

CARRYOVER AQUATIC EFFECTS ON SURVIVAL OF METAMORPHIC FROGS DURING POND EMIGRATION

NATHAN D. CHELGREN,^{1,3} DANIEL K. ROSENBERG,¹ SELINA S. HEPPELL,¹ AND ALIX I. GITELMAN²

¹Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331-3803 USA

²Department of Statistics, Oregon State University, Corvallis, Oregon 97331 USA

Abstract. In organisms with complex life cycles, physiological stressors during early life stages may have fitness-level impacts that are delayed into later stages or habitats. We tested the hypothesis that body size and date of metamorphosis, which are highly responsive to aquatic stressors, influence post-metamorphic survival and movement patterns in the terrestrial phase of an ephemeral pond-breeding frog by examining these traits in two populations of northern red-legged frogs (*Rana aurora aurora*). To increase variation of body size at metamorphosis, we manipulated food availability for 314 of 1045 uniquely marked tadpoles and estimated the probability that frogs survived and emigrated using concentric rings of drift fencing surrounding ponds and Bayesian capture–recapture modeling. The odds of surviving and emigrating from the ponds to the innermost drift fences, ~12 m, increased by factors of 2.20 (95% credibility intervals 1.39–4.23) and 2.54 (0.94–4.91) with each millimeter increase in snout–vent length and decreased by factors of 0.91 (0.85–0.96) and 0.89 (0.80–1.00) with each day’s delay in metamorphosis for the two ponds. The odds of surviving and moving to the next ring of fencing, 12 m to ~40 m from the ponds, increased by a factor of 1.20 (0.45–4.06) with each millimeter increase in size. Our results demonstrated that body size and timing of metamorphosis relate strongly to the performance of newly metamorphosed frogs during their initial transition into terrestrial habitat. Carryover effects of aquatic stressors that reduce size and delay metamorphosis may have population-level impacts that are not expressed until terrestrial stages. Since changes in both aquatic and terrestrial systems are implicated in many amphibian declines, quantifying both immediate and delayed effects of stressors on demographic rates is critical to sound management.

Key words: Bayesian analysis; body size; delayed effects; emigration; individual variation; movement; post-metamorphosis; *Rana aurora aurora*; survival.

INTRODUCTION

In organisms with complex life cycles, metamorphosis is often associated with major shifts in habitat use. However, from an individual organism’s perspective, this ontogenetic niche shift (Wilbur 1980) does not constitute a “new beginning” (Pechenik et al. 1998). It is increasingly recognized that conditions experienced during one life stage affect organisms in later stages, and these carryover effects between stages or between habitats may have important impacts on fitness (Beckerman et al. 2002, Phillips 2002, Giménez et al. 2004). Carryover effects are perhaps most well studied in marine invertebrates, where effects of the larval environment on juvenile growth and, under controlled conditions, survival are well documented (Wendt 1998). Although carryover effects are important in elucidating factors affecting population change in organisms with complex life cycles, the magnitude of car-

ryover effects on demographic rates has rarely been measured in situ (Semlitsch 1987, Pechenik et al. 1998, Altwegg and Reyer 2003, Ng and Keough 2003, Giménez et al. 2004). In amphibians, the shift between aquatic and terrestrial habitats following metamorphosis has been espoused as justification for their value as indicators of environmental health (Blaustein and Kiesecker 2002). Yet even for this group, there is insufficient information to evaluate the extent to which aquatic vs. terrestrial stressors impact populations. Understanding their relative importance is critical in addressing global amphibian declines (Alford and Richards 1999, Houlahan et al. 2000).

In the search for mechanisms responsible for global amphibian declines, a large number of experimental and observational studies have linked treatments or conditions experienced by larvae to their survival, growth, and ontogeny. Overwhelmingly, such studies terminate at or before completion of metamorphosis. However, sublethal effects of aquatic stressors on larvae, such as reduced body size, delayed metamorphosis, developmental deformities, and immunosuppression, may persist into subsequent life stages (Goater 1994, Morey and Reznick 2001, Belden and Blaustein

Manuscript received 25 February 2004; revised 10 February 2005; accepted 6 April 2005; final version received 6 May 2005.
Corresponding Editor: R. D. Semlitsch.

³ Present address: USGS Forest and Rangeland Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, Oregon 97331 USA. E-mail: nathan_chelgren@usgs.gov

2002, Blaustein and Kiesecker 2002), potentially confounding the stressor's population-level impact and the impact of terrestrial habitat conditions. One of the most apparent factors affecting success in terrestrial habitats for anurans is body size (Berven and Gill 1983, Smith 1987, Goater 1994, Morey and Reznick 2001). Although less well studied in amphibians, later metamorphosis may also impact future performance (Smith 1987, Semlitsch et al. 1988).

A suite of globally significant anthropogenic changes have been shown to reduce body size at metamorphosis or larval growth rate in amphibians. Body size at metamorphosis or larval growth rate is lowered by (1) the presence of introduced predators (Kupferberg 1997, Kiesecker and Blaustein 1998, Lawler et al. 1999, Kiesecker et al. 2001*b*), (2) increased ultraviolet UV-B radiation (Bruggeman et al. 1998, Belden and Blaustein 2002), (3) chemical pollution (Lefcort et al. 1998, Schuyttema and Nebeker 1999), (4) acidification (Dunson et al. 1992), (5) competition with invasive species (Kupferberg 1997, Adams 2000, Kiesecker et al. 2001*b*), and (6) shortened hydroperiod of ponds (Leips et al. 2000, Kiesecker and Skelly 2001). There is clear evidence that body size at metamorphosis positively relates to multiple components of fitness: younger age at first reproduction (Smith 1987, Semlitsch et al. 1988), increased fecundity (Howard 1980, Berven 1981, 1988, Berven and Gill 1983, Semlitsch 1987), and increased survival (Smith 1987, Morey and Reznick 2001, Altwegg and Reyer 2003). In addition, delaying metamorphosis has been shown to affect future performance in amphibians (Beck and Congdon 2000) and especially in marine invertebrates (Gebauer et al. 1999, Maldonado and Young 1999). Such evidence suggests the delayed effects of aquatic stressors, considered in total, may be important contributors to declining amphibian populations.

Body size and timing of metamorphosis affect fitness components at a population level, but they may also affect metapopulation dynamics. Connectivity and spatial population dynamics are thought to be important factors in amphibian ecology (Pechmann et al. 1991, Alford and Richards 1999, Marsh and Trenham 2001), and the juvenile stage may be primary for dispersal (Gill 1978, Breden 1987, Berven and Grudzien 1990). We should expect body size to be an important factor influencing long-distance dispersal ability in amphibians because of the negative association of body size with desiccation rate (Thorson 1955, Ray 1958), the positive relationship of size with locomotor ability (John-Alder and Morin 1990), and because multiple physiological mechanisms of movement are compromised by desiccation (Hillman 1984, 1987, Gatten 1987, Preest and Pough 1989). In addition, delaying metamorphosis has survival costs associated with stranding pre-metamorphic individuals in drying ponds, but it may also limit the ability of frogs to coordinate emigration with favorable humidity condi-

tions for terrestrial movement (Chelgren 2003). Impacts of reduced body size and delayed metamorphosis on population persistence will be strongest for amphibians in ephemeral and isolated habitat patches (Hanski 1999).

The red-legged frog is an exemplary species for which ephemeral ponds are important for breeding (Adams 2000) and which is known for long-distance movements through terrestrial habitats (Hayes et al. 2001, Bulger et al. 2003, Chan-McLeod 2003). Red-legged frogs breed in low-elevation ponds (<1500 m; Bulger et al. 2003), areas often encroached upon by intensive human-dominated land uses. However, their use of terrestrial habitats is poorly known beyond anecdotal accounts of adult frogs observed in forests far from open water (Hayes et al. 2001, Bulger et al. 2003). Importantly, there is little known of the autecology of recently metamorphosed red-legged frogs, precisely the stage that would be most impacted by terrestrial habitat degradation and at which the potential for carryover effects are greatest.

The magnitude of carryover effects of aquatic stressors is germane in understanding declining numbers of red-legged frogs. Sublethal effects of aquatic stressors have been demonstrated for red-legged frogs (Kiesecker and Blaustein 1998, Belden and Blaustein 2002), and both aquatic and terrestrial conditions have been implicated in population declines (Hayes and Jennings 1986, Kiesecker and Blaustein 1998, Blaustein and Kiesecker 2002). Our objective was to measure variation in the probability of surviving from metamorphosis through pond emigration that was attributable to variation in body size and timing of metamorphosis under natural conditions. We discuss the magnitude of these effects in the context of complex causes of amphibian declines. Our work contributes to a small number of studies (Pechenik et al. 1998, Wendt 1998, Altwegg and Reyer 2003) that have measured, in situ, the scale of carryover effects on demographic rates in organisms with complex life cycles.

METHODS

Study areas

We studied frog survival and emigration at two ephemeral ponds in Lincoln County along the Oregon coast, USA, from the first completion of metamorphosis 6 June 2002 until the fall rains flooded pitfall traps 8 November 2002. We selected ponds for their densities of metamorphic frogs to allow for a minimum of 500 marked individuals at each site and for the suitability of surrounding landscape for pitfall trapping. Our non-random sample of two ponds does not permit a larger scope of inference at the pond level. However, replication at the individual level and the difficulty and resulting rarity of juvenile frog studies under natural conditions lend relevance to our work. Burdue's Pond, with a maximum surface area of ~0.36 ha, was sur-

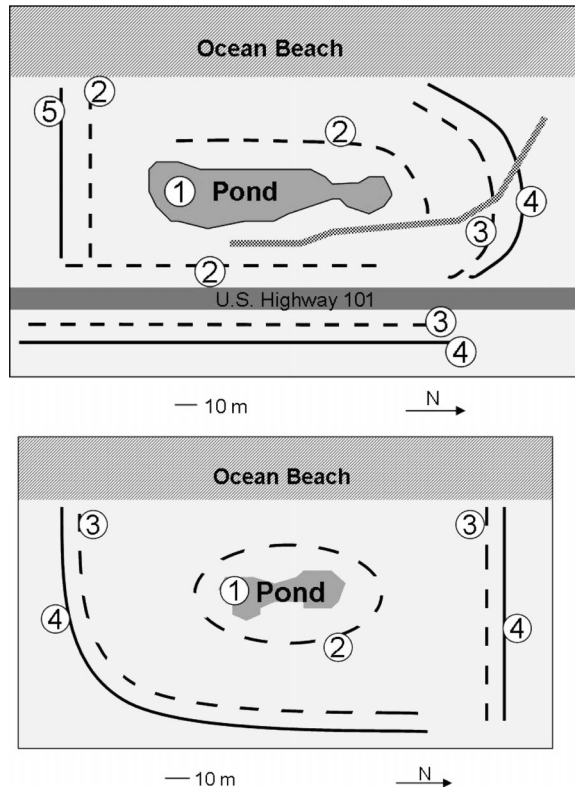


FIG. 1. Drift fence layout and strata at Burdue's Pond (upper panel) and State Pond (lower panel) in Lincoln County along the Oregon coast, USA. Locations of 7.6-m discontinuous drift fences are shown with dashed black lines. Locations of continuous drift fences are shown with solid black lines. A cliff (hatched line) at Burdue's Pond was largely impassible to frogs. Numbers associated with fence lines indicate their stratum number as used in the analysis to quantify probabilities of survival and movement.

rounded by disturbed forest characterized by large areas of bare ground, sparse beach grass (*Ammophila arenaria*), patchy understory predominated by salal (*Gaultheria shallon*) and young pines (*Pinus contorta*), and patchy mixed-canopy cover (*Alnus*, *Pinus*, *Pseudotsuga*). The trapping area was bisected by U.S. Highway 101 with associated disturbed roadside vegetation. Aerial percent cover of vegetation (means \pm SE), based on 498 photographs taken skyward in a regular 10-m grid over the study area was $27.3 \pm 2.2\%$ and $47.7 \pm 2.4\%$ at 1.5 m above the ground surface and at ground surface, respectively. Burdue's Pond dried completely on 23 July 2002 and remained so until 8 November 2002.

State Pond, approximately 0.15 ha, was more densely vegetated than Burdue's Pond, with nearly continuous forest canopy and little disturbed ground. State Pond was immediately surrounded by a strip of thick emergent wetland plants dominated by the forb *Sanguisorba officinalis* and sedge (*Carex* spp.). The surrounding upland habitat was a patchwork of closed-canopy pine-salal forest, open-canopy salal-twinberry (*Lonicera in-*

volucrata) beach scrub, sedge-willow (*Salix* spp.) scrub-shrub wetland, and mowed lawn. Aerial percent cover of vegetation, based on 332 photographs at State Pond was $61.0 \pm 2.6\%$ and $84.1 \pm 1.8\%$ at 1.5 m above and at the ground surface, respectively. State Pond dried completely on 4 August 2002 and remained dry until the end of the trapping period. The two ponds were similar in their amphibian communities with larvae and adults of Pacific treefrog (*Pseudacris regilla*), Northwestern salamander (*Ambystoma gracile*), and rough-skinned newt (*Taricha granulose*).

Field methods

When the surface areas of ponds were at their maximum in March and April 2002, we constructed concentric rings of drift fence encircling ponds (Fig. 1). Fences were constructed of black polyethylene plastic sheeting suspended with wooden stakes and nylon string to a height of 40–50 cm above ground level (Gibbs 1998) and buried at the base. Discontinuous drift fences were 7.6 m in length and were separated by 7.6-m gaps; length was determined by available materials. We placed the innermost fences \sim 12 m from pond edges (Fig. 1). Middle and outer fences were placed \sim 40 m and 45 m from pond edges where landscape features permitted and at the nearest possible location otherwise. At Burdue's Pond, we used a total of 323 m of discontinuous drift fence partially surrounded by 368 m of continuous drift fence. At State Pond, 308 m of discontinuous drift fencing was partially surrounded with 310 m of continuous drift fencing. We did not complete drift fence rings in areas where landscape features or landowner permission prohibited, nor adjacent to the ocean beach as previous work showed no propensity for frog movement there (N. D. Chelgren, unpublished data).

On the inner (pond) side of drift fences we placed pitfall traps approximately every 1.9 m at Burdue's Pond (363 traps) and State Pond (323 traps). Pitfall traps were constructed of two 3.1-L cans taped end to end and buried such that the rim was slightly below duff level. Cans were fitted with black (Crawford and Kurta 2000) funnel tops to prevent escape by scaling (Corn 1994). We provided small mammal escape devices, modified from Karraker (2001), of jute twine anchored in the soil with galvanized steel wire. We maintained a moistened cellulose sponge in each can to provide consistently humid conditions and for floatation when traps flooded.

At Burdue's Pond we built 87 in-pond enclosures to isolate samples of tadpoles for food manipulation treatments in order to increase the variation in body size at metamorphosis. Enclosures were constructed of 11.4-L plastic tubs perforated with holes to allow for water circulation. Enclosures were placed on the pond bottom, provided with a wooden perch, and covered with hardware cloth to prevent predation. At State Pond, because of limited pond area and rapid pond drying,

food manipulation was performed similarly except that the 31 11.4-L enclosures were kept in 1.83 m diameter plastic wading pools at the pond's edge.

From 14 May through 2 July 2002, we captured tadpoles using dip nets to include in food manipulation treatments. We assigned three animals per enclosure, grouped by Gosner (1960) developmental stage; only stages ≥ 25 were retained. We then randomly assigned enclosures to either a high- or low-food treatment. Both treatments received five pellets of commercial rabbit chow two times weekly until growth stage 37, when the appearance of all hind toes is distinct, was reached. At stage 37, the high-food treatment enclosures continued to receive the same food allotment. The low-food treatment individuals then received no supplemental food, similar to the Group III treatment of Audo et al. (1995), which reduced size at metamorphosis but did not affect the timing of metamorphosis in their study. Tadpoles in both treatments could graze algae that grew naturally on the enclosures and wooden perches. We removed loose algae, feces, and extraneous food pellets and circulated water with a hand-operated bilge pump twice weekly. At State Pond, because it appeared the natural pond might entirely dry before tadpoles metamorphosed, we collected additional animals that we raised in 1.83 m diameter wading pools outside of the 11.4-L feeding enclosures. These individuals are described further below.

Upon reaching the final stages of ontogeny, from 12 June to 31 July, we terminated feeding trials and marked animals for release into ponds. At Gosner stages 43, when the mouth broadens following eruption of the forelimbs, to 46, essentially complete metamorphosis, we anesthetized individuals in a 0.25-g/L solution of 3-aminobenzoic acid ethyl ester (MS-222; Nauwelaerts et al. 2000) buffered with sodium bicarbonate (Fellers et al. 1994). We measured snout-vent length (SVL) to the nearest 0.01 mm using a dial caliper and marked animals using three-digit soft alphanumeric VIAAlpha tags (Northwest Marine Technology, Shaw Island, Washington, USA; Buckley et al. 1994) injected subcutaneously in the dorsal thigh. We then massaged tags to the ventral side where the skin was transparent and to avoid tag loss through the incision. We clipped a single front digit to indicate the animal was VIAAlpha marked and held animals in enclosures for 24 h to ensure recovery from anesthesia and tag retention before randomly assigning animals to release groups. We then released frogs in their assigned groups at randomly selected sites around the edges of their natal pond.

At Burdue's Pond, coincident with the marking and release sessions for feeding trial animals, we captured and marked samples of free-living individuals in the range of Gosner developmental stages 43–46 from the pond using dip-nets and hand capture. These animals were handled identically to animals of the feeding trials through the marking and release process. However, at State Pond, we used the tadpoles that had been captured

from drying portions of the pond at intermediate developmental stages (stages 25–30, beginning of limb bud development to initial toe development) that were raised in the same 1.83 m diameter wading pools at the pond's edge that housed the 11.4-L feeding trial enclosures described above. Tadpoles outside the 11.4-L feeding trial enclosures were fed commercial rabbit pellets ad libitum and were provided with logs for structural cover. We changed 25% of pool water and removed feces and uneaten pellet food twice weekly.

We opened pitfall trap arrays at the appearance of the first metamorphic individuals. We considered Gosner stage 45 as metamorphosed since these animals were fully formed frogs capable of terrestrial movement but had a remnant tail bud (Gosner 1960). From 6 June to 31 July 2002, we checked and emptied traps daily at Burdue's Pond and on alternate days at State Pond. More frequent trap checks were necessary at Burdue's Pond, the more xeric and less shaded site, in order to minimize desiccation. From 1 August to 8 November, at both sites, we checked and emptied traps on alternate days. Captured frogs were re-released on the opposite side of the drift fence adjacent the trap from which they were captured.

Outside the main trapping arrays, we constructed three supplemental test-release pens for the purpose of establishing prior probabilities for capture probability parameters. Test pens consisted of an inner octagon of four discontinuous 7.6-m fences separated by 7.6-m gaps. We placed an enclosing continuous drift fence 2 m outside the discontinuous fences. We set pitfall traps only on the inner sides of drift fences, similar to the main trapping arrays. At the center of the test pens we released a total of 255 juvenile frogs that had been captured in the outer fences of the main trapping arrays. As animals radiated from the pen centers, some were captured in the traps of the inner fence rings. These animals were identified and re-released immediately outside the fence at which they were captured. Animals captured in the outer fences were noted and then released in the forest outside of the test pens.

Statistical methods

We measured the relationships of body size and date of metamorphosis with the probability of surviving and moving to two distances from the ponds using capture-recapture models. We used the Cormack-Jolly-Seber (CJS) model (Lebreton et al. 1992) and its multistrata extension (Hestbeck et al. 1991), where the multinomial cells represented each pattern of captured vs. not captured in the drift fence lines as frogs dispersed from the ponds. We made the application Bayesian (e.g., Link et al. 2002, Barry et al. 2003) to incorporate the supplemental information we collected in test-release pens as empirical prior distributions and to account for dependence among animals within release groups. We implemented Markov chain Monte Carlo (MCMC) simulation following Gelman et al. (1995), using software

WinBUGS version 1.4 (Spiegelhalter et al. 1994). The measures of precision we reported for the Bayesian analysis were 95% credibility intervals. We used the deviance information criterion (DIC) to compare models in terms of parsimony in numbers of parameters vs. model fit (Spiegelhalter et al. 2002).

In our spatial capture–recapture application, there were three types of probabilities: the probability of surviving and moving as a product (Ψ), capture probability (p), and the product of surviving, moving, and being captured in the outermost fences (χ). We did not separately estimate probabilities of survival and movement. Our measure of survival, Ψ , quantified survival across spatial intervals during exodus from the drying ponds. Timing of movement remained important for this spatial analysis in that frogs that had not yet emigrated or that had settled within the trapping arrays before the end of the trapping period were not distinguished from individuals that had died. We modeled the multinomial cell probabilities as functions of Ψ , p , and χ (see Supplement). We used the log-odds function to link individual covariate data and their coefficients, hereafter referred to as β parameters, to Ψ , p , and χ . Subscripts of Ψ , p , χ , and β parameters indicate stratum number and pond (S, State; B, Burdue's Pond). At Burdue's Pond we were unable to achieve three tiers of drift fencing in the southern portion of the study area (Fig. 1). For this reason, at Burdue's Pond we accommodated an additional parameter, π , the probability a frog oriented toward strata 3 and 4 vs. stratum 5.

We fit three models to the main capture–recapture data set. In the first of these, the Basic Model, we used the following covariates: stage (Gosner stage at the time of marking); date (date at marking); SVL; strata; pond; and trial, an indicator variable for the feeding trial individuals that were raised in 11.9-L enclosures. The structure of the Basic Model was as follows, where the terms to the right of approximate signs indicate the covariate included in each component of the model and to which the β coefficients correspond:

$$\begin{aligned} \text{logit}(\Psi_{1-2}) &\sim 1 + \text{SVL} + \text{date} + \text{pond} \\ &\quad \times (1 + \text{SVL} + \text{date}) + \text{stage} \\ &\quad + \text{trial} + g_k, \end{aligned} \quad (1)$$

$$\text{logit}(\Psi_{2-3}) \sim 1 + \text{SVL} + \text{pond} \times (1 + \text{SVL}) + g_k, \quad (2)$$

$$\text{logit}(p) \sim 1 + \text{SVL} + \text{pond} + \text{strata}, \quad (3)$$

$$\text{logit}(\chi) \sim 1 + \text{SVL} + \text{pond} \times (1 + \text{SVL}). \quad (4)$$

In Eqs. 1 and 2, g_k was a release group (k) random effect, common to Ψ_{1-2} and Ψ_{2-3} , for each of the 40 releases; this term was included in the model to account for dependence within release groups.

To estimate capture and handling effects on survival for frogs that were captured in pitfall traps, we modified the multinomial cell probabilities of the Basic Model. We inserted a pond-specific survival cost of handling

parameter h into the multinomial cell probabilities following each pitfall capture. For example at State Pond, the multinomial cell probability for the capture history (1, 1, 0, 1) in the Basic Model, $\text{Pr}(1, 1, 0, 1) = \Psi_{1-2,S} p_{2,S} \Psi_{2-3,S} (1 - p_{3,S}) \chi_{3-4}$, representing frogs that were initially released at stratum 1, captured at strata 2 and 4, and not captured at stratum 3, became $\text{Pr}(1, 1, 0, 1) = \Psi_{1-2,S} p_{2,S} h_S \Psi_{2-3,S} (1 - p_{3,S}) \chi_{3-4}$ in the Handling Model (see Supplement). The additional parameters of the Handling Model were estimable only because we included as prior probabilities the information pertaining to p from the test-release pens. In response to an anonymous reviewer's comments, we also fit the Handling Model to a reduced data set excluding individuals that had not completed metamorphosis to Gosner stage 45 or 46 at the time of marking, since individuals may not be physiologically capable of emigrating at earlier stages.

In our final model, the Treatment Model, we postulated that the effects we observed on the probability of surviving and emigrating may be due ultimately to genetic factors that positively impact both size and survival. We evaluated this hypothesis by comparing the effect of size for tadpoles that were experimentally fed to the individuals that were not experimentally fed. If the effects on Ψ were similar for same-sized tadpoles in these two groups, we could attribute the effect of body size as a direct response to size. The Treatment Model and Handling Model were identical, except for the inclusion of an interaction term $\text{Trial} \times \text{SVL}$ in Eq. 1.

Specification of prior distributions is an important issue in the context of Bayesian capture–recapture modeling (Link et al. 2002). We used the data from the test-release pens, described above, to form empirical prior distributions for capture probability β 's. This was done using the subset of animals known to have reached the outer test-release pen fences (172 animals) and considering whether each animal in the sample had been captured in the inner fence ring as the response variable in a generalized linear model with regressor variable SVL. This resulted in the prior distribution $\text{Normal}(0.17, \text{var} = 1.11)$, for the intercept, and $\text{Normal}(-0.006, \text{var} = 0.002)$, for the slope of SVL. For the remainder of the β parameters, we sought prior distributions that reflected our naiveté. We used $\beta \sim \text{Normal}(0, \text{var} = 5)$ for all regression intercepts and slopes following Barry et al. (2003), $\text{Uniform}(0, 1)$ prior distributions for π and for handling effects on survival, and $\text{Uniform}(0, 100)$ for the random effects standard deviation. We examined the sensitivity of posterior distributions to the choice of priors by varying the specification of prior distributions (see Appendix).

We used a traditional Frequentist statistical approach to examine variation in body size at metamorphosis. We used linear mixed models in S-plus (S-PLUS 1999) to relate SVL to feeding treatment, trial, stage, and date, with pond interactions for all variables in a general model. We accounted for lack of independence among

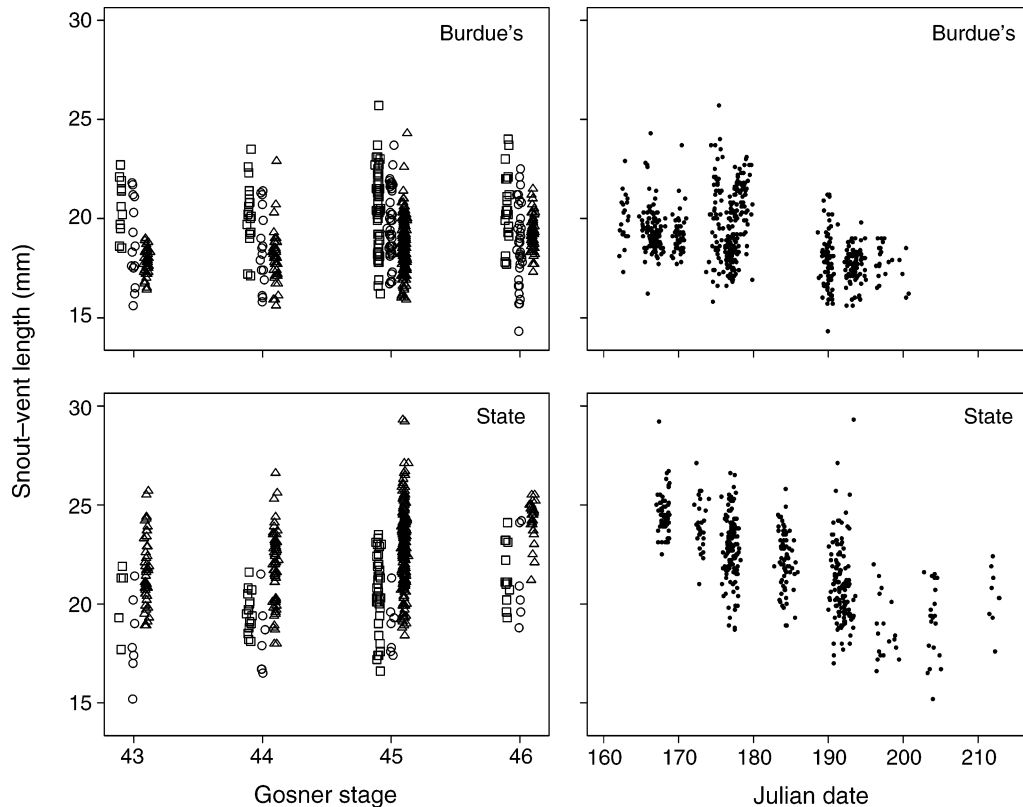


FIG. 2. Variation in snout-vent length by Gosner stage, food treatment, Julian date (day 1 = 1 January 2002), and pond. Individuals that were raised in 11.4-L feeding enclosures are represented by squares for high-food and circles for low-food treatments, whereas triangles indicate individuals that developed freely in Burdue's Pond or in 1.83 m diameter wading pools adjacent to State Pond.

tadpoles within 11.4-L feeding enclosures using random effects for enclosures. We used likelihood ratio tests to compare the general model to reduced models where the effect and its interaction with pond were removed. The significance of the effect of pond was tested as a main effect at the mean of the other variables. The measure of precision we report for the linear mixed model is one standard error.

RESULTS

We released 583 and 462 frogs with unique marks during the final stages of metamorphosis at Burdue's and State Ponds, respectively. Of these animals, 314 were from the feeding trials (180 in the high-food treatment and 134 in the low-food treatment). Releases were made in 24 and 16 groups at Burdue's and State Ponds, distributed across the range of metamorphosis dates at each pond. We subsequently recaptured 23% and 47% of these animals in forest pitfall traps at Burdue's and State Ponds, respectively. We observed two individuals (<1%) with likely toe clips but no VIAAlpha tag, indicating their tags may have been lost. Because of the apparent low rate of missing tags, we did not account for tag loss in the analysis.

Snout-vent length was variable by stage, food treatment, trial, date, and pond (Fig. 2). Size (means \pm SE) was higher ($\chi^2 = 666.5$, $df = 1$, $P < 0.001$) at State Pond (22.4 ± 0.1 mm) than at Burdue's Pond (18.8 ± 0.1 mm), and lower ($\chi^2 = 42.1$, $df = 2$, $P < 0.001$) for the low-food treatment (19.9 ± 0.2 mm) compared to the high-food treatment (21.3 ± 0.2 mm). Housing tadpoles in the feeding enclosures ($\chi^2 = 30.7$, $df = 2$, $P < 0.001$) had a positive effect on size at Burdue's Pond (0.7 ± 0.2 mm) and a negative effect at State Pond (-1.7 ± 0.4 mm). The coefficient of variation of SVL increased from 6.4% to 8.7% and from 8.5% to 10.0% at Burdue's and State Ponds, respectively, when individuals from the food manipulation treatments were included in the sample. Body size at metamorphosis decreased significantly with increasing date of metamorphosis ($\chi^2 = 252.6$, $df = 2$, $P < 0.001$) by -0.07 ± 0.01 mm/d and -0.11 ± 0.01 mm/d across the range of dates observed at Burdue's and State Ponds, respectively. After accounting for the other variables in the model, a single Gosner stage transition ($\chi^2 = 24.3$, $df = 2$, $P < 0.001$) was associated with a small decrease in SVL at Burdue's Pond (-0.05 ± 0.07 mm), and an increase at State Pond (0.37 ± 0.07 mm).

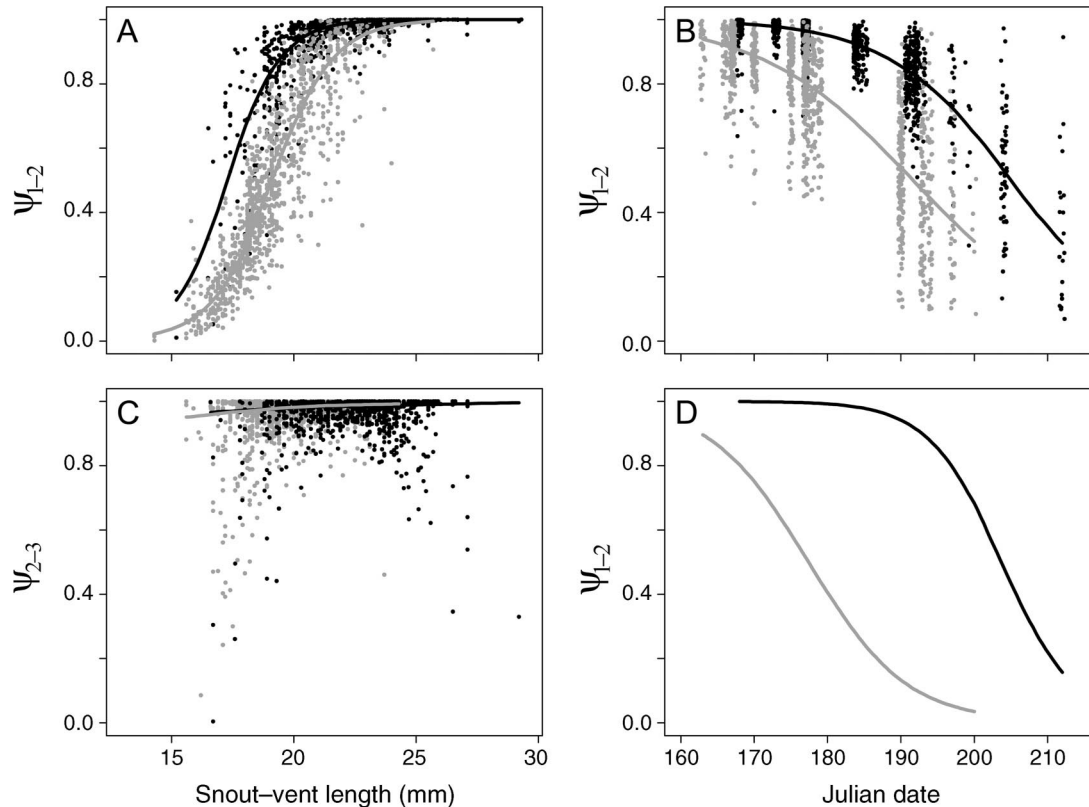


FIG. 3. Probability of surviving and emigrating from ponds into terrestrial habitat ~ 12 m (Ψ_{1-2}) and from 12 m to ~ 40 m (Ψ_{2-3}), for nonexperimentally fed individuals of Gosner stage 45 at Burdue's Pond (gray) and State Pond (black). In (A) and (C), lines represent 50% quantiles of the posterior distribution of Ψ_{1-2} and Ψ_{2-3} at the mean Julian date (day 1 = 1 January 2002) and given snout-vent length (SVL). In (B), lines represent 50% quantiles of the posterior distribution of Ψ_{1-2} at the mean SVL and given date. In (D), lines represent combined effects of SVL and date on Ψ_{1-2} using the expected value of SVL at the given date from our linear mixed-effects model of size at and date of metamorphosis. Uncertainty in the relationships is depicted with 1000 random draws from the posterior distribution of Ψ weighted by the distribution of SVL or date in the data.

The Handling Model was favored over the Treatment Model (+2.8 units) and the Basic Model (+6.7 units) based on DIC. Because the Handling Model was strongly favored, we present the results of the Handling Model, except where noted. The probability of surviving and emigrating was positively related to body size at metamorphosis and negatively related to date of metamorphosis (Fig. 3). The analyses strongly supported the hypotheses that larger (Probability = 1.00) and earlier metamorphosing (Probability = 1.00) frogs were more likely to survive and emigrate to 12 m, Ψ_{1-2} , than smaller and later individuals. The odds of surviving and emigrating from the ponds to the innermost drift fences increased by a factor of 2.39 (1.53–3.95) with each millimeter increase in SVL (Table 1). When stages 43 and 44 individuals were removed from the data, estimated effects of SVL increased for both ponds and intervals (Table 1). With each day's delay of metamorphosis, Ψ_{1-2} decreased by a factor of 0.91 (0.85–0.96) at Burdue's Pond and 0.89 (0.80–1.00) at State Pond. Effects of date changed by at most 0.01 when stages 43 and 44 individuals were removed from the

data. At the mean size and date, Ψ_{1-2} still was lower (Probability = 0.97) at Burdue's Pond, the disturbed site. There was little support (Probability = 0.61) that body size continued to be important to survival and movement in the second distance interval Ψ_{2-3} , where the odds increased by a factor of 1.20 (0.45–4.06) on average between ponds (Table 1). There was no support (Probability = 0.53) for a stronger effect of body size on Ψ_{2-3} at Burdue's Pond. The Treatment Model revealed that there was no support (Probability = 0.50) for differences in SVL effects on Ψ_{1-2} for the individuals of the food manipulation treatments. We concluded that the positive relationships we observed of Ψ with SVL were largely due to environmental factors that affected size rather than differences in potential correlates of size such as genotype.

We estimated capture probabilities and other parameters that will be important for planning and in the formation of prior probabilities of future studies. In the main trapping arrays, capture probabilities of fence rows averaged 0.21 and varied primarily between strata (Table 1). The odds of surviving increased by a factor

TABLE 1. Capture probability p with 95% credibility intervals (in parentheses) and the probability of surviving and moving between strata Ψ , with the multiplicative change in odds for a 1-mm increase in snout-vent length.

Probability	Probability estimate	Change in odds
$p_{2,B}$	0.23 (0.17–0.34)	0.99 (0.96–1.02)
$p_{2,S}$	0.27 (0.23–0.33)	0.99 (0.96–1.02)
$p_{3,B}$	0.15 (0.11–0.25)	0.99 (0.96–1.02)
$p_{3,S}$	0.19 (0.15–0.24)	0.99 (0.96–1.02)
$\Psi_{1-2,B}$	0.74 (0.37–0.95)	2.20 (1.39–4.23)
$\Psi_{1-2,S}$	0.89 (0.56–0.99)†	3.48 (1.83–8.12)
$\Psi_{1-2,S}$	0.95 (0.76–0.99)	2.54 (0.94–4.91)
$\Psi_{1-2,S}$	0.97 (0.74–1.00)†	3.79 (0.81–12.13)
$\Psi_{2-3,B}$	0.98 (0.86–1.00)	1.24 (0.35–4.57)
$\Psi_{2-3,B}$	0.98 (0.84–1.00)†	1.25 (0.38–4.45)
$\Psi_{2-3,S}$	0.98 (0.81–1.00)	1.20 (0.41–5.61)
$\Psi_{2-3,S}$	0.98 (0.80–1.00)†	1.48 (0.46–6.61)

Notes: Except where noted, estimates are from the Handling Model and represent nonexperimentally fed individuals of mean size and date at Gosner stage 45. Estimates when individuals that were younger than Gosner stage 45 were removed from the data are indicated with †. Subscripts indicate stratum (see Fig. 1) and pond specificity (B, Burdue's Pond; S, State Pond). Experiments were conducted at two ephemeral ponds in Lincoln County along the Oregon coast, USA.

of 1.82 (1.14–2.91) per Gosner stage transition from 43 to 46. This amounts to a 5.5-fold increase in the survival odds or, at the average of the other variables, a survival probability of 0.68, for transitioning from stage 43 to stage 46. We are aware of no other studies that have estimated survival probabilities associated with Gosner stage transitions in natural populations. There was some support (Probability = 0.79) for Ψ_{1-2} being different for treatment animals: the odds being 0.88 (0.34–2.19) times lower for treatment animals. Especially important for future studies of threatened populations, we estimated the probability of surviving capture and handling was 0.74 (0.40–0.98) and 0.71 (0.48–0.93) at Burdue's and State Pond, respectively. All of the estimates we reported have been corrected for the effect of handling. Of the 255 frogs released in the test release pens, 172 were ultimately captured in the enclosing outer fences, an additional 23 were captured in the inner rings but were not captured in the outer rings, and the remaining 60 were not detected after release. Individuals that were captured in pitfall traps of the test release pens were 1.7 mm larger than the original sample released in the pens.

DISCUSSION

It is increasingly well documented that in organisms with complex life cycles, stressors acting on early life stages may have important impacts on future survival and reproduction and that the impacts of these stressors may be moderated by conditions experienced in later stages. Ontogenetic niche shift then presents a simple mechanism for the interactions of stressors between what might otherwise be disparate habitats. During the initial transition of newly metamorphosed red-legged

frogs from aquatic to terrestrial habitat, we found strong carryover effects of body size at metamorphosis and timing of metamorphosis, two traits that are highly responsive to conditions faced by amphibian larvae.

Our findings of strong carryover effects were consistent at two sites and contribute to a small number of studies that have measured, in situ, the magnitude of carryover effects. Our findings agree with recent studies of carryover effects on survival of newly metamorphosed water frogs (*R. lessonae* and *R. esculenta*; Altwegg and Reyer 2003), spadefoot toads (*Spea hammondi*; Morey and Reznick 2001), and southern toads (*B. terrestris*; Beck and Congdon 1999) in field enclosures, demonstrating initial strong effects of body size at metamorphosis that subsided within weeks. Using artificial enclosures, Goater (1994) and Goater and Vandebos (1997) also showed that conditions faced by larvae continued to affect survival immediately post-metamorphosis in European toads (*B. bufo*) and wood frogs (*R. sylvatica*), respectively. Field studies such as ours contribute to the interpretation of laboratory studies in which carryover effects were measured under artificial conditions, since environmental context may be important in their expression (Peacor and Werner 2001, Phillips 2002). In contrast to our study, no effect of body size or timing of metamorphosis was observed on survival in field studies of chorus frogs (*Pseudacris triseriata*; Smith 1987) or mole salamanders (*Ambystoma talpoideum*; Semlitsch et al. 1988). Further, our consistent finding that lower survival was associated with later metamorphosis was similar for brown frogs (*R. temporaria* and *R. arvalis*; Lyapkov et al. 2000), but contrasted the results of Beck and Congdon (1999) in southern toads. Though size at and date of metamorphosis strongly impacted the performance of newly metamorphosed frogs at our sites, they did not explain all of the variation we observed between ponds. Environmental context appears to be important in the expression of carryover effects of larval conditions on survival, as mediated through body size at and timing of metamorphosis.

The context of our survival study was exodus from ephemeral ponds in the dry period of late summer, potentially a harsh scenario for the osmoregulation of small frogs. Though we demonstrated strong carryover effects, we did not observe variation in the magnitude of these effects between sites for either survival interval, from the ponds to ~12 m or from 12 m to ~40 m, despite contrasting terrestrial conditions at the two ponds. However, we should expect body size to be more important in dispersal success of amphibians in xeric habitats, because of three basic principles of amphibian physiology. It has been well documented that desiccation rate decreases with increasing body size (Thorson 1955, Ray 1958) and that body size positively relates to locomotor performance (John-Alder and Morin 1990, Goater et al. 1993, Beck and Congdon 2000, Tejedo et al. 2000, Álvarez and Nicleza 2002). Further,

desiccation directly suppresses the physiological mechanisms of movement (Hillman 1984, Gatten 1987, Hillman 1987, Preest and Pough 1989) and has been directly observed to negatively impact locomotory performance (Rogowitz et al. 1999, Preest and Pough 2003). The importance of size to dispersing or migrating amphibians is supported at a landscape scale by evidence of differential selection of forests or humid conditions by smaller individuals. For example, wood frogs captured in fragmented areas were larger than those in pristine areas (Mazerolle 2001), the propensity of adult red-legged frogs to enter clearcuts increased with body mass (Chan-McLeod 2003), which may suggest greater risk to smaller individuals, and newly metamorphosed amphibians may differentially select forested habitats relative to adults (deMaynadier and Hunter 1999, Rothermel and Semlitsch 2002). Finally, field studies of marked individuals showed positive relationships between size and distance dispersed (e.g., Lyapkov et al. 2000, Vasconcelos and Calhoun 2004). Body size affects vagility at an individual level, but size at metamorphosis is important at a metapopulation level because this is the most common stage for amphibian dispersal (Gill 1978, Breden 1987, Berven and Grudzien 1990) and because metapopulation dynamics are thought to be important for amphibians (Pechmann et al. 1991, Alford and Richards 1999, Marsh and Trenham 2001). Expansion of the spatial scale of individual movement and survival studies of juvenile frogs is needed to adequately evaluate interactions among stressors in aquatic and terrestrial habitats.

To illustrate the potential magnitude of carryover effects of aquatic stressors in our study, we consider an example, the presence of bullfrogs (*R. catesbeiana*), invasive competitors with and predators on red-legged frogs. Taking the results of Kiesecker and Blaustein (1998), the presence of adult bullfrogs caused a delay in metamorphosis by 11 d and a reduction in mass at metamorphosis from 1.72 to 1.38 g for red-legged frogs in field enclosures. The combined effects of delayed metamorphosis and reduced size, 1.24 mm by our correlation of the log of mass with snout-vent length, would have decreased the probability of surviving and emigrating to 40 m for a frog of mean size and date at our sites from 86% survival to 41%. In situations in which density dependence is weak and abundance responds appreciably to changes in survival of this magnitude, carryover effects of aquatic stressors into terrestrial habitat could have an important impact on population dynamics, even when size effects on age at first reproduction, fecundity, and long-term survival are not considered. Here it is notable that several recent life cycle demographic syntheses (Vonesh and De la Cruz 2002, Conroy and Brook 2003) emphasized the importance of juvenile survival in affecting population change.

Carryover effects between life stages or between habitats may not be adequately considered by popu-

lation and conservation biologists, but collectively for all demographic rates, their impacts at a population level may be large. Considering that multiple fitness components often are affected indirectly (Metcalf and Monaghan 2001, Peacor and Werner 2001) or long after exposure to stressors (Lindström 1999, Metcalf and Monaghan 2001, Beckerman et al. 2002), the potential for populations to be impacted by carryover effects is large (Caswell 1996, Peacor and Werner 2001). Holistic examples of population-level responses that incorporate carryover effects on multiple demographic rates are remarkably rare, despite early applications of sensitivity analysis in size-classified matrix models that showed asymptotic population growth rates were most sensitive to early mass gain in small mammals (Sauer and Slade 1986, 1987). In an example involving indirect predator effects on *Daphnia*, Walls et al. (1991) showed that at low food availability, predator-induced reduction in *Daphnia* fitness was driven primarily by reduced individual growth rate of early instars. Although important to conservation and population biologists, impacts of carryover or delayed effects at a population level are far from obvious (Caswell 1996, Metcalf and Monaghan 2001), and understanding their full effect will require measuring impacts under natural conditions, which are often difficult.

An important issue for the interpretation of our results is that we could not distinguish between animals that settled within the study areas and animals that died. However, we hypothesize that the majority of disappearances were the result of mortality and not settling, because of the patterns of movement we observed. Our analysis of these same capture-recapture data in the time dimension (Chelgren 2003) does not reveal any delayed emigration at Burdue's Pond, which would be expected if animals aestivated until the fall rains began to occur in September. However, at State Pond we captured 16 individuals in pitfall traps after 1 September, suggesting that our expectation of increased frog activity during that period was valid. No individuals were captured after 1 September at Burdue's Pond. Since the majority of disappearances occurred at Burdue's Pond, where frogs were smaller and where aerial cover of vegetation was half that of State Pond, we believe that mortality was a more likely explanation than aestivation. Hastened emigration from Burdue's Pond was also consistent with the increased travel velocity of salamanders in disturbed vs. natural patches (Rosenberg et al. 1998) and with habitat selection studies showing preference for forests over unforested areas by newly metamorphosed American toads (*B. americanus*; Rothermel and Semlitsch 2002) and wood frogs (deMaynadier and Hunter 1999). Expansion of the temporal scale of our study to include future breeding efforts of these frogs may be the most efficient and valuable method for resolving the issue of mortality vs. aestivation.

Widespread declines in amphibian numbers may commonly be a result of multiple and interacting stressors (Kiesecker et al. 2001a, Blaustein and Kiesecker 2002, Collins and Storfer 2003). Body size at metamorphosis and timing of metamorphosis are highly plastic traits that influence components of fitness and are affected by numerous stressors (see *Introduction* for citations). Recent studies have begun to focus on the importance of estimating demographic rates in situ and the consideration of all stages of the life cycle for the interpretation of laboratory and microcosm amphibian studies (Biek et al. 2002, Vonesh and De la Cruz 2002, Grafe et al. 2004). Efforts to elucidate the relative impact of various anthropogenic changes to population and metapopulation dynamics will be misleading where no account is made for fitness-level carryover effects of stressors between life cycle stages.

ACKNOWLEDGMENTS

We thank Earl Gonsolin and Roxanne Barker for their work in the field. Cynthia Anderson, Jennifer Gervais, Christopher Pearl, and James Sedinger contributed insightful discussion and comments on an earlier version of this manuscript. A Cooperative Training Grant was provided to N. Chelgren by the U.S. Environmental Protection Agency, National Health and Environmental Effects Laboratory, Western Ecology Division. Additional funding and support was provided by the U.S. Fish and Wildlife Service, Portland field office, the Oregon Agricultural Experiment Station under project ORE00102, and the Oregon Cooperative Wildlife Research Unit.

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APPENDIX

A figure presenting sensitivity of selected posterior distributions to the choice of prior distribution (*Ecological Archives* A016-013-A1).

SUPPLEMENT

Winbugs version 1.4 code for the Cormack-Jolly-Seber model with random effects and its modification for accommodating handling effects at State Pond (*Ecological Archives* A016-013-S1).