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Oregon Spotted Frog (*Rana pretiosa*) Movement and Demography at Dilman Meadow: Implications for Future Monitoring

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Prepared in cooperation with the *Sunriver Nature Center*

Open-File Report 2007-1016

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ACKNOWLEDGEMENTS

This analysis was made possible by a grant from the Interagency Special Status/Sensitive Species Program. We thank C. Korson and L. Zakrejsek at the US Bureau of Reclamation for their work in all aspects of the translocation. Reviews by L. Bailey and two anonymous reviewers improved the manuscript. We thank R. B. Bury for suggestions on field techniques and assistance throughout the early years of the study. We thank S. Ackley, R. Diehl, B. McCreary, and C. Rombough for assistance with field work. We also thank Deschutes National Forest, US Fish and Wildlife Service, North Unit Irrigation District, and Sunriver Nature Center for the logistical and personnel support they dedicated.

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 (121° 39' 52" W, 43° 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 °C), 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 $\text{logit}(\delta)$, 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 $\mu_i^{RT} = \alpha_i^T / (1 - \alpha_i^R)$, 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 *sex*, *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 $site_{i,t} \sim \text{Mult}(1; \theta_1, \theta_2, \theta_3, \dots, \theta_8)$. 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, $n_{day,site} \sim \text{Binomial}(N_{year,site}, P_{day,site})$, 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. $\text{Pr}(Y > 0) = 0.93$ 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 $\text{Pr}(\beta_{\text{Female}} > 0) = 1.00$ during the breeding/post-breeding redistribution period but was not supportive of gender differences in the other seasons: spring redistribution, $\text{Pr} = 0.37$; summer, $\text{Pr} = 0.13$; fall redistribution, $\text{Pr} = 0.27$; and over-winter, $\text{Pr} = 0.23$. There was strong support ($\text{Pr} = 0.99$) 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 ($\text{Pr} = 1.00$) 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 ($\text{Pr} = 0.41$) 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

