

# Demography and reproductive ecology of the Columbia spotted frog (*Rana luteiventris*) across the Palouse

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**Abstract:** Here we report on the demography and reproductive ecology of the Columbia spotted frog (*Rana luteiventris* Thompson, 1913) breeding in ponds across the Palouse Bioregion of Washington and Idaho. Spotted frogs are unusual, if not unique, among temperate ranids in that males establish the oviposition site before females become active. Females laid at one or two communal sites in shallow water. Our breeding populations were small, never exceeding 50 adults counted, and most displayed male-biased sex ratios. We estimated effective population sizes ( $N_e$ ) as ranges determined by extremes in male breeding success; these varied between 3.2 and 37.8. Even the latter falls below the minimum required for long-term population viability. Small population size may make spotted frogs vulnerable to genetic problems and environmental insults. Communal oviposition certainly renders a population's reproductive effort vulnerable to variation in hydroperiod, which we observed during the dry spring of 2004. In the absence of information on the degree of "connectedness" among our ponds as subunits of more resilient metapopulations, we suggest that small population size and communal oviposition likely render *R. luteiventris* vulnerable to anthropogenic disturbance. Furthermore, the status of *R. luteiventris* on the Palouse may be less secure than assumed currently.

**Résumé :** Notre travail porte sur la démographie et l'écologie de la reproduction de la grenouille maculée de Columbia (*Rana luteiventris* Thompson, 1913) qui se reproduit dans des étangs dans toute la biorégion de la Palouse au Washington et en Idaho. Les grenouilles maculées mâles établissent le site de ponte avant que les femelles ne deviennent actives; c'est une caractéristique inusitée, sinon unique, chez les ranidés. Les femelles pondent à un ou deux sites communautaires en eau peu profonde. Les populations étudiées sont petites avec des densités inférieures à 50 adultes et la plupart contiennent plus de mâles que de femelles. Les tailles effectives des populations ( $N_e$ ) s'estiment par l'étendue des valeurs extrêmes du succès reproductif des mâles qui varient de 3,2 à 37,8. Même cette dernière valeur est trop faible pour assurer la viabilité à long terme de la population. La taille réduite des populations peut rendre la grenouille maculée vulnérable aux problèmes génétiques et aux insultes environnementales. La ponte communautaire rend certainement l'effort reproductif de la population vulnérable aux variations de l'hydropériode, comme cela s'est produit au printemps sec de 2004. Sans information sur le degré de connectivité entre les étangs comme sous-unités d'une métapopulation plus résistante, nous croyons que la taille des populations et la ponte communautaire rendent vraisemblablement *R. luteiventris* vulnérable aux perturbations anthropiques. De plus, le statut de *R. luteiventris* dans la Palouse peut être moins assuré qu'on ne le croit généralement.

[Traduit par la Rédaction]

## Introduction

Much has been written about the "sixth extinction" (Eldredge 1998). This refers to our current global "biodiversity crisis" in which estimates of extinction rates appear to be higher than can be explained by natural processes alone (Wilson 1998). An ever-growing body of literature suggests that amphibians (especially anurans) are declining on a global scale (e.g., Blaustein et al. 1994). The permeable skins and complex (at least biphasic) life cycles typical of amphibians

are regarded as naturally evolved traits that may be decidedly disadvantageous in the face of anthropogenic change (Beebee 1996). Anuran taxa that reside at high altitudes and in northern latitudes seem especially vulnerable, as do those that are habitat specialists and those that occur naturally as isolated populations (Wake 1991). Finally, physiological constraints, low vagility, and high philopatry may make unlikely the recolonization of sites that have suffered local extinction (Blaustein et al. 1994; Smith and Green 2005).

Within western North America, the spotted frog complex has become a case study of anthropogenic population decline. Spotted frogs recently were separated into two species based on allozyme differences (Green et al. 1997). In the United States, the Oregon spotted frog (*Rana pretiosa* Baird and Girard, 1853) occurs in western Oregon and Washington; the Columbia spotted frog (*Rana luteiventris* Thompson, 1913) is found to the north and east, and has a wider range.

In the last 100 years, *R. pretiosa* has declined precipitously. It has been found at only 13 of 59 locations in which

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it was present historically (McAllister and Leonard 1997), and Hayes (1997) suggests that *R. pretiosa* today occupies about 10% of its original range. West of the Cascade Mountains of Oregon, the species appears to be extinct.

*Rana luteiventris* has a distribution from extreme southeast Alaska, southwestern Yukon Territory, northern British Columbia, and western Alberta south through eastern Washington, eastern Oregon, Idaho, and western Montana (U.S. Fish and Wildlife Service 2002). Disjunct populations occur in the southern part of this range in central and northeastern Nevada, western and north-central Wyoming, and northern Utah (Green et al. 1997). These populations are fairing poorly. In the Wasatch Front of Utah, presence of *R. luteiventris* was confirmed at only 5 of 13 historical locations, suggesting a major range reduction in an area where this species likely once was the most abundant anuran (U.S. Fish and Wildlife Service 2002). Remaining populations in this area consist of relatively few individuals and are considered to be below long-term sustainable population sizes. *Rana luteiventris* populations in Nevada have been extirpated from 50% of their historic range, with remaining frogs clustered in just four isolated populations (Reaser 2000).

The status of *R. luteiventris* in the more northern part of its range is largely unstudied but should not be considered secure. It is clear that this species faces multiple anthropogenic threats. One critical factor in the decline of *R. luteiventris* clearly is habitat alteration and destruction, which has greatly increased since the 19th century. Non-native reed canary grass (*Phalaris arundinacea* L.) has covered many of the shallow, open-water areas favored by these frogs with thick growths of vegetation (McAllister and Leonard 1997). Increased use of uplands for grazing livestock, growing crops, and construction has led to habitat fragmentation and drainage of wetlands (Sisk 1998). Conversion of wild land to agricultural use not only alters or eliminates habitat but also introduces many environmental contaminants, such as nitrogenous fertilizers and pesticides (Blaustein and Kiesecker 2002). The latter may flow downstream or blow upwind to affect populations in areas that are relatively undisturbed otherwise.

The status of *R. luteiventris* indicates a need for careful management of existing populations. This species is considered to be of "concern" in Washington (Washington Department of Fish and Wildlife at [www.wdfw.wa.gov](http://www.wdfw.wa.gov)), of "special concern" in Idaho (Idaho Department of Fish and Game at [www.fishandgame.idaho.gov](http://www.fishandgame.idaho.gov)), and is classified as a "conservation agreement species" in Utah (State of Utah 2003). Population declines have been well documented, and many contributing factors have been implicated. What we need now is a better understanding of the demography and reproductive ecology of spotted frogs. Such information is needed to identify the factors to which they are vulnerable and to aid in sound management of remaining populations.

This paper reports data on the demography and reproductive ecology of *R. luteiventris* in the Palouse Bioregion of southeast Washington and adjacent northwest Idaho. Once dominated by short-grass prairie, the Palouse has been greatly altered by human activity since 1900 (Sisk 1998), largely as a result of agriculture and, more recently, urbanization. Our primary goal was to explore two aspects of frog natural history that may increase vulnerability to human

disturbance: small, isolated populations and communal egg laying at specific locations within breeding ponds. We accomplished this primary goal by examining Palouse frogs at seven ponds in 1 year, and at two ponds, in great detail, in 2 years. Ponds were selected to be representative of the Palouse landscape. We conclude that certain aspects of the biology of *R. luteiventris* likely increases its vulnerability to anthropogenic problems, including those faced by other anuran species.

## Methods

### Pond locations and characteristics

All ponds surveyed were located in Whitman (Washington) and Latah (Idaho) counties, within which the majority of the Palouse Bioregion lies (Sisk 1998; see Table 1). Ponds were chosen across the landscape based on several factors. Recently reported (Monello and Wright 1999; Eareckson 2001) or personally observed presence of *R. luteiventris* was essential. The presence of emergent vegetation is believed to be a key indicator of frog reproduction (Monello and Wright 1999); therefore, it was a determining factor in our selection of sites. The two most abundant emergent plants were reed canary grass and cattails (species of the genus *Typha* L.). All ponds in this survey had one or both types of vegetation present.

Also taken into consideration was the distribution of ponds across the Palouse ecotype and how representative these sites were of ponds in the region. Our ponds ranged in surface area from approximately 1200 to 5200 m<sup>2</sup> and in elevation from 697 to 896 m. All ponds were shallow, ranging from approximately 0.6 to 1.5 m in depth; only at Eden Valley did maximum depth ever exceed 1.5 m.

### Phillips Farm and Eden Valley — primary study sites

Phillips Farm and Eden Valley were surveyed for frogs during the springs of 2003 and 2004. Both ponds were visited daily, and water and air temperatures, numbers and locations of egg clutches, and the presence of other vertebrate species were recorded. Frogs were caught and measured for snout-vent length (SVL) to the nearest 1 mm owing to the small amount of "bend" associated with a live, struggling frog. We used mean within-year measurements for each individual in our analyses. A frog's location within the pond, its sex, its collection method (net, trap, or hand), and whether it was in amplexus were recorded. A unique toe combination was clipped for each individual (see Heyer et al. 1994). A minimum number of toes was removed for each individual; thumbs were never clipped to avoid effects on amplexus and no more than one toe per foot was removed. On front appendages the entire toe was taken. On rear digits, the toe was cut to where webbing began to minimize bleeding, chance of infection, and interference with swimming. Scissors were heat-sterilized with a butane lighter between the processing of consecutive individuals. There was no evidence of infection caused by toe-clipping; therefore, no antibiotic was applied. Individual toes were stored in 70% ethanol solution.

In the spring of 2003, collapsible minnow traps (Nylon Net Company, Memphis, Tennessee) were placed in the water on 11 March. Traps were checked daily and were re-

**Table 1.** Locations, elevations, and approximate surface areas of 10 ponds within the Palouse Bioregion with known or suspected presence of *Rana luteiventris* in 2003 and 2004.

Site	County (State)	Latitude (N)	Longitude (W)	Elevation (m)	Approximate surface area (m <sup>2</sup> )
Phillips Farm	Latah (Idaho)	46°48.90'	117°01.28'	835	1230
Eden Valley	Whitman (Washington)	46°56.23'	117°12.01'	759	4780
West Twin	Latah (Idaho)	46°46.20'	116°57.74'	815	5210
Smoot Hill	Whitman (Washington)	46°49.76'	117°13.84'	697	3310
Eareckson	Latah (Idaho)	46°50.32'	116°58.68'	879	—
Waste Water	Latah (Idaho)	46°43.86'	117°02.36'	768	—
Paradise Creek	Latah (Idaho)	46°47.45'	116° 58.93'	826	—
Moscow Mountain Road	Latah (Idaho)	46°45.36'	116°57.48'	810	—
Beaver Ponds	Latah (Idaho)	46°51.58'	116°56.28'	838	—
Four Mile	Latah (Idaho)	46°50.37'	116°58.89'	896	—

moved from their respective ponds once the first adult frog was caught (12 March for Eden Valley and 20 March for Phillips Farm). Traps were removed at that time because the interval from first capture to onset of breeding was unknown. Dip netting and hand capture subsequently were employed to catch frogs.

Attempts were made to catch all frogs seen within or on the surface of the ponds, and every effort was made to ensure that sampling was distributed equally, both spatially and temporally. Sampling continued through the breeding season and beyond (until 15 May) for Phillips Farm. Because of the difficulty catching adults and limited netting success at the communal oviposition site at Eden Valley, the vegetation was cut back and an "egg cradle" was created from fine nylon mesh and wooden dowels. This egg cradle provided greater accessibility with a net to catch adult frogs while allowing the oviposition site to remain at the location where active breeding was occurring. This apparatus was lowered as the water level dropped to assure that eggs could develop and hatch normally. The egg cradle was removed on 14 April after all eggs had hatched and sampling was terminated at this site for 2003.

For the spring of 2004, Phillips Farm and Eden Valley were visited daily from 21 February to 1 April. Traps were placed in water and checked daily until they were removed at the first indication of breeding (first female present, males aggregating, pairs in amplexus, or eggs laid). This longer prebreeding period for trapping was possible in the second season because it was determined in the previous year that there was a span of approximately 2 weeks between first capture and onset of breeding. Traps were removed when breeding began to eliminate interference with pairing and choice of egg deposition site. Collection continued by dip netting and hand capture until 10 days after the last clutch of eggs was laid, after which time trapping was again used.

#### Additional ponds surveyed in 2004

Two ponds (West Twin and Smoot Hill) were included for full observation in the spring of 2004 using the same methods as described above for Phillips Farm and Eden Valley in the same year. Five additional ponds (Waste Water, Paradise Creek, Moscow Mountain Road, Eareckson, and Beaver) were surveyed only for the number of egg clutches present over a period of 2 weeks in 2004. These seven ponds were

added to expand our understanding of *R. luteiventris* breeding dynamics, examined in greatest detail at Phillips Farm, to a broader landscape scale.

One other pond (Four Mile) was visited daily from 21 February to 10 April, a site at which breeding had occurred in previous years (Eareckson 2001). Traps were in place over this entire period, but no frogs were captured and no eggs were observed. Visitation ceased after frogs in adjacent ponds had completed breeding and the eggs at these other ponds were beginning to hatch. It was concluded that frogs did not breed at Four Mile in 2004.

## Results

### Mating and breeding

The first individuals of *R. luteiventris* seen/captured at all ponds and in both years were males. Females were first seen/captured after males (median interval 6.5 days, range 1–36 days, for all ponds and both years). Males encountered early in the spring were widely distributed spatially throughout the pond. However, they later moved to and aggregated within a specific location in the pond (approximately 4 m<sup>2</sup> in size) and vocalized as a chorus during daylight hours at all ponds and in both years.

We examined the spatial dynamics of the male population of Phillips Farm in 2003 in greater detail and found that a linear regression of distance from the eventual egg-laying site on day was significant ( $P < 0.023$ ). We also found that a quadratic regression of distance on day<sup>2</sup> was significant ( $P < 0.045$ ; Fig. 1). These regressions were bootstrapped with 2000 randomizations in which one observation per individual was selected for each run (thus,  $N = 7$ ) and  $P$  values were calculated as indicated by Efron and Tibshirani (1993). This conservative approach to regression analyses was taken because of the serially correlated nature of our data (arising from repeated observations of individual frogs) and the irregular nature of the timing of captures (necessitated by field conditions and frog behavior). The minimum of the quadratic regression lies at approximately 20 days after sampling had begun. This corresponds to when the males in the population were most aggregated at the site of egg laying during the time of active egg laying, 6–8 April (Fig. 1).

The mating call of male *R. luteiventris* consists of a series of 6–9 rapid, low-pitched clucking notes (Leonard et al.



**Table 2.** Summary of demographic information obtained for *R. luteiventris*.

	Phillips Farm		Eden Valley			West Twin, 2004	Smoot Hill, 2004	Eareckson, 2004	Waste Water, 2004	Paradise Creek, 2004	Moscow Mountain Road, 2004	Beaver Pond, 2004
	2003	2004	2003	2004	2004							
Number of males caught	7	23	7	19	29	8	—	—	—	—	—	—
Number of females caught	5	10	2	9	16	3	—	—	—	—	—	—
Sex ratio (male/female)	7/5	23/10	7/12	19/12	29/16	8/5	—	—	—	—	—	—
Two-tailed binomial <i>P</i> value	0.774	0.035	0.358	0.28	0.072	0.58	—	—	—	—	—	—
Number of clutches counted	4	7	12	12	14	5	9	4	3	4	7	—
Juveniles observed	Yes	Yes	No	Yes	Yes	Yes	—	—	—	—	—	—

**Note:** Phillips Farm and Eden Valley were sampled in both 2003 and 2004. All other ponds were sampled in 2004 only. The number of females represented in the sex ratio is the greater of either the number of females caught or the number of egg clutches counted.

**Fig. 2.** Three male *R. luteiventris* calling from around and atop eggs (two clutches) at the primary oviposition site of Phillips Farm in 2004. Note a single amplexant pair in the upper lefthand corner. Reproduced with permission of John Clark, Washington State University, Pullman.



Median SVL (and range) for males was 56.5 mm (46–71 mm,  $N = 86$ ), for females was 67.0 mm (43–86 mm,  $N = 41$ ), and for juveniles was 33.0 mm (22–45 mm,  $N = 46$ ).

### Population parameters

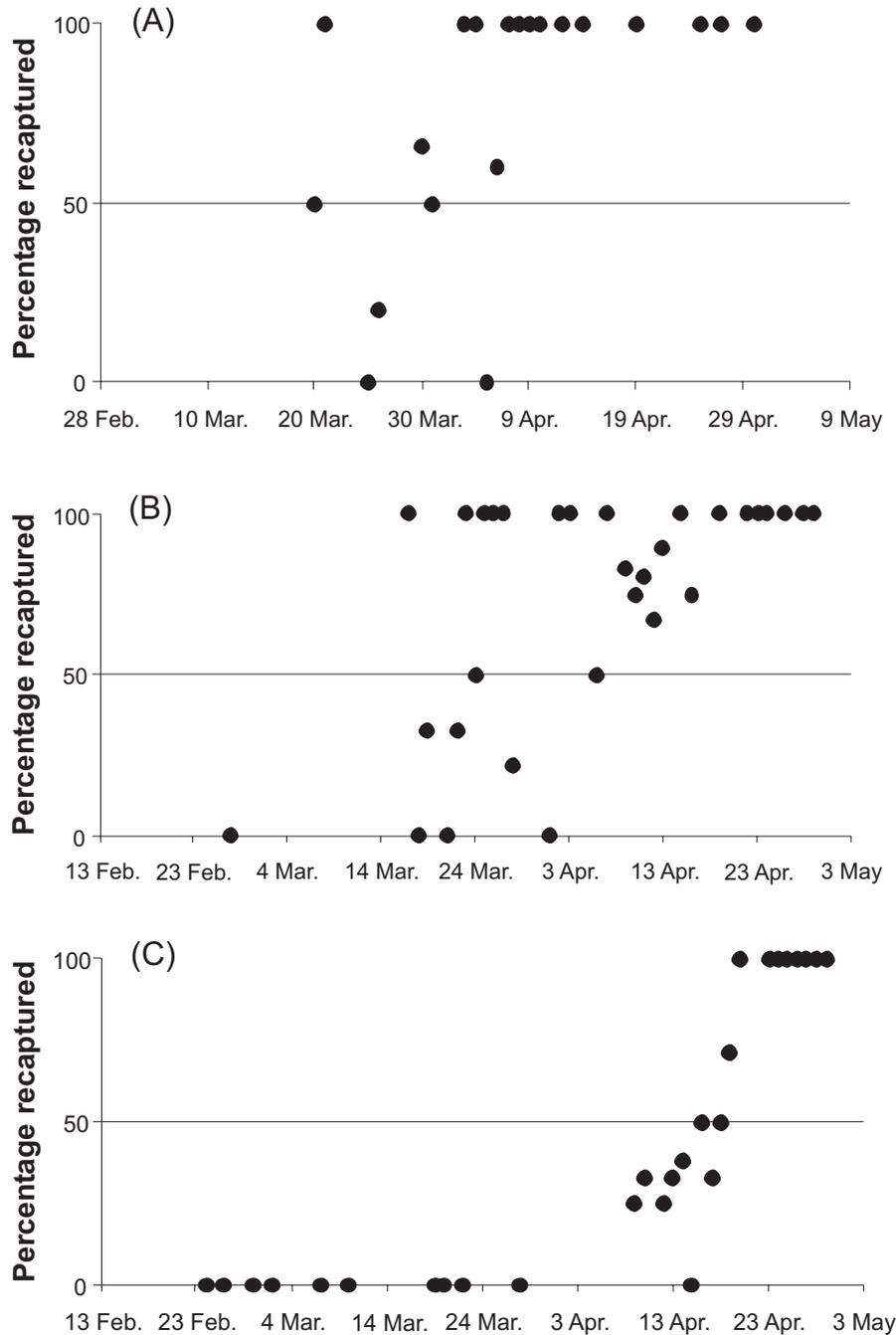
Three parameters of behavioral, ecological, and genetic significance for animal populations are (1) population size (total number of adult males and adult females present), (2) adult sex ratio (number of adult males to number of adult females; discussed above), and (3) effective population size ( $N_e$ ).

Population size usually is estimated rather than measured directly for large populations. However, direct measurement is possible for populations that are small and (or) aggregated spatially, as was the case for our populations of *R. luteiventris*. On the basis of recapture saturation over time for marked and released individuals at Phillips Farm (2003 and 2004) and West Twin (2004), we concluded that our surveys of adult population sizes at these sites were comprehensive in that all (or almost all) of the adults present were captured (Fig. 3). In addition, our data indicated that these populations were not large (Table 2).

The effective size of a population,  $N_e$ , provides an index of the extent to which a population (regardless of its census population size) will lose genetic heterogeneity as a consequence of genetic drift (Freeman and Herron 2001). For populations with unequal adult sex ratios, as was the case for our study populations of *R. luteiventris*, Wright (1931) proposed that  $N_e$  can be estimated as  $4N_fN_m/(N_f + N_m)$ , where  $N_f$  is the number of breeding females and  $N_m$  is the number of breeding males.

For *R. luteiventris*, the number of egg masses in a pond provides an exact value for  $N_f$ . We consider this valid because females do not lay more than one clutch per season (Licht 1975). Additionally, using egg masses to determine  $N_f$  is more accurate than using the number of females captured because (i) not all gravid females deposited eggs and (ii) we sometimes counted more clutches than the number of fe-

**Fig. 3.** Evidence for complete recapture saturation over single seasons, shown as percentages of recaptured adults after being previously captured and marked, for (A) Phillips Farm in 2003, (B) Phillips Farm in 2004, and (C) West Twin in 2004.



males caught. However, in the absence of data on male breeding success,  $N_m$  can be measured neither directly nor accurately. Thus, we estimated  $N_m$  according to two extreme models of male breeding success. In the first, a single male monopolizes all breeding females, and thus all fertilizations, so that  $N_m = 1$ . In the second model, each clutch is fertilized by every male in the population so that  $N_m$  is the number of males seen/captured. In this way, we estimated  $N_e$  for each pond/year not as a point value but as a range of possible values bracketed by the above extremes. We believe that the “true”  $N_e$  lies within this range and that this is more useful than an uncertain point estimate. We estimated our largest

population (West Twin) to have a  $N_e$  of 3.73–37.8, and our smallest populations (Moscow Mountain Road, Phillips Farm in 2003 and Smoot Hill) to have  $N_e$ s of 3.2–10.2 (see Table 3). Even the maximum values of these ranges are not large.

**Discussion**

**Demography**

Population number provides a measure of how many individuals are present in a pond, competing for resources and potentially mating. The ponds included in our study con-

**Table 3.** Estimates of ranges of effective population sizes ( $N_e$ ) for four populations of *R. luteiventris* determined for one or both of 2 years.

$N_e$	Phillips Farm		Eden Valley		West Twin, 2004	Smoot Hill, 2004
	2003	2004	2003	2004		
	3.2–10.2	3.5–21.5	3.7–17.7	3.7–29.4	3.73–37.8	3.3–12.3

**Note:**  $N_e$  was calculated with number of egg clutches determining the number of females. Number of males sets the range; minima were calculated with one male per population fertilizing all of the eggs in that population, and maxima with every male contributing to the fertilization of every clutch.

tained very few adults. For the populations surveyed most thoroughly and exhibiting recapture saturation of 100%, the largest had 45 adults (West Twin in 2004) and the smallest had 12 adults (Phillips Farm in 2003). Juveniles were seen at most ponds (see Table 2), suggesting that there may have been successful reproduction and recruitment within them in years previous to this study. However, it is possible that at least some of the juveniles had dispersed into our ponds from other sites nearby.

Adult sex ratios at all ponds and in both years (except for Eden Valley in 2003) were biased toward an excess of males. This differs from Turner (1960, 1962), Reaser (2000), and Hovingh (1993), all of whom reported female-biased adult sex ratios for *R. luteiventris*. Pilliod et al. (2002) reported a mixed adult sex ratio across years when all habitats in their study area were combined. Only Morris and Tanner (1969) reported a male-biased sex ratio. The timing of and procedures used for sampling are not clearly reported for all of the above studies, but it seems unlikely that the male-biased adult sex ratio which seems common for the Palouse is typical for *R. luteiventris* across its complete geographic range.

The breeding dynamics of *R. luteiventris* (and *R. pretiosa*, its western sister taxon) appear to be unusual for a temperate ranid frog. *Rana luteiventris* is an explosive breeder (sensu Wells 1977), with a breeding season no more than 3 weeks in duration. Males establish a common calling site within a pond before females appear. Males do not disperse within the pond to search actively for females, as has been described for other anurans with egg deposition at communal sites (Wells 1977; Seale 1982). For example, the wood frog (*Rana sylvatica* LeConte, 1825) exhibits a breeding system in which males are active before females, call from individual territories within the pond, and search actively for mates; once paired, females move to the egg-laying site with males attached (Berven 1981, 1988).

Male *R. luteiventris* congregate in a very small area of the pond from which they call and do not search actively for females across the pond. As a result, male *R. luteiventris* establish the site of egg deposition, not females. It has been suggested that females overwinter near breeding sites and emerge in response to the vocal cues of calling males (Licht 1969). This is consistent with our observations, but we do not have sufficient data to confirm this idea.

Amplexus is initiated within the male calling area and egg masses are laid there. While the female is responsible for any movements shown by an amplexant pair, females do not appear to make any efforts to lay their clutches away from the male calling site. As a result, eggs are laid communally within a pond at a site determined by the males of that popu-

lation. This site within each pond appears to be the same from year to year and is always near the margin of the pond (our data; Licht 1969; Morris and Tanner 1969).

The breeding dynamics and male-biased adult sex ratios observed in our populations strongly suggest the possibility of sexual selection via intermale competition and, perhaps, female mate choice (Sullivan et al. 1995). The operational sex ratio was always male-biased, with as many as 11 males in the presence of a single female. Emlen and Oring (1977) state that the greater the disparity in the abundance of reproductively active individuals of each sex, the more intense the opportunity for sexual selection in the more numerous sex (typically males). This situation is ripe for male–male conflict, which is supported by the multiple clasping by two males of one female seen at Phillips Farm in 2004. Morris and Tanner (1969), who also reported a male-biased sex ratio, observed a single female embraced by more than one male. We also observed males kicking at one another with their hind limbs while calling atop communal egg masses. Although males did not establish individual breeding territories across the pond, there may be a hierarchy of positions at the egg mass. Because the call of an individual male likely does not travel far, males may also vie for call sites nearest the POS.

If pairs remain clasped for prolonged periods of time, as has been reported (Svihla 1935; Middendorf 1957) and as suggested by our limited data, then amplexus could serve as a form of mate guarding. Prolonged amplexus also might allow a female to mate with the male that is most able to retain his grip on her (a form of indirect female choice). Both of these possibilities require further investigation.

### Reproductive ecology and the frogs' fate

Effective population size ( $N_e$ ) is determined by the number of reproductive individuals in a population, not the total number of individuals present (Wright 1931). Previous authors have estimated  $N_e$  in anurans by multiplying the number of egg clutches by two so that  $N_e = 2N_f$  (Merrell 1968; Berven and Grudzien 1990; Seppa and Laurila 1999; U.S. Fish and Wildlife Service 2002), by reporting the number of clutches ( $N_f$ ) alone (Seppa and Laurila 1999), or by estimation using capture–recapture information (Merrell 1968). We chose to represent  $N_e$  as a range rather than as a point estimate. Our minimum value derives from a model in which one male monopolizes all of the fertilizations within a single breeding season ( $N_m = 1$ ). The maximum value of our range represents the case in which every male contributes to the fertilization of every clutch ( $N_m = \text{number of males present}$ ). True  $N_e$  must lie somewhere within this range. Given that

males may be polygynous (Licht 1975) and that unpaired males surreptitiously may fertilize eggs in recently laid clutches via “piracy” (see Vietites et al. 2005), it is likely that true  $N_e$  lies nearer to the upper limit of the range but that our maximum values are overestimates. It is also important to note that not all gravid females deposited a clutch during the breeding period. The reason for and significance of this are not known; however, counting all gravid females as reproductive could overestimate  $N_f$  and thus  $N_e$ .

It is crucial to note that, even if our maximum estimate of  $N_e$  does approximate true effective population size, the largest effective population in our survey consisted only of about 38 individuals (West Twin in 2004). Shaffer (1981) proposed minimum viable population (MVP) sizes in the region of 50 for sexual organisms with complex life histories. Halley et al. (1996) found that the MVP for European toads (*Bufo bufo* (L., 1758)) with a male-biased sex ratio was 300. Soulé (1980) gave a rule-of-thumb estimate of  $N_e$  equal to 500 to avoid genetic problems (inbreeding, excess levels of homozygosity, etc.). All of our populations studied across the Palouse fell well below these minimum numbers required for successful, sustainable populations (overall range 10.2–37.8; Table 3), suggesting that our populations may be vulnerable to local extinction. Of course, regardless of genetic problems, small populations are also less able to withstand environmental insults and stochastic events.

Additionally, the breeding system of spotted frogs is such that the success or failure of a communal egg mass is either enjoyed or suffered by the entire population (establishment of a SOS not withstanding). An unpredictable environmental event, such as drought, could very easily eliminate an entire year of later recruitment to that population.

The major advantage of communal laying is thermal insulation (Waldman and Ryan 1983). Spotted frogs are among the earliest amphibians to breed vernal in the Northwest (Leonard et al. 1993), allowing for a longer hydroperiod that likely facilitates metamorphosis before ponds dry in the summer. Spotted frog eggs that are laid communally retain heat from the day into the night (Licht 1971) and, in *R. sylvatica*, are often warmer than surrounding water (Waldman and Ryan 1983). Female *R. sylvatica* lay eggs in shallow water on top of vegetation, in open areas, and often with many eggs above the surface. This also works to the thermal advantage of clutches by maximizing solar exposure (Seale 1982). The vegetation on which eggs are laid reduces water flow around the masses, thus maintaining elevated temperatures (Licht 1971; Howard 1980).

The same factors that make communal oviposition a successful tactic in cool and (or) wet years may result in a devastating loss of eggs in dry years. If an unusually dry period occurs after deposition but before hatching, eggs could be stranded on the bank or tangled in emergent vegetation, and so not be permitted to drop with the water level. An entire year's reproductive effort could be lost to desiccation. This was the case for Smoot Hill in the spring of 2004. Without our intervention (shifting egg masses a few centimetres toward the center of the pond until again at the new margin), the entire reproductive output of that year would have been completely lost. Eden Valley also would have lost the 9 clutches (of 12 total in the pond) laid at the POS in the

spring of 2004. Licht (1971, 1974) observed stranding of egg clutches in Yellowstone National Park and British Columbia after only a few days without rain.

Secondary oviposition sites, SOSs, were established in 2004 at both Smoot Hill and Eden Valley after POSs were completely dry. If a female was to arrive at the POS and perceive that it is no longer a viable egg site, it would serve as a strategy to minimize the loss of that individual's clutch of eggs to create a SOS. However, waiting to determine the success of the POS carries with it the risk of eggs failing to develop before the pond dries, especially in dry years when the success of the POS would be most compromised. The establishment of a SOS does not necessarily assure hatching success. The SOS at Smoot Hill ended up above the water line as well, and again would have been a complete loss without our intervention.

Individual breeding populations that may be vulnerable to local extinction also may be components of more resilient metapopulations. The latter consist of arrays of populations among which there is dispersal and gene flow, and for which simultaneous extinction of all units in an array is unlikely (Smith and Green 2005). For *R. luteiventris*, Pilliod et al. (2002) provide evidence for metapopulation structure across an undisturbed montane landscape in Idaho. However, since 1900, 97% of the wetlands of the Palouse bioregion have been converted to cropland, hay, or pasture (Sisk 1998). Overall, 94% of native types of land cover have been converted (Sisk 1998). The degree of demographic and genetic connectedness among populations of *R. luteiventris* across the Palouse is unknown empirically, but interpond dispersal may be low. The sites in which spotted frogs breed on the Palouse almost entirely are small, isolated, man-made farm ponds: apparent islands in a sea of agriculture.

Although agricultural ponds have been shown to support amphibian populations (Knutson et al. 2004), spotted frogs surely are exposed to numerous agrochemicals, with possible detrimental consequences (Alford and Richards 1999). For example, Marco et al. (1999) demonstrated that *R. pretiosa* (the western sister taxon to *R. luteiventris*) is one of the most sensitive amphibian species in the Pacific Northwest to both nitrite and nitrate used in fertilizers. Distance from agricultural land is one variable that has been determined to be important for successful reproduction of *R. luteiventris* (Monello and Wright 1999).

### Final remarks

What data are needed to determine whether and how to manage a species of conservation concern? First, we need a thorough understanding of those factors (natural and anthropogenic) that are causative of population declines. Often this is fairly straightforward. Second, and more difficult, we need to determine how different aspects of that species' natural history may predispose it to the negative influences of the above factors. Only with a thorough understanding of a species' natural history can we develop management plans that will stabilize or, even better, recover a vulnerable species. Our study of *R. luteiventris* is a case-in-point. For example, only by knowing that these frogs lay their eggs communally in shallow water could a biologist make sensible recommendations concerning the manipulation of hydroperiods in a

managed wetland. Natural-history data are crucial for both generating and then testing the effectiveness of conservation management plans.

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