

AN ABSTRACT OF THE THESIS OF

Nathan D. Chelgren for the degree of Master of Science in Wildlife Science. Presented on June 17, 2003.

Title: Effects of Body Size on the Survival and Timing of Emigration of Newly Metamorphosed Northern Red-legged Frogs.

Abstract approved:

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The purpose of this study was to investigate the survival and movements of newly metamorphosed Northern Red-legged frogs (*Rana aurora aurora*) as they emigrated from two ephemeral breeding ponds. Quantifying survival and movement rates will be important to our understanding how changes to terrestrial and aquatic systems affect behavior and population dynamics. I manipulated food availability for a subset of uniquely marked metamorphic frogs and then analyzed temporal and spatial aspects of their recapture in forest pitfall traps relative to body size and date of metamorphosis. The probability of surviving and emigrating increased strongly with increasing body size and declined for

frogs metamorphosing later in the season. Larger body size was associated with earlier emigration and greater correlation of movements with rainfall events. Within a pond, the time elapsed between metamorphosis and emigration was not affected by the pond drying. My results demonstrate that conditions during the tadpole stage which affect body size and the timing of metamorphosis may have a dramatic impact on the performance of frogs during their initial transition into the terrestrial environment.

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Effects of Body Size on the Survival and Timing of Emigration of Newly
Metamorphosed Northern Red-legged Frogs

by

Nathan D. Chelgren

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Nathan D. Chelgren, Author

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CONTRIBUTION OF AUTHORS

Dr. Alix I. Gitelman assisted with the interpretation of data and analysis for Chapters 2 and 3.

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DEDICATION

To my Mother Peggy Chelgren-Smith and Father Karl Chelgren for their
unfailing support, limitless understanding, faith, and love.

Effects of Body Size on the Survival and Timing of Emigration of Newly Metamorphosed Northern Red-legged Frogs

CHAPTER 1

GENERAL INTRODUCTION

The Northern Red-legged frog *Rana aurora aurora* is declining in portions of its historic range (Nussbaum et al. 1983, Hayes and Jennings 1986, Kiesecker and Blaustein 1998) and the California sub-species, *R. a. draytonii*, is listed federally as Threatened (USFWS, 1996). Meanwhile, there is concern among scientists that amphibians worldwide are declining at a more rapid rate than other taxa (Houlahan et al. 2000). Syntheses of amphibian population studies are in agreement that there is no single cause for the declines, but rather various stressors acting and interacting on populations with differing intensities depending on local conditions (Kiesecker et al. 2001, Blaustein and Kiesecker 2002, Collins and Storfer 2003). A large number of studies have been conducted during the aquatic stages of the life-cycles of these animals. However, the post-metamorphic and juvenile periods have received disproportionately little focus relative to their importance to population dynamics (Morey and Reznick 2001, Biek et al. 2002). Knowledge of the basic ecology and demographics during all life-cycle stages is important for elucidating the complex causes of population declines.

A broad suite of anthropogenic changes have been shown to affect larval survival, growth and ontogeny (see Chapter 3 for citations). Larval mortality is the most direct link of aquatic stressors to population declines, but the effects of lowered growth rates and delayed metamorphosis on population change are more difficult to decipher. This dilemma is made more pronounced by our lack of basic knowledge of frog ecology during the post-metamorphic and juvenile periods which immediately follow metamorphosis and can last for years in some species (Nussbaum et al. 1983).

Understanding the continued impacts of aquatic stressors on the demographics and behavior of frogs in the terrestrial realm is critical to discerning impacts of anthropogenic change to terrestrial habitats. Terrestrial habitat degradation is implicated in the declines of both sub-species of Red-legged frogs (Hayes and Jennings 1986, Kiesecker and Blaustein 1998, Blaustein and Kiesecker 2002). For amphibians, body size is strongly negatively correlated with desiccation rate (Shelford 1913, Thorson 1955, Ray 1958, Spight 1968). Body size and the timing of metamorphosis may, therefore, play a critical role in the survival of newly metamorphosed frogs as they emigrate from drying ponds, especially where terrestrial habitat degradation has lowered the relative humidity, intensified extremes of temperature, and created obstacles that slow frog movements.

We initiated a study of Northern Red-legged frog movements and survival from metamorphosis through emigration from two ephemeral breeding ponds located in Lincoln County, Oregon, USA. We focused our work on the continued impacts of body size and timing of metamorphosis on performance as frogs transitioned into the terrestrial realm.

We used a Bayesian approach to statistical modeling and inference in our study for two reasons. In both of our applications, the study of the timing of frog movements and of frog survival, the complexity of our statistical models was such that available likelihood based software was inadequate. A second and bigger issue is that the Bayesian paradigm in general better suits the nature of terrestrial frog studies. The study of frog terrestrial ecology has lagged behind the aquatic stage because of methodological difficulties in experimentation and observation. An inferential framework is needed for the synthesis of information and uncertainty from demographic studies that can span only a limited spatial or temporal extent, and for the incorporation of imprecisely calibrated field methods such as capture techniques. The Bayesian paradigm is the ideal modeling framework for synthesis of multiple and hierarchical sources of uncertainty (Cox and Hinkley 1974, Dixon and Ellison 1996).

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CHAPTER 2

TIMING OF EMIGRATION OF NEWLY METAMORPHOSED RED-
LEGGED FROGS: INTERACTING EFFECTS OF BODY SIZE AND
RAINFALL

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

Alix I. Gitelman

Abstract

Quantifying the timing of emigration of newly metamorphosed frogs from their natal ponds will be important to our understanding how changes to terrestrial and aquatic systems affect population dynamics. We studied the timing of emigration of newly metamorphosed Red-legged frogs (*Rana aurora*) relative to their date and body size at metamorphosis, and the occurrence of rainfall at two ephemeral ponds. We manipulated food availability for a sample (322) of 1062 uniquely marked metamorphic frogs and released them at their natal ponds. We recaptured 33% of released frogs in forest pitfall traps surrounding ponds as they emigrated. The median age at emigration was 4 and 10 days at the two sites. Larger body size was associated with earlier emigration and greater correlation of movements with rainfall events. Within a pond, the time elapsed between metamorphosis and emigration was not affected by the pond drying. These findings are important to understanding the life-history of Red-legged frogs and their behavior relative to body size, an often measured response to aquatic conditions.

Introduction

The dearth of ecological studies of amphibians in the period immediately following metamorphosis is unfortunate as this is a dynamic period that likely has important population consequences (Biek et al.

2002). The extreme plasticity in timing of ontogeny and body size at metamorphosis entering into this period is well documented (Wilbur and Collins 1973, Collins 1979). Both variables have fitness related consequences for amphibians: timing (Licht 1974, Tevis 1966, Shoop 1974, Smith 1987, Semlitch et al. 1988, Skelly 1996), and body size (Martof 1956, Smith 1987, Semlitsch 1987, Semlitsch et al. 1988, Morey and Reznick 2001). Moreover, the post-metamorphic and juvenile periods may be primary for dispersal (Dole 1971, Schroeder 1976, Berven and Grudzien 1990). Considering the extreme spatiotemporal variability in factors related to reproductive success (Gill 1978, Berven 1990, Berven and Grudzien 1990, Pechmann et al. 1991, Sjögren 1991), natal dispersal should be an important contributor to the regional persistence of populations. Newly metamorphosed frogs, because of small body size, face important mortality risk from desiccation during terrestrial movements (Shelford 1913, Thorson 1955, Ray 1958, Spight 1968). This comes at a time when frogs are experiencing a novel environment and in the case of ephemeral breeding ponds may be forced to emigrate during drought.

The use of permanent ponds by non-native predators and competitors places increased importance on ephemeral ponds for native frog breeding (Adams 2000). However, the stochastic nature of frog productivity in ephemeral ponds (e.g. Licht 1974, Skelly 1996) will result in an increased role for dispersal in maintaining connectivity between

populations and the persistence of populations regionally. In the case of ephemeral pond breeding, we also should expect weather to play a key role in terms of survival and timing of movements in the terrestrial habitat matrix, especially since body size is positively correlated with pond permanence (Tejedo and Reques 1994, Leips et al. 2000) and negatively correlated with desiccation rate (Shelford 1913, Thorson 1955, Ray 1958, Spight 1968). Increased reliance on ephemeral ponds for breeding may create a dilemma for the regional persistence of frog populations involving interacting effects of body size, weather variability and terrestrial habitat quality on post-metamorphic survival and natal dispersal.

The correspondence of mass-movements of newly metamorphosed frogs with periods of wet weather is evident (e.g. Martof 1953, Heatwole 1961, Bellis 1962, Dole 1965). Yet, there is much to be learned in this dynamic by studying the variation between individuals in response to weather changes. There are few quantitative individual-based studies of frog emigration as a result of the difficulty of individually marking and recapturing frogs and in the analytical methodology of incorporating time-dependent weather variables and dependence among individuals.

We used mark-recapture methods to study the timing of emigration of newly metamorphosed Red-legged frogs at two contrasting ephemeral ponds. We specifically examined effects of date of metamorphosis and interactions of body size, and rainfall events. Because body size and

desiccation rate are negatively correlated, we hypothesized that smaller size at metamorphosis should be associated with delayed emigration for continued growth at the ponds. However, as ponds dry, metamorphosed frogs may be forced to emigrate to reach areas for favorable water balance, survival and growth. For this reason, we hypothesized that animals metamorphosing late in the season should emigrate sooner following metamorphosis than frogs metamorphosing early in the season. Finally, larger animals at metamorphosis may have more flexibility in their timing of emigration as they are more robust to extremes in weather. We hypothesized that rainfall influences the timing of movements more severely for smaller than larger animals.

Methods

Study Areas

We studied the timing of frog emigration at two ephemeral, off-channel ponds located within 1km of the ocean beach in Lincoln County, Oregon, USA from June to November, 2002. Ponds were selected for their densities of metamorphic frogs to allow for a minimum of 500 marked animals at each site. The latitude of the sites was central for the species range (Nussbaum et al. 1983). Because it was immediately adjacent the ocean, the area was mild in its extremes of temperature and relative

humidity fluctuation (Figure 2.1). Bullfrogs (*R. catesbeiana*) were not present at or near the study ponds.

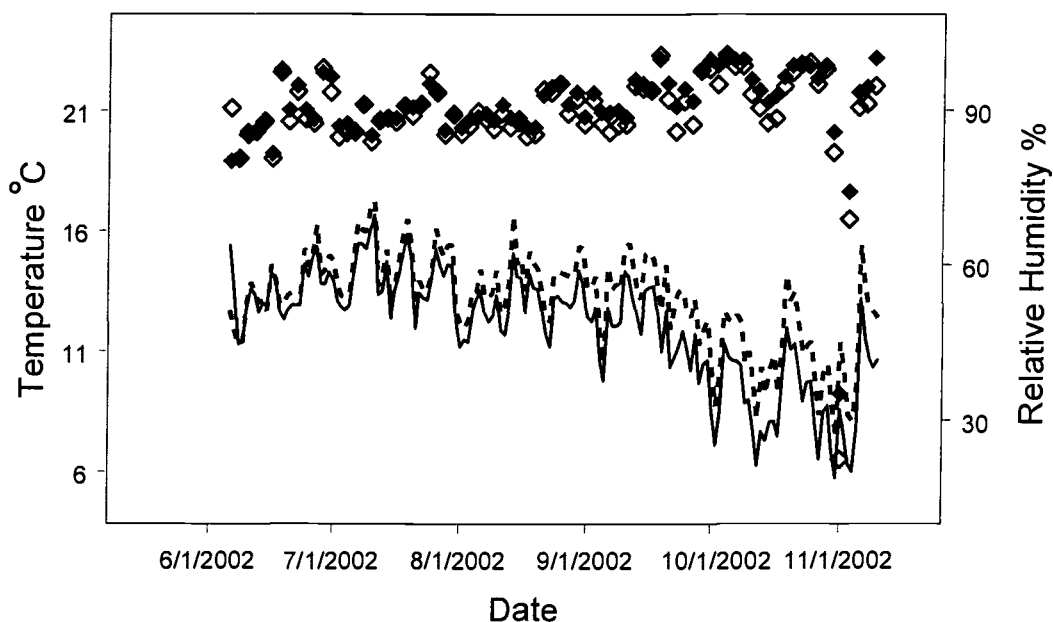


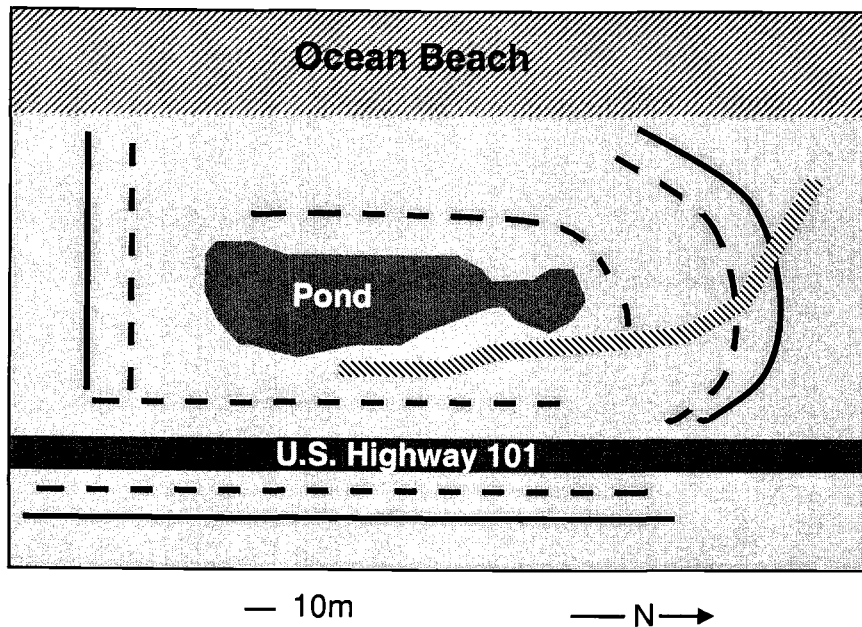
Figure 2.1. Relative humidity (diamonds) and air temperature (lines) at Burdue's Pond (open symbols and dashed line) and State Pond (filled symbols and solid line).

The site referred to hereafter as Burdue's Pond (Figure 2.2), approximately 0.36ha, was surrounded by a matrix of sparse beachgrass (*Ammophila arenaria*) and rush community interspersed with patches of salal (*Gaultheria shallon*) and young pines (*Pinus contorta*), sparse roadside grasses and forbs, and patches of remnant older salal with a mixed tree canopy (*Alnus*, *Pinus*, *Pseudotsuga*). The trapping area surrounding Burdue's Pond was bisected by Interstate Highway 101, had a single residence, and power line right-of way. Burdue's Pond was a

disturbed site characterized by large areas of bare ground, sparse understory, and patchy canopy cover. The bank inclined gradually and the deepest areas of the pond were un-shaded. We marked and released animals in Burdue's Pond during the final stages of metamorphosis from June 12 to July 17, 2002. The pond dried completely on July 23, 2002.

The site referred to hereafter as State Pond (Figure 2.2), approximately 0.15ha, was immediately surrounded by a strip of thick emergent wetlands dominated by forbs (*Sanguisorba officinalis*) and sedge (*Carex spp.*). Encircling was a dense scrub-shrub wetland of willow (*Salix spp*) and sedge (*Carex spp.*). The surrounding upland matrix was a patchwork of closed canopy pine-salal forest, open canopy salal-twinberry (*Lonicera involucrata*) beach scrub, sedge-willow scrub-shrub wetland, and one patch of manicured lawn. A canal with full canopy cover, which drained a nearby ephemeral wetland, bisected the northern portion of the study area. State Pond was lushly vegetated relative to the disturbed site, with nearly continuous forest canopy and little disturbed ground. State Pond also had a gradually inclined bank but was shaded in its deepest region. We marked and released metamorphic frogs at State Pond from June 17 to July 12, 2002. State Pond dried completely on July 17, 2002.

A)



B)

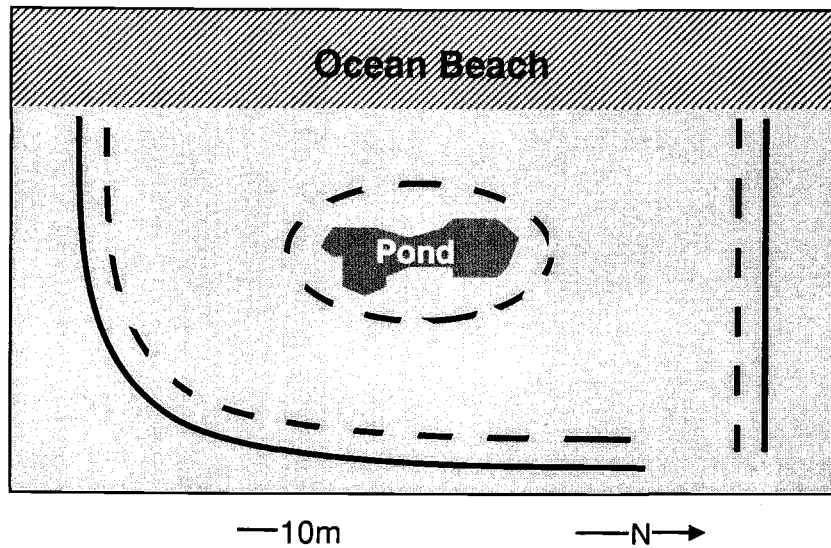


Figure 2.2. Schematics of A) Burdue's Pond, and B) State Pond. Discontinuous fence rows are depicted with dashed lines. Solid lines are continuous drift fence rows. A cliff (cross-hatched line) at Burdue's Pond substantially influenced movements by frogs.

Field Methods

Around each pond we constructed concentric rings of drift fencing with pitfall traps (Figures 2.2). At the time of fence construction, when the ponds were at maximum size in March and April 2002, the fences nearest ponds were placed at 10-12m from the pond edges. Outer-most fences were placed at approximately 40m and 45m from pond edges where landscape features permitted and the nearest possible location otherwise. At Burdue's Pond, 323m of discontinuous 7.7m drift fences were partially surrounded by 368m of continuous drift fence. At State Pond 308m of discontinuous drift fencing was partially surrounded with 310m of continuous drift fencing. On the inner (pond) side of drift fences, we placed pitfall traps approximately every 1.9m at Burdue's Pond (363 traps) and State Pond (323 traps), respectively. Pitfall traps were constructed of two #10 cans taped end to end and buried such that the rim was slightly below duff-level following Corn (1994). Pitfall traps were fitted with black funnel tops (Crawford and Kurta 2000) to prevent escape by scaling. 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 in case of flooding.

At Burdue's Pond we built 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 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 the pond's rapid drying, food manipulation was performed similarly except that 11.4L enclosures were kept in 1.83m diameter plastic wading pools at the pond's edge.

From June through July 2002, we dip-netted tadpoles for inclusion in food manipulation treatments. We measured tadpole snout to vent length (SVL) and categorized metamorphic development into Gosner stages (Gosner 1960) before assigning three animals per enclosure, grouped by developmental stage. We then randomly assigned enclosures to one of two treatments. Both treatments received five pellets of commercial rabbit chow two times weekly until growth stage 37 was reached, at which time the high food treatment enclosures continued to receive the same food allotment. The low food treatment then received no supplemental food, similar to Audo et al. (1995). 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.

Upon reaching metamorphosis, Gosner stages 43 to 46, we terminated feeding trials on a per tub basis. All animals which were marked for study were anesthetized in a 0.25g/L solution of MS-222 (3-aminobenzoic acid ethyl ester; Nauwelaerts et al. 2000) buffered with sodium bicarbonate (Fellers et al. 1994). We measured SVL to the nearest 0.01mm using a dial caliper. We marked animals with soft, three-digit alphanumeric VIAAlpha tags (Northwest Marine Technology Inc., Shaw Island, WA; Buckley et al. 1994) injected subcutaneously in the dorsal thigh. We then massaged tags to the ventral side of the thigh to avoid tag loss through the incision and allow tags to be seen clearly through the transparent skin. To evaluate tag loss, we clipped a single front digit to indicate the animal was VIAAlpha marked. We held animals in enclosures for 24h to ensure recovery from the 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 mark and release of feeding trial tadpoles, we captured and marked free-living animals in the range of Gosner developmental stages 43 to 46 from the pond using dip-nets and hand-capture. These animals were handled, marked, and released identically to those of the feeding trials. At State Pond, again because of limited pond area and pond's rapid drying, we raised tadpoles that did not

enter the feeding trial enclosures in 1.83m diameter wading pools from intermediate developmental stages (stages 25 to 30). These animals had been captured from drying portions of State Pond. Tadpoles were fed commercial rabbit pellets ad lib and were provided with logs for structural cover. We changed 25% of pool water, removed feces and uneaten pellet food twice weekly.

At the appearance of the first metamorphic individuals we opened pitfall trap arrays. From June 6 to July 31 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 in order to minimize mortality and desiccation at this sparsely vegetated, more arid site. From 1 August to 8 November traps at both sites were checked and emptied on alternate days. Frogs that had been marked with VIAAlpha tags were re-measured and then released on the opposite side of the drift fence adjacent the trap from which they were captured.

Statistical Methods

To study timing of movements relative to rainfall events, date and body size at metamorphosis, we used a likelihood-based discrete-time relative-risk survival model (Prentice and Gloeckler 1978). Our response variable was age in days since metamorphosis at first pitfall trap recapture, hereafter referred to as age at emigration. Importantly for the

scope of inference, the only animals that entered this timing of movement analysis were those that were captured in a forest drift fence before traps were closed at the end of the study period November 8, 2002: 139 of 591 marked animals at Burdue's Pond and 213 of 471 marked animals at State Pond. Of the animals originally marked we thus excluded three distinct groups of frogs from the analysis: frogs that died at the ponds or during their exodus from the trapping area before they were captured, frogs that escaped the trapping area without being captured, and animals that were never recaptured but remained alive within the trapping areas as of November 8, 2002.

We used the BUGS software (Spiegelhalter et al. 1994) to incorporate non-informative prior probabilities on regression parameters as well as on the baseline hazard rate in a Bayesian application. The Bayesian approach easily allowed us to incorporate random effects (frailty) of the 39 release groups (g) which had at least one recapture to account for the possibility that animals within groups might not behave independently.

The model structure was a temporal chain of conditional, interval specific 'survival' rates or hazard rates. Here 'surviving' in the normal time-to-event sense pertains to animals remaining un-captured in the pitfall traps. We accounted for gross differences in the timing of movements between ponds with pond-specific baseline hazards. The

daily hazard rate, $hazard_{i,j,p}$, at pond p for individual i over interval j is related to the baseline daily hazard rate $\alpha_{j,p}$. We incorporated the time specific (t) regression variables $Z(t_j)$, the length of the interval between trap checks in days (d) and the random group effects (g) with the following link function

$$hazard_{i,j,p} = \alpha_{j,p}^{d \exp(Z(t_j)\beta + g)}.$$

For intervals of two days, therefore, we assumed equal daily hazard rates for the two days. The hazard link function we used related the properties of individual frogs, the length of the interval between trap checks, and the random effects of release groups to the binary response, captured versus not captured in the respective interval for the marked animals that had yet to be captured at the start of the interval.

We sought to relate date and relative body size during the final stages of metamorphosis as well as Gosner stage to the timing of emigration. Since animals were still developing and growing at the time of marking, we used the residual SVL (rSVL) from an ANOVA model relating size to Gosner stage as the regressor variable in the timing of movement study.

We structured our regression data to estimate pond-specific effects of date of metamorphosis (Date), Gosner stage at release (Stage), rSVL, indicators for rainfall occurring in the time interval (Rain; 1 = measurable

rainfall, 0 = no measurable rainfall) and the interaction of rain with rSVL (Rain*rSVL). To account for the distance from the pond where the frog was first captured we also included an indicator for the fence ring (0 = innermost fence ring versus 1 for any of the surrounding fences) where the frog was first re-captured. The continuous variables Date and rSVL were standardized to one standard deviation about the mean for better comparison of the magnitude of their effects on emigration timing.

Our specification of prior probabilities was intended to be non-informative in the sense that the mass of the prior distributions were spread 'evenly' across the range that was reasonable biologically (Figure 2.3):

$$\begin{aligned} g &\sim \text{Normal}(\text{mean} = 0, \text{var} = \tau^{-1}) \\ \tau &\sim \text{Gamma}(1.0\text{e} - 3, 1.0\text{e} - 3) \\ \beta &\sim N(0, 1.0\text{e} + 6) \\ \alpha_{j,p} &\sim \text{Beta}(1, 1). \end{aligned}$$

We used alternative prior specifications

$$\begin{aligned} \tau &\sim \text{Gamma}(1, 0.01), \\ \beta &\sim \text{Normal}(\text{mean} = 0, \text{var} = 1), \text{ and} \\ \alpha_{j,p} &\sim \text{Beta}(10, 1) \end{aligned}$$

to judge sensitivity of the posterior distributions to our choice of prior distributions. For prior sensitivity analysis we altered only one parameter at a time from the original specifications.

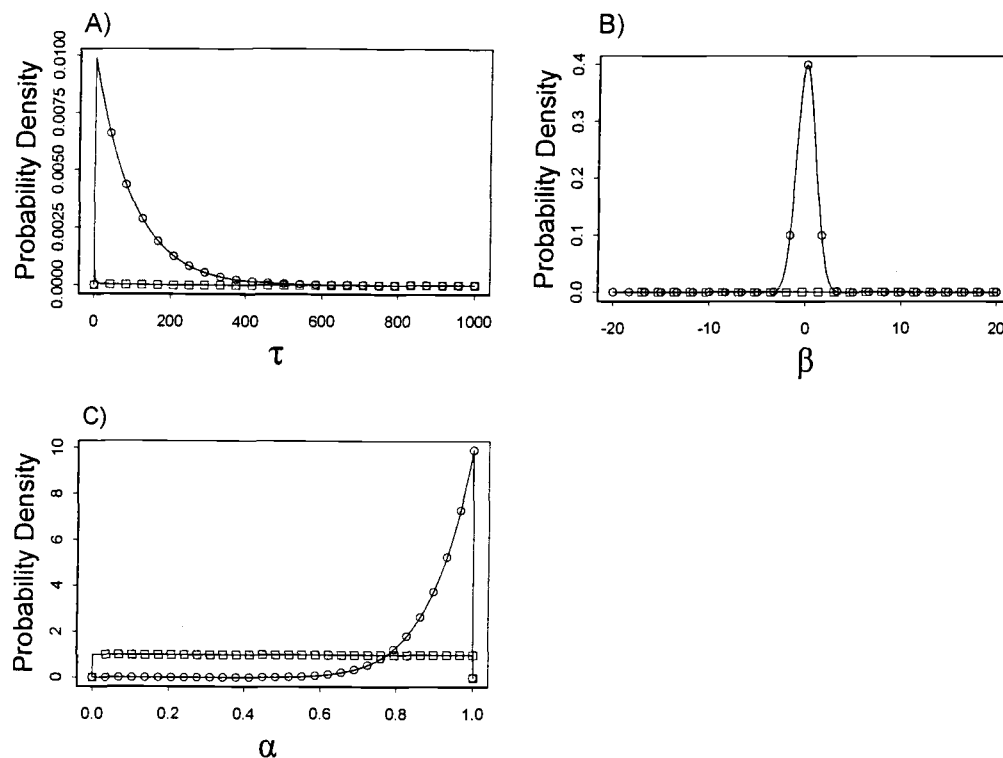


Figure 2.3. Prior distributions for model parameters with alternates. Prior distributions A) the $\text{Gamma}(0.001, 0.001)$ density (squares) and the $\text{Gamma}(1, 0.01)$ density (circles) for the random effect precision. Prior distributions B) the $\text{Normal}(\text{mean}=0, \text{var}=1.0\text{E}+6)$ density (squares) and the $\text{Normal}(\text{mean}=0, \text{var}=1)$ density (circles) for regression coefficients. Prior distributions C) the $\text{Beta}(1, 1)$ density (squares) and $\text{Beta}(10, 1)$ density (circles) for baseline hazard rates.

The Markov chain Monte Carlo simulation of posterior probabilities was made up of draws from three independent streams begun from over-dispersed starting values (Gelman 1996). We discarded the first 1000 iterations of each stream as the chain converged to the stationary distribution. We established that the streams had converged with the Gelman-Rubin diagnostic (Gelman 1996). Finally, we accumulated the next 5,000 iterations of each stream, resulting in 15,000 samples.

We used these samples from the simulated marginal posterior probabilities of each parameter to examine the statistical support for each of our hypotheses (Anderson et al. 2001). Our hypothesis that smaller animals would wait longer to emigrate than larger animals was supported with the probability equal to the proportion of samples where

$\exp((\beta_{rSVL*Burdue's} + \beta_{rSVL*State})/2) > 1$. Based on data from both ponds, the computation represents the probabilistic support that the contribution of the effect of rSVL to the exponent of the baseline hazard rate was greater than one. Similarly, our hypothesis that frogs metamorphosing later in the season would emigrate sooner after metamorphosis than those metamorphosing early in the season was supported with the probability equal to the proportion of samples where

$\exp((\beta_{Date*Burdue's} + \beta_{Date*State})/2) > 1$. Third, our hypothesis that smaller animals were more closely tied to periods of wet weather for their movements than larger animals was supported with the probability equal to the proportion of samples where

$\exp((\beta_{Rain*rSVL*Burdue's} + \beta_{Rain*rSVL*State})/2) < 1$.

To determine if our feeding treatments affected body size we compared SVL at metamorphosis between food treatment animals and across time within ponds using linear regression in S-plus (S-PLUS 1999). Then, in order to determine if growth rates post-metamorphosis were of a

magnitude great enough to account for the delay in emigration of smaller animals, we modeled frog growth from measurements taken at the time of marking and at recapture in forest drift fences using linear mixed models (Verbeke and Molenbergs 2000) in S-plus (S-PLUS 1999). We fit a model with Gosner stage as a factor, days since metamorphosis (Age), Pond, and Age by Pond interaction with random intercepts and slopes for individuals to account for repeated measurements in the precision of our estimates.

Results

At Burdue's Pond we individually marked a total of 591 frogs at metamorphosis, of which 222 animals were from the feeding trials (111 high food treatment, 111 low food treatment) and 369 were captured from the pond just prior to metamorphosis and did not enter the feeding trials. At State Pond we marked 471 animals at metamorphosis, of which 100 animals were from the feeding trials (70 high food treatment, 30 low food treatment) and 371 were reared in 1.83m diameter wading pools outside of feeding tubs at the pond edge with ad lib food availability.

Body size at metamorphosis varied by pond, feeding regime, and date of metamorphosis. Overall, size at metamorphosis (\pm SE) was 15% greater for the marked frogs at State Pond ($22.1 \pm 0.15\text{mm}$) compared to those at Burdue's Pond ($19.3 \pm 0.071\text{mm}$; $F=1503.5$, $df=1$, $P<0.0001$),

and lower for the low food treatment ($20.2 \pm 0.17\text{mm}$) compared to the high food treatment ($21.4 \pm 0.13\text{mm}$; $\text{Chisq}=30.96$, $\text{df}=2$, $P<0.0001$; Figure 2.4). Housing tadpoles in the 11.4L feeding enclosures had a positive effect on size at metamorphosis at Burdue's Pond and a negative effect on size for animals raised at State Pond. Body size at metamorphosis decreased significantly with increasing date of metamorphosis ($F=194.2$, $\text{df}=2$, $P<0.0001$) by $0.075 \pm 0.0051\text{mm}$ and $0.128 \pm 0.0098\text{mm}$ per day across the range of dates observed at Burdue's and State Ponds, respectively (Figure 2.5).

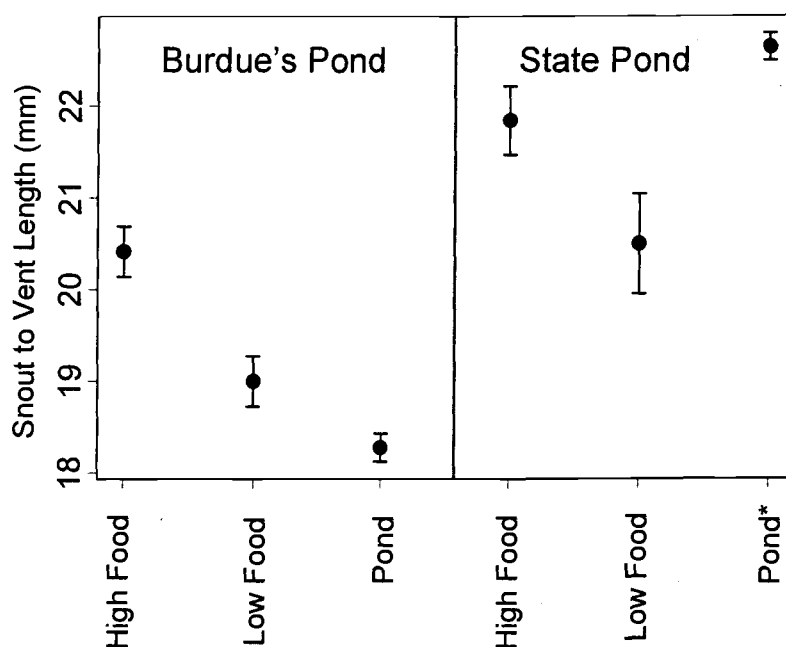


Figure 2.4. Mean body size at metamorphosis by food treatment and pond adjusted for June 29, 2002. Intervals are 95% confidence intervals computed using Scheffe's method for multiple comparisons. Marked animals at State Pond that did not enter the feeding trials (Pond*) were raised in 1.83m diameter wading pools at the pond edge.

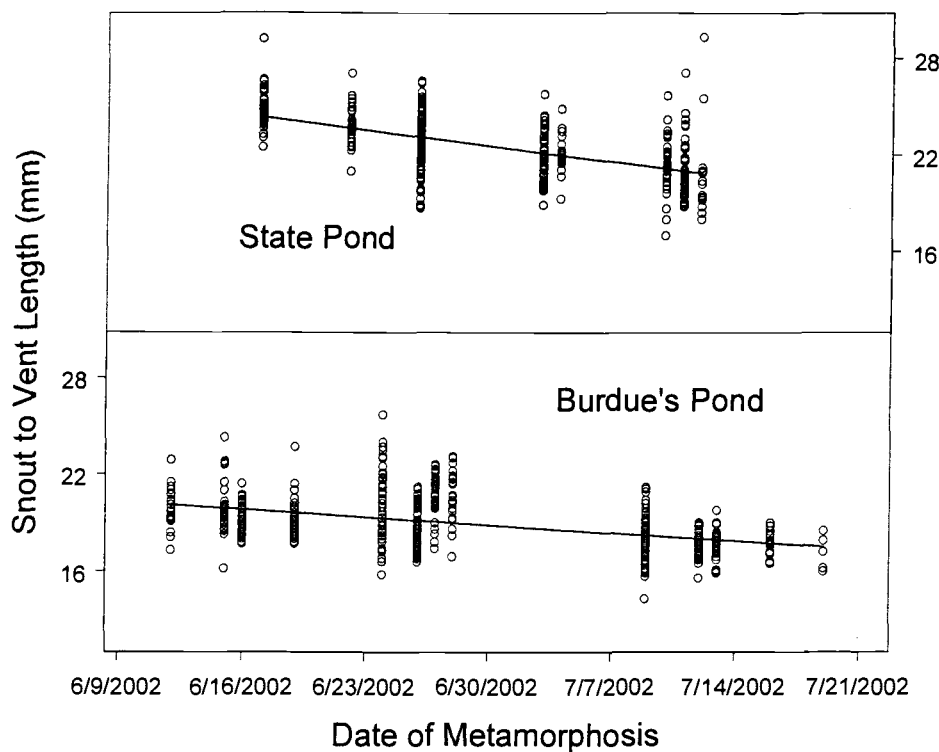


Figure 2.5. Body size at metamorphosis by date and pond.

The growth we observed post-metamorphosis was small in comparison with the variation in body size at metamorphosis. Growth rate post-metamorphosis did not vary significantly by pond (Chisq=1.05, df=1, $P=0.306$). Frogs grew at a rate of 0.014 ± 0.010 mm/day at Burdue's Pond and 0.024 ± 0.0074 mm/day at State Pond.

The timing of emigration behavior differed drastically between sites (Figure 2.6). We captured 24 and 53 percent of the frogs we marked in forest pitfall traps at Burdue's and State Pond, respectively. Median age at emigration was smaller at Burdue's Pond (4 days) than at State Pond (10 days). The 2.5% and 97.5% quantiles of age at emigration were 1 and

13 days at Burdue's Pond and 2 and 70 days at State Pond, respectively. No frogs were first captured in forest pitfall traps after Burdue's Pond dried completely, whereas 17 frogs were first captured at State Pond after its dry date.

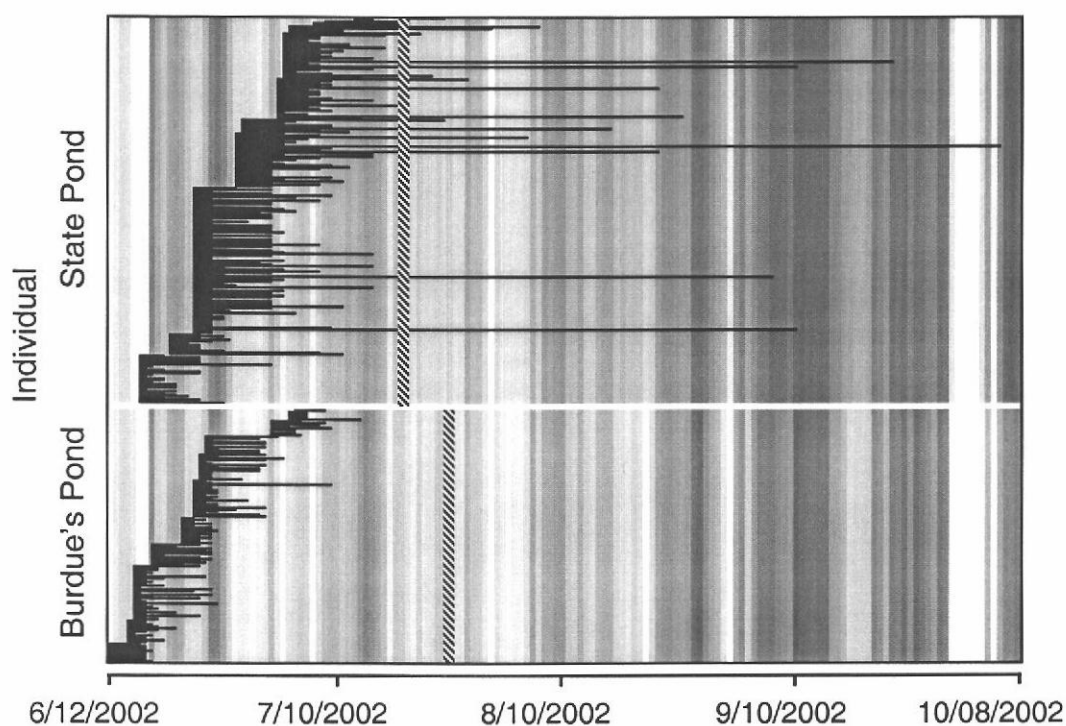


Figure 2.6. Residence times (horizontal lines) for individual frogs depicting release date at left and date of first capture in forest traps at right. Vertical shading represents nightly (1800hr to 0600hr) average relative humidity grading from arid (light bars) to humid (dark bars). The dates on which ponds dried are indicated with cross-hatched vertical bars.

Age at emigration was linked to body size at metamorphosis in a consistent manner between ponds (Figure 2.7). Our hypothesis that smaller animals wait longer to emigrate than larger animals was supported

with $\Pr(\exp((\beta_{rSVL*Burdue's} + \beta_{rSVL*State})/2) > 1) = 0.94$. One millimeter increase in SVL at metamorphosis would decrease the probability of remaining at the pond an additional day by a power of 1.09 (0.98, 1.21). The occurrence of rainfall decreased the daily probability of remaining at the pond following metamorphosis by a power of 3.81 (2.24, 6.23) at Burdue's Pond and by a power of 1.13 (0.74, 1.67) at State Pond. However, simply because precipitation was infrequent, 45% of the frogs in our study emigrated during dry periods. Smaller animals were less tied to periods of wet weather in their movements than larger animals, even after accounting for the developmental stage at which the animal was released. This outcome was counter to our original hypothesis. In fact our analysis strongly supports with $\Pr(\exp((\beta_{Rain*rSVL*Burdue's} + \beta_{Rain*rSVL*State})/2) > 1) = 1.00$ that larger animals were more closely tied to periods of wet weather for their movements than smaller animals. Intervals with rainfall decreased the daily probability of remaining at the ponds by a power of 1.26 (1.07, 1.49) for each additional millimeter of body size at metamorphosis. There was no support, $\Pr(\exp((\beta_{Rain*rSVL*Burdue's} + \beta_{Rain*rSVL*State})/2) < 1) = 0.35$, that age at emigration decreased over the course of the season after accounting for the decline in body size through time.

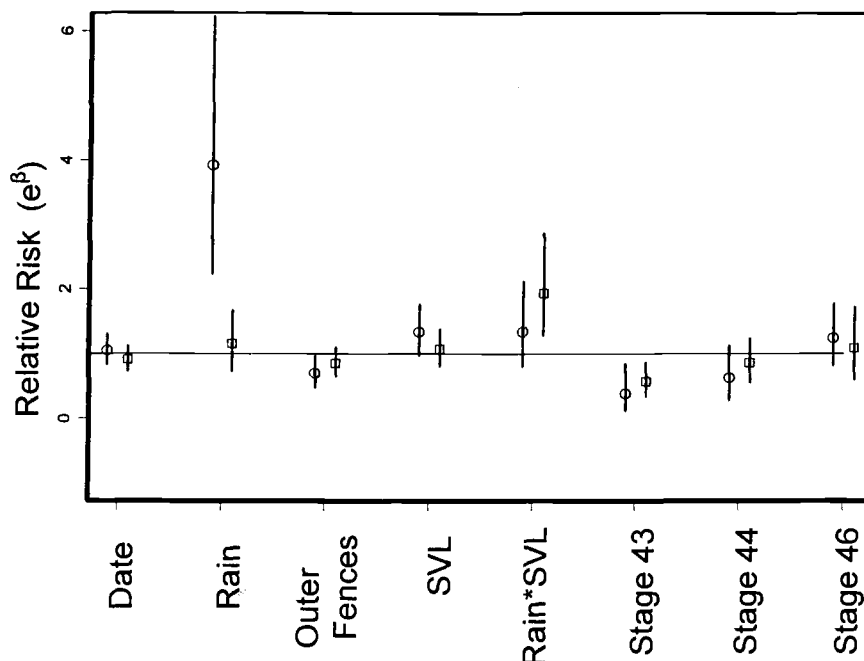


Figure 2.7. Relative risk estimates for age at emigration at Burdue's Pond (round symbols) and State Pond (square symbols). Plotted are e^{β} which relate to the baseline daily hazard rates as exponents. In this way an estimate of 1.0 (horizontal line) had no effect on the baseline daily risk of emigrating. Effects greater than 1.0 increased the daily probability of emigrating. Bars are 95% credibility intervals.

Our inference was generally insensitive to changes in prior probability specification except for the case of examining the effect of date of metamorphosis on age at emigration (Figure 2.8) when the prior distribution for the baseline hazard rate was changed from Beta(1,1), which is flat over the interval (0,1), to Beta(10,1), which had an accumulation of mass near one (Figure 2.3a). Even in this case, there was no substantive change in the role of date of metamorphosis on the timing of emigration.

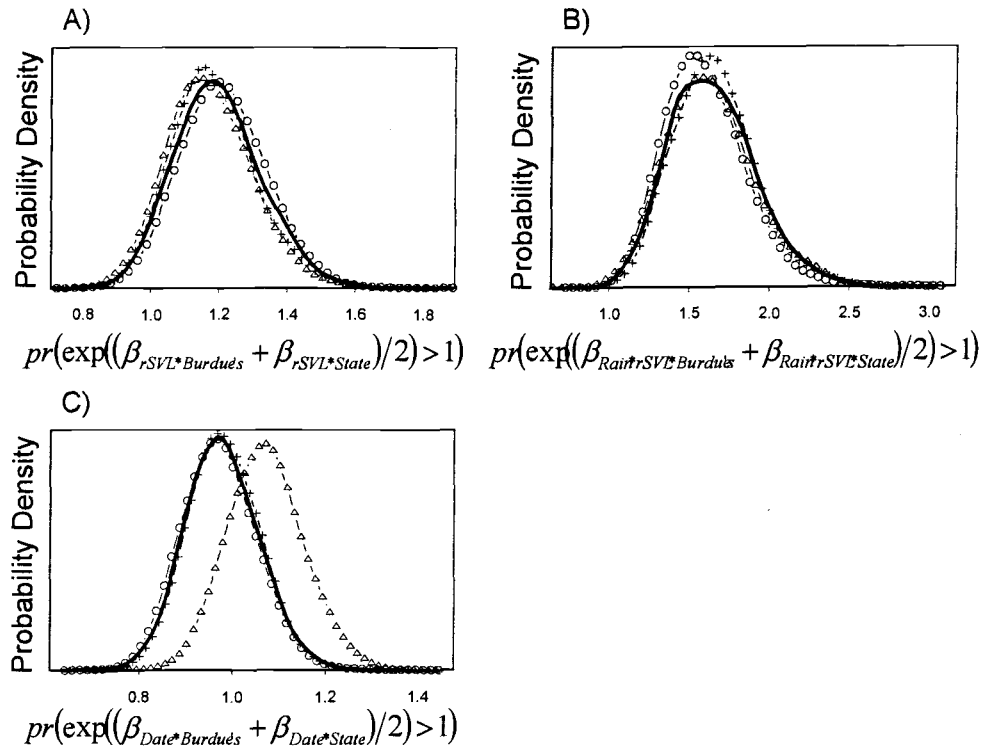


Figure 2.8. Sensitivity of selected posterior distributions to prior probability specification. We judged the sensitivity of posterior probabilities associated with hypothesis tests to the choice of prior distribution of A) the main effect of residual snout to vent length (rSVL), B) interaction of the occurrence of rain and rSVL, and C) date of metamorphosis. Solid heavy lines depict the original prior distributions. Posterior distributions associated with alternative prior distributions are shown as lines with circles for $\beta \sim \text{Normal}(\text{mean}=0, \text{var}=1)$, shown as lines with plus symbols for $\tau \sim \text{Gamma}(1, 0.01)$ and shown as lines with triangles for $\alpha \sim \text{Beta}(10, 1)$.

Discussion

Aquatic stressors which lead to reduced growth rates and size at metamorphosis have immediate survival costs for juvenile anurans (Goater 1994, Morey and Reznick 2001) which may be related to vagility. An analysis of survival during emigration of the same animals in our study

showed that body size strongly positively relates to the probability of surviving and emigrating from the natal pond (Chapter 3). Size related mortality may act through changes in animal behavior or performance that are associated with smaller size such as reduced activity (John-Alder and Morin 1998, Downes 2002), or frogs may alter behaviors because of a perceived risk of mortality that changes with body size, such as from the negative relationship between body size and desiccation rate (Shelford 1913, Thorson 1955, Ray 1958, Spight 1968, Spotila 1972). Animals that remain at drying pools are a concentrated source for predators (Arnold and Wassersug 1978) and may be at higher risk of infection (Kiesecker and Skelly 2001) but those that emigrate face the risk of desiccating. Consistently at our sites, smaller frogs waited longer to emigrate after metamorphosing than larger frogs and were more likely to forego rainfall events in their movements, contrary to our prediction. This may relate to development of the physiological basis for aerobic metabolism (Taigen and Pough 1981, Pough and Kamel 1984, John-Alder and Morin 1998, Carrier 1996) or to a size biased trade off in the risk of remaining at the natal pond versus emigrating.

We demonstrated that rainfall decreased the daily probability of remaining at the ponds following metamorphosis by a power of 2.08 on average between ponds. However, simply as a matter of the infrequency of precipitation, a large percentage (45%) of frogs emigrated during dry

periods. These results and captures of un-marked frogs agree with Dole's (1971) observation that some emigration occurs on almost every night for newly metamorphosed leopard frogs (*R. pipiens*), and with Greenbergs (2001) work that showed substantial frog movements during dry periods. In light of terrestrial habitat selection studies that have suggested juvenile anurans favor forested habitats more so than adults (deMaynadier and Hunter 1999, Rothermel and Semlitsch 2002) it is likely that desiccation risk is an important factor in determining emigration behavior and survival of newly metamorphosed frogs. Aquatic stressors which result in reduced body size at metamorphosis will increase mortality to desiccation during emigration and will lead to a more important role for terrestrial habitat quality as a buffer for survival in providing favorable temperature and humidity conditions.

Since desiccation rate negatively relates to body size (Shelford 1913, Thorson 1955, Ray 1958, Spight 1968, Spotila 1972) small frogs may wait at their natal pond to grow prior to emigrating. This is supported by our observation that larger frogs emigrate sooner after metamorphosis than smaller frogs. However, the post-metamorphic growth we observed ($<0.03 \text{ mm} \cdot \text{day}^{-1}$) was miniscule in comparison to the variation in body size at metamorphosis (standard deviation = 2.22mm). Given the growth rate we estimated, 10 day's growth would have decreased the daily probability of remaining at the ponds by a power of 1.03 (0.99, 1.06) for

dry days and by 1.07 (1.02, 1.13) for days with rain. Frogs that remain at ponds do not benefit appreciably from post-metamorphic growth at the ponds prior to emigrating. Rather, the size related delay in emigration may be a result of retarded physiological development of smaller animals which appears to change rapidly relative to physical growth (Pough and Kamel 1984).

We observed gross differences between ponds in the timing of frog emigration. Emigration occurred sooner after metamorphosis at Burdue's Pond, the disturbed site, even though the animals there were smaller than at State Pond. Our analysis indicates the importance of differences between ponds over properties of individual frogs within ponds. Rapid emigration at Burdue's Pond is consistent with the increased travel velocity of *Ensatina eschscholtzii* in disturbed versus natural patches (Rosenberg et al. 1998) and with habitat selection studies that have shown preference for forests over un-forested areas by newly metamorphosed *Bufo americanus* (Rothermel and Semlitsch 2002) and *R. sylvatica* (deMaynadier and Hunter 1999). Of the variables we examined, only the response to rainfall strongly contrasted between ponds. The direction of the difference supports the findings of Mazerolle (2001) that precipitation events will be more important to animals faced with emigration through a disturbed surrounding terrestrial matrix. In conjunction with the spatial survival analysis (Chapter 3) for the same

marked animals of our timing of emigration study here, it appears that desiccation during emigration and its negative relationship with body size are important risks under field conditions even at our coastal sites which we are cooler and more humid than sites located inland.

Frogs showed little affinity for their natal ponds following metamorphosis. At Burdue's and State Ponds 50% of frogs emigrated by the 4th and 10th days following metamorphosis, respectively. If newly metamorphosed frogs favored natal ponds as habitat we would expect to see frogs that metamorphosed early in the season remaining longer than frogs metamorphosing later as ponds reduced in size and finally dried. We observed no such hastening of emigration as pond size and depth dwindled and no pulse of emigration following drying dates which we interpret as little or no affinity of these animals to their ephemeral natal pools post-metamorphosis. These results are in agreement with Schroeder's (1976) observation of immediate emigration of green frogs (*R. pipiens*) following metamorphosis. Newly metamorphosed frogs may be dissociating with concentrations of predators at pond margins (e.g. Arnold and Wassersug 1978), or be seeking increased food resources in terrestrial habitats (e.g. Lamoureux et al. 2002). Future experimentation and field studies conducted at larger spatial extent and of frog movement and survival in wetland complexes will be necessary for understanding the

emigration behavior of newly metamorphosed frogs at the level needed for decision making in conservation action.

It is clear from the timing of movements at State Pond that even newly metamorphosed frogs may survive in intact forests away from any open water sources during the dry period of late summer. However, at least some newly metamorphosed *R. aurora* sought surface water in roadside ditches and ponds based on our capture and sighting of marked animals in areas surrounding the trapping arrays. Newly metamorphosed animals may seek deeper and more permanent pools during the dry periods of late summer for the maintenance of water balance and predator escape (Nussbaum et al. 1983), and for favorable growth conditions (Freed 1980). Historically, permanent pools may also have provided refuge from predation (e.g. Nussbaum et al. 1983). However, *R. aurora* in permanent wetlands that were historically free from fish and bullfrogs may be naive to predation risk by these exotic animals (Kiesecker and Blaustein 1997).

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CHAPTER 3

BODY SIZE AND DATE EFFECTS ON SURVIVAL OF NEWLY METAMORPHOSED RED-LEGGED FROGS DURING EMIGRATION

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Abstract

The post-metamorphic period is a little studied yet dynamic period in the life-cycle of anurans many of which are in decline globally. We studied survival during emigration relative to body size and date of metamorphosis for newly metamorphosed Red-legged frogs (*Rana aurora*) at two ephemeral ponds. To affect body size at metamorphosis we manipulated food availability for a sample (244) of the 963 uniquely marked tadpoles. We then used Bayesian capture-recapture modeling with data from forest pitfall traps to quantify survival and movements into the terrestrial matrix relative to body size and date of metamorphosis. The odds of surviving and emigrating increased strongly with increasing body size and decreased with later metamorphosis. Our results showed that conditions during the tadpole stage which affect body size and the timing of metamorphosis may strongly affect the performance of frogs during their initial transition into the terrestrial environment.

Introduction

In the search for mechanisms responsible for global amphibian declines (Alford and Richards 1999, Houlihan et al. 2000), many experimental and observational studies have linked treatments or conditions experienced by tadpoles to their survival, growth and ontogeny within the aquatic setting. Direct mortality is the most apparent link of

aquatic stressors to population declines, however the sub-lethal effects of aquatic stressors such as reduced body size, delayed metamorphosis, developmental deformities and immunosuppression may persist into subsequent life-history stages (Goater 1994, Morey and Reznick 2001, Belden and Blaustein 2002, Blaustein and Kiesecker 2002) clouding our understanding of the stressor's full impact and the impact of terrestrial habitat degradation. One of the most apparent factors affecting success in the terrestrial realm for anurans is body size (Berven and Gill 1983, Smith 1987, Goater 1994, Morey and Reznick 2001).

A suite of globally significant anthropogenic changes have been shown to reduce body size at metamorphosis. Body size at metamorphosis or larval growth rate is lowered by (1) the presence of exotic predators (Kupferberg 1997, Kiesecker and Blaustein 1998, Lawler et al. 1999, Kiesecker et al. 2001b), (2) increased ultraviolet UV-B radiation (Bruggeman et al. 1998, Belden and Blaustein 2002), (3) chemical pollution (Lefcort et al. 1998, Schuytema and Nebeker 1999), (4) acidification (Dunson et al. 1992), (5) competition with invasive species (Kupferberg 1997, Adams 2000, Kiesecker et al. 2001b), (6) parasitic infection (Kiesecker and Skelly 2001), and (7) shortening hydroperiod (Leips et al. 2000, Kiesecker and Skelly 2001). Also, it may be common for multiple stressors to impact systems simultaneously (Kiesecker et al. 2001a, Blaustein and Kiesecker 2002, Collins and Storfer 2003). The

consequences of reduced larval growth rates and body size at metamorphosis to subsequent performance have been under-studied (Morey and Reznick 2001).

There is clear evidence that body size at metamorphosis does impact fitness. Body size at metamorphosis has been linked to age at first reproduction (Semlitsch et al. 1988, Smith 1987), and to body size at reproduction (Berven and Gill 1983), which in turn has been linked to fecundity (Howard 1980, Berven 1981). Growth rates for newly metamorphosed frogs are affected by the conditions faced by tadpoles and growth compensation in subsequent life stages may not occur in some populations (Goater 1994, Morey and Reznick 2001). Quantifying the magnitude of carry-over effects of aquatic conditions is crucial for our understanding the population level impacts of anthropogenic changes to aquatic and terrestrial systems.

In populations where aquatic stressors result in reduced body size at metamorphosis we should expect an important role for the quality of surrounding terrestrial habitat to either buffer or intensify these impacts as frogs disperse (Mazerolle 2001). Connectivity and spatial population dynamics are important factors in amphibian ecology (Alford and Richards 1999, Marsh and Trenham 2001, Pechmann et al. 1991) and the post-metamorphic and juvenile stages may be primary for dispersal (Martof 1953, Dole 1971, Gill 1978, Breden 1987, Berven and Grudzien 1990). In

addition to natal dispersal, the complex life-cycle and diverse habitat requirements of frogs also encourages seasonal migration (Bulger et al. 2003, Nussbaum et al. 1983). Because of risk of desiccation, however, amphibians may be less suited for terrestrial movements than other vertebrates (Sinsch 1990, Rothermel and Semlitsch 2002). This is particularly the case for newly metamorphosed amphibians as they are more susceptible to desiccation than larger conspecifics due to their greater surface area to volume ratio (Shelford 1913, Thorson 1955, Ray 1958, Spight 1968, Spotila 1972), and they may be forced to emigrate from natal ponds during drought (Chapter 2).

There have been few quantitative field studies of amphibian ecology during the metamorphic and juvenile periods (Nussbaum et al. 1983, Beebee 1996, Alford and Richards 1999, Morey and Reznick 2001), disproportionate to their potential importance in population and metapopulation dynamics (Biek et al. 2002). This is especially true considering the variation in body size at metamorphosis, the demonstrated impacts of aquatic stressors on size and timing of ontogeny, and the fitness consequences of body size. For many species we lack even basic knowledge of movements and habitat preference in the period following metamorphosis (Beebee 1996). This is critical especially for species breeding in areas of human encroachment. Juvenile Red-legged frogs (*Rana aurora*) are not frequently observed at breeding ponds (Nussbaum

et al. 1983), yet it is noteworthy that terrestrial land use change is commonly implicated in amphibian declines (Pechmann and Wilbur 1994, Alford and Richards 1999, Blaustein and Kiesecker 2002, Collins and Storfer 2003).

The paucity of field studies of amphibian ecology during early terrestrial stages is largely due to the difficulties of working with small frogs *in situ*; study methodologies to isolate confounding factors affecting survival are in desperate need of advancement (Wood et al. 1998). We used a novel arrangement of forest drift fences and capture-recapture statistical methods to study survival across space (e.g. Hestbeck et al. 1991, Schwarz et al. 1993). The study described here quantifies survival and emigration of newly metamorphosed frogs over a range of body sizes and dates of metamorphosis at two ephemeral ponds that vary in their percentage and intensity of disturbed ground and vegetative cover. We provide estimates of the probability that animals survive metamorphosis and emigrate across two distance intervals from these ponds relative to their body size, developmental stage, and timing of metamorphosis. We discuss the magnitude of these effects in the context of the complex causes of amphibian declines (Alford and Richards 1999, Blaustein and Kiesecker 2002, Collins and Storfer 2003).

Methods

Study Areas

We studied frog survival and emigration at two ephemeral, off-channel ponds in Lincoln County along the Oregon coast, USA from the first completion of metamorphosis 6 June, 2002 until the fall rains raised the water table sufficiently to flood pitfall traps 8 November, 2002. The study ponds were described in detail in Chapter 2. The site referred to hereafter as Burdue's Pond, with maximum surface area approximately 0.36ha, was surrounded by disturbed forest characterized by large areas of bare ground, sparse under-story, and patchy mixed canopy cover (*Alnus*, *Pinus*, *Pseudotsuga*). The trapping area was bisected by U.S. Highway 101 with associated disturbed roadside vegetation. Burdue's Pond dried completely on 23 July, 2002 and remained so until 8 November, 2002. The deepest area of the pond was un-shaded and emergent vegetation is sparse.

The site referred to as State Pond, approximately 0.15ha, was lushly vegetated relative to Burdue's Pond with nearly continuous mixed forest canopy, abundant under-story, and little disturbed ground. State Pond dried completely on 17 July, 2002 and remained dry until the end of the trapping period. The deepest area of the pond was shaded and wetland plants (*Sanguisorba officinalis*, *Carex* spp.) extend into forested areas.

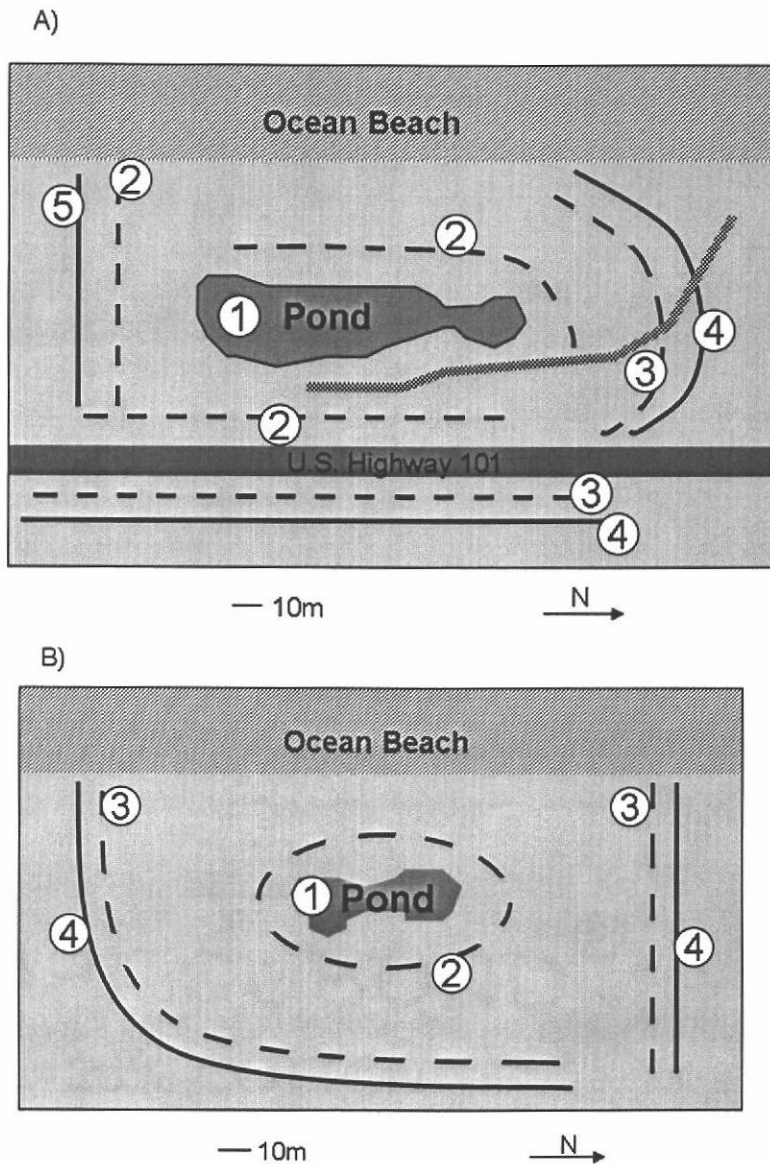


Figure 3.1. Drift fence layout and strata at A) Burdue's Pond, and B) State Pond. Locations of 7.7m discontinuous drift fences (dashed black lines) and continuous drift fences (solid black lines) are depicted. A cliff (checkered line) at Burdue's Pond substantially influenced movements by frogs. Numbers associated with fence lines indicate their stratum number as used in the analysis to quantify probabilities of movement between the strata.

We used concentric rings of discontinuous drift fencing to quantify the probability that frogs reached two distances from their natal ponds as they dispersed into the terrestrial habitat matrix. The discontinuous fences accommodated frogs' return movement to ponds from temporary forays into the terrestrial habitat (Lamoureux et al. 2002), allowed movements of predators, as well as enabled our expanding the spatial extent of the trapping areas by distributing trapping effort. Figure 3.1 depicts drift fence placement relative to pond edges and dominant landscape features for Burdue's and State Ponds.

Field Methods

When the surface areas of ponds were at their maximum in March and April 2002 we constructed concentric rings of drift fencing encircling ponds. Fences were constructed of black polyethylene plastic sheeting, which we suspended with wooden stakes and nylon string to a height of 40 to 50cm above ground level (Gibbs 1998). We buried the base of fences to prevent underpass by frogs. Discontinuous drift fences were 7.7m in length and were separated by 7.7m gaps. We placed the innermost fences approximately 12m from pond edges. Middle and outer fences were placed approximately 40m and 45m from pond edges where landscape features permitted and at the nearest possible location otherwise. At Burdue's Pond we used a total of 323m of discontinuous

drift fence partially surrounded by 368m of continuous drift fence. At State Pond, 308m of discontinuous drift fencing was partially surrounded with 310m of continuous drift fencing. We did not complete drift fence rings in areas adjacent to the ocean beach as previous work showed no propensity for frog movement there (N. Chelgren unpublished data).

On the inner (pond) side of drift fences we placed pitfall traps approximately every 1.9m at Burdue's Pond (363 traps) and State Pond (323 traps). Pitfall traps were constructed of two #10 cans taped end to end and buried such that the rim was slightly below duff-level and were fitted with funnel traps to prevent escape by scaling (Corn 1994). To increase capture probabilities we painted funnel tops black (Crawford and Kurta 2000). 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 in case of flooding.

At Burdue's Pond we built 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 the pond's rapid drying, food

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

During June through July 2002 we captured tadpoles using dip-nets for inclusion in food manipulation treatments. We measured tadpole snout to vent length (SVL) and categorized metamorphic development into stages (Gosner 1960) before assigning three animals per enclosure, grouped by developmental stage. We then randomly assigned enclosures to one of two treatments. Both treatments received five pellets of commercial rabbit chow two times weekly until growth stage 37 was reached, at which time the high food treatment enclosures continued to receive the same food allotment. The reduced food treatment then received no supplemental food, similar to Audo et al. (1995). 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.

Upon reaching the final stages of ontogeny, Gosner stages 43 to 46, we terminated feeding trials on a per tub basis and marked animals for release into ponds. All animals which were marked for study were anesthetized in a 0.25g/L solution of MS-222 (3-aminobenzoic acid ethyl ester; Nauwelaerts et al. 2000) buffered with sodium bicarbonate (Fellers et al. 1994). We measured SVL to the nearest 0.01mm using a dial

caliper. We marked animals using three-digit soft alphanumeric VIAAlpha tags (Northwest Marine Technology Inc., Shaw Island, WA; Buckley et al. 1994) injected subcutaneously in the dorsal thigh. We then massaged tags to the ventral side where the skin is transparent and to avoid tag loss through the incision. To evaluate tag loss, we clipped a single front digit to indicate the animal was VIAAlpha marked. We held animals in enclosures for 24h to ensure recovery from the 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. Release groups were distributed temporally across the dates over which metamorphosis occurred naturally in the ponds (Figure 3.2).

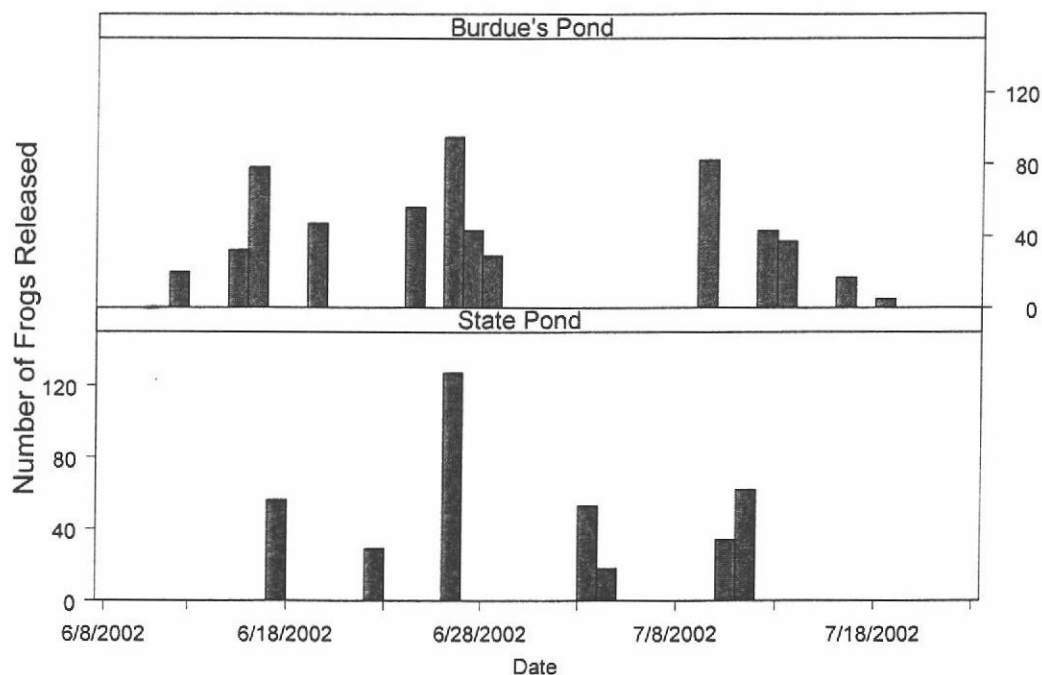


Figure 3.2. Temporal distribution of frog releases by pond.

At Burdue's Pond, coincident with the marking and release sessions for feeding trial animals, we captured and marked samples of free-living animals in the range of Gosner developmental stages 43 to 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. At State Pond, again because of limited pond area and the pond drying rapidly, we raised tadpoles that did not enter the feeding trial enclosures in 1.83m diameter wading pools from intermediate developmental stages (stages 25 to 30). These animals had been captured from drying portions of State Pond. Tadpoles were fed commercial rabbit pellets ad lib and were provided with logs for structural cover. We changed 25% of pool water, and removed feces and uneaten pellet food twice weekly. At State Pond the animals that did not enter the feeding trials experienced similar conditions to those of the supplemental food treatment at State Pond except that they were not confined in 11.4L enclosures.

We consider Gosner stage 45 as metamorphosed for the purposes of this paper since these animals are fully formed frogs capable of terrestrial movement but have a remnant tail bud (Gosner 1960). We opened pitfall trap arrays at the appearance of the first metamorphic individuals. 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 traps at both sites were checked and emptied on alternate days. Frogs that had been marked with VIAAlpha tags 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 evaluating assumptions of our capture-recapture models and to establish prior probabilities for some model parameters. Test pens consisted of an inner ring of four discontinuous 7.7m fences separated by 7.7m gaps similar to the main trapping arrays. Two meters outside of discontinuous fences we placed a circle of continuous drift fence. We set pitfall traps only on the inner sides of drift fences, similarly 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 inner fence rings. These animals were identified and re-released immediately outside the fence from 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 estimated the effect of body size, date of metamorphosis and Gosner stage at marking on the probability of surviving and moving to two distances from the breeding ponds using capture-recapture modeling. We implemented the Cormack-Jolly-Seber (CJS) model (Lebreton et al. 1992) and its multi-strata extension (Hestbeck et al. 1991) with accommodation for individual covariate data (Skalski et al. 1993). These likelihood models were based on the multinomial distribution with cells that represented each pattern of captured versus not captured in the drift fence lines as frogs dispersed outward from the ponds. We made the application Bayesian by specifying prior probabilities for the model parameters and implementing Markov chain Monte Carlo simulation of the posterior distributions of model parameters using the *BUGS* software (Spiegelhalter et al. 1994).

In this spatial capture-recapture application, there were three types of parameters: the probability of surviving and moving as a product (ψ), capture probability (p) conditional on the animal reaching a given drift-fence line, and the product of surviving, moving and being captured for the outer-most fences (χ) before the frogs were lost from the areas of trapping. Capture probabilities and χ 's were estimated here only as nuisance parameters to arrive at estimates of the ψ 's which were then

unbiased by differences in capture effort so long as standard capture-recapture assumptions (see Lindberg and Rexstad 2002, Lebreton et al. 1992) were met. The multinomial cell probabilities were modeled as functions of the ψ , p , and χ parameters (Appendix). We used the log-odds ratio (logit) to link individual covariates and their coefficients (β parameters) to these three types of probabilities.

At State Pond we used a CJS model with four capture occasions referred to here as strata (Figure 3.1) including (1) the initial capture of tadpoles near the completion of metamorphosis in the ponds upon which the analysis was conditional, (2) capture at the innermost ring of discontinuous fences, (3) capture at the middle set of discontinuous fences, and (4) capture at the outer-most drift fence lines. For State Pond we let $\psi_{1-2, \text{State}}$, and $\psi_{2-3, \text{State}}$ be the probabilities of surviving and moving over the intervals 1 to 2 and 2 to 3, respectively. Let $p_{2, \text{State}}$ be the capture probability of fence ring 2 conditional on animals reaching that distance from the pond, and similarly $p_{3, \text{State}}$ the capture probability for the middle set of fencing. Finally, the parameter $\chi_{3-4, \text{State}}$ was the probability an animal survived and moved from the middle ring of fencing to the outer-most fence lines and was captured there.

At Burdue's Pond we were unable to achieve three rings of fencing (Figure 3.1). For this reason in the analysis we used the multi-strata

extension of the CJS model. In this application the change amounted to a minor modification in the capture-recapture model from that of State Pond. Let $\psi_{1-2, \text{Burdue's}}$ be the probability of surviving and moving from Burdue's Pond itself (stratum 1) to the innermost fences (stratum 2). Here let $\psi_{2-3, \text{Burdue's}}$ be the probability of surviving and moving from stratum 2 to the northern and eastern middle rows of fencing (stratum 3). Let $\chi_{2-5, \text{Burdue's}}$ be the probability of surviving and moving from stratum 2 to the southern continuous outer fence (stratum 5) and being captured there. Let $\chi_{3-4, \text{Burdue's}}$ be the probability of surviving and moving from stratum 3 to the northern and eastern continuous outer fence (stratum 4) and being captured there. Finally, we have the probabilities of capture for stratum 2 ($p_{2, \text{Burdue's}}$) and stratum 3 ($p_{3, \text{Burdue's}}$).

The focus of this paper was the relationship between body size and date of metamorphosis with the probabilities $\psi_{1-2, \text{State}}$, $\psi_{1-2, \text{Burdue's}}$, $\psi_{2-3, \text{State}}$, and $\psi_{2-3, \text{Burdue's}}$. Since we studied the frogs' success at reaching two distances from their natal pond, we modeled only the outward expansion of the population with no account for return movement or repeated captures within strata, and there was no movement between ponds. In this way, the time-element was collapsed. See Chapter 2 for an analysis of the timing of movements for these same marked animals. 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 frogs that had died. The implication was that true survival rates were under-estimated by the proportion of marked animals that remained inside the trapping arrays as of the end of the trapping period. This bias could not exceed 1 minus the probability of surviving and emigrating which we present below.

Because animals were still developing and growing at the time of marking we used the residual snout to vent length (rSVL) from an ANOVA relating SVL to Gosner stage as our regressor variable. The continuous variables, date of metamorphosis (Date) and rSVL were standardized to one standard deviation about the mean for better comparison of the magnitude of their effects and for considerations of prior specification. We used a linear trend (-2, -1, 0, and 1) for Gosner stages 43-46 (Stage) such that baseline estimates represented stage 45, fully formed frogs retaining a tail-bud.

Several recent studies have introduced Bayesian methods for capture-recapture survival modeling (e.g. Brooks et al. 2000a,b, Link et al. 2002). In a Bayesian analysis, prior probability distributions are specified for each model parameter. Prior distributions convey a probability statement about the value of the parameter before the data set is analyzed. The Bayesian analysis then combines the information provided by the data with the prior probability distributions resulting in the posterior

probability distributions of model parameters. Prior probability distributions may reflect naivety of the value of the parameter before the information provided by the data is considered, or reflect some probabilistic expert knowledge of the parameter value. The specification of prior probabilities can also be an opportunity for the incorporation of supplemental data, or empirical priors. This approach can be used to greatly strengthen inference in complex problems. It enables the incorporation of data from side-studies, which can be specifically designed to focus on critical aspects of the problem for which the main data may provide little information (Gelman et al. 1998).

We established empirical prior probabilities for capture β parameters using the supplemental test release pens. This was done using the subset of animals known to have reached the outer test release pen fences (172 animals). We then considered whether each animal in the sample had been captured in the inner fence ring as the response variable in a generalized linear model (GLM) with an intercept and regressor variable rSVL. Since the link function in the GLM (logit link) corresponded with that in the main capture-recapture analysis, we used the parameter estimates and standard errors directly in forming normal prior probabilities for the associated capture probability coefficients of our main survival and movement analysis.

We fit a small number of models to the main capture-recapture data set. We considered the estimation of size and date effects the primary goal and differences between ponds as secondary. Consequently, we structured the regression data to enable concise sensitivity analysis to prior specification regarding differences between ponds. In the Basic Model, we fit ψ_{1-2} with an intercept and slopes for rSVL, Date, Stage, and for the feeding trial animals (Trial) with adjustments for Pond (Burdue's = 0.5, State = -0.5) to the intercept, rSVL, and Date terms. We modeled ψ_{2-3} with an intercept for pond and slope for rSVL and included adjustments for both terms by Pond. We modeled capture probabilities with an average intercept and slope on rSVL along with adjustments to the intercept by Pond and Strata (stratum 2 = -0.5, stratum 3 = 0.5). We modeled χ_{3-4} with an intercept and slope for rSVL again with adjustments for Pond. Finally χ_{2-5} had its own intercept and slope for rSVL. The structure of the Basic Model is summarized:

$$\text{Basic Model} = \left\{ \begin{array}{l} \psi_{1-2} \sim 1 + \text{rSVL} + \text{Date} + \text{Stage} + \text{Trial} + \\ \quad + (\text{Pond}) * (1 + \text{rSVL} + \text{Date}) \\ \psi_{2-3} \sim 1 + \text{rSVL} + \text{Pond} * (1 + \text{rSVL}) \\ p \sim 1 + \text{rSVL} + \text{Pond} + \text{Strata} \\ \chi_{3-4} \sim 1 + \text{rSVL} + \text{Pond} * (1 + \text{rSVL}) \\ \chi_{2-5} \sim 1 + \text{rSVL} \end{array} \right\},$$

incorporating a total of 22 parameters. Multinomial cell probabilities for the basic model are provided in appendix Table A.1.

To the basic model we made generalizations to assess the impacts of several issues of concern. We fit a model with random effects of release groups on ψ_{1-2} (Release Model) to address possible lack of independence within the groups of animals that were released together. We fit a model that incorporated capture and handling effects for frogs that were captured in pitfall traps on ψ and χ in the intervals immediately following capture (Handling Model). This was done by including an adjustment term for captured versus not captured to ψ and χ within the multinomial cell probabilities. The changes to the Basic Model are

$$\begin{aligned}\psi_{2-3} &\sim 1 + rSVL + \text{Pond} * (1 + rSVL) + \text{Captured}_{\text{Stratum 2}}, \\ \chi_{3-4} &\sim 1 + rSVL + \text{Pond} * (1 + rSVL) + \text{Captured}_{\text{Stratum 3}}, \text{ and} \\ \chi_{2-5} &\sim 1 + rSVL + \text{Captured}_{\text{Stratum 2}},\end{aligned}$$

where the estimated $\text{Captured}_{\text{Stratum 2}}$ and $\text{Captured}_{\text{Stratum 3}}$ coefficients pertain to the data captured = 0.5 and not captured = -0.5 in the respective strata. Multinomial cell probabilities for the Handling Model are provided in the appendix Table A.2.

Finally, we fit a model which incorporated an additional strata transition to an unobservable state, namely escape from the study areas through one of the gaps in coverage of the middle and outer fences (Escape Model). Since escape through the gaps in fence coverage was an unobservable and terminal state there was no information provided by the capture-recapture data which was relevant to the estimation of the

additional parameter. For this reason, differences between parameter estimates of the Escape Model and the Basic Model were based solely on the information provided in the prior distributions. This model was included to provide an indication of the sensitivity of parameter estimates to a pattern of movement, which we cannot observe. We used the prior distribution $\text{Beta}(1, 5)$ which has mean $1/6$ (Figure 3.3a.) for the probability an animal escaped the study area via gaps in the middle and outer fence lines after having reached stratum 2. Multinomial cell probabilities for the Escape Model are provided in the Appendix Table A.3.

For each model the Markov chain Monte Carlo simulation of posterior probabilities consisted of draws from three independent streams begun from over-dispersed starting values (Gelman 1996). We discarded the first 1000 iterations of each stream as the chain converged to the stationary distribution and established that the streams had converged with the Gelman-Rubin diagnostic (Gelman 1996). We pooled the next 5,000 iterations of each stream, resulting in 15,000 samples from the posterior distributions of each parameter. The measures of precision we report for the Bayesian capture-recapture analysis are 95% credibility intervals, the 2.5th and 97.5th quantiles of the Markov chain samples. Credibility intervals are the quantiles of the posterior probability of a parameter. The 95% credibility intervals for functions of parameters are

the 2.5th and 97.5th quantiles of the solution of that function for each of the 15,000 samples.

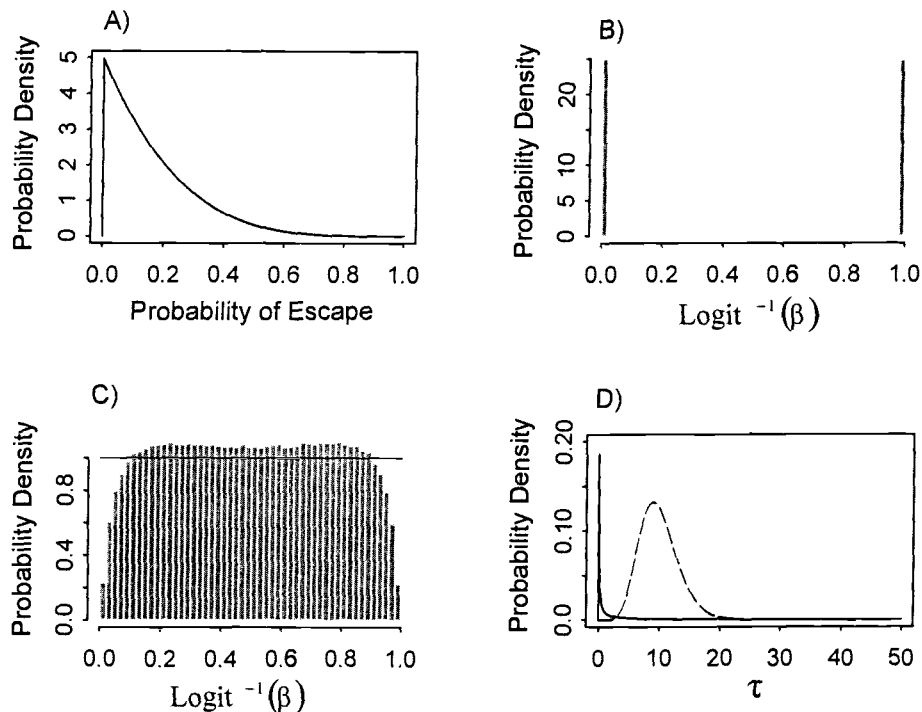


Figure 3.3. Comparison of prior distributions. Prior distributions for A) the probability of escaping between areas sampled with drift fences conditional on reaching 12m from the pond edges ($\text{Pr}(\text{Escape}) \sim \text{Beta}(1, 5)$), B) the regression coefficients (β 's) relating individual frog properties to survival and capture probabilities ($\beta \sim N(\text{mean}=0, \text{var}=1.0\text{E-}6)$) shown after back-transformation, C) the regression coefficients with reduced prior variance ($\beta \sim N(\text{mean}=0, \text{var}=0.45^{-1})$) shown as a histogram. The probability distribution $\text{Uniform}(0,1)$ is provided as a reference (horizontal line). Shown in D) is the prior distribution for the random effect precision, τ , of release groups on the probability of reaching approximately 12m from the pond edges. The main prior distribution used for inference, $\tau \sim \text{Gamma}(0.01, 0.01)$, is shown as a solid line. The alternate prior distribution, $\tau \sim \text{Gamma}(10, 1)$, is shown as a dashed line and imparts lower variance in random effects.

Specification of the prior distributions is an important issue in the context of Bayesian capture-recapture modeling (Dupuis 1995, Brooks et al. 2000a,b, Link et al. 2002). For capture parameters we used the empirical data from the test release pens and GLM analysis described above. Our prior distribution for the intercept was Normal(mean=0.167, var=1.114). Our prior distribution for the slope of rSVL was Normal(mean=-0.00624, var= 0.00211). For ψ and χ parameters we sought prior distributions that would reflect our naivety. There are two approaches to the specification of non-informative priors, which have been used in the capture-recapture setting. Link et al. (2002) used a diffuse normal prior distribution centered at zero with variance $1.0e+6$ for regression intercepts and coefficients, which were in logit space. This distribution has accumulations of mass near 0 and 1 when back-transformed to real space (Figure 3.3b). More commonly for Bayesian capture-recapture models without covariate modeling, flat prior distributions have been placed on the survival and capture probabilities themselves by using a uniform distribution on the interval (0, 1) (e.g. Brooks et al. 2000a,b). We used the latter approach for our primary inference because the approach of Link et al. (2002) resulted in failure of the Markov chain to reach convergence. Since our coefficients (β 's) were in logit space however, this required the transformation

$$\log\left(\frac{\beta}{1-\beta}\right) \sim \text{Uniform}(0,1),$$

which in the *BUGS* software resulted in a prohibitive reduction in the speed of the simulations. To overcome this problem, we used $\beta \sim \text{Normal}(\text{mean} = 0, \text{var} = 2.22)$, which approximates the $\text{Uniform}(0,1)$ distribution once the β 's are back-transformed into real space (Figure 3.3c).

Our approach to incorporating model selection uncertainty in inference follows Gelman et al. (1998). We fit an inference model (Global Model) incorporating all effects simultaneously, with the exception of those of the Escape Model, and tightened prior probabilities for those parameters we considered as secondary to the main questions. Namely, we used normal prior distributions with mean 0.0 and variance 1.0 for all of the regression parameters except the intercepts which we left at $\text{Normal}(\text{mean}=0, \text{var}=2.22)$. We also changed the prior distribution for the precision of the random effects from $\text{Gamma}(0.01,0.01)$ which imparts low precision (high variance) to $\text{Gamma}(10,1)$ which imparts higher precision (lower variance) in the random effects (Figure 3.3d).

We examined the sensitivity of our estimates and precision by varying the specification of prior distributions. For the Global Model, we modified the prior distribution of the effect of rSVL on p from the empirical priors to $\text{Normal}(\text{mean} = 0, \text{var} = 2.22)$. Second, we used the approach to

non-informative prior specification of Link et al. (2002), namely

$\beta \sim N(\text{mean} = 0, \text{var} = 1.0e + 6)$ for all regression intercepts and coefficients.

Third, we modeled regression intercepts with $\beta \sim N(\text{mean} = 0, \text{var} = 2.22)$,

and all other regression parameters with $\beta \sim N(\text{mean} = 0, \text{var} = 1.0e + 6)$.

Results

We released 584 and 379 frogs with unique marks during the final stages of metamorphosis at Burdue's and State Ponds, respectively. Of these animals, 244 were from the feeding trials (130 ad lib and 114 low food). Releases were made in 24 and 14 groups at Burdue's and State Ponds, respectively, distributed across the range of metamorphosis dates at each pond (Figure 3.2). We subsequently recaptured 24 and 53 percent of these animals in forest pitfall traps at Burdue's and State Ponds, respectively.

Mean body size (\pm SE) at metamorphosis was 11% higher at State Pond ($21.7 \pm 1.52\text{mm}$) than at Burdue's Pond ($19.2 \pm 1.80\text{mm}$), and lower for the low food treatment ($19.7 \pm 2.55\text{mm}$) compared to the ad lib food treatment ($21.1 \pm 1.98\text{mm}$). These results are reported in detail in Chapter 2. Housing tadpoles in the feeding enclosures had a positive effect on size at metamorphosis at Burdue's Pond and a negative effect on size at State Pond. Body size at metamorphosis decreased by $0.075 \pm$

0.0051mm and 0.128 ± 0.0098 mm per day across the range of dates observed at Burdue's and State Ponds, respectively. Our calculation of standardized rSVL was based on SVL residuals with standard deviation 2.45 and mean SVL of 20.2, 20.3, 20.45 and 21.8 for Gosner stages 43 to 46, respectively.

Our estimates of capture probability (95% credibility intervals) of the inner fence rings for frogs of average size were $p_{2,\text{Burdue's}} = 0.24$ (0.20, 0.31), and $p_{2,\text{State}} = 0.08$ (0.07, 0.11). Considering that these fences covered 50% of the circumference of each pond, our conditional probability of capturing a frog given it encountered a 7.7m fence segment was 0.49 (0.40, 0.61) and 0.17 (0.13, 0.22) for Burdue's and State Ponds, respectively. Capture probabilities of the middle fences (p_3) were 0.47 (0.41, 0.55) and 0.20 (0.16, 0.25) for Burdue's and State Ponds, respectively. The odds of capturing a frog given it reached a discontinuous fence line decreased by a factor of 0.99 (0.95, 1.02) per millimeter increase in body size.

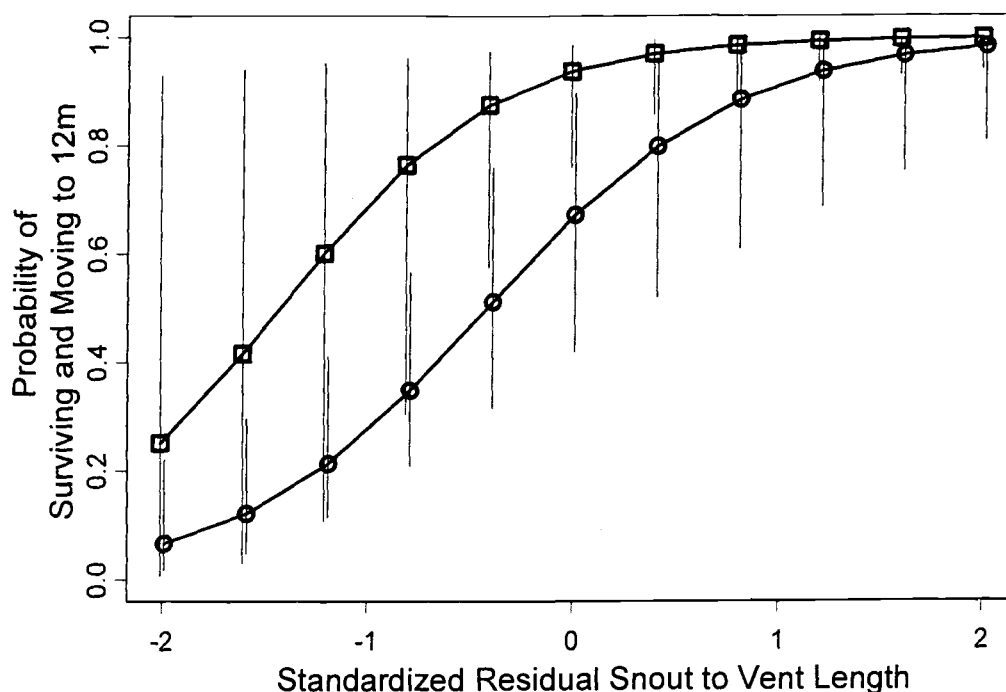


Figure 3.4. Effects of rSVL on the probability of surviving and moving from the pond to approximately 12m (ψ_{1-2}) at Burdue's Pond (circles) and State Pond (squares) with 95% credibility intervals.

Successful emigration to 12m (ψ_{1-2}) was related positively to body size at metamorphosis (Figure 3.4). The data provided overwhelming support (Probability = 1.00) that larger animals were more likely to survive and emigrate to 12m than smaller animals. For each millimeter increase in snout to vent length the odds of surviving and emigrating to 12m increased with factors of 1.98 (1.37, 3.18) and 2.15 (1.13, 4.39) for Burdue's Pond and State Pond, respectively. There was no support (Probability = 0.42) that body size positively influenced the probability of surviving and emigrating to 12m more strongly at Burdue's Pond, the

disturbed site, than at State Pond, the natural site; in fact, the direction of the difference was the reverse. There was strong support (Probability = 0.99) for a higher probability of surviving and emigrating to 12m at State Pond relative to Burdue's Pond after accounting for size and date differences. The random effect standard deviation for release groups was 0.31 (0.24, 0.43), which amounts to a 0.73 and 1.36 times change in the odds of reaching 12m for -1 and +1 standard deviation in the release group heterogeneity. This is less than the effect of a millimeter change in SVL.

Later metamorphosing animals also showed a reduced probability of successfully reaching 12m (figure 3.5, Probability = 0.99) after accounting for their being smaller. The odds of surviving and emigrating decreased by factors of 0.90 (0.85, 0.96) and 0.85 (0.73, 1.06) per day an animal was delayed in metamorphosing at Burdue's and State Ponds, respectively. Similarly, the odds of surviving increased by a factor of 1.85 (1.22, 2.91) for each Gosner stage transition from 43 to 46.

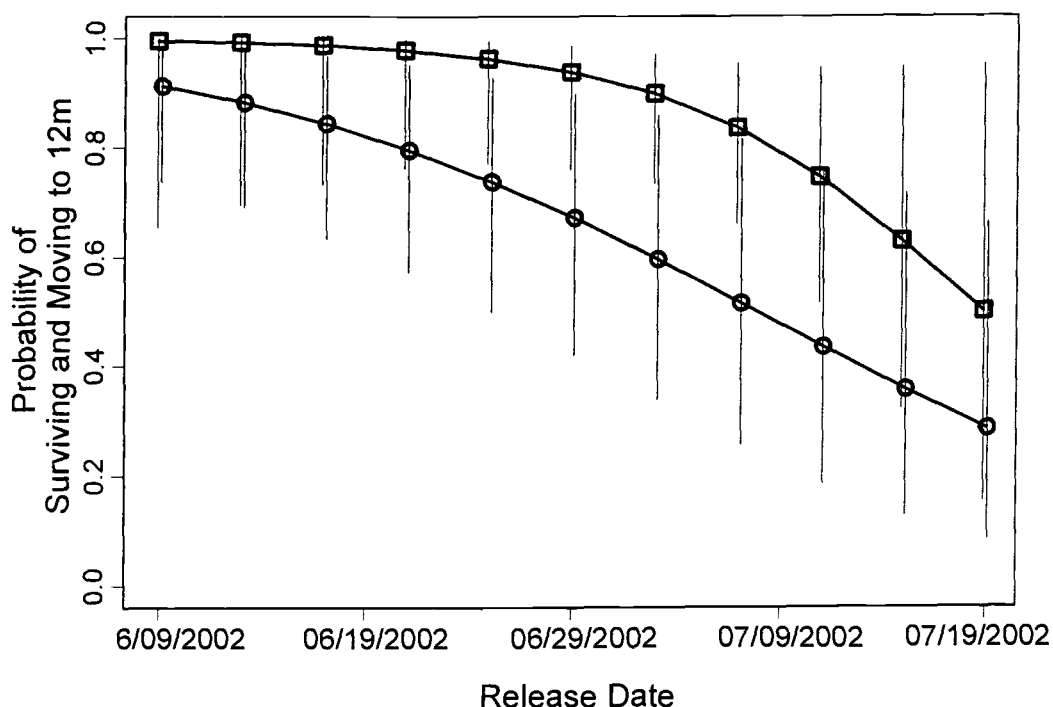


Figure 3.5. Effects of date of metamorphosis on the probability of surviving and moving from the pond to approximately 12m (ψ_{1-2}) at Burdue's Pond (circles) and State Pond (squares) with 95% credibility intervals.

The probability of surviving and moving over the second distance interval from 12m to 40m continued to be positively related to a frog's relative size at metamorphosis (Probability = 0.89, Figure 3.6), but there was very little support for a stronger effect of rSVL at Burdue's Pond, the disturbed site (Probability = 0.59) as a result of low precision. At Burdue's and State Ponds, the odds of surviving and moving from stratum 2 to stratum 3 increased by factors of 1.56 (0.85, 2.79) and 1.45 (0.69, 3.04) per millimeter increase in SVL, respectively. At Burdue's Pond, many more movements occurred to the north and east than to the south which

was reflected in the estimates $\psi_{3-4} = 0.85$ (0.63, 0.97) and $\chi_{2-5} = 0.02$ (0.01, 0.05) for animals of average size and release date. The Handling Model permitted estimation of a cost of capture in the forest pitfall traps in terms of survival following the frogs' re-release. We estimated the probability of surviving capture and handling was 0.96 (0.86, 1.01). All of the estimates we report have factored out the effect of handling.

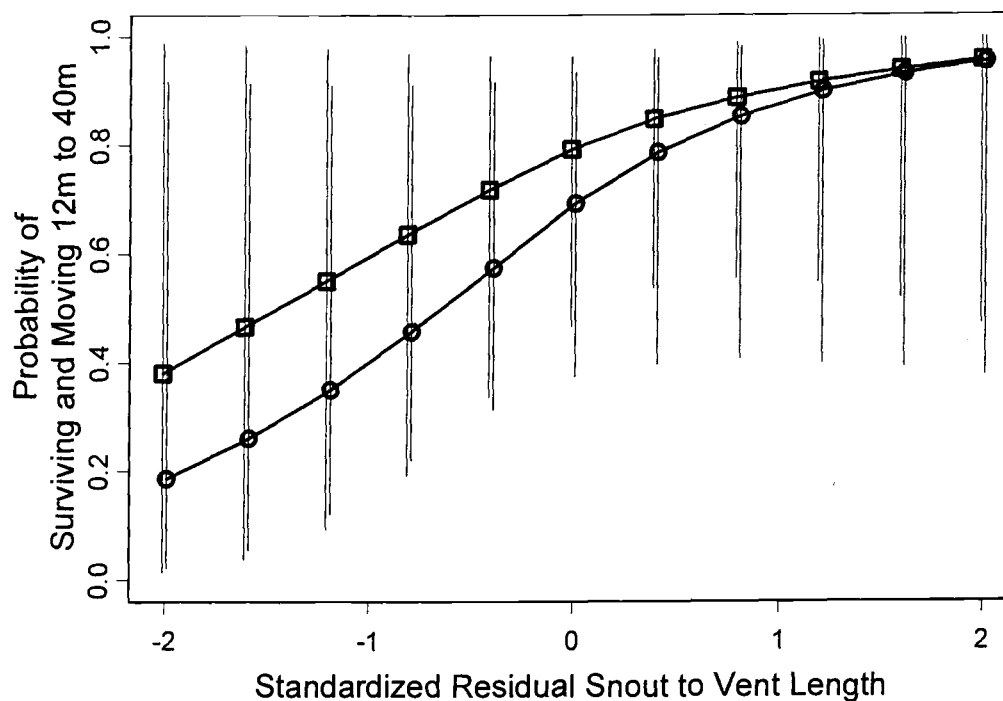


Figure 3.6. Effects of rSVL on the probability of surviving and moving from approximately 12m to 40m (ψ_{2-3}) from pond edges at Burdue's Pond (circles) and State Pond (squares) with 95% credibility intervals.

All of the models we considered resulted in similar parameter estimates (Figure 3.7). The most extreme differences among models

were in the estimates of ψ_{2-3} when comparing models with and without the handling effect, and with and without the escape parameter. Inclusion of the random effect of release group had little influence on the other parameters or their precision.

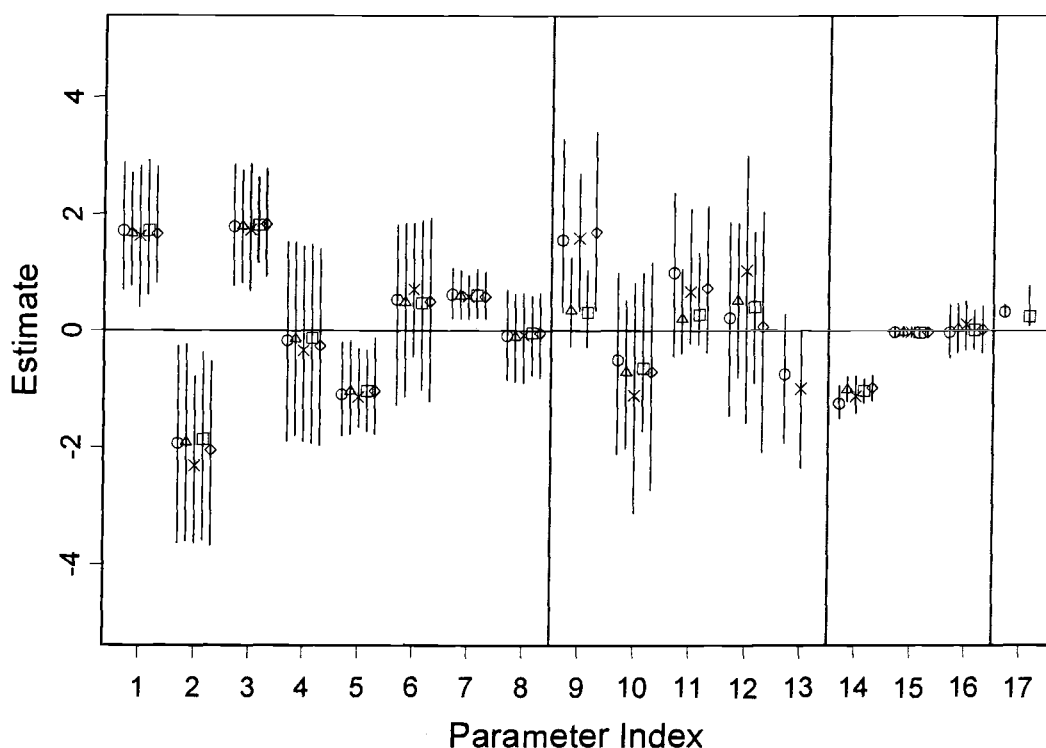


Figure 3.7. Selected parameter estimates and 95% credibility intervals for the Global (Circle), Basic (Triangle), Handling (x), Release (square), and Escape (diamond) models. Estimates are in logit space and relate to the standardized regression data. The index to parameter numbers is as follows: Parameters 1-8 pertain to ψ_{1-2} , survival and movement from the pond to 12m (1, intercept; 2, Pond; 3, rSVL; 4, Pond*rSVL; 5, Date; 6, Pond*Date; 7, Stage; 8, Trial), parameters 9-13 pertain to ψ_{2-3} , the probability of surviving and moving from 12m to 40m (9, intercept; 10, Pond; 11, rSVL; 12, Pond*rSVL; 13, Handling), parameters 14-16 pertain to capture probability (14, intercept; 15, rSVL; 16, Pond), and parameter 17 is the random effect standard deviation for release groups on ψ_{1-2} .

In comparison with the variation in parameter estimates among models, prior specification had a larger effect on parameter estimates and their precision. We did not achieve convergence within 5,000 iterations when $\beta \sim N(\text{mean} = 0, \text{var} = 1.0e + 6)$ was used for all regression parameters. When we used $\beta \sim N(\text{mean} = 0, \text{var} = 2.22)$ for prior distributions on intercepts and $\beta \sim N(\text{mean} = 0, \text{var} = 1.0e + 6)$ for all other regression parameters the Markov chain converged readily. The effect of loosening the prior variance from 2.22 to $1.0e+6$ had a predictable effect on parameter estimates and their precision. With the high variance prior, posterior means shifted away from 0 and their precisions decreased. This demonstrates that our estimates of the effect of rSVL and the differences between ponds were reduced by our choice of prior distribution in the model we used for inference. It also shows that the precisions of our estimates were greater due to our considering ponds as similar *a priori*. Estimates of the effects of rSVL on ψ_{1-2} and ψ_{2-3} were 23% and 79% greater, respectively, with the alternative prior specification. Estimates of the Pond*rSVL interactions on ψ_{1-2} and ψ_{2-3} were 74% smaller and 161% smaller, respectively, with the alternative prior specification (Figure 3.8).

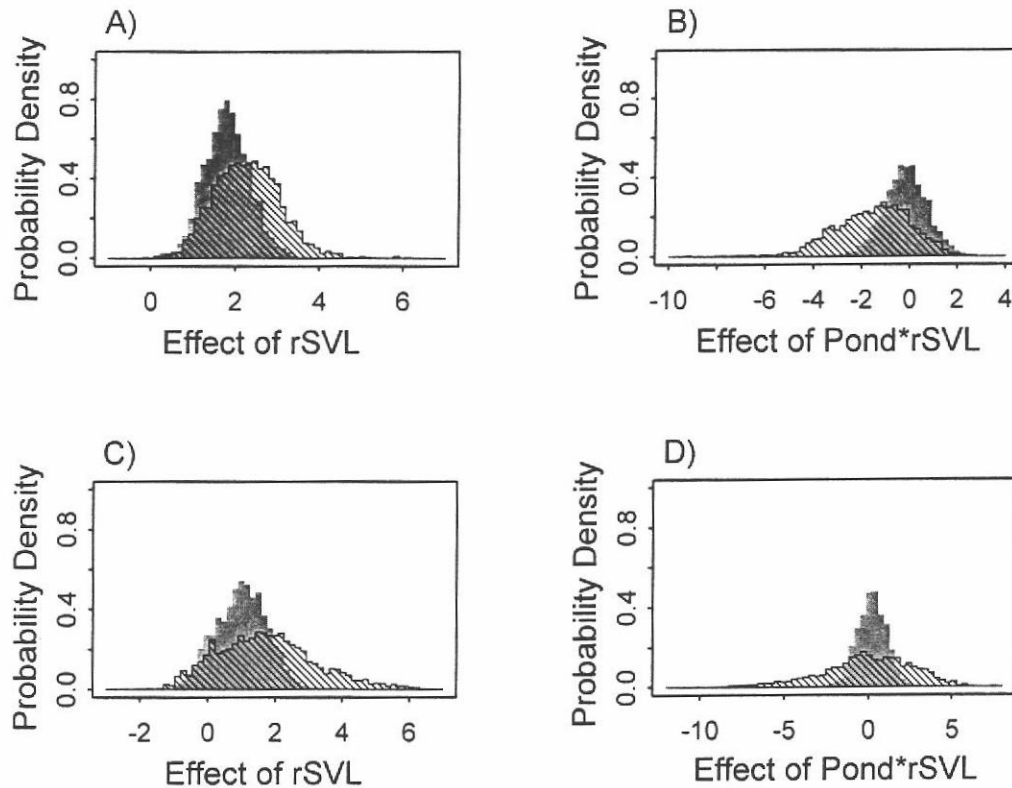


Figure 3.8. Sensitivity of selected estimates and their precision to the specification of prior distributions. Separate plots represent the parameter estimates in logit space which relate to the standardized regression data for the effect of A) rSVL on the probability of reaching 12m from the pond ($\psi_{1,2}$), B) the effect of Pond*rSVL on $\psi_{1,2}$, C) the effect of rSVL on the probability of surviving and moving from 12m to 40m from the pond edge ($\psi_{2,3}$), and D) the effect of Pond*rSVL on $\psi_{2,3}$. The Global Model with the prior distributions on which reported inference is based is shown in gray. The barred histogram represents the Global Model with alternate prior distributions: intercepts, $\beta \sim N(\text{mean} = 0, \text{var} = 2.22)$; and all other regression parameters $\beta \sim N(\text{mean} = 0, \text{var} = 1.0e + 6)$.

Discussion

These results we present demonstrate the profound importance of body size and timing of metamorphosis to the initial transition from ephemeral breeding ponds into the surrounding terrestrial matrix. As an

example of the scale of these carry-over effects we present an example. Kiesecker and Blaustein (1998) showed that the presence of adult bullfrogs (*R. catesbeiana*) caused a reduction in mass at metamorphosis from approximately 1.72g to 1.38g, and delayed metamorphosis by 11 days for Red-legged frogs in field enclosures. Based on a linear regression of SVL against the logarithm of mass using our data, this reduction in mass would equate to a reduction in SVL of approximately 1.24mm. The combined effects of reduced size and delayed metamorphosis would have decreased the odds of successful emigration to 12m at our sites by factors of 0.14 (0.05, 0.29) and 0.06 (0.01, 0.95) for Burdue's and State Ponds, respectively and reduced the odds of reaching 40m by another factor of 0.47 (0.18, 1.32) and 0.54 (0.15, 1.88), respectively. This suggests the carry-over effects of aquatic stressors in the terrestrial stage could have an extreme impact on population dynamics.

Reduction in the dispersal ability of newly metamorphosed frogs associated with reduced body size at metamorphosis may influence the persistence of populations regionally by reducing connectivity between breeding sites. Ephemeral ponds, which are highly variable in the production of young (e.g. Pechmann et al. 1991), may be increasingly important sources for Red-legged frog reproduction due to the takeover of more permanent sites by invasive species (Adams 2000). Metapopulation

theory predicts that connectivity between populations will be more important when populations exhibit a high rate of local extinction (Hanski 1999), which is expected with the stochastic nature of reproduction at ephemeral ponds. However, ephemeral ponds produce smaller animals (Tejedo and Reques 1994, Leips et al. 2000), which are more susceptible to desiccation (Shelford 1913, Thorson 1955, Ray 1958, Spight 1968, Spotila 1972), and they may be forced to emigrate during drought (Chapter 2). The combined effects of a shift away from stable permanent wetlands for breeding, reduction in body size at metamorphosis, and an increased role for connectivity is a dilemma for the persistence of frog populations especially where terrestrial habitat changes have harshened conditions for dispersing frogs. More work should be done to quantify the impacts of aquatic stressors on frog movement behavior and survival following metamorphosis with a focus on the role of desiccation in the context of degraded terrestrial habitats.

We did not see strong support for pond effects on solely terrestrial survival and movement rates relative to body size. In contrast Mazerolle (2001) found that Wood frogs (*R. sylvatica*) captured in fragmented areas were larger than those in pristine areas. Similarly, Bellis (1961) observed smaller Wood frogs associated with humid conditions. However, our sites were selected for their large numbers of newly metamorphosed animals and may be less variable in their temperature and relative humidity

fluctuations than sites not located directly adjacent to the Pacific Ocean. In addition, the spatial extent of our trapping areas may have been insufficient to observe differing roles for body size between sites that may have resulted from differing terrestrial habitat conditions.

We agree with the recommendation of deMaynadier and Hunter (1999) that expansion of the spatial scale typical of terrestrial movement studies is needed for understanding factors relating to survival, growth and habitat use, particularly for metamorphic and juvenile frogs. We sampled the movements of individuals spatially in order to spread limited resources to a larger area of study and to probabilistically account for uncertainties in the observation process. These measures will be necessary in order to expand the spatial extent of terrestrial frog studies to a scale that is meaningful from the standpoint of estimation of *in situ* survival rates. The estimation of survival rates under field conditions is a necessary step in understanding amphibian population declines (Biek et al. 2002) by placing survival and its variation in context with the other demographic rates that together determine population change. Our findings are important in the interpretation of stage based population projection modeling (e.g. Biek et al. 2002) in that these efforts would best incorporate size class specific transitions (e.g. Wood et al. 1998) to accommodate carry-over effects of conditions in earlier life-history stages and the variation between individuals in demographic rates.

An important point for the interpretation of the analyses presented here is that animals which had settled within the study areas were not distinguishable from animals that had died. Our analysis of these same capture-recapture data in the time dimension (Chapter 2) does not reveal any delayed emigration at Burdue's Pond, which would be expected if animals aestivated until rainfall events increased in frequency in the fall. However, at State Pond 17 frogs were first captured in the forest after the pond dried, some of these greater than a month after drying (Chapter 2, Figure 2.2). Therefore, newly metamorphosed Red-legged frogs can survive during the dry period of late summer in the forest away from surface water. We attribute this ability to the largely intact, undisturbed nature of vegetation at State Pond. Chelgren et al. (Chapter 2) also showed that smaller animals waited longer to emigrate than larger animals. The direction of this effect is consistent with the positive relationship between body size and the probability of surviving and emigrating that we found in the current study if aestivation accounts for a portion of the frogs' disappearance. However, the magnitude of the body size effect on timing of movements would not explain the size-based differences in apparent survival we estimated here.

The study of frog terrestrial ecology has lagged behind the aquatic stage because of methodological difficulties in experimentation and observation. Newly metamorphosed frogs, because of their small size,

are difficult to individually mark and difficult to observe in their natural state. Their movements are punctuated and probably dependent between individuals, and their numbers can vary annually by orders of magnitude (e.g. Pechmann et al. 1991, Greenberg 2001). These challenges will continue to make large-scale demographic studies in the terrestrial realm difficult, where frogs are less concentrated than in the aquatic setting. An inferential framework is needed for the synthesis of information and uncertainty from demographic studies that can span only a limited spatial or temporal extent, and for the incorporation of imprecisely calibrated field methods such as capture techniques and visual encounter surveys. To accommodate these issues, we used a Bayesian approach (see Dixon and Ellison 1996, Ellison 1996, Wade 2000). Bayesian results, as probability distributions of model parameters, have an interpretation that is suitable for complex problems in that they lend themselves ideally to meta-analysis and synthesis (Cox and Hinkley 1974) which have seen use in amphibian studies (e.g. Pechmann and Wilbur 1994, Houlahan 2000, Marsh 2001, Biek et al. 2002) and are essential for diagnosing large-scale, complex and variable problems (Dixon and Ellison 1996). The complexity and scale of the global amphibian crisis (Kiesecker et al. 2001a, Blaustein and Kiesecker 2002, Collins and Storfer 2003), as much as any other ecological problem, warrants the consideration of Bayesian thought.

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CHAPTER 4

SYNOPSIS AND CONCLUSIONS

Body size at metamorphosis and the timing of ontogeny are strongly linked to the performance of newly metamorphosed frogs as they transition to become terrestrial animals. Factors which reduce larval growth rates resulting in later metamorphosis and smaller body size may lead to changes in behavior and lowered survival rates in the next life-cycle stage. Studies examining impacts of stressors in either realm, the aquatic or terrestrial, should account for the carry-over effects of previous life-cycle stages because these can be extreme.

A suite of confounded anthropogenic changes to the aquatic and terrestrial habitats of Red-legged frogs are responsible for reductions in their populations. The introduction of invasive predators and competitors, the physical loss of breeding ponds as well as changes to existing ponds and the surrounding terrestrial habitat matrix, increased ultraviolet radiation and chemical pollution play mixed roles as causes of population declines. Determining a single factor responsible for any particular decline is unlikely since multiple factors may be acting on different life-cycle stages, all affecting fitness components that together determine the rate of population change. Quantitative measures of all demographic rates under

field conditions along with experimental approaches will be necessary for the implementation of effective conservation measures.

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APPENDIX

MULTINOMIAL CELL PROBABILITIES FOR SELECTED CAPTURE-RECAPTURE MODELS

The capture-recapture models we used are based on the multinomial distribution with 10 cells, one cell for each possible capture history. The capture histories are records of the strata in which individual frogs were or were not captured. All frogs were released initially in the ponds (stratum 1). Frogs that were captured in the innermost drift fences (stratum 2) are represented with a 2 in the second column of the capture history, otherwise the frog was not captured in stratum 2 and it is represented with a 0. The capture history is completed similarly for the remaining strata 3, 4 and 5. We represent transitions between strata that are not possible with (-). The multinomial cell probabilities are functions of the frogs' probabilities of survival and moving between strata ψ , being captured p , and surviving, moving, and being captured in the outer-most fences χ . The multinomial cell probabilities for the Basic Model are given below in Table A.1.

Table A.1. Multinomial cell probabilities for the Basic Model.

| Cell | Capture history | Multinomial cell probability |
|------|-----------------|--|
| 1 | 1,2,0,0,- | $\psi_{1-2}p_2((1-\psi_{2-3}-\chi_{2-5})+\psi_{2-3}(1-p_3)(1-\chi_{3-4}))$ |
| 2 | 1,0,3,0,- | $\psi_{1-2}(1-p_2)\psi_{2-3}p_3(1-\chi_{3-4})$ |
| 3 | 1,0,0,4,- | $\psi_{1-2}(1-p_2)\psi_{2-3}(1-p_3)\chi_{3-4}$ |
| 4 | 1,2,3,0,- | $\psi_{1-2}p_2\psi_{2-3}p_3(1-\chi_{3-4})$ |
| 5 | 1,2,0,4,- | $\psi_{1-2}p_2\psi_{2-3}(1-p_3)\chi_{3-4}$ |
| 6 | 1,0,3,4,- | $\psi_{1-2}(1-p_2)\psi_{2-3}p_3\chi_{3-4}$ |
| 7 | 1,2,3,4,- | $\psi_{1-2}p_2\psi_{2-3}p_3\chi_{3-4}$ |
| 8 | 1,0,-,-,5 | $\psi_{1-2}(1-p_2)\chi_{2-5}$ |
| 9 | 1,2,-,-,5 | $\psi_{1-2}p_2\chi_{2-5}$ |
| 10 | 1,0,0,0,0 | $1 - \sum(\text{cells 1 to 9})$ |

The Handling Model is similar to the Basic Model except that animals that were captured in a stratum are given a different survival ψ^* or product χ^* term in the following survival and movement interval than animals that were not captured in that stratum. The multinomial cell probabilities for the Handling Model are given in Table A.2.

Table A.2. Multinomial cell probabilities for the Handling Model.

| <u>Cell</u> | <u>Capture history</u> | <u>Multinomial cell probability</u> |
|-------------|------------------------|---|
| 1 | 1,2,0,0,- | $\psi_{1-2} p_2 \left((1 - \psi_{2-3}^* - \chi_{2-5}) + \psi_{2-3}^* (1 - p_3) (1 - \chi_{3-4}) \right)$ |
| 2 | 1,0,3,0,- | $\psi_{1-2} (1 - p_2) \psi_{2-3} p_3 (1 - \chi_{3-4}^*)$ |
| 3 | 1,0,0,4,- | $\psi_{1-2} (1 - p_2) \psi_{2-3} (1 - p_3) \chi_{3-4}$ |
| 4 | 1,2,3,0,- | $\psi_{1-2} p_2 \psi_{2-3}^* p_3 (1 - \chi_{3-4}^*)$ |
| 5 | 1,2,0,4,- | $\psi_{1-2} p_2 \psi_{2-3}^* (1 - p_3) \chi_{3-4}$ |
| 6 | 1,0,3,4,- | $\psi_{1-2} (1 - p_2) \psi_{2-3} p_3 \chi_{3-4}^*$ |
| 7 | 1,2,3,4,- | $\psi_{1-2} p_2 \psi_{2-3}^* p_3 \chi_{3-4}^*$ |
| 8 | 1,0,-,-,5 | $\psi_{1-2} (1 - p_2) \chi_{2-5}$ |
| 9 | 1,2,-,-,5 | $\psi_{1-2} p_2 \chi_{2-5}^*$ |
| 10 | 1,0,0,0,0 | $1 - \sum (\text{cells 1 to 9})$ |

The Escape Model is similar to the Basic Model except that there is an unobservable transition (γ), which enters the multinomial cell probabilities. Since it is unobservable and also a terminal state it can only be separated from mortality by the specification of its prior distribution. The multinomial cell probabilities for the Escape Model are given in Table A.3.

Table A.3. Multinomial cell probabilities for the Escape Model.

| <u>Cell</u> | <u>Capture history</u> | <u>Multinomial cell probability</u> |
|-------------|------------------------|---|
| 1 | 1,2,0,0,- | $\psi_{1-2} p_2 [(1-\gamma)\{(1-\psi_{2-3}-\chi_{2-5})+\psi_{2-3}(1-p_3)(1-\chi_{3-4})\}+\gamma]$ |
| 2 | 1,0,3,0,- | $\psi_{1-2}(1-p_2)(1-\gamma)\psi_{2-3}p_3(1-\chi_{3-4})$ |
| 3 | 1,0,0,4,- | $\psi_{1-2}(1-p_2)(1-\gamma)\psi_{2-3}(1-p_3)\chi_{3-4}$ |
| 4 | 1,2,3,0,- | $\psi_{1-2}p_2(1-\gamma)\psi_{2-3}p_3(1-\chi_{3-4})$ |
| 5 | 1,2,0,4,- | $\psi_{1-2}p_2(1-\gamma)\psi_{2-3}(1-p_3)\chi_{3-4}$ |
| 6 | 1,0,3,4,- | $\psi_{1-2}(1-p_2)(1-\gamma)\psi_{2-3}p_3\chi_{3-4}$ |
| 7 | 1,2,3,4,- | $\psi_{1-2}p_2(1-\gamma)\psi_{2-3}p_3\chi_{3-4}$ |
| 8 | 1,0,-,-,5 | $\psi_{1-2}(1-p_2)(1-\gamma)\chi_{2-5}$ |
| 9 | 1,2,-,-,5 | $\psi_{1-2}p_2(1-\gamma)\chi_{2-5}$ |
| 10 | 1,0,0,0,0 | $1 - \sum (\text{cells 1 to 9})$ |