

Individual variation affects departure rate from the natal pond in an ephemeral pond-breeding anuran

Nathan D. Chelgren, Daniel K. Rosenberg, Selina S. Heppell, and Alix I. Gitelman

Abstract: Frogs exhibit extreme plasticity and individual variation in growth and behavior during metamorphosis, driven by interactions of intrinsic state factors and extrinsic environmental factors. In northern red-legged frogs (*Rana aurora* Baird and Girard, 1852), we studied the timing of departure from the natal pond as it relates to date and size of individuals at metamorphosis in the context of environmental uncertainty. To affect body size at metamorphosis, we manipulated food availability during the larval stage for a sample (317) of 1045 uniquely marked individuals and released them at their natal ponds as newly metamorphosed frogs. We recaptured 34% of marked frogs in pitfall traps as they departed and related the timing of their initial terrestrial movements to individual properties using a time-to-event model. Median age at first capture was 4 and 9 days postmetamorphosis at two sites. The rate of departure was positively related to body size and to date of metamorphosis. Departure rate was strongly negatively related to time elapsed since rainfall, and this effect was diminished for smaller and later metamorphosing frogs. Individual variation in metamorphic traits thus affects individuals' responses to environmental variability, supporting a behavioral link with variation in survival associated with these same metamorphic traits.

Résumé : Les grenouilles possèdent durant la métamorphose une plasticité extrême et une variation individuelle de leur croissance et de leur comportement qui s'expliquent par les interactions des facteurs d'état intrinsèques et des facteurs environnementaux extrinsèques. Nous étudions chez la grenouille à pattes rouges du nord (*Rana aurora* Baird et Girard, 1852) le calendrier des départs de l'étang natal en relation avec la date et la taille individuelle à la métamorphose dans un contexte d'incertitude environnementale. Pour pouvoir agir sur la taille corporelle à la métamorphose, nous avons manipulé la disponibilité de la nourriture durant la vie larvaire dans un échantillon (317) tiré de 1045 individus marqués de façon particulière que nous avons relâché dans l'étang natal au stade de grenouilles récemment métamorphosées. Nous avons recapturé 34 % des grenouilles marquées dans des pièges à fosse lors de leur départ et nous avons mis en relation le moment du début de leurs déplacements au sol avec leurs caractéristiques individuelles à l'aide d'un modèle « temps pour un événement ». L'âge médian de la première capture est respectivement de 4 et de 9 jours après la métamorphose à deux sites. Le taux des départs est en forte relation négative avec le temps depuis la dernière pluie, mais cet effet est moins marqué chez les grenouilles plus petites et celles qui se métamorphosent plus tardivement. La variation individuelle des caractéristiques de la métamorphose affecte ainsi les réactions des individus à la variabilité environnementale, créant ainsi un lien comportemental avec la variation de la survie associée à ces mêmes caractéristiques de la métamorphose.

[Traduit par la Rédaction]

Introduction

Population processes such as dispersal and migration are affected by individual variation in the life history traits of animals (Cam et al. 2002; Clark 2003; Bowler and Benton 2005). Dispersal decisions may be influenced by the animal's state, where costs and benefits depend on properties of the individual (e.g., van der Jeugd 2001). This is particularly important for amphibians that have an aquatic larval state but disperse over land. Many amphibians that metamorphose at ephemeral ponds may be forced to migrate into habitats that are more stable hydrologically or more suitable

for the terrestrial life stages. The optimal timing for departure of newly metamorphosed frogs from their natal ponds may depend on metamorphic traits that are strongly shaped by their early aquatic environment. This phenotypic plasticity and variability are well documented for the life history traits of anurans (Martof 1956; Wilbur 1972) and offer opportunities to evaluate how individual variation interacting with environmental variability influences components of fitness and behavior.

For newly metamorphosed anurans, the decision to emigrate includes the risk of desiccation during overland move-

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N.D. Chelgren,^{1,2} D.K. Rosenberg, and S.S. Heppell. Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331-3803, USA.

A.I. Gitelman. Department of Statistics, Oregon State University, Corvallis, OR 97331, USA.

¹Corresponding author (e-mail: nathan_chelgren@usgs.gov).

²Present address: Present address: USGS Forest and Rangeland Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, OR 97331, USA.

ments. Desiccation risk is itself tempered by growth via three allometric relationships. First, larger individuals are more robust to environmental variability because of their smaller surface area to volume ratio (Shelford 1913; Thorson 1955; Ray 1958; Newman and Dunham 1994). Second, multiple aspects of vagility, including metabolic rate, sprint speed, and endurance increase with increasing size (John-Alder and Morin 1990; Goater et al. 1993; Beck and Congdon 2000; Álvarez and Nicleza 2002). Finally, these two general principles of scaling compound through other physiological mechanisms whereby desiccation leads to reduced locomotor performance (e.g., Weinstein et al. 1994; Rogowitz et al. 1999; Preest and Pough 2003). Desiccation negatively impacts physiological mechanisms that affect movement and stamina including reduced circulatory oxygen delivery and other cardiovascular effects (Hillman 1987, 1991) and cellular energetics (Churchill and Storey 1995). On these grounds, the propensity for terrestrial movement should depend strongly on body size for newly metamorphosed frogs. Aquatic stressors that reduce larval growth rates and prolong the larval period can result in smaller size at metamorphosis and, therefore, affect the physiological ecology of individuals after metamorphosis.

A variety of natural and anthropogenic stressors, in addition to affecting size at metamorphosis, further limit movement opportunities by prolonging the larval period. Delayed ontogeny has been linked with colder water temperatures (Loman 2002), the presence of exotic predators (Kiesecker and Blaustein 1998), and exposure to ultraviolet-B radiation (Belden and Blaustein 2002). There is some evidence that the length of the larval period may affect mobility in anurans (Beck and Congdon 2000) via changes in limb morphology (Emerson 1978, 1986). However, for anuran larvae that develop in ephemeral ponds, impacts of a prolonged larval period on vagility manifest through changes in physiology or morphology are likely outweighed by the increased risk of stranding associated with delayed metamorphosis. Delayed ontogeny, even for individuals that complete metamorphosis, may result in animals missing favorable climatic conditions for emigration. Others that forego emigration during wet conditions and remain in the vicinity of their natal pond for continued growth may not have opportunity again to emigrate under favorable conditions before their pond dries. Our study is the first to use a longitudinal approach in considering how individual characteristics of metamorphic frogs influence emigration behavior in the uncertainty of climatic and hydrologic conditions. The longitudinal approach allowed us to address unique hypotheses that would not be possible to address with more commonly collected cross-sectional data.

This experiment was designed to examine how individual variation and its interaction with environmental conditions influence the emigration behavior of newly metamorphosed northern red-legged frogs (*Rana aurora* Baird and Girard, 1852) from two ephemeral ponds. We specifically examined the interacting effects of date of metamorphosis, body size, and time since rainfall to address three hypotheses: (1) individuals metamorphosing late in the season would emigrate sooner following metamorphosis than individuals metamorphosing early in the season; (2) smaller size at metamorphosis would be associated with delayed emigration; and (3) rain-

fall would influence the timing of movements more strongly for smaller than larger individuals.

Materials and methods

Study species

Northern red-legged frogs breed in ephemeral and permanent ponds in the Pacific Northwest of North America (i.e., southwest British Columbia, western Washington and Oregon, and northwestern California). Though there is little information about movements and habitat preference by newly metamorphosed red-legged frogs, radiotelemetry (Chan-McLeod 2003) and anecdotal accounts of adults associated with lotic and permanent lentic water shorelines during the dry period of late summer (Nussbaum et al. 1983) suggest the importance of successful migration from natal ponds to these microhabitats favorable for hydration and predator avoidance.

Study sites

Our experiment took place in 2002 at two ephemeral study ponds in Lincoln County, Oregon. Ponds were selected for their densities of metamorphic northern red-legged frogs to allow for a minimum of 500 marked individuals at each site and for the suitability of surrounding landscape for pitfall trapping. Burdue's Pond (0.36 ha) was a "disturbed" site where surrounding vegetation was characterized by large areas of bare ground, sparse understory, and patchy canopy cover. Burdue's Pond dried completely on 23 July 2002. The vegetation surrounding State Pond (0.15 ha) was more densely vegetated than at Burdue's Pond, with nearly continuous forest canopy and little disturbed ground. State Pond dried completely on 4 August 2002. Aerial percentage cover of vegetation was two times greater at State Pond than at Burdue's Pond (Chelgren et al. 2006). The amphibian communities of the two ponds also included larvae and adults of the Pacific treefrog (*Pseudacris regilla* (Baird and Girard, 1852)), northwestern salamander (*Ambystoma gracile* (Baird 1859)), and rough-skinned newt (*Taricha granulosa* (Skilton, 1849)).

Field methods

We constructed concentric rings of polyethylene plastic drift fencing with pitfall traps around each pond, described in detail in Chelgren et al. (2006). The innermost discontinuous fences (7.6 m fences separated with 7.6 m gaps) were placed 10–12 m from the pond edges when the ponds were at their maximum size in March and April 2002. Outermost fences were placed approximately 45 m from the pond edges. Outer fences were continuous except where roads and other landscape features prohibited. We buried 363 (Burdue's Pond) and 323 (State Pond) pitfall traps on the inner (pond) side of drift fences spaced 2–3 m apart. Traps were made of two No. 10 cans attached end to end, were fitted with black (Crawford and Kurta 2000) funnel tops to prevent escape by scaling, with small mammal escape devices (Karraker 2001), and with moistened cellulose sponges. We recorded daily rainfall to the nearest 1.0 mm with rain gauges placed within the drift fence arrays at each pond.

Drought during spring of 2002 in western Oregon forced us to use different methods of acquiring study animals at

each site. State Pond appeared to be on a trajectory to dry completely after the fences were constructed, but before we expected significant metamorphosis to occur. In response to this, we set up 1.83 m diameter plastic wading pools on the shore of the drying pond. During May we captured tadpoles of Gosner stages 25–30 (i.e., beginning of limb bud development to initial toe development; Gosner 1960) as they became stranded by the dropping water level and raised them in the wading pools. Tadpoles were fed commercial rabbit pellets *ad libitum* and were provided with logs for structural cover. We replaced 25% of the pool water from a nearby slough and removed feces and uneaten pellet food twice weekly. Acquisition of subjects at Burdue's Pond is described in the following section.

We manipulated food availability to increase the variation in body size at metamorphosis for a subset of tadpoles at each pond. Enclosures were 11.4 L plastic tubs perforated with holes to allow water circulation, were covered with hardware cloth to prevent predation, and were provided with a wooden basking platform. At Burdue's Pond 87 enclosures were placed on the pond bottom. At State Pond, because of the limited pond area and the pond's rapid drying, the 31 enclosures were kept inside 1.83 m diameter plastic wading pools at the pond's edge.

We collected tadpoles by hand and with dip nets for inclusion in food manipulation treatments from 14 May through 2 July 2002. At Burdue's Pond, these individuals were captured in the natural pond, whereas at State Pond, they were a subset of the individuals being held in the plastic wading pools described previously. We collected tadpoles over this protracted period because of the variation that existed naturally in the timing of metamorphosis, but also because this allowed us to control for developmental stage in examining the relationship between date of metamorphosis and departure rate. We categorized metamorphic development into Gosner stages before assigning three tadpoles grouped by developmental stage to each enclosure. We then randomly assigned enclosures to high- or low-food treatments. Both treatments received five pellets of commercial rabbit chow twice weekly until tadpoles reached growth stage 37 (i.e., the appearance of all hind toes as distinct). We then continued to provide the high-food treatment enclosures with the same food allotment. The low-food treatment enclosures received no supplemental food, similar to Audo et al. (1995), but these individuals could graze algae that developed in the enclosures. We removed loose algae, feces, and extraneous food pellets and circulated water with a hand-operated bilge pump twice weekly.

We terminated the feeding trials when tadpoles reached Gosner stages 43–46 (i.e., broadening of the mouth following eruption of the forelimbs to essentially complete metamorphosis). We then anesthetized animals in a 0.25 g·L⁻¹ solution of MS-222 (3-aminobenzoic acid ethyl ester; Nauwelaerts et al. 2000) buffered with sodium bicarbonate (Fellers et al. 1994), and measured snout–vent length (SVL) to the nearest 0.1 mm using a dial caliper. We marked animals with soft, three-digit alphanumeric VIAAlpha tags (Northwest Marine Technology Inc., Shaw Island, Washington) injected subcutaneously in the dorsal thigh (Chelgren et al. 2006), and clipped a single front digit to indicate that the individual was marked. Following marking, we held animals

in enclosures for 24 h to ensure recovery from the anesthesia and tag retention before randomly assigning them to 24 and 16 release groups and locations in Burdue's and State Pond, respectively. This research was conducted under an animal care and use permit issued by Oregon State University and a collection permit issued by the state of Oregon. Animal care complied with the Guidelines for Use of Live Amphibians and Reptiles in Field and Laboratory Research (available from <http://www.asih.org/files/hacc-final.pdf> [accessed 22 February 2008]).

We supplemented the sample of marked individuals from the food manipulation enclosures (317 individuals) with 728 additional marked metamorphic frogs that were not raised in the 11.4 L food manipulation enclosures. At Burdue's Pond, coincident with marking, we captured 366 free-living individuals using a dip net in the range of Gosner stages 43–46. At State Pond, we used 362 metamorphosing individuals that had been raised outside of the 11.4 L enclosures, but in the 1.83 m diameter wading pools, as described previously.

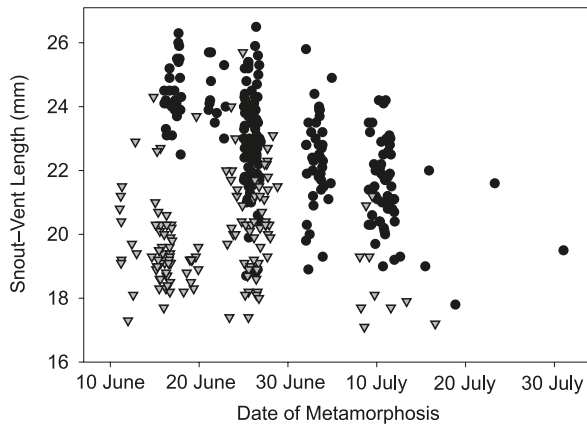
We opened the pitfall-trap arrays when the first metamorphic individuals appeared. We checked and emptied traps daily at Burdue's Pond and on alternate days at State Pond through 31 July. Traps at both sites were checked and emptied on alternate days from 1 August to 8 November. Individuals that were captured in pitfall traps were remeasured and then released on the opposite side of the drift fence adjacent the trap from which they were captured.

We acknowledge that methodological differences between ponds preclude the meaningful comparison of departure rates between ponds. However, the focus of the work and our hypotheses relate to individual animal properties and how these interact with weather variation in affecting departure rate. In the next section, we describe how gross differences in the timing of first captures associated with nuisance variables (pond, including their different trap checking intervals; capture in inner versus outer fences; and developmental stage at marking) were controlled for using separate strata.

Statistical methods

We used the Cox proportional hazards model for time-to-event data (Cox 1972) to study factors affecting the timing of initial terrestrial movements. A time-to-event model was well suited to address our hypotheses about the links between time since rainfall and departure rate because of the time-variable and repetitive nature of this explanatory variable; some frogs skipped one or more episodes of rain, a situation that would be difficult to accommodate using other analytical methods, but that fit easily in a time-to-event approach. The Cox proportional hazards model is a semiparametric model for time-to-event data in the sense that the overall group pattern of events is immaterial as are the exact event times. The only pertinent information about the actual response times are their ranks within strata (Efron 1977). Inference from the model is based on the method of maximum likelihood. The only individuals that entered our analyses were those that were captured in a forest drift fence before traps were closed at the end of the study period, 8 November 2002: 137 of 583 marked animals at Burdue's Pond and 219 of 462 marked animals at State Pond. We believe these accounted for the vast majority of surviving frogs as xeric

Fig. 1. Relationship between date of metamorphosis and body size at metamorphosis for northern red-legged frogs (*Rana aurora*) that entered the departure rate analysis. Symbols (gray triangles for Burdue's Pond and black circles for State Pond) have been jittered along the *x* axis for clarity.



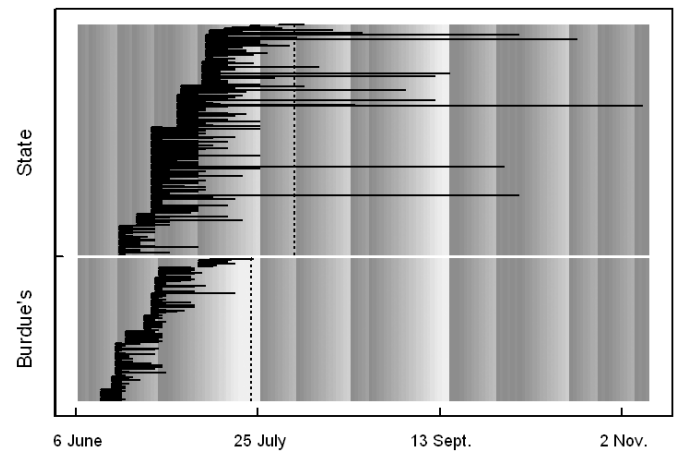
conditions inside the fence arrays appeared averse to survival after the ponds had dried completely.

We related date of metamorphosis, body size at metamorphosis, and days since rainfall last occurred to the timing of first recapture while accounting for variation associated with Gosner stage, pond, and capture in inner versus outer fences using separate strata. The response variable was age at first pitfall trap recapture, measured in days since metamorphosis (Age). We standardized SVL and date of metamorphosis (Day) to one standard deviation (SD) about their means. Because the Cox proportional hazards model is sensitive to asymmetric covariates, we used $\log(\text{days since rainfall} + 1)$ standardized to 1 SD about its mean as our measure of time since rainfall (LagRain). We included the interaction $\text{SVL} \times \text{LagRain}$ to test our hypothesis about size affecting the correlation of movement with rainfall and the interaction $\text{Day} \times \text{LagRain}$ to isolate the $\text{SVL} \times \text{LagRain}$ interaction from a temporal effect and to account for the correlation of SVL and Day (Fig. 1). We measured the effect of housing tadpoles in 11.4 L feeding enclosures with the indicator variable, Trial. We accommodated dependence in the timing of movements within each of the 40 release groups with the random effect, Group. Hence, the analysis was conservative in terms of what was considered true replication. Because they were not the focus of our hypotheses, but still were likely to affect Age, we accounted for variation associated with Gosner stage, pond, and capture in inner versus outer drift fences using different strata for each combination of these variables. By using a different stratum for each combination of Gosner stage, pond, and capture in inner versus outer fence, we focused inference on the relative risk associated with the terms of the linear model

$$\text{SVL} + \text{Day} + \text{LagRain} + \text{Trial} + \text{Day} \times \text{LagRain} \\ + \text{SVL} \times \text{LagRain} + \text{Group}$$

Gross differences in Age between strata were accounted for because each stratum had its own baseline pattern of departure or baseline hazard. A posteriori, in response to reviewer comments we fit the same analysis to data from

Fig. 2. Residence times of individual frogs (horizontal black lines) at Burdue's and State ponds from release date at left to first capture in forest traps at right. Vertically oriented shading, ranging from gray to white, represents days since rainfall (darkest shading represents 0 days). Dashed vertical lines indicate the date the pond dried.



Burdue's Pond and State Pond separately and to data from the inner and outer fences separately.

The timing of departure analysis was performed in S-PLUS (Mathsoft Inc. 1999) using the counting process Cox formulation (Andersen and Gill 1982) and Efron method for tied event times (Mathsoft Inc. 1999). The data conformed to the proportional hazards assumption according to observed and expected scaled Schoenfeld residuals (Grambsch and Therneau 1994). We examined whether differences between individuals in capture probability could have explained the timing of frog captures. We found no evidence that the probability of capture, given an animal reached a fence, was related to the main effects in the timing of departure analysis. This was determined by examining SVL, Day, LagRain, and Trial effects on the probability of capture at inner fences for all individuals that were captured at outer fences using a generalized linear model.

To measure postmetamorphic growth, we used measurements taken at the time of marking and at each recapture in forest drift fences using a linear mixed-effects model in S-PLUS (Mathsoft Inc. 1999). We modeled the response $\log(\text{SVL})$ with random intercepts and slopes across Age grouped by individual. We estimated the fixed effects Pond, Pond \times Age, and the factor Gosner stage (Stage). The measures of precision we report for both analyses are ± 1 standard error (SE).

Results

Of the 583 and 462 frogs that were originally marked at Burdue's and State Ponds, respectively, we captured 23% and 47%, respectively, in the pitfall traps. At Burdue's Pond, 67 frogs were first captured in inner fences and 70 were first captured in outer fences. At State Pond, 94 and 125 frogs were first captured in inner and outer fences, respectively. Age differed strongly between sites (Fig. 2). Median Age was younger at Burdue's Pond (4 days) than at State Pond (9 days). The 2.5 and 97.5 percentiles of Age were 1 and 12 days at Burdue's Pond and 1 and 86 days at State Pond, respectively. Variation in body size for the org-

Table 1. Cox proportional hazards model coefficients and relative risk (exp(Coefficient)).

Variable	Coefficient	Relative risk	SE	<i>z</i>	<i>P</i>
SVL	0.43	1.53	0.07	5.74	<0.0001
Day	0.26	1.29	0.12	2.16	0.031
LagRain	-0.48	0.62	0.08	-6.13	<0.0001
Trial	0.11	1.12	0.19	0.59	0.56
Day × LagRain	0.43	1.53	0.09	4.95	<0.0001
SVL × LagRain	-0.15	0.86	0.07	-1.96	0.050

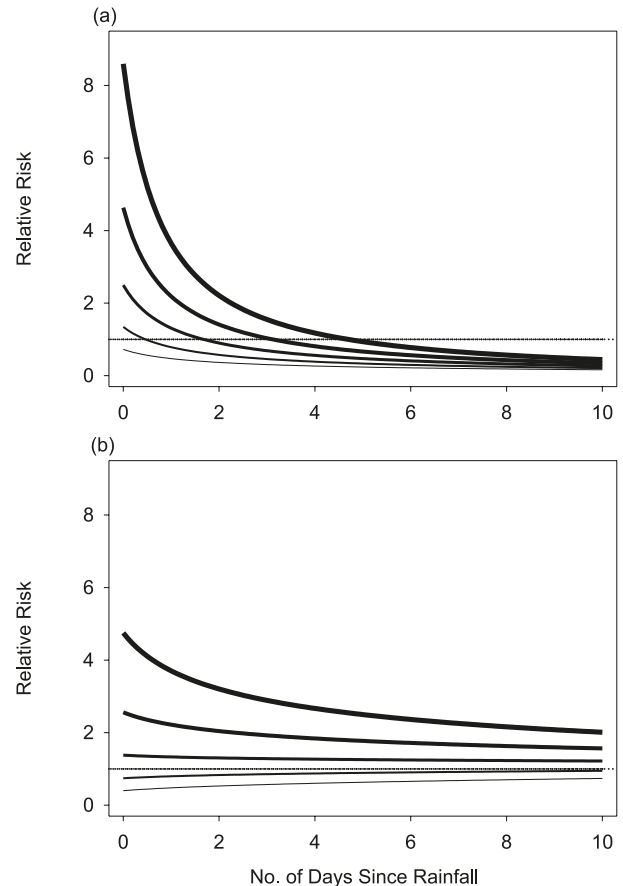
Note: The relative risk is the multiplicative effect of a unit change in the variable (e.g., a change of 1 SD of snout-vent length (SVL) or a change in the indicator variable Trial from 0 to 1) on the instantaneous probability of departing the natal pond. The SE reported is the robust SE of the coefficient.

inal marked sample was reported in Chelgren et al. (2006); frogs were significantly larger at State Pond (22.4 ± 0.1 mm) than at Burdue's Pond (18.8 ± 0.1 mm), and frogs were significantly larger from the high-food treatment (21.3 ± 0.2 mm) than from the low-food treatment (19.9 ± 0.2 mm). The variable Trial did not affect the probability that individuals survived and emigrated (Chelgren et al. 2006). The coefficient of variation of SVL increased by 36% and 18% at Burdue's and State ponds, respectively, when individuals from the food manipulation were combined with the other sample (Chelgren et al. 2006), which achieved our goal of increasing variation in size.

Although frogs waited longer to emigrate at State Pond and were also larger, the rate of departure was positively related to body size and to date of metamorphosis within ponds. The relative risk, interpreted as the multiplicative increase in the probability of departing, increased significantly with increasing SVL and with increasing Day, and decreased significantly with LagRain (Table 1). However, the positive coefficient for the Day × LagRain interaction indicated that the effect of LagRain was lessened for later metamorphosing individuals (Fig. 3). That is, individuals that metamorphosed early in the season tended to tie their movements to rainfall more so than later metamorphosing animals. Finally, the negative coefficient for SVL × LagRain indicated that, even after accounting for the temporal variables Day and Day × LagRain, the effect of LagRain was diminished for individuals that were smaller at metamorphosis, the very individuals most vulnerable to desiccation and with the lowest vagility. This result contradicted our hypothesis that smaller animals would be more closely tied to periods of rain for their movements than larger frogs. When data were analyzed separately by pond and by inner versus outer fences a posteriori, the direction of effects always remained consistent with Table 1 except for the variable Trial, which was not nearly significant.

The postmetamorphic growth we observed was small in comparison with the variation in body size at metamorphosis. Postmetamorphic growth differed significantly between ponds ($\chi^2 = 18.1$, *df* = 1, and *P* < 0.001). SNL length increased negligibly by 0.05% per week ($\pm 0.25\%$ SD) at Burdue's Pond. Snout-to-vent length increased by 1.25% per week ($\pm 0.09\%$ SD) at State Pond. Based on the fitted growth curves, growth at the 95th percentile of age at emigration was <1% at Burdue's Pond (12 days) and 16% at State Pond (86 days). Postmetamorphic growth clearly did not benefit the smallest frogs, which occurred at Burdue's Pond where growth was negligible.

Fig. 3. The relative risk for departure rate (interpreted as the multiplicative change in the instantaneous probability of departing the natal pond) by snout-vent length (SVL), date of metamorphosis (Day), and days since rain (LagRain). Line width is proportional to SVL at metamorphosis (-2, -1, 0, 1, and 2 SD about the mean SVL). Early metamorphosing individuals (-1 SD of the mean Day) are depicted in (a) and late metamorphosing individuals (+1 SD of the mean Day) are depicted in (b).



Discussion

This is the first longitudinal study of the timing of exodus of newly metamorphosed frogs from their natal pond. Other studies regarding timing of anuran movements have been cross-sectional (e.g., Todd and Winne 2006; Timm et al. 2007), which limits their ability to relate timing of movements to the states of individuals when these interact with temporally variable climatic factors. We found that the timing of initial terrestrial captures was related to size and date

at metamorphosis, which are highly plastic in ranid frogs (Wilbur and Collins 1973; Collins 1979). Furthermore, significant interactions of these variables with LagRain showed that the propensity of frogs to time movements with rain was compromised for smaller and later metamorphosing individuals. In a study of survival for the same individual frogs examined here, we found a strong positive relationship between the probability of surviving and emigrating natal ponds with larger body size, and a negative relationship with delayed metamorphosis (Chelgren et al. 2006). Aquatic stressors that reduce growth rates and size at metamorphosis have immediate survival costs for newly metamorphosed anurans (Goater 1994; Morey and Reznick 2001; Altwegg and Reyer 2003); our study links these same metamorphic traits to the propensity to time terrestrial movements with favorable climatic conditions.

Because desiccation rate negatively relates to body size in amphibians (Shelford 1913; Thorson 1955; Ray 1958; Newman and Dunham 1994), small frogs may wait at their natal pond to grow before attempting overland movement. Our observation that larger frogs emigrate sooner after metamorphosis than smaller frogs is consistent with this hypothesis, a pattern also observed by Lyapkov et al. (2000) in brown frogs (*Rana arvalis* Nilsson, 1842 and *Rana temporaria* L., 1758). Size-related variation in mortality risk may lead to differences in behavior between frogs of different sizes. However, the positive relationship we observed between size and departure rate may simply have been a consequence of the positive relationship of size with locomotor activity, which has firmly established bases in physiology for amphibians (Taigen and Pough 1981; Pough and Kamel 1984; John-Alder and Morin 1990). Size-related dispersal patterns in cane toads (*Bufo marinus* (L., 1758)) have also been attributed to physiological scaling (Phillips et al. 2006).

In some environmental conditions delayed emigration in favor of continued growth may be beneficial. Frogs remained in the vicinity of State Pond, the more densely vegetated site, for up to 5 months. Inconsistent methodologies between ponds and lack of replication at the pond level limit interpretation of the difference that we observed between ponds. However, the gross difference in timing of emigration between ponds is consistent with the preference of forested habitats by juvenile anurans. Habitat selection of newly metamorphosed American toads (*Bufo americanus* Holbrook, 1836; Rothermel and Semlitsch 2002) and wood frogs (*Rana sylvatica* LeConte, 1825; deMaynadier and Hunter 1999) demonstrated preference for forests over un-forested areas. Also supportive that forest cover is beneficial, postmetamorphic growth rate was substantially higher at State Pond where the percentage of aerial cover was twice that of Burdue's Pond. Greater mass was associated with a higher propensity of adult northern red-legged frogs to enter clearcuts (Chan-McLeod 2003), indicating that larger frogs may have more flexibility for movement through disturbed landscapes.

Our observation that later metamorphosing frogs hastened emigration indicates frogs modify behavior according to local conditions. However, a higher emigration rate for later metamorphosing frogs is also consistent with interspecific differences reported by Pough and Kamel (1984), where longer larval period was associated with faster postmetamor-

phic development of the physiological machinery for aerobic metabolism. Also consistent with our result, vagility in the direct-developing common coqui (*Eleutherodactylus coqui* Thomas, 1966) was lower for early hatching frogs (Buckley et al. 2005). The pattern we observed of younger age at emigration for later metamorphosing frogs does not support negative effects of delayed ontogeny on vagility as observed by Beck and Congdon (2000) and Emerson (1986). Pond drying may be a factor driving the hastened departure of later metamorphosing frogs. Although we did not estimate separate departure rates for before and after pond drying dates in the model, these dates do not appear to be associated with distinct pulses of departure (Fig. 2).

Counter to our third hypothesis, larger frogs were more tightly linked with rainfall in their movements than were smaller frogs. This pattern may be simply explained by increased locomotor performance associated with larger body size under the condition that rainfall triggers emigration. As a result of their lower stamina (Taigen and Pough 1981; Pough and Kamel 1984) and travel speed (Emerson 1978; John-Alder and Morin 1990), small individuals take longer to filter through the forest during emigration, leading to greater cumulative exposure to dry conditions for smaller frogs. Dehydration then leads to reduced performance in several physiological processes that should further reduce stamina including cellular energetics (Churchill and Storey 1995) and cardiovascular processes (Hillman 1987, 1991). We hypothesize that a large proportion of the size-related variation in postmetamorphic survival observed in Chelgren et al. (2006) was from desiccation rather than from predation. Anurans are vulnerable to predation near the completion of metamorphosis because they neither swim nor hop efficiently (Arnold and Wassersug 1978). However, the relationship between body size and predation rate of anurans is equivocal. For example, predation rates by a vertebrate and an invertebrate predator were negatively related to tadpole size in two ranid frogs (Elköv and Werner 2000), and predation by an invertebrate predator on adult male Pacific treefrogs was positively related to frog size (Benard 2007). Field studies designed to elucidate mortality factors for newly metamorphosed amphibians are remarkably rare despite their relevance to amphibian populations.

As a matter of the infrequency of precipitation, a large percentage (49%) of frogs emigrated during dry periods. These results and captures of unmarked frogs agree with Dole's (1971) observation that some emigration occurred on almost every night for newly metamorphosed northern leopard frogs (*Rana pipiens* Schreber, 1782), and with substantial movements during dry periods by Florida gopher frogs (*Rana capito* LeConte, 1855) (Greenberg 2001). Rain and other weather variables were important factors in explaining the timing of terrestrial captures of eight amphibian species at Savannah River, South Carolina (Todd and Winne 2006) and of pond-breeding amphibians in Massachusetts (Timm et al. 2007). Whereas mass movement of metamorphic frogs during rainy nights is a conspicuous phenomenon, it is important to consider that a large proportion of emigrating frogs may face dry conditions. Variation among individuals in body size and timing of metamorphosis affects age at emigration and the propensity to coordinate movements with rainfall. Because of the relationships of size with desiccation

rate and size with locomotor activity and of desiccation with locomotor activity, landscape features that impede movement, e.g., roads (Marsh and Beckman 2004), or landscapes void of microhabitats favorable for enduring drought, e.g., burrows and forest cover (Chan-McLeod 2003; Rothmel and Luhring 2005), should disproportionately impact smaller individuals, providing a simple mechanism for synergistic effects of changes in aquatic and terrestrial habitats on amphibian survival.

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