and 2 after emergence and the

second on days 29 and 30. We assessed performance for each froglet by conducting maximum jump trials on day 1 and 29, and endurance trials on day 2 and 30 following Boes and Benard (2013). We conducted maximum jump distance trials by placing a newly metamorphosed froglet in the center of a circular arena (1.5 m diameter plastic tub) under an opaque cup. The froglet rested under the cup during a 2 min adjustment period before the cup was lifted and the distance of the first jump was recorded. Froglets that did not immediately jump were gently tapped on the urostyle. Three trials (separated by 6 min) were conducted for each froglet on the same day. The maximum jump distance (Jump) from the three trials in a day was used in analyses. To conduct endurance trials, we placed a froglet under an opaque cup on a circular track approximately 10 cm wide with walls 10 cm high for a 2 min adjustment period. Upon lifting the cup, we recorded the total distance moved (Dist) and duration of movement (Duration) and calculated average speed (Speed). When a froglet did not immediately jump or came to a rest, it was gently tapped on the urostyle up to three times to encourage movement. Once a froglet did not jump after being tapped three times, the trial was concluded. On days 2 and 30, we measured SVL, mass, and hind leg length (following Boes and Benard 2013). We anesthetized froglets using MS-222 (Gentz 2007) prior to measurement to ensure their safety. After measurement, froglets were bathed in aged tap water with their head above the water until they regained locomotor ability.

Relating larval and adult responses: Morphology measures

During the 2 years prior to adult sampling (2014–2015), we measured tadpoles in the 9 pools where adults were sampled. We collected these data to predict breeding male size because breeding adult males likely represent multiple cohorts and may have hatched within the previous 2 years. We conducted weekly tadpole surveys (Eakin CJ (2018) Wildlife use of vernal pools in an urbanizing landscape, in review) between 15 June–26 August, and measured SVL and mass of Gosner stages 40–41 tadpoles. Tadpoles at these developmental stages are typically at their largest size prior to completion of metamorphosis. We conducted ANCOVAs to determine if there were differences in SVL and relative mass (residuals of mass regressed against SVL) between years or developmental stages. Because there were no substantial differences (for those models where $P < 0.1$, $\eta^2 \leq 0.05$ indicated small effect size; Levine and Hullett 2002), we pooled observations across years and/or stages and calculated median SVL and relative mass.

In 2016, we captured and measured adult male frogs to assess how population level responses of breeding adults were related to conditions experienced by larvae and pool-wide larval responses. Due to logistic constraints, we could not capture enough females across pools to incorporate into analyses. Since wood frog survival to first reproduction is not different between sexes (Berven 1990), we used adult males as a proxy for adult wood frog responses. We used minnow traps to capture adult male wood frogs in 9 breeding pools (4 of the same pools from which tadpoles in the microcosm-rearing portion of the study were captured) from April 13–24. We weighed frogs, measured SVL, and toe-clipped new captures to prevent resampling. Given wood frog's high breeding fidelity to their natal pool (Berven and Grudzien 1990; Vasconcelos and Calhoun 2004), we assume that a high percent (>80%) of males were sampled at their natal pool.

Statistical analysis

All statistical analyses were completed using program R (R Core Team 2016). Initially we conducted ANCOVAs for a subset of lab-reared individuals and a subset of adults from the four most rural and four most suburban pools in each full dataset to examine if suburbanization level influenced the relationships (i.e., rate of change) between pairs of likely size- or developmental stage-dependent responses and SVL or Gosner stage (Table 1). We used impervious cover within 300 m (lab-reared individuals: rural pools: 3–6%, suburban: 22–27%; adults: 0.02–2% rural, 14–27% suburban) to represent suburbanization intensity because this was identified as an important site characteristic for predicting larval wood frog morphology (Eakin CJ (2018) Wildlife use of vernal pools in an urbanizing landscape, in review). Because there were no

Table 1 Larval, froglet, and adult frog response variables. Where a regressor variable is listed, pairs of response-regressor variables were examined for differences in relationship between rural and suburban pools using ANCOVA. Relationships with regressors were examined for early and late froglet morphology and performance responses

Response variable	Regressor variable
ln(larval SVL)	Larval Gosner stage
ln(larval mass)	ln(larval SVL (mm))*
ln(froglet SVL)	–
ln(froglet mass)	ln(froglet SVL(mm))*
ln(froglet leg length)	ln(froglet SVL(mm))*
ln(maximum jump distance)	ln(froglet SVL(mm))
ln(duration)	ln(froglet SVL(mm))
ln(speed)	ln(froglet SVL(mm))
ln(distance moved)	ln(froglet SVL(mm))
ln(adult SVL)	–
ln(adult mass)	ln(adult SVL(mm))*

Regressor variables with an (*) were included as a covariate in linear mixed effect models

substantial differences in these relationships between suburbanization levels (for those models where $P < 0.1$, $\eta^2 \leq 0.08$ indicated small effect size), we pooled all sites in each respective dataset for further analysis.

We tested for differences among sites using MANOVAs with response vectors of larval and early froglet responses ($P < 0.05$) and logistic regression to test for differences in probability of survival to emergence ($X^2 < 0.05$). Because of unexpectedly low survival to the second round of froglet measurements (1–6 observations per site; median = 2), we did not test for differences among sites for second measurements, but instead relied on differences among sites for early froglet measurements to indicate likely differences at the late froglet stage. We used ANOVA to test for among-site differences in adult responses ($P < 0.05$) because of highly uneven sample sizes (8–53) and because we were examining only two responses. Prior to larval and early froglet MANOVAs, we conducted an ANOVA for each pair of variables used in ANCOVAs to identify which responses were size- or developmental stage-dependent and should be corrected for size or stage. For all response-regressor pairs except larval SVL-Gosner stage and duration-froglet SVL, the regressor was significant ($P < 0.1$) with at least a moderate effect size ($\eta^2 > 0.2$). All regressions were interpreted using Type II sum of squares to reduce the influence of uneven sample sizes. We extracted residuals from significant relationships for use in MANOVAs. We conducted MANOVAs for early froglet responses (round 1) from sites with ≥ 4 complete cases to maintain similar sample sizes among sites (53 froglets from 8 sites, 4–8 individuals per site).

If differences among sites were detected for morphology, performance, and/or survival metrics, we used a two-step model selection process to identify which predictors within

each predictor category (site characteristics, larval morphology) were likely influential and then compare the relative influence among those variables. Site characteristic variables were used to predict all responses (Fig. 3a); larval morphology variables from lab-housed individuals were used to predict all froglet morphology and performance and survival metrics (Fig. 3b); median larval morphology from late-stage field measured tadpoles was used to predict adult metrics (Fig. 3c).

First we created a set of linear models for each morphology and performance response variable using R package ‘lme4’ (Bates et al. 2017) for continuous data and logistic regression models using package ‘nlme’ (Pinheiro et al. 2017) for binary survival data. For all responses except those from late stage froglets we nested by Site (random effect). We did not nest by Site for late stage froglets because of the small sample size and low per-site replicates (individuals). A single predictor was added to create competing models. Models of relative mass and leg length always included natural log-transformed SVL as a covariate because we were interested in the effect of these responses independent of body size. The influence of SVL was not interpreted in these models. We grouped models of each response by predictor category and selected the top models for a response within each category. We used library ‘AICcmodavg’ (Mazerolle 2017) to rank models using Akaike’s information criterion adjusted for small sample size (AICc). We considered models $\Delta\text{AICc} < 2$ that ranked above the null model to be plausible (Burnham and Anderson 2002). If > 1 model met these criteria, we tested additive models that included all combinations of covariates in plausible models. Secondly, for each response, we compared all plausible models across predictor categories to determine the relative importance of predictors. Similar to the first step, if > 1 model had $\Delta\text{AICc} < 2$ we tested additive models that included all combinations of covariates these highly-ranked models. We examined the 85% confidence intervals (Arnold 2010) of each covariate in this final set of models (i.e., that ranked above the null model and had $\Delta\text{AICc} < 2$ within its respective predictor category) to determine effect. An effect (predictor with an 85% CIs different from zero) of site characteristics but not

of larval morphology suggests that site characteristics may influence later stages via an unmeasured morphology or physiologically related variable. In contrast, an effect of larval morphology but no effect of site characteristics suggests that an unmeasured difference among sites is responsible for the persistent effect of larval morphology on terrestrial stages.

Results

Summary statistics

Of 100 tadpoles captured, 57 froglets survived to emergence and were used in froglet model selection analyses. Of those 57, 21 survived until the second froglet performance trials (6 from suburban pools, 13 from rural pools, and 2 from intermediate development intensities) and 14 completed second performance trials (5 from suburban pools, 7 from rural pools). Larval morphology and early froglet morphology-performance profiles differed by site (MANOVA, Larval: $F_{9,90} = 8.88$, $P < 0.001$; Froglet: Pillai test $F_{7,45} = 2.06$, $P < 0.001$), as did survival to emergence ($X^2_{9,100} = 22.85$, $P = 0.007$). We measured 266 unique adult male frogs (8–53 per site), and adult SVL and mass adjusted for SVL differed by site (SVL: $F_{8,257} = 13.52$, $P < 0.001$, $\eta^2 = 0.30$; Mass: $F_{8,256} = 13.51$, $P < 0.001$, $\eta^2 = 0.17$).

Pool characteristic metrics for the set of 15 focal pools did not vary with suburbanization (as indicated by impervious cover within 300 m; $P > 0.1$) with one exception. The hydrology metric (Hydro) decreased with suburbanization ($F_{1,8} = 13.23$, $P = 0.01$) for the 10 tadpole source pools, but this trend was not universal across the set of 30 pools used to calculate principal component values for 2015 ($F_{1,28} = 0.078$, $P = 0.78$).

At least one site characteristic had a statistical effect ($\Delta\text{AICc} < 2$ within each predictor category and with 85% CI excluding zero) on all larval, froglet, and adult responses except for late froglet leg length (Figs. 4 and 5, Online resource Table 2). Of those early froglet responses predicted by site characteristics, all except duration were also predicted

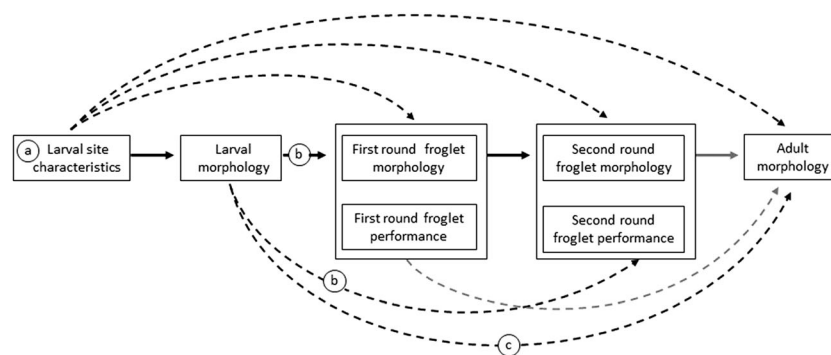


Fig. 3 Direct and indirect effect pathways among site characteristics and stages of wood frog development. Solid lines represent direct effects and dashed lines represent indirect effects. Effects represented by black

arrows were explored in our study; grey arrows were not addressed with our study design. Circled letters are for reference in the text

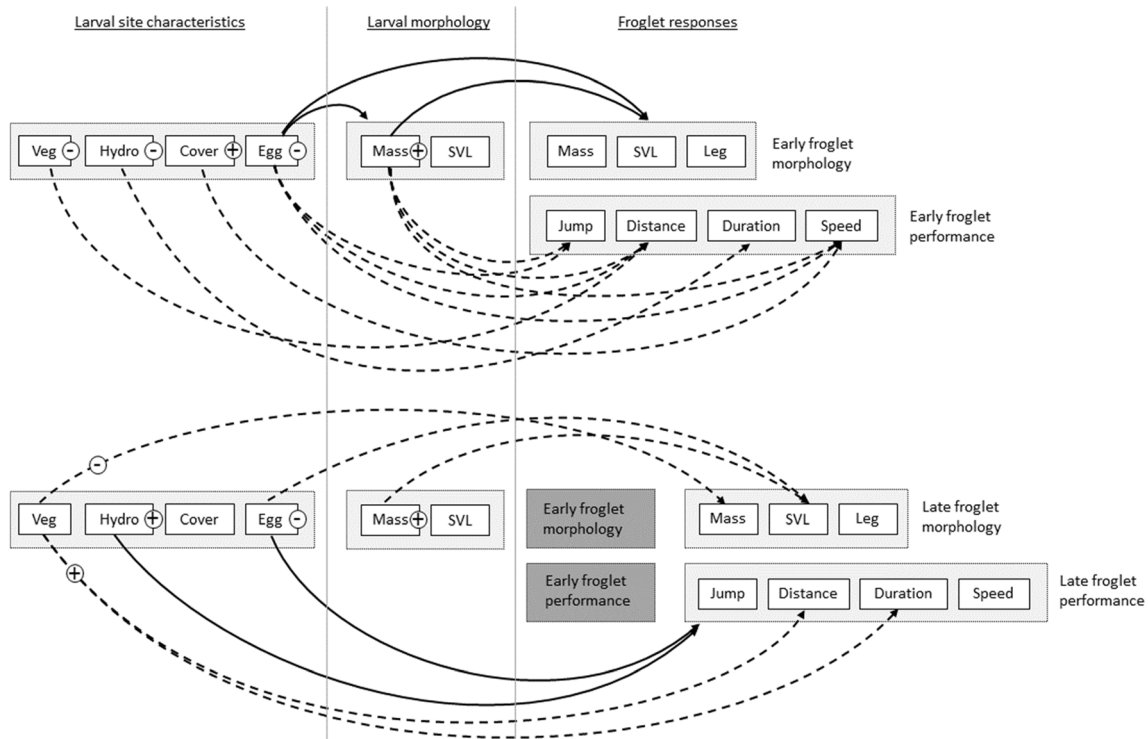


Fig. 4 Carry-over effects of site characteristics and morphology on early froglet (top half) and late froglet (bottom half) morphology and performance. Arrows originate at the predictive parameter and point at the response. Arrows represent explanatory parameters from models with $\Delta AICc < 2$ and that had 85% CIs excluding zero. Solid arrows that point at categories of variables (enclosed in gray boxes) indicate a statistical

effect on all variables within a box. Dashed lines indicate an effect of one predictor on one response variable. Circled “+” and “-” indicate the direction of effect of a predictor on responses. Vegetation (Veg) has both positive and negative effects associated with different responses at the late froglet stage and thus the direction of effect is indicated on the appropriate arrow

by larval morphology. SVL was the only late stage response and mass was the only adult response predicted by site characteristics and larval morphology (Figs. 4 and 5, Online resource Table 2). For those responses for which both site

characteristics and larval morphology had an effect, models with larval morphology predictors ranked above those with site characteristic predictors (Figs. 4 and 5, Online resource Tables 1-2).

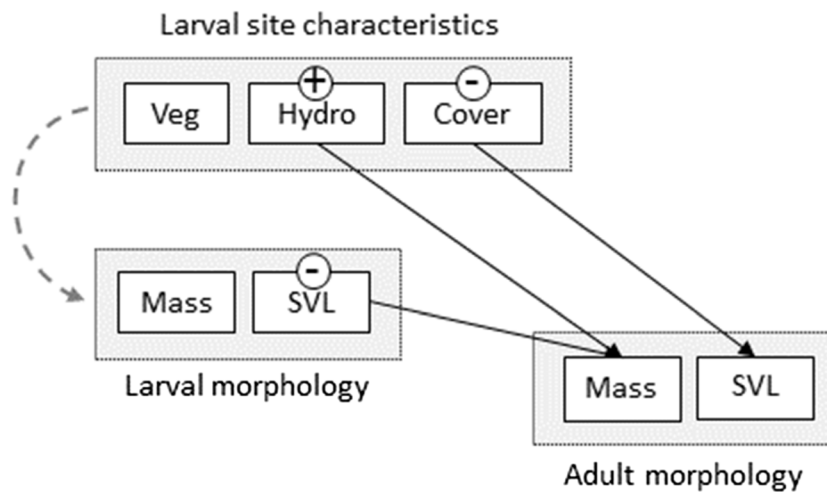


Fig. 5 Relationships among site characteristics and larval and adult morphology. Solid arrows originate at the predictive parameter and point at the response and represent explanatory parameters from models with $\Delta AICc < 2$ and that had 85% CIs excluding zero. The dashed arrow

indicates the unmeasured but likely influence of site characteristics on larval morphology. Circled “+” and “-” indicate the direction of effect of a predictor on responses

Table 2 Predictors of larval, froglet, and adult frog responses

Variable	Description
Site characteristics	
Veg	Vegetation PC1: canopy cover (+, 0.573, 0.589); shrub (–, –0.346, –0.128), emergent (–, –0.623, –0.603), and submerged vegetation cover (–, –0.404, –0.523)
Cover	Cover PC1: tree cover within 100 (+, 0.582) and 1000 m (+, 0.573), impervious cover within 300 m (–, –0.576)
Hydro	Hydrology PC1: hydroperiod (+, 0.601, 0.629) and maximum depth (+, 0.571, 0.547), surface water temperature (–0.560, –0.552)
Egg	ln(Wood frog egg masses/m ²)
Larval morphology of tadpoles raised in the lab (individual measures)	
L.Mass	Relative larval mass: ln(Larval mass (g)) ¹
L.SVL	Larval SVL: ln(SVL (mm))
Larval morphology of tadpoles at pools where adults were measured (cohort measures)	
L.Mass	Relative larval mass: Within-pool median of residuals of ln(Larval mass (g)) regressed against ln(Larval SVL (mm)) ¹
L.SVL	Larval SVL: Within-pool median ln(SVL (mm))

Within a principal component, (–) indicates a negative relationship, and (+) indicates a positive relationship. Pairs of numbers listed in parentheses after each variable in a PC refer to eigenvalue contributions within the 2015 and 2014–2016 datasets. Only one number is listed for each cover variable because cover was consistent among years

¹ Larval or froglet ln(SVL) is included as a covariate to account for variation in larval or froglet response, respectively, attributed to body size

² Froglet morphology was assessed early (F1) and late (F2) in froglet development

Site characteristic predictors

Tadpoles from pools with a higher egg density were predicted to have lower SVL and mass, and become froglets with shorter and slower jumps and lower endurance (but no effect on duration in early froglets; Fig. 4, Online resource Tables 1–2). Vegetation (Veg), hydrology (Hydro), and land cover type (Cover) each had somewhat conflicting statistical effects across responses (Fig. 4, Online resource Tables 1–2). Tadpoles from pools with vegetation characterized by less canopy and more herbaceous cover (negative Veg values, Table 2) were predicted to have lower mass and move shorter distances in endurance trials as early-stage froglets but farther distances in endurance trials and greater duration as late-stage froglets (Fig. 4, Online resource Tables 1–2). Tadpoles from pools with higher hydrology values (primarily corresponding with longer hydroperiod and deeper water and secondarily with cooler water, Table 2) were predicted to have shorter jump duration as early-stage froglets, but be better jumpers (positive effect on all performance metrics) as late-stage froglets (Fig. 4, Online resource Tables 1–2). Adults breeding in pools with greater hydrology values were predicted to have greater mass. Land cover type (characterized by more tree cover and less impervious cover, Table 2) was positively associated with early froglet jump speed (Fig. 4, Online resource Tables 1–2). Land cover type was weakly negatively associated with adult SVL (small effect size as indicated by β estimate; Fig. 5, Online resource Tables 1–2).

Larval morphology predictors

Froglet responses were positively associated with larval predictors; all larval predictors in top-ranked froglet response models that also had covariate estimates with 85% CI different

from zero had a positive effect on responses (Fig. 4, Online resource Table 2). Survival models with larval SVL and mass as predictors ranked above the null model, but only SVL had an 85% CI that did not include zero (β Mass: –0.517, 2.02; Online resource Table 2); tadpoles with greater larval SVL were predicted to have a greater probability of survival to emergence (Online resource Tables 1 and 2). Tadpoles with greater mass were predicted to have greater early froglet morphology and performance responses (for 6 of 7 metrics) and late froglet SVL. Pool-wide larval SVL was the predictor in the top-ranked model of adult mass, with a negative effect on mass.

Discussion

In a suburban landscape in the greater Bangor, Maine region, characteristics of pools influenced larvae and had latent effects on morphology and performance at terrestrial stages, with larval density having a stronger influence relative to that of vegetation and hydrology. In contrast, cover types in suburban landscapes have little to no lasting influence on terrestrial stage wood frogs via impacts on aquatic stages. Although cover type had statistical effects on terrestrial wood frog responses, the small effect size for adult SVL and the small proportion of froglet responses for which there was a statistical effect (1 of 15) suggest that biological significance is limited. The overall lack of effect of cover type on larval and froglet metrics is unexpected as it is well-demonstrated that suburban land cover can impact aquatic amphibians (Lambert et al. 2016) and specifically wood frog (Smits et al. 2014; Lambert et al. 2015; Holgerson et al. 2017).

Our work is consistent with some other papers showing limited harm of suburban development on some aspects of

wood frog development and ecology (larval development, Shepack et al. 2017; Eakin CJ (2018) Wildlife use of vernal pools in an urbanizing landscape, in review; genetic connectivity, Gabrielsen et al. 2013; Furman et al. 2016; terrestrial stage habitat suitability, Nagy et al. 2011). However, it seems more relevant that three other concurrent studies in our study area found negative effects for wood frogs (smaller breeding population size, Eakin CJ (2018) Wildlife use of vernal pools in an urbanizing landscape, in review; genetic isolation, Homola 2018; restricted adult movements, Hoffmann and Hastings unpublished data). Thus, it is unlikely that our results indicate that there is minimal harm from suburban development to wood frogs. Our work more likely suggests that harm from suburbanization realized at terrestrial stages is not attributable to the influence of suburban land conversion on conditions experienced during larval development or that we failed to detect an effect of suburbanization where one existed because of an unmeasured yet relevant factor. For example, we did not account for sex in froglet and larval analyses because wood frogs completing metamorphosis in forested landscapes have 1:1 sex ratios (Berven 1990); however, recent work shows several suburban-associated factors, such as lawn, landscaping vegetation, domestic wastewater contamination, and road salt contamination (Smits et al. 2014; Lambert and Skelly 2016; Lambert et al. 2017) can alter the sex ratio of amphibians as well as sex-specific morphological responses of wood frog (Lambert et al. 2018). Additionally, we may not have detected an effect of suburbanization if it is driven by a specific factor not accurately represented by our integrated metric of suburban cover (impervious and forest), such as road salt, which is not applied to all impervious cover, or spatial configuration of terrestrial habitat. Low survival to the late froglet stage also may have compromised our ability to detect an effect of suburbanization; i.e., the resulting low sample size prevented accounting for the common influence of Site among individuals from the same developmental pool (i.e., nesting by Site). Although for this study we assumed land cover to have a separate influence from within-pool characteristics, we cannot discount the possibility that suburban land conversion may have influenced within-pool vegetation, hydrology, and egg density and that these may represent indirect effects of suburbanization on wood frogs.

Our observation that egg density negatively affects larval morphology and froglet locomotor performance aligns with well-studied relationships of increased conspecific density resulting in smaller (mass, volume, or body length) wood frogs at metamorphic climax (emergence of front legs; Wilbur 1977; Smith-Gill and Berven 1979; Berven and Chandra 1988; Berven 2009) including in an urban landscape (Scheffers and Paszkowski 2016). Additionally, Goater and Vandenbos (1997) observed that the effects of experimentally

controlled larval density on froglet morphology are detectable months after metamorphosis. Our results suggest that conspecific density in the field may have similarly long-lasting effects on juveniles, including consequences for post-emergence movement ability. Additionally, egg density may affect froglets indirectly via larval morphology: we observed that relative larval mass, which decreased with egg density, affected froglet morphology and performance and models with egg density as a predictor out-ranked competing models with egg density as a predictor. However, our findings that larval SVL (pool-wide) was negatively associated with relative adult mass suggest a possible disconnect between egg density effects on larval stages and adult morphology. Terrestrial habitat quality may explain these conflicting effects between juvenile and adult stages: high-quality terrestrial habitat could be expected to support a relatively large population of fecund adults that would produce a greater egg density, which could have negative effects on larval size. Alternatively, land conversion that removes breeding pools but maintains ample terrestrial habitat could funnel all adults from a relatively large terrestrial area into a few remaining breeding pools, increasing the egg densities in remaining pools and reducing larval size. Similarly, our observed negative relationship between relative larval mass and adult size is unexpected based on published positive correlations between size of newly emerged froglets and one-year old size and survival (Berven 1990), but aligns with other work demonstrating that variation in terrestrial areas can mask effects of larval environments (Earl and Semlitsch 2013).

The positive relationships between larval and froglet mass and between larval SVL and survival in wood frog aligns with other studies (Goater and Vandenbos 1997; Relyea 2001; Berven 2009). Additionally, the positive effect of larval mass, froglet mass, and leg length across froglet performance measures is consistent with other research on wood frogs (Boes and Benard 2013) and newly emerged froglets of other species (Álvarez and Nicieza 2002; Orizaola and Laurila 2009). Our results indicate that larval mass, which corresponds with the amount of fats and other energetic reserves relative to body size (i.e., condition; reviewed by Green 2001), is a better predictor of froglet morphology (SVL, relative mass, and relative leg length) than is larval SVL and thus may be of greater importance to fitness. The effect of larval mass on froglet morphology suggests that greater late-stage larval metabolic reserves may help froglets move faster and farther immediately after emergence from a pool. This may be particularly important in fragmented urbanized landscapes where longer movements may be necessary to locate suitable overwintering areas and for juveniles to disperse to sustain genetic connectivity and colonize suitable breeding pools.

Although we did not detect an effect of hydrology on larval morphology, hydrology conditions that primarily corresponded with longer hydroperiod and deeper water, and secondarily with cooler water, indicated greater late stage

froglet performance and larger relative mass of adults. The effect on late stage performance suggests that hydrology conditions experienced during larval development could benefit frogs at terrestrial stages and persist through adulthood. Other studies have noted wood frog larvae size and relative mass increased with hydroperiod, pool depth, and cooler water (Karraker and Gibbs 2009; Eakin CJ, Hunter MLJ, Calhoun AJK (2018) Indicators of wood frog (*Lithobates sylvaticus*) condition in an urbanizing landscape, in review; Herreid and Kinney 1967; Watkins and Vraspir 2006; however, see Rowe and Dunson 1995). In our study, we detected an effect of hydrology conditions experienced during larval development on *terrestrial* stages.

Vegetation indicative of high-light conditions (consistent with less-dense canopy cover) was correlated with greater mass in late stage froglets and aligned with other studies that have demonstrated that froglets from open-canopy pools emerge at greater size than those from closed-canopy pools (Werner and Glennemeier 1999; Skelly et al. 2002; Schiesari 2006). However, there is some inconsistency within the literature; both Halverson et al. (2003) and Boes and Benard (2013) observed larger wood frogs developing in closed-canopy pools. The inconsistent effect of vegetation that we observed between early and late performance (i.e. individuals from high-light pools jumped farther in early stage endurance trials (Distance), but had shorter jumps (Distance and Duration) as late stage froglets) may suggest that vegetation during the larval stage can influence terrestrial stages, but the direction of effect changes with time since emergence.

Conclusion

Our findings indicate that egg mass density, vegetation, and hydrology experienced during larval development can influence terrestrial stages even though their effects may not be expressed in larval and/or froglet morphology. Although the influences of cover type near larval development pools may not have persistent effects on terrestrial stages, suburban cover type experienced during terrestrial stages may affect population persistence. Alternatively, suburbanization may have lasting effects via larval development but be better represented by factors other than forest and impervious cover such as water chemistry metrics or the spatial configuration of habitat components. As indicated by recent studies (Lambert et al. 2015; Lambert and Skelly 2016), the presence of environmental sex determination in wood frog makes determining the sex of individuals critical in future comparisons among urban, suburban, and rural wood frog populations. The effect of pool hydrology on adult mass supports the idea that site conditions experienced during larval development have life-long consequences, but may not be adequately captured by larval or froglet morphology measurements alone. Although some

researchers have examined the relative effects of pool and landscape-scale characteristics on morphology and survival throughout the wood frogs' life-cycle (Berven 2009; Green and Bailey 2015), understanding these relationships in suburbanizing landscapes will help ensure that conservation actions are effective. Further study that examines the relative influence of larval and terrestrial conditions on adult morphology and performance, as well as survival to breeding in suburbanizing landscapes, can enhance our understanding of which aspects of suburbanization contribute to wood frog population declines. Although our research did not identify a mechanism of suburbanization acting at the larval stage and affecting terrestrial stage responses, our research in the context of others' findings strongly suggests that suburbanization harms at least some wood frog populations. These findings support the idea that planners should strive to maintain connected and high-quality habitat for aquatic and terrestrial stage wood frogs when possible.

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