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Oregon spotted frog (*Rana pretiosa*) movement and demography at Dilman Meadow: Implications for future monitoring

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Abstract

From 2001 to 2005, we studied the demography and seasonal movement of Oregon spotted frogs (*Rana pretiosa*) translocated into created ponds in Dilman Meadow in central Oregon. Our objectives were to inform future monitoring and management at the site, and to elucidate poorly known aspects of the species' population ecology. Movement rates revealed complementary use of sites seasonally, with one small spring being preferred during winter that was rarely used during the rest of the year. Growth rates were significantly higher in ponds that were not used for breeding, and larger size resulted in significantly higher survival. When variation in survival by size was accounted for there was little variation among ponds in survival. Seasonal estimates of survival were lowest for males during the breeding/post-breeding redistribution period, suggesting a high cost of breeding for males. Overwintering survival for both genders was relatively high. Our study supports others in suggesting Oregon spotted frogs are specific in their overwintering habitat requirements, and that predator-free springs may be of particular value. We suggest that any future monitoring include measures of the rate of pond succession. Demographic monitoring should include metrics of both frog reproduction and survival: counts of egg masses at all ponds during spring, and capture-recapture study of survival in mid and late summer when capture rates are highest. Additional study of early life stages would be particularly useful to broaden our understanding of the species' ecology. Specifically, adding intensive capture and marking effort after larval transformation in fall would enable a full understanding of the annual life cycle. Complete study of the annual life cycle is needed to isolate the life stages and mechanisms through which Oregon spotted frogs are affected by stressors such as nonnative predators. Dilman Meadow, which lacks many hypothesized stressors, is an important reference for isolating the life stages most responsive to management elsewhere in the species' range.

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Introduction

The Oregon spotted frog (*Rana pretiosa*) is a highly aquatic frog that has been extirpated from a large portion of its historic range in the Pacific Northwest, and remaining populations are reduced and isolated (Hayes 1997, Pearl and Hayes 2005). Loss and alteration of marsh habitat, predation and competition from exotic fish and bullfrogs, and degraded water quality from agriculture and livestock grazing are implicated in their decline (Hayes 1997, Pearl and Hayes 2005). In 2001, an interagency team translocated a population of frogs from a site that was to be eliminated by the renovation of the dam impounding Wickiup Reservoir, to newly created ponds at Dilman Meadow (121º 39' 52" W, 43º 41' 58" N), 2.5 km from the original site in central Oregon, USA. We monitored Oregon spotted frog demography and movements at Dilman Meadow for > 4 yr to assess the efficacy of these mitigation efforts, determine metrics for long-term monitoring, and inform future management at the site. More broadly, many aspects of Oregon spotted frog life history are poorly known, so understanding demography and movement patterns is likely to be useful in its conservation. Although wildlife translocations have been attempted extensively as conservation means, few such projects have been sufficiently monitored for demographic rates to understand the causes for the translocation's success or failure (Dodd and Seigel 1991). Our objective here is to document demographic and movement patterns in the population of Oregon spotted frog at Dilman Meadow so that this information will be available to guide management decisions.

To better evaluate amphibian population responses to management actions it is important to consider the contribution of each life history stage and both genders to the balance of reproduction and mortality. Population growth or contraction occurs as a complicated function of the probability of breeding, fecundity, and survival during multiple life history stages and size classes and the transition between these classes. Body size in amphibians is strongly positively linked with the probability of breeding (Semlitsch et al. 1988, Smith 1987), fecundity (Howard 1980, Berven 1981, Berven and Gill 1983), and survival (Altwegg and Reyer 2003, Chelgren et al. 2006). Thus, growth of individuals is an important component of population change. Estimates of demographic rates for one gender are often used to infer population growth rates or population viability (Caswell 2001). However, in anurans such as Ranid frogs, gender is thought to affect survival rate (Wood et al. 1998, Lyapkov et al. 2004), probability of dispersal (Austin et al. 2003, Palo et al. 2004), age at sexual maturation (Lyapkov et al. 2004), and breeding probability (Muths et al. 2006). Moreover, males and females differ in energetic costs associated with breeding (Feder and Burggren 1992) and in growth rate (Lyapkov et al. 2004). Differences in demographic rates between genders will generally affect population growth rate for small populations (Engen et al. 2003, Sæther et al. 2004, Husby et al. 2006), so it is important to distinguish these differences during monitoring. For example, it has been hypothesized that differences in the frequency at which male and female western toads (*Bufo boreas*) visit breeding sites have led to differential mortality from Chytridiomycosis, resulting in highly skewed sex ratios and diminished reproductive output (Muths et al. 2003). We examined sex- and size-specific demography at Dilman Meadow with particular focus on *a priori* hypotheses regarding survival, movement, and growth.

It is generally no longer defensible to use captures or sightings of individuals to estimate demographic rates when numbers are uncorrected for differences in the probability of capture. Instead, capture, survival, and movement probabilities are modeled simultaneously to reduce bias in estimates of demographic rates (Williams et

al. 2001). The missing-data factorization of the multi-state model (Dupuis 1995) and Bayesian estimation allowed us to incorporate important features of Oregon spotted frog ecology, central to our hypotheses, into our statistical modeling.

Specific hypotheses

We examined several *a priori* hypotheses regarding variation in survival at Dilman Meadow. Potential losses to emigration, frogs' unfamiliarity with the new site, and handling effects led us to hypothesize that survival would be initially lower for individuals translocated to Dilman Meadow than for individuals produced in the meadow in subsequent years, hereafter 'native'. We also hypothesized that density effects associated with a growing frog population in the meadow should lead to decreased survival with increasing time since ponds were established. As has been seen in other amphibians, we hypothesized that survival should be higher for larger frogs, and should be higher for females than males. In addition to hypotheses about survival, we examined two hypotheses regarding movement and growth to illuminate the value of specific ponds for growth versus reproduction. We hypothesized that 1) after breeding and prior to the dry summer when most growth is expected to occur, frogs disproportionally moved away from breeding sites to non-breeding sites, and 2) that the sites not used for breeding had higher growth rates than sites which were used for breeding. Other objectives were to compare the magnitude of the hypothesized effects with the magnitude of variation among ponds and seasons, and to estimate movement probabilities among ponds to determine how specific ponds were used seasonally.

Methods

Study Area Description

Dilman Meadow is an emergent wetland located at approximately 1300 m elevation in the Deschutes National Forest, Oregon. In the 2 years prior to pond construction, open water in the meadow was limited to a narrow channel that conveyed steady ground-water flow.   Our observation wells indicated that most of the meadow was saturated to near the surface throughout the year. The meadow is largely isolated from other surface water during summer, with the exception of the small outflow stream that drains to the Deschutes River located 0.5 km distant. The nearest permanent lentic water is Wickiup Reservoir, 2.5 km distant. Dilman Meadow did not support breeding frogs at the beginning of the translocation effort in 2001. From 2001 to 2005, 5 adult western toads and many long-toed salamanders (*Ambystoma macrodactylum*) were observed at the meadow. The nearest known Oregon spotted frogs are a small number that breed sporadically in upper Wickiup Reservoir, circa 5 km distant, and separated from Dilman Meadow by the dam, a road, and arid upland forest. The landscape surrounding Dilman Meadow is ponderosa (*Pinus ponderosa*) and lodgepole pine (*Pinus contorta*) forest, with the exception of a thin willow (*Salix* sp.) – sedge (*Carex* sp.) riparian strip downstream of Dilman Meadow and along the Deschutes River. Dilman Meadow itself is relatively undisturbed: livestock grazing does not occur, and there is no agriculture in the wetland's catchment other than timber harvest. Neither bullfrogs nor fish are present at the meadow. As a result of the absence of these stressors, Oregon spotted frog demography at Dilman Meadow is invaluable as a reference to which other populations may be compared.

Field Methods

In fall and winter of 2000-2001, six ponds were created at Dilman Meadow as mitigation for the loss of Oregon spotted frog habitat associated with the renovation of the Wickiup Reservoir dam. Ponds were constructed by blasting and ranged from circa 100 to 800 square meters in surface area (0.01 - 0.08 ha.) and the deepest water in all ponds was circa 2 m. Pond succession prompted the creation of three additional ponds around the margin of the meadow in 2004 by mechanical excavation using heavy equipment. In spring 2001, we moved 9 Oregon spotted frog egg masses from the ditch below Wickiup Reservoir to ponds in Dilman Meadow. During intensive search and trapping efforts in June through September 2001, 48 frogs (9 females, 11 males, and 28 post-metamorphic sub-adults) were captured at the Wickiup ditch and were translocated to Dilman Meadow. All adult frogs captured had unique passive integrated transponder (PIT) tags from an extensive survey of the site the prior year, and presumably represented the entire adult population.

We counted egg masses during complete searches of Dilman Meadow in April-May each year from 2002 to 2005. In addition, we captured frogs by hand and with funnel traps (circa 3-cm gape) during bi-monthly sampling occasions. In winter months, when water temperatures were cold (< 12 ℃), traps were submerged. Otherwise traps were placed at the water's surface to enable captured animals to exchange air. Captured frogs were measured for snout-urostyle length (*sul*) and snout-vent length (*svl*), and sex was determined. Based on limb morphology, we attempted to independently determine the sex of frogs each time the individual was captured. If gender could not be determined, or if our field determination at one capture conflicted with the individual's final gender determination, the gender data were treated as missing. We marked frogs >40 mm *svl* with PIT tags inserted subcutaneously through incisions made on the anterior dorsum. To avoid additional tissue damage, we did not close incisions with medical glue, but rather massaged tags to the posterior dorsal side to prevent tag loss back through the incision. McAllister et al. (2004) reported "negligible or no side effects" of PIT tagging on Oregon spotted frogs in Washington. At each capture, frogs were checked for PIT tags using a Destron Fearing Mini Portable Reader™.

Statistical Methods

Survival and movements

We used a modified version of the Arnason-Schwarz multi-state capture-recapture model (Arnason 1972, 1973; Brownie et al. 1993; Schwarz et al. 1993) to relate characteristics of individual frogs to survival, movement, and capture probabilities. The Arnason-Schwarz model differs from other models in that it allows the estimation of survival and movement rates among multiple sites when capture probabilities are less than 1.0. Because sex is thought to strongly affect survival in Ranid frogs, and because improper treatment of missing gender data can lead to substantial bias in sex-specific survival estimates (Nichols et al. 2004), we modified the Arnason-Schwarz model to account for missing sex data. We augmented the Arnason-Schwarz model to simultaneously model the probability of being female and the mechanism, δ, of the sex data being observed in a manner analogous to sampling situation A of Nichols et al. (2004). Model A of Nichols et al. (2004) may be written in a missing data factorization as a joint model with 2 factors: a model for sex with informative missing (Little and Rubin 2002) data and a model for survival and capture equivalent to the Cormack-Jolly-Seber model (Lebreton et al. 1992). Our new model amounts to simply substituting, for the Cormack-Jolly-Seber component its multi-state generalization, the Arnason-Schwarz model. We modeled logit(δ), as a linear function of *sex*; *large*, an indicator for animals greater than 57 mm snout-vent length; and the interaction *sex*large*. To make this augmentation, we monopolized the tractability of the missing data likelihood (Dupuis 1995) for the Arnason-Schwarz model, which can be concisely coded in program WinBugs 1.4. In summary, the estimation procedure used the pattern of whether or not gender was determined among all captures to adjust survival, movement, and growth rates for the sampling bias that large individuals and males were more likely to have their gender determined than small and female frogs.

To accommodate the large number of potential movement patterns among sites and seasons, we also factored site transition probabilities into probabilities of emigration and immigration conditional on the frog having emigrated (Grosbois and Tavecchia 2003), then simplified the model for immigration. Transition probabilities, ψ, of the Arnason-Schwarz multi-state model were decomposed in the $\pi\mu$ formulation of Grosbois and Tavecchia (2003) into probabilities of emigrating sites and probabilities of immigrating sites conditional on emigration having occurred. Adopting the notation of Grosbois and Tavecchia (2003), let ψ_i^{RT} be the probability that an individual which originates in site R in period i and survives the interval, moves to site T at the end of the interval. Grosbois and Tavecchia (2003) factored ψ_i^{RT} into two processes, defining $\pi_i^R = \sum_{T \neq R} \psi_i^{RT}$, as the probability of emigrating from site R; and μ_i^{RT}, as the probability of immigrating to site T given emigration from R occurred, with the constraint that $\sum_{T \neq R} \mu_i^{RT} = 1$. Although the $\pi\mu$ formulation provides opportunity to separately model leaving and settlement decisions (Grosbois and Tavecchia 2003), with even a moderate number of states (here sites), a large number of movement parameters exist. In our case, with 8 sites and 5 seasons, there were 8*7*5 = 280 movement probabilities to be accounted for. To stabilize parameter estimates, and to summarize frog movements seasonally in

a manner that could be easily interpreted, we considered the immigration probabilities to be non-Markovian, or independent of the site of origin. To accomplish this under the constraint that transition probabilities sum to 1, we define the relative

probability of preference, α_i^T, as the probability site T is preferred as a destination. Here we assume that animals do not emigrate and immediately immigrate back to the same site within the same interval. The probability that site T is preferred as a destination, relates to immigration probability by $\mu_i^{RT} = \alpha_i^T / \left(1 - \alpha_i^R\right)$, where $\sum_{j=1}^{K} \alpha_i^j = 1$ and K is the total number of sites. In this way the μ_i parameters drop from the likelihood, and the number of immigration parameters for an interval reduces from K(K-1) to K. To reduce the parameter space further, and because seasonally we expected that environmental conditions such as desiccating conditions in summer would largely determine the probability that individuals redistribute among sites, we used random effects of *site* nested within 5 discrete *seasons* as fixed effects to model π. The total number of transition parameters was thus reduced from 280 to between 40 and 75 depending on the amount of shrinkage associated with the random effects.

Because body size of amphibians is an important factor affecting survival, sexual maturation, and fecundity, feeding areas favorable for growth are important to population change. In addition to spatial movements among 8 sites, our multi-state model also accounted for size-transition probabilistically between 2 discrete size-classes (Wood et al. 1998). As described above, we used the indicator *large* = 1 for size greater than 57 mm snout-vent length, otherwise large = 0. The cutoff between size classes, 57 mm, was the average minimum snout-vent length for individuals in the study. Because of sexual size dimorphism, we considered size-class transition probabilities to be sex-specific. See below for a more detailed analysis of logistic growth separate from the capture-recapture modeling effort.

We tabulated the capture-recapture data for bi-monthly survival and movement rates at the network of 8 sites which comprise Dilman Meadow. Of the 8 sites, 6 were created in 2001 for mitigation and one (site 3) was a natural spring. Three ponds were newly excavated in 2004 as mitigation. The 3 new ponds, which were excavated in 2004, were grouped as a single site (site 8) for the purpose of this analysis because of the small numbers of captures and identical search schedule at these ponds. Relative preference for site 8 was set to 0.0 in the model during intervals that occurred prior to the ponds' excavation. We used a bi-monthly survival-movement interval as a compromise between the time-scale of frog movements, our search efforts, and the dimension of the problem computationally. We constrained bi-monthly parameter estimates to be equal within 5 discrete *seasons*: spring redistribution (March), breeding/post-breeding redistribution (April-May), summer growth (June-September), fall redistribution (October), and over-winter (November-February). Seasons were chosen based on *a priori* knowledge of spotted frog ecology and to address our hypotheses about seasonal movements.

We used a generalized linear mixed model framework to relate the survival and capture probabilities to explanatory variables. With the logit link function, we used normally distributed random effects to stabilize parameter estimates while still allowing generality (Barry et al. 2003). We modeled survival with the fixed effects: *sex*; *trans*, an indicator for the original translocated individuals in the first year of the study; *large*; and *year*, a continuous pond-specific variable for years since pond construction. We included random effects on survival for *season* nested within *sex*, and for the *site* in use at the start of the survival interval. We accounted for variation in capture probabilities with the fixed effects: *sex*; *year*; and *days*, the number of days the site was searched in the 14 day interval; and included random effects of *site* and *season* for capture probability.

Logistic growth

In a separate analysis from the multi-state capture recapture modeling just described, we used a 2-parameter discrete-time logistic growth model for 251 PIT tagged frogs that had two or more measurements and for which gender was known. We modeled *sul* at time t as the response, conditioning on initial size at marking

$$sul_{t+1} \sim sul_t + \rho * sul_t * \left(1 - \frac{sul_t}{\gamma}\right).$$

We modeled the growth rate parameter, ρ, by s*ex*, *trans*, *site*, and *season*, with a continuous effect of *year*, and modeled asymptotic size, γ, by *sex* and *trans*. *Site* was treated as a normal random effect. We handled missing *site* data for individual i by imputing missing values based on the proportion of observed data at each site. Specifically, we treated the *site* values for each individual at each time as single multinomial trials where the multinomial probabilities, θ, were common to all individuals and time intervals $site_{i,t} \sim \mathrm{Mult}(1; \theta_1, \theta_2, \theta_3, \cdots, \theta_8)$. Bivariate normal random effects of individuals for ρ and γ accounted for repeated measures in the precision of estimates. In addition to the random *site* model, we ran a similar model without the random *site* effect, but where we estimated an offset, *breeding*, for growth rate in the ponds primarily used for breeding (i.e. *breeding* = 1 for ponds 1, 5, 6, and 7; *breeding* = 0 for ponds 2, 3, 4, and 8).

Abundance

We estimated abundance of juvenile, small adult, and large adult frogs at each *site* during September each year prior to the majority of fall movement. We used the Bayesian estimates of capture probability from the capture-recapture analysis of PIT tagged adults at each pond and bi-monthly interval, to adjust the number of captures of frogs in each size class for differences in capture probability. Because juvenile frogs, *svl* < 40 mm, were not individually marked and we could not know the total numbers of individuals captured in the bimonthly intervals, we computed the Bayesian estimators of capture probabilities for *days* = 1, then modeled the numbers of juveniles captured each day, $n_{day,site}$, as binomially distributed, $n_{day,site} \sim \mathrm{Binomial}(N_{year,site}, P_{day,site})$, to estimate year and site-specific population size $N_{year,site}$. To estimate numbers of small (40 - 57 mm) and large (> 57 mm) adults, we took the same approach, but used bi-monthly capture rates and numbers of unique frogs captured in bi-monthly intervals to estimate *site-* and *year-* specific numbers.

Notation

We report 95% credibility intervals for Bayesian parameter estimates. Credibility intervals are interpreted as the values between which we are 95% certain the true parameter lies. Statistical significance is evaluated at the level of $\alpha = 0.05$. We do not report P-values, but report the probability (Pr) a parameter is greater than or less than a specified value [*e.g.* Pr(Y > 0) = 0.93 states that we are 93% certain the value of Y is greater than 0].

RESULTS

Survival

Survival rate had a strong, positive relationship to size, was lower for translocated individuals than frogs native to Dilman Meadow, and differed seasonally by sex (Table 1). Estimates of sex-specific seasonal survival rates reveal different seasonal patterns for the genders that suggest an acute cost of breeding for males. Mortality was highest for males in the breeding/post-breeding redistribution period (April-May), and during summer (June-September), whereas females tended to die later in the year, during June-September and October (Figure 1). The lowest mortality rate occurred over winter, November through February (Figure 1). The probability that the survival odds for females exceeded that for males was $\mathrm{Pr}(\beta_{Female} > 0) = 1.00$ during the breeding/post-breeding redistribution period but was not supportive of gender differences in the other seasons: spring redistribution, Pr = 0.37; summer, Pr = 0.13; fall redistribution, Pr = 0.27; and over-winter, Pr = 0.23. There was strong support (Pr = 0.99) that survival was higher for large frogs than small. Female frogs survived at an annual rate of 0.19 (0.06, 0.37) and 0.69 (0.57, 0.82) for small and large individuals, respectively. Males survived at an annual rate of 0.08 (0.03, 0.16) and 0.57 (0.49, 0.66) for small and large individuals, respectively, these estimates being computed for individuals native to Dilman Meadow at the median *site* and in 2003. There was strong support (Pr = 1.00) that translocated frogs had lower survival during the first year following relocation, the odds of survival being lower by a factor of 0.39 (0.20, 0.78; Figure 2). However, there was no support (Pr = 0.41) for a trend by *year* and there was little variation between *sites* in survival (Figure 1). There was little probabilistic support for *site* differences based on pair-wise

comparisons of the survival odds between sites: the largest measure of support being Pr = 0.87 comparing sites 5 and 6. The pattern of variation in survival rate at Dilman Meadow was dominated by the translocation effect, size, and differences between the sexes seasonally.

Movements

Movements between sites occurred primarily during March prior to breeding, and during October, following the dry summer (Figure 3). Frogs did not redistribute appreciably during the breeding/post-breeding period prior to the summer dry season when growth conditions are most favorable. In addition, the pattern of movements post-breeding did not support preference for non-breeding sites. On the contrary, the ratio of emigration to immigration π/α during the breeding/post-breeding redistribution period was actually lower at the sites most important for breeding: site 1, 0.03; site 5, 1.12; site 6, 2.43; and site 7, 0.73, compared with sites with little or no breeding: site 2, 5.08; site 3, 8.81; site 4, 0.80; and site 8, 13.85. The pattern of movements for site 3, the natural spring, was distinctly different than for the other ponds. Animals used site 3 during the over-winter period, emigrating site 3 during the March redistribution period, and immigrating site 3 during the fall redistribution period (Figures 3, 4). The pattern of movements for site 5, the closest pond to site 3, was consistent with steppingstone movement. The group of 3 ponds excavated in 2004 (Site 8) were not used preferentially within the first year following construction; relative probability of preference for the site was intermediate to preference for other sites (Figure 4).

Capture probability

Capture probability varied considerably and by all sources examined (Table 2). There was strong support (Pr = 1.00) that capture probability was higher for females than males, the odds of capture given presence in the pond were 1.86 (1.55, 2.22) times higher for females than males. There was substantial variation among ponds, capture probability being generally negatively related to pond size. Capture probability was highest at site 3, the natural spring, and lowest at site 6. The odds of capture increased (Pr = 1.00) with increasing *year* at a rate of 1.29 (1.18, 1.41) times per year, a pattern consistent with the negative correlation of capture probability with pond size considering that pond succession led to reduced pond area over the course of the study. The odds of capture also increased with the number of days the site was visited (Pr = 1.00), by 1.77 (1.63, 1.92) times per day.

Missing gender

Gender was significantly less likely to be determined for females than for males, and for smaller than larger individuals (Table 3). Our estimates of survival and movement appropriately account for this sampling bias.

Logistic growth

Growth rate and asymptotic size were variable; *breeding* and *trans* were important factors affecting growth rate, and animals that were translocated from the Wickiup site appeared able to attain larger maximum size than frogs native to Dilman. Males grew at a significantly faster rate, relative to their asymptotic size, than females (Pr = 1.00). Growth rate was significantly higher for translocated frogs than those native to Dilman Meadow (Pr = 1.00), again this was relative to asymptotic size. An increasing trend in growth rate with increasing *year* was also significant (Pr = 1.00), which may be explained by increased productivity of ponds as they acquired natural communities subsequent to construction. Growth rate did not vary importantly among *sites* according to the estimated standard deviation, but seasonal differences were substantial (Table 4). Growth rate was highest in summer and was negligible during the fall redistribution and over-winter periods. The growth model that estimated separate growth rates for breeding sites revealed significantly lower growth rates at breeding sites than at sites where little or no breeding occurred (Pr = 0.99). Asymptotic size was significantly higher for translocated animals (Pr = 1.00), and higher for females than males (Pr = 1.00; Figure 5). The significant *trans* effect for asymptotic size is

consistent with inter-population variation in maximum size among other populations (C. Pearl unpublished data) and suggests the differences may have important environmental causes over strictly genetic ones.

Egg masses, adult abundance and recruitment

Numbers of egg masses laid at Dilman Meadow increased steadily from a minimum of 2 masses in the first year following translocation to 49 masses in 2005 (Table 5). Numbers of large adult frogs also increased steadily from 2001 to 2005, with total numbers in this group reaching 179 (154, 205) individuals by 2005 (Figure 6). Numbers of small adults reached a total of 93 (76, 112) animals by 2005. The ratio of numbers of egg masses to numbers of large adults in the previous fall varied significantly among years and was lowest in 2002, the year following translocation: 2002, 0.06 (0.04, 0.09); 2003, 0.32 (0.25, 0.40); 2004, 0.22 (0.17, 0.29); and 2005, 0.38 (0.30, 0.48). There was no evidence that density dependence acted on numbers of egg masses laid. However, density dependence, or a decreasing temporal trend in embryo or larval survival is apparent. Numbers of egg masses increased five fold from 2001 to 2005 (Table 5), though numbers of juveniles during September did not increase over this same period (Figure 6A).

DISCUSSION

Numbers of adult Oregon spotted frogs at Dilman Meadow reached greater than 5 times their original number in 5 years. Both the numbers of egg masses and the number of egg masses per large adult increased since the translocation was completed, while adult survival stabilized. As a result of intensive seasonal capture efforts annually, a large proportion of the frog population has been marked, enabling unique insight to gender and seasonal variation in survival and growth. The detailed demography we present is invaluable for understanding the potential for population growth of the species because stressors thought responsible for its demise elsewhere were not acting at Dilman Meadow.

Low survival rates of small frogs in the first year of the study emphasize the importance of translocating mature individuals for rapid population growth provided these individuals do not attempt to home. Attempts by translocated individuals to home may explain the lower apparent survival of translocated frogs at Dilman than frogs native to the meadow. Homing has been observed in frogs (*e.g.* Sinsch 1992, Matthews 2003). However, this was not supported by a telemetry study conducted at Dilman Meadow which revealed no inclination to home for radio tagged adults (C. Pearl, J. Bowerman and R. B. Bury, unpublished data). Handling effects, unfamiliarity with the new site or unexplained annual variation may also be responsible for significantly lower survival in the first year of this study. Translocated mountain yellow-legged frogs (*Rana muscosa*) lost more weight than a random sample of individuals that were not translocated (Matthews 2003), but annual variation in frog demography is also commonly observed (*e.g.* Richter and Seigel 2002).

Annual survival rates for adult frogs at Dilman Meadow differed substantially between size classes, but large frogs native to the meadow survived at rates comparable to other species. Large frogs that were native to Dilman Meadow survived at rates (55 – 70%) comparable with other anurans: 72-84%, *R. lessonae* (Peter 2001); 53-70%, *R. esculenta* (Peter 2001); 65-92%, *R. sevosa* (Richter and Seigel 2002); 52-71% *Bufo bufo* (Frétey et al. 2004). Size strongly affected survival at Dilman Meadow consistent with studies of European toads (*Bufo bufo*; Goater 1994), water frogs (*R. lessonae*, *R. esculenta*; Altwegg and Reyer 2003), and Northern red-legged frogs (*Rana aurora*; Chelgren et al. 2006). No size effect was detected on survival of chorus frogs (*Pseudacris triseriata*; Smith 1987). Estimates of survival for small adults (7 – 20%) were intermediate to rates for adults and juveniles in other studies. Monthly survival rate estimates for juvenile pig frogs (*R. grylio*; Wood et al. 1998) extrapolate to 3% survival annually. Any effort to promote growth of individuals at Dilman Meadow could benefit the population growth rate by increasing survival probability, but we do not know how current survival rates affect population viability. Unfortunately, estimates of annual survival of Oregon spotted frogs from other sites are not currently available for comparison. Obtaining annual demographic rates from other Oregon spotted frog populations, where suspected stressors are acting, would be most valuable in understanding the mechanisms underlying the species declines and in prescribing management actions focused on appropriate life history stages.

Few studies have properly dealt with bias due to missing sex data (Wood et al. 1998, Nichols et al. 2004) and ours is the first that we know of to do so in a multi-state model. Here we show that sex-specific survival rates varied by season. The highest mortality of frogs at Dilman Meadow occurred for males after breeding. This is consistent with recent work on boreal toads (*Bufo boreas*) that suggests breeding is costly for males (Muths et al. 2006). Also, monthly survival during autumn through winter was higher than during spring through summer in water frogs (*R. lessonae*, *R. esculenta*; Peter 2001), consistent with our study. Oregon spotted frogs migrate seasonally to special habitats for over-wintering (Watson et al. 2003, our study) where they are relatively concentrated in space. We hypothesize that the high over-winter survival we observed at Dilman Meadow related to the absence of predatory fish from over-winter sites.

Size is rarely controlled for in studies of sex-specific survival in frogs. In our analysis, which controlled for size, survival rate still tended to be higher for females, as in other studies (Wood et al. 1998), but this difference was not statistically significant. We suggest that differences in survival rates between genders in other studies are confounded by size variation between genders. Body size tends to be sexually dimorphic in frogs (Shine 1979) and is highly plastic (*e.g*. Peacor and Pfister 2006). Because size may be affected by management, whereas sex generally cannot, we suggest that future studies attempt to isolate gender and size effects on demographic rates.

The results of our study were consistent with other studies of Oregon and Columbia spotted frogs (*R. luteiventris*) that demonstrate seasonal migrations and the importance of specialized wintering habitats. Watson et al. (2003) showed that Oregon spotted frogs reduced movements in summer, re-occupied the breeding range in September through January, and used specialized habitats as refuge during the coldest periods. Columbia spotted frogs in the mountains of central Idaho used multiple wetland sites seasonally and were able to traverse uplands (Pilliod et al. 2002). We do not know whether Oregon spotted frogs from Dilman Meadow are able to travel to the nearest lentic site outside of Dilman Meadow, Wickiup Reservoir (ca. 2.5 km). We would expect such movements, be they seasonal or permanent (*i.e*., emigration), to show up in our capture-recapture data as greater mortality during the fall and spring (wet, warm months when longer movements are most likely). While Oregon spotted frogs appear capable of substantial movements (*e.g*., Watson et al. 2003), there is little indication in literature or in our observations that they make such moves outside of riparian areas. Clearly, the differential use of site 3, the natural spring, emphasizes the importance of movement within the meadow. We conclude that Oregon spotted frogs at Dilman Meadow behave as a single population with exchange of individuals among ponds, which were complementary in their value to the population.

Striking and significant differences in asymptotic size were observed between the animals originally translocated to Dilman Meadow and those native to the meadow. Studies of body size at metamorphosis and subsequent growth have shown variation in the capacity of frogs to make up for size differences at metamorphosis after their transformation. Such catch-up growth has been shown to occur in 4 species of anuran (Boone 2005), though it was not detected in European toads (*Bufo bufo*; Goater 1994), wood frogs (*R. sylvatica*; Goater and Vandenbos, 1997), or spadefoot toads (*Spea hammondii*; Morey and Reznick 2001). Currently, we cannot determine if the variation in asymptotic size we observed resulted from difference in conditions faced by larvae, by frogs, or both. There is some evidence, provided by the lower growth trajectories of 3 individuals originally translocated to Dilman as sub-adults (Figure 5), that the environment of adults plays a role in the differences in asymptotic size. Because of the importance of size in the demography of amphibians, this difference is likely to affect the performance of the Oregon spotted frog population at Dilman Meadow.

We observed a decreasing trend in embryo or larval survival over the course of the study. This pattern is consistent with density dependent effects on survival, but could be explained by other factors which were not studied, such as the growth of predator populations or other changes in pond communities. Density dependence has been regularly observed in mesocosms (Loman 2001) and in some whole-pond experiments (Van Buskirk and Smith 1991, Loman 2004; but see Beebee et al. 1996). Perhaps most importantly for the future of Oregon spotted frogs at Dilman Meadow, open water in the mitigated ponds is rapidly decreasing due to pond succession. Our study suggests that the Dilman population may be impacted by succession initially via the reduced survival of larvae. There is some indication that density dependence affected the growth of adults as evidenced by differences in growth rate between breeding and non-breeding ponds. Density dependence could have occurred if a higher density of young frogs at breeding sites reduced growth relative to non-breeding sites.

At Dilman Meadow, increasing numbers of egg masses were laid at sites which were used previously for breeding, whereas there was little evidence of true dispersal (resulting in breeding) to sites which were not previously used for breeding. Breeding has yet to occur at the 3 ponds newly excavated in 2004 (Site 8), but neither did breeding occur immediately at sites 2, 3, or 4. Site 8 has been used increasingly by frogs since 2005 (C. Pearl unpublished data) though not for breeding. In other frog species, dispersal is most prevalent in young animals. If this is true of Oregon spotted frogs, then spring of 2005 may have been too early to anticipate the deposition of eggs at site 8. Sites 2 and 4, the first to be naturally colonized, did not produce an egg mass until the 4th year of natural egg deposition. Age-related dispersal in Oregon spotted frogs is an important information gap. To confirm age-related dispersal, it will be necessary to mark young animals, and use genetic techniques or intensive breeding season observation to link egg masses to the individual frogs that laid them. Apparent density dependent effects on survival during the larval stage coupled with the pattern of true dispersal at Dilman Meadow suggest an advantage of careful distribution of egg masses during translocation to minimize tadpole density. Our survival study, and others (Smith 1987, Semlitsch et al. 1988, Chelgren et al. 2006) demonstrate that conditions which positively affect growth rates of tadpoles should increase the probability of success of translocation efforts by improving multiple components of fitness.

Recommendations for future monitoring

To continue monitoring frog dynamics at Dilman Meadow, we recommend the following components in order of priority:

1) Obtain a complete count of egg masses at all ponds during spring.

2) Monitor pond succession or the extent of surface water at each pond during the dry period of summer.

3) Continue capture-recapture sampling of adult and sub-adult frogs during summer when frogs are most easily captured.

4) Conduct capture-recapture sampling during late summer following metamorphosis, applying year- and pond-specific batch marks to newly metamorphosed juveniles.

Components 1 and 2 are minimum metrics for documenting short-term success of the translocation effort. Component 1 is the most effective single measure of population performance but at a minimum should be combined with component 2 because without management, pond succession appears inevitable and will ultimately negate the population dynamics of frogs. Components 1 and 2 together would relate frog population size to area of open water, clarifying the urgency of management.

The combination of components 1, 2, and 3 would provide information necessary to assess recruitment of adult breeders, and survival as well as breeding probability. Including component 3 in monitoring efforts would provide a more complete picture of the life history, but it would not permit analysis of the entire annual life cycle. That is, without component 4, demography during the two most variable and dynamic periods, the larval period from egg to metamorphosis and the juvenile period from metamorphosis to the small adult stage, would be missed. Without the fourth component it would not be possible to link recruitment of adults to the numbers of egg masses laid, because of variation in both size at metamorphosis and post-metamorphic growth rates. With the fourth component, it would be possible to estimate the complete suite of demographic rates annually, which has never been done for a single amphibian population. Intensified efforts to sample juveniles during fall would benefit our understanding of the ecology of larval and juvenile life stages including the importance and form of density dependence during the larval period and the impacts of size at metamorphosis on juvenile survival and proportional age of recruitment into the breeding population.

This work provides context for studies of other Oregon spotted frog populations, particularly populations confronted with exotic predators. For example, Pilliod et al. (2002) reported that the presence of fish in overwintering sites reduced Columbia spotted frog survival. Our finding of high overwinter survival in a system lacking fish is consistent with focused winter effects of fish. Comparison of demographic rates between sites with introduced fish or bullfrogs and sites lacking predators (such as Dilman Meadow) is a necessary component for proceeding with informed, effective management elsewhere in the species range.

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Table 1. Summary statistics of the posterior distributions of capture-recapture model parameters pertaining to survival: model coefficients (1-5), random sex*season effects (6-15), random site effects (16-23), and random effect standard deviations (24-25). Random effects were zero-centered. Lower and Upper refer to the 0.025[th] and 0.975[th] percentiles of posterior distributions, respectively. The logit link function relates linear combinations of parameters to bi-monthly survival rates.

Index	Parameter	Mean	St. dev.	Lower	Median	Upper
1.	Intercept	3.585	0.927	2.092	3.473	5.684
2.	Female	-0.083	1.054	-2.232	-0.022	1.878
3.	Year	-0.020	0.101	-0.209	-0.024	0.184
4.	Trans	-0.941	0.349	-1.617	-0.945	-0.247
5.	Large	1.700	0.274	1.175	1.696	2.245
6.	male, March	0.997	1.648	-1.776	0.807	4.786
7.	male, April-May	-2.691	0.981	-5.012	-2.568	-1.136
8.	male, June-Sept.	-1.021	0.938	-3.114	-0.906	0.527
9.	male, Oct.	1.308	1.549	-1.118	1.084	5.018
10.	male, Nov.-Feb.	1.735	1.502	-0.608	1.529	5.275
11.	female, March	0.406	1.721	-2.615	0.274	4.255
12.	female, April-May	0.970	1.679	-2.119	0.809	4.785
13.	female, June-Sept.	-1.413	1.054	-3.762	-1.355	0.530
14.	female, Oct.	0.148	1.730	-3.007	0.036	3.927
15.	female, Nov.-Feb.	0.585	1.500	-2.162	0.452	4.028
16.	Site 1	-0.034	0.189	-0.418	-0.030	0.334
17.	Site 2	-0.058	0.262	-0.602	-0.051	0.448
18.	Site 3	0.007	0.286	-0.548	0.003	0.586
19.	Site 4	0.006	0.224	-0.436	0.005	0.453
20.	Site 5	-0.119	0.186	-0.505	-0.113	0.229
21.	Site 6	0.173	0.238	-0.238	0.154	0.708
22.	Site 7	-0.014	0.186	-0.386	-0.015	0.355
23.	Site 8	0.057	0.293	-0.489	0.042	0.694
24.	$\sigma_{sex*season}$	1.791	0.833	0.758	1.604	3.905
25.	σ_{site}	0.275	0.109	0.141	0.251	0.555

Table 2. Summary statistics of the posterior distributions of capture-recapture model parameters pertaining to capture probability: model coefficients (1-4), random site effects (5-12), random season effects (13-17), and the random effect standard deviation (18). Random effects were zero-centered. Lower and Upper refer to the 0.025[th] and 0.975[th] percentiles of posterior distributions, respectively. The logit link function relates linear combinations of parameters to capture probability.

Index	Parameter	Mean	St. dev.	Lower	Median	Upper
1.	Intercept	-3.962	0.504	-4.894	-3.965	-2.945
2.	Female	0.620	0.092	0.435	0.621	0.799
3.	Year	0.255	0.046	0.164	0.254	0.347
4.	Days	0.569	0.042	0.487	0.569	0.651
5.	Site 1	-0.409	0.306	-1.033	-0.405	0.175
6.	Site 2	-0.246	0.378	-1.041	-0.234	0.462
7.	Site 3	1.888	0.410	1.104	1.879	2.705
8.	Site 4	0.157	0.327	-0.492	0.160	0.784
9.	Site 5	-0.166	0.303	-0.784	-0.158	0.414
10.	Site 6	-1.030	0.329	-1.714	-1.018	-0.416
11.	Site 7	-0.827	0.306	-1.444	-0.824	-0.241
12.	Site 8	0.404	0.552	-0.675	0.399	1.511
13.	March	0.041	0.363	-0.738	0.048	0.748
14.	April-May	-0.262	0.368	-1.052	-0.252	0.444
15.	June-Sept.	0.808	0.355	0.023	0.815	1.500
16.	Oct.	-0.292	0.369	-1.087	-0.283	0.409
17.	Nov.-Feb.	-0.770	0.389	-1.611	-0.758	-0.033
18.	σ	0.818	0.193	0.532	0.790	1.280

Table 3. Summary statistics of the posterior distributions of coefficients for the mechanism of the missing gender data. Parameters relate to the probability that gender was observed using the logit link function. Lower and Upper refer to the 0.025^{th} and 0.975^{th} percentiles of posterior distributions, respectively.

Index	Parameter	Mean	St. dev.	Lower	Median	Upper
1.	Intercept	-0.414	0.169	-0.748	-0.412	0.091
2.	Female	-1.651	0.292	-2.235	-1.651	-1.075
3.	Large	3.467	0.301	2.892	3.458	4.089
4.	Female*Large	0.893	0.410	0.087	0.898	1.673

Table 4. Summary statistics of the posterior distributions of logistic growth model parameters: coefficients for growth rate (1-9), random site effects on growth rate (10-17), coefficients for asymptotic size (18-20), and the random effect standard deviation (21). Random effects were zero-centered. Lower and Upper refer to the 0.025[th] and 0.975[th] percentiles of posterior distributions, respectively. The log link function relates linear combinations of parameters to growth rate and asymptotic size.

| Index	Parameter	Mean	St. dev.	Lower	Median	Upper
1.	March	-3.137	0.486	-4.176	-3.132	-2.275
2.	April-May	-2.994	0.456	-3.960	-2.951	-2.200
3.	June-Sept.	-2.444	0.283	-3.005	-2.421	-1.946
4.	Oct.	-774.525	594.123	-2186	-633.85	-33.284
5.	Nov.-Feb.	-807.054	598.731	-2233	-690.90	-36.290
6.	Female	-0.455	0.190	-0.810	-0.464	-0.092
7.	Year	0.210	0.067	0.074	0.216	0.330
8.	Translocation	1.520	0.328	0.825	1.548	2.132
9.	Breeding	-0.563	0.207	-0.949	-0.572	-0.121
10.	Site 1	-0.295	0.354	-0.977	-0.316	0.463
11.	Site 2	0.039	0.465	-0.932	0.071	0.830
12.	Site 3	-0.518	0.602	-1.926	-0.447	0.457
13.	Site 4	0.609	0.323	-0.031	0.627	1.203
14.	Site 5	-0.109	0.318	-0.75	-0.094	0.499
15.	Site 6	-0.070	0.408	-0.934	-0.048	0.710
16.	Site 7	0.003	0.331	-0.615	-0.005	0.663
17.	Site 8	-0.180	0.666	-1.635	-0.129	0.969
18.	Intercept	4.067	0.012	4.046	4.067	4.091
19.	Female	0.181	0.019	0.143	0.181	0.217
20.	Translocation	0.089	0.023	0.044	0.088	0.134
21.	σ	0.707	0.222	0.414	0.664	1.264

Table 5. Numbers of egg masses laid in 2000 at the original ditch near Wickiup Reservoir, numbers translocated to Dilman Meadow in 2001, and numbers laid at Dilman Meadow subsequently. Site 8 was constructed after the completion of oviposition in 2004.

| Year	Count	Site Number							
		1	2	3	4	5	6	7	8
2000	11	-	-	-	-	-	-	-	-
2001	9	2.25	0	0	0	2.25	2.25	2.25	-
2002	2	0	0	0	0	2	0	0	-
2003	25	12	0	0	0	4	2	7	-
2004	30	10	0	0	0	6	6	8	-
2005	49	13	1	0	1	14	8	12	0

Figure 1. Variation in bimonthly survival rate by season, gender, and pond. Bimonthly survival rates were constrained to be equal within the 5 seasons (x-axis): 1) Spring redistribution (March), 2) Breeding/post-breeding redistribution (April-May), 3) Summer (June-September), 4) Fall redistribution (October), 5) Over-winter (November-February). Female frogs are depicted in gray, males in black, and plotting symbols represent sites 1-8. Estimates are computed for frogs native to Dilman Meadow at the median year.
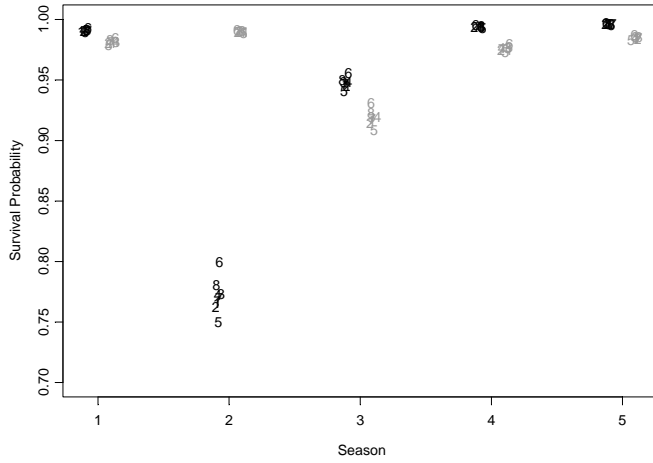
Figure 2. Variation in annual survival rate for small (snout-vent length < 57 mm, triangles) and large frogs (snout-vent length > 57 mm, circles) by year and sex. Males are depicted in black, females in gray. Bars are 95% credibility intervals. The linear combination for 2001 incorporates a translocation effect additive to the trend across years.
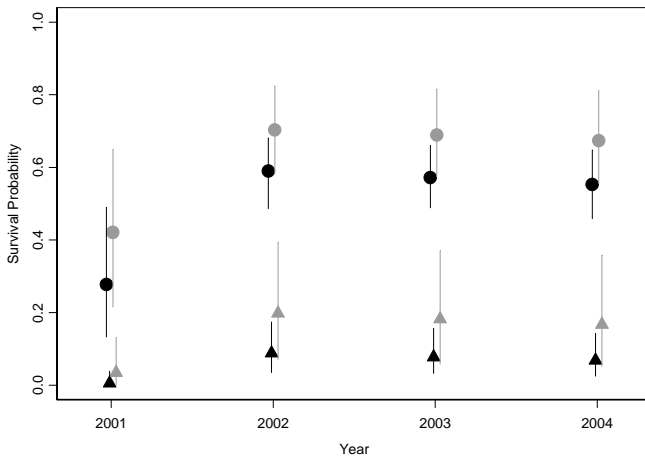
Figure 3. Probability of emigrating a site given the animal was present in the pond at the start of a bimonthly interval (π). X-axis represents season: 1) Spring redistribution (March), 2) Breeding/post-breeding redistribution (April-May), 3) Summer (June-September), 4) Fall redistribution (October), 5) Over-winter (November-February). Parameter estimates were constrained equal within seasons. Plotting symbols represent the site of origin.
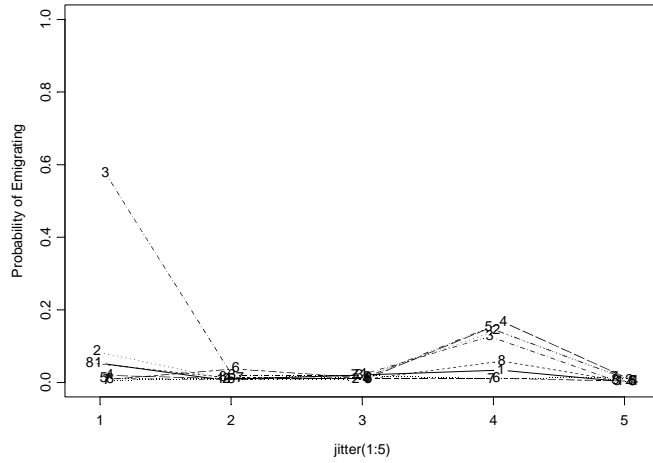
Figure 4. Season-specific relative probability of preference of sites conditional on frogs having emigrated. X-axis represents season: 1) Spring redistribution (March), 2) Breeding/post-breeding redistribution (April-May), 3) Summer (June-September), 4) Fall redistribution (October), 5) Over-winter (November-February). Within seasons, relative probabilities of preference sum to 1.0. Plotting symbols represent the site of destination.
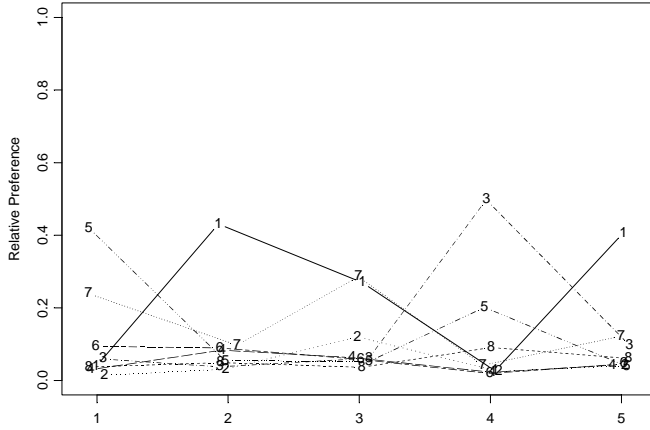
Figure 5. Growth of female (upper panel) and male (lower panel) Oregon spotted frogs. Original translocated individuals are represented with solid lines. X-axis represents days since first marked.
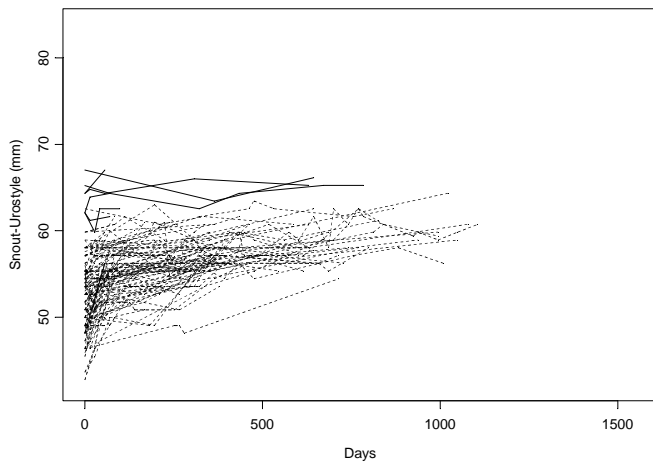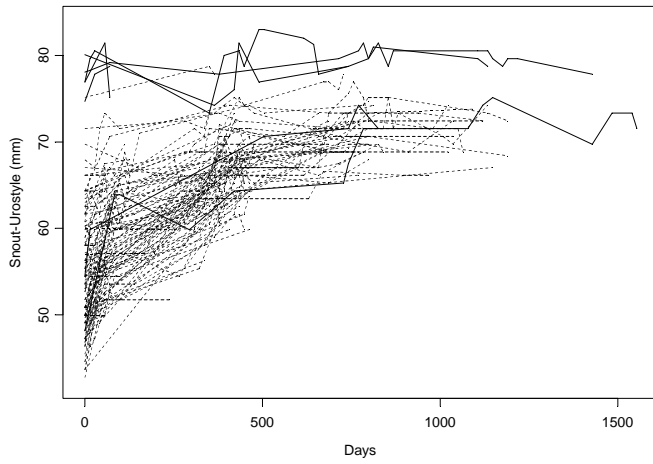
Figure 6. Estimated abundance of A) juvenile (< 40 mm snout-vent length), B) small adult (40-57 mm) and C) large adult frogs (> 57 mm). Plotting symbols represent sites 1-8. In A), No juvenile frogs were captured at sites 3, 4, and 8.