

NORTHWESTERN SALAMANDER (*AMBYSTOMA GRACILE*) OVIPOSITION SITES AND HATCHING SUCCESS IN THE CASCADE MOUNTAINS OF SOUTHERN WASHINGTON

JAMES G. MACCRACKEN

Longview Timberlands LLC, Box 667, Longview, Washington 98632, USA
e-mail: jmac@longfibre.com

Abstract.—Reproductive success of amphibians is influenced by choice of oviposition sites, including Northwestern Salamanders (*Ambystoma gracile*) whose egg masses are fixed to vegetation. During summers of 1999-2002, I surveyed 33 permanent ponds in a 26 ha wetland (935 m elevation) for Northwestern Salamander egg masses, quantified oviposition site characteristics, and tracked embryonic development and survival. The number of egg masses found ranged from 141-235 annually, and the active oviposition period was 4-8 weeks. An average (\pm SE) of $63.4 \pm 3.7\%$ of egg masses were attached to stems of Sitka Sedge (*Carex sitchensis*), $23.3 \pm 3.4\%$ to overhanging shrub stems or completely submerged sticks, and $8.3 \pm 4.9\%$ were unattached. On average, $62.0 \pm 6.1\%$ of egg masses were in deep water, $25.7 \pm 4.9\%$ in shallow water, and $12.3 \pm 2.6\%$ along the edge of deep and shallow areas. Egg masses were deposited at an average depth of 24.4 ± 0.5 cm. A mean of $53.1 \pm 3.5\%$ of egg masses had at least one embryo hatch, which on average took 9.0 ± 0.5 weeks. Rough-skinned Newts (*Taricha granulosa*) were observed feeding on embryos. Regression tree models indicated that use of ponds for oviposition was negatively influenced by the relative abundance of Rough-skinned Newts, and positively related to the relative abundance of larval Northwestern Salamanders. Hatching success was greatest in intermediate sized ponds where the number of overhanging shrubs was greatest. These results suggest that Northwestern Salamanders avoided ponds where potential predators were most abundant (including Brook Trout, *Salvelinus fontinalis*) and that the presence of larval conspecifics was indicative of favorable oviposition and rearing habitats.

Key Words.—*Ambystoma gracile*; breeding; egg; habitat use; Northwestern Salamander; predation risk; regression trees; reproduction; Washington.

INTRODUCTION

The Northwestern Salamander (*Ambystoma gracile*) breeds in a variety of lentic habitats ranging from the backwaters of coastal rivers to alpine lakes (Nussbaum et al. 1983; Leonard et al. 1993). The species also exhibits substantial plasticity in breeding ecology and morphology (Petranka 1998). Northwestern Salamander oviposition behavior is likely subject to strong selection pressures (*sensu* Resetarits 1996) that affects progeny at both the embryonic and larval life stages. Embryos develop in egg masses fixed in place by attachment to vegetation (Nussbaum et al. 1983; Petranka 1998; Fig. 1). Consequently, conditions at oviposition sites (e.g., water flow, depth, and temperature) could have a substantial influence on embryonic development and survival. However, larval salamanders can move to other areas within a pond as conditions change, but are confined to that particular water body until metamorphosis.

Females should choose oviposition sites that maximize offspring survival, but several factors confound site selection. For example, variation in lentic habitats may present individuals with a wide array of suitable sites, and environmental conditions after egg deposition are unpredictable. The introduction of trout (*Salvelinus fontinalis*, *Oncorhynchus spp.*) into many watersheds has



FIGURE 1. Northwestern Salamander (*Ambystoma gracile*) depositing an egg mass on an overhanging, partially submerged stem of Bog Laurel (*Kalmia microphylla*) (Photograph by James G. MacCracken).

been shown to negatively affect Northwestern Salamanders, and they may avoid ponds with trout

MacCracken—*Ambystoma gracile* reproduction



FIGURE 3. Photograph of a series of Beaver (*Castor canadensis*) ponds illustrating the extent of shallow water emergent vegetation (left side of pond in foreground, 10% of the surface area) and open water areas. The pond in the foreground has a surface area of 365.3 m² and a maximum depth of 0.9 m. In the foreground is 19 L plastic bucket (Photograph by James G. MacCracken).

(Hoffman et al. 2004; Larson and Hoffman 2002; Taylor 1983; Tyler et al. 1998a). Another factor that may influence oviposition is the presence of larval conspecifics. Northwestern Salamander larvae and some other ambystomatids do not metamorphose for 1-3 years (Petranka 1998), and ponds with larvae may be a reliable indicator of favorable habitat. However, to my knowledge, that aspect of habitat selection has not been examined.

This paper describes the oviposition sites of

Northwestern Salamanders, and examines relationships among abiotic and biotic conditions, and pond use for oviposition, and embryonic development and survival. I used tree-based models to assess the relative importance of pond characteristics, predators, and conspecifics on pond use and hatching success of Northwestern Salamanders.

MATERIALS AND METHODS

Study Area.—I conducted this study in a 25.5 ha wetland that was a mix of shallow water, fen, and bog habitats (*sensu* Pielou 1998) in the Cascade Mountains of southwestern Washington (Fig. 2). The wetland had a southeast aspect, 3% slope, and contained numerous ponds of various sizes and in various stages of vegetation encroachment. The southern portion of the wetland was typical of a Beaver (*Castor canadensis*) engineered shallow water wetland (Fig. 3). It was composed of a series of 11 impoundments along the primary drainage course (Fig. 2); however, Beaver did not occupy the wetland during this study. The northern half of the study area, as well as the forest-wetland edge in the southern half, was primarily a fen intermixed with small, isolated, poorly drained portions with bog characteristics (Pielou 1998).

The larger Beaver ponds had wide shallow (≤ 0.5 m) margins, excluding the dams, which supported emergent vegetation: primarily Sitka Sedge (*Carex sitchensis*),

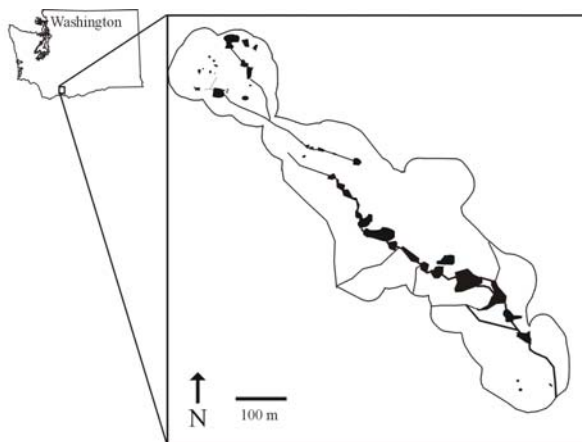


FIGURE 2. Location of the 25.5 ha wetland study site in Washington, U.S.A and the distribution and size of ponds surveyed for *Ambystoma gracile* egg masses and major stream courses. Width of streams indicates relative flow levels. Surveys were conducted from 1999-2002.



FIGURE 4. A photograph of a smaller pond with steep margins, little emergent vegetation, but several partially submerged, overhanging shrub stems. The net to the left is approximately 1.5 m long, the surface area of this pond is 8.9 m², and the maximum depth is 1.3 m (Photograph by James G. MacCracken).

Narrow-leaved Burr-reed (*Sparganium angustifolium*), and Yellow Pond-lily (*Nuphar polysepalum*). These ponds also had an abrupt transition to deep water (> 0.5 m) that contained little to no aquatic vegetation, creating a distinct open water-emergent vegetation edge. In contrast, the smaller ponds in the fen area had steep margins that went directly to the pond bottom (Fig 4). These ponds often had overhanging, partially submerged, stems of Bog Laurel (*Kalmia microphylla*), Bog Blueberry (*Vaccinium uliginosum*), and Sitka Alder (*Alnus crispa*) and, occasionally, relatively small areas of emergent vegetation. In addition, some ponds in the fen/bog areas were relatively deep given their small surface area, which appeared to be the result of perimeter encroachment by a floating mat of sedges, shrubs (*V. uliginosum*, *K. microphylla*) and Peat Moss (*Sphagnum spp.*)

The fen wetland was dominated by Sitka Burnet (*Sanguisorba canadensis*), Marsh Marigold (*Caltha sp.*), sedges (*Carex spp.*), Cottongrass (*Eriophorum angustifolium*), Hardhack Steeplebush (*Spirea douglassi*), Bog Blueberry, and Sitka Alder. The entire wetland was surrounded by Noble Fir-Western Hemlock (*Abies procera-Tsuga heterophylla*) forest that was managed for timber production (see MacCracken 2005). Elevation ranged from 915-940 m.

I surveyed 33 ponds from 1999-2002. In 1999, I estimated pond volume by multiplying pond surface area by pond depth, measured at the deepest point. Surface area was estimated by determining the geometric shape (circle, ellipse, rectangle, etc.) that best represented the pond surface (some ponds were segmented into two or more shapes), and I took the appropriate measurements with a meter stick

or tape. This procedure overestimated volume, but this bias was consistent across ponds and provided a useful index of pond size. Surface area estimates ranged from 0.3-800.0 m², depths from 0.3-2.5 m, and volumes from 0.5-1040 m³. At the same time, I visually estimated the percentage of the surface area of a pond occupied by emergent vegetation, and I counted the number of overhanging, partially submerged shrub stems, and completely submerged sticks \leq 4 cm diameter. Observations over the four years of study indicated that Brook Trout (*Salvelinus fontinalis*) were present in 10 of the ponds in the southern half of the wetland, but the other ponds were not connected to the drainage system that contained fish or a downstream barrier prevented fish occupation.

Egg Mass Surveys.—I surveyed each pond every 5-7 days beginning with the start of the active oviposition period until all egg masses had completed hatching. An egg mass was considered to have been successful if at least one embryo hatched. I characterized hatching by tear-shaped capsules in an egg mass, formed as the embryos pushed through the jelly, to exit an egg mass.

I searched each pond for egg masses by traversing the perimeter and wading sections where egg masses could not be seen from the shore. Water clarity permitted viewing to 2 m depth. When an egg mass was first discovered, I inserted a numbered pin flag into the substrate next to the egg mass. I also estimated the depth (cm) of the top of each egg mass below the water surface with a meter stick, recorded the substrate to which the egg mass was attached, and whether it was in shallow water, deep water, or along the edge of deep and shallow areas. If an egg mass had been fed upon (portions missing, ragged and irregular edges, hanging pieces of jelly, etc.), I estimated the proportion of an egg mass missing and recorded observations of predator activity. In addition, I also estimated the percentage of embryos that appeared dead (white, desiccated, physically damaged, etc.). I recorded

TABLE 1. Total number of Northwestern Salamander (*Ambystoma gracile*) egg masses, percentage lost, percentage attached to various substrates, percentage in three pond habitats, and number of ponds with egg masses in 1999-2002 in the Cascade Mountains of southwestern Washington, U.S.A.

	1999	2000	2001	2002	Mean (SE)
Total egg masses	191	141	235	195	190.5 (95.2)
Egg masses lost (%)	44	30	23	49	36.5 (6.0)
Due to <i>Taricha granulosa</i> (%)	9	2	12	5	7.0 (2.2)
Attachment substrate (%)					
<i>Carex sitchensis</i> stem	56	no data	68	66	63.4 (3.7)
stick/shrub stem	19	no data	21	30	23.3 (3.4)
other	7	no data	6	2	5.0 (1.5)
not attached	18	no data	5	2	8.3 (4.9)
Pond habitat					
deep water	72	no data	63	51	62.0 (6.1)
shallow water	16	no data	29	32	25.7 (4.9)
edge (of deep and shallow areas)	12	no data	8	17	12.3 (2.6)
Number of ponds	31	31	33	33	32.0 (0.7)

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water temperature for each pond at the outflow at every visit with a liquid thermometer about 12 cm below the surface. In addition, I established four weather stations, each equipped with a maximum-minimum thermometer and two rain gauges (about 100 m apart) in the wetland, which I checked and reset at every visit.

Embryonic Development.—I recorded embryonic development at each visit. I devised a 6-stage development classification scheme by combining the 46 stages used by Brown (1976). The six developmental stages could be recognized through the water without magnification, which minimized disturbance to egg masses and reduced any effect that handling might have had on the integrity of their attachment, as well as embryonic survival and development. Stage 1 ranged from egg deposition to development of the neural plate. Stage 2 advanced to development of the head, stage 3 included development of the heart, Stage 4 was recognized by development of gills, Stage 5 coincided with the emergence of forelimbs, and Stage 6 was at hatching.

Amphibian and trout surveys.—I also conducted visual encounter surveys (Crump and Scott 1994) for Northwestern Salamander larvae and adult Rough-skinned Newts (*Taricha granulosa*) each time I visited a pond. These surveys consisted of traversing the perimeter of each pond and counting all individuals observed. In addition, I noted the presence of Brook Trout during these surveys.

Data Analyses.—I compared abiotic or biotic variables with egg mass numbers, pond use, or hatching success using Pearson correlation coefficients. I used *T*-tests to compare the number of egg masses in ponds with trout, to ponds where trout were not observed. Actual *P*-values and effect sizes are presented in lieu of setting an arbitrary significance level (Johnson 1999; Anderson et al. 2000, 2001; Ridley et al. 2007).

I used regression tree models (Breiman et al. 1998) to estimate the influence of pond characteristics, and the presence of predators and conspecifics on use of ponds for oviposition and on hatching success. Tree-based models are powerful tools for ecological data analyses (e.g., Sutherland and Bunnell 2001; Steele et al. 2003; Sullivan et al. 2006) as they often perform better, and are unencumbered by the assumptions of most parametric statistical models (De'ath and Fabricius 2000). They also incorporate both continuous and categorical variables, reveal important structure in complex data sets characterized by nonlinear relationships, higher-order interactions, and missing values, and they are easy to interpret and use for prediction (De'ath and Fabricius 2000).

Two separate trees were estimated, each with a different response variable indicative of either pond

use or quality. Because large ponds had more potential oviposition sites and habitat types than smaller ponds, the first tree was based on the number of egg masses/m³ of pond. The second tree had the percentage of egg masses/pond that successfully hatched as the response variable. The explanatory variables for each tree were: (1) the percentage of the surface area of a pond in emergent vegetation; (2) the number of overhanging, partially submerged shrub stems; (3) the number of completely submerged sticks; (4) mean water temperature; (5) maximum water temperature; (6) the presence of Brook Trout; and (7) the maximum number of Rough-skinned Newts and larval Northwestern Salamanders counted during any single visit to a pond for each year. A pond was considered occupied by trout if they had been observed in the pond at least once during the study. The maximum number of newts and salamanders observed during any one visit/year provided a better measure of the abundance of these species due to imperfect detections associated with visual encounter surveys (Crump and Scott 1994).

Trees were pruned using 10-fold cross-validation and the one standard error rule (Breiman et al. 1998). Tree stability was assessed with 50 replicates of the cross-validation procedure for each model. Program DTREG (<http://www.dtreg.com>) was used for the regression tree analyses. All means reported in the text are followed by their standard error in parentheses.

RESULTS

I observed 762 egg masses during this study, with the greatest number occurring in 2001 (Table 1). I found 88% more egg masses (*P* = 0.005) in ponds where trout were not observed than in ponds with trout (Table 2). The earliest egg mass I discovered was on 5 April 2001. On that date, the average pond water temperature was 4°C and the average maximum and minimum air temperatures were 11 and -9°C, respectively. The latest I observed a Stage 1 egg mass was 20 July 1999, when the average pond temperature was 11°C and the average maximum and minimum air temperatures were 24 and 1°C, respectively. The number of new egg masses I observed on each visit

TABLE 2. Mean (standard error) number of Northwestern Salamander (*Ambystoma gracile*) egg masses/pond, number of egg masses/pond adjusted for pond volume (m³), percentage of egg masses hatching, and days to hatching for ponds with and without Brook Trout (*Salvelinus fontinalis*) in the Cascade Mountains of southwestern Washington, sampled in 1999-2002. Results of *t*-tests comparing means of each metric between pond types are also presented.

	<i>Salvelinus fontinalis</i>		<i>t</i> -statistic	<i>P</i> -value
	Present	Not Observed		
Number of egg masses	4.8 (0.4)	9.8 (1.3)	2.0	0.07
Egg masses/m ³	0.1 (0.1)	0.9 (0.3)	3.1	0.005
Percentage hatching	49.9 (4.8)	54.5 (4.1)	0.7	0.24
Weeks to hatching	8.8 (2.0)	9.3 (1.6)	1.0	0.15

TABLE 3. Mean (standard error) depth of Northwestern Salamander (*Ambystoma gracile*) egg masses below the water surface and number of egg masses by attachment substrate and pond habitat in the Cascade Mountains in southwestern Washington, USA from 1999-2002.

	Depth (cm)	Egg Masses (n)
Substrate		
<i>Carex sitchensis</i> stem	24.0 (1.0)	332
Stick	28.6 (1.6)	126
<i>Nuphar polysepalum</i> stem	31.5 (4.0)	9
unidentified root	26.2 (4.7)	5
nylon string ¹	10.0 (3.5)	4
<i>Potamogeton gramineus</i>	27.0 (10.3)	3
<i>Vaccinium uliginosum</i> , <i>Kalmia microphylla</i> , or <i>Alnus crispa</i> stem	8.0 (1.0)	2
Habitat		
deep water (≥ 0.5 m)	30.9 (0.9)	295
shallow water (< 0.5 m)	17.5 (1.0)	138
edge	27.8 (1.4)	55

¹Used to secure funnel traps and water temperature data loggers.

was moderately correlated ($r = 0.52$, $P = 0.02$) with pond water temperature. However, I found 88% of new egg masses when water temperatures ranged from 10-15°C, the balance when temperatures were between 4-9°C and none when temperatures exceeded 15°C. Onset of oviposition coincided with a combination of water temperatures reaching 4°C and maximum air temperatures exceeding 10°C.

The majority of egg masses were attached to stems of Sitka Sedge, followed by shrubs and sticks, and other substrates (Table 1). An average (\pm SE) of $8.3 \pm 4.9\%$ of egg masses were unattached or became unattached shortly after being deposited. Egg masses were laid primarily in deep water habitat (Table 1). Egg mass depth ranged from 0 to 100 cm below the surface and averaged 24.4 ± 0.5 cm. Egg masses were attached to emergent vegetation 27-31 cm deep, 26-29 cm deep on sticks and exposed roots, but only 8-10 cm deep attached to overhanging shrubs (Table 3).

On average, $36.5 \pm 6.0\%$ of egg masses disappeared, most from unknown causes (Table 1). However, I observed Rough-skinned Newts feeding on egg masses on 19 separate occasions, accounting for $7.0 \pm 2.2\%$ of the losses, and the appearance of another 14% of the egg

TABLE 4. Mean (standard error) percentage of Northwestern Salamander (*Ambystoma gracile*) egg masses that had at least one embryo hatch, weeks to hatching, and duration, in weeks, of six embryonic developmental stages in the Cascade Mountains of southwestern Washington from 1999-2002.

	1999	2000	2001	2002
Percent hatching	53.6 (5.5)	62.8 (5.8)	48.1 (7.2)	48.0 (5.6)
Duration of stage 1	2.3 (1.0)	2.5 (0.8)	1.6 (1.1)	2.9 (0.5)
Duration of stage 2	2.0 (1.5)	1.8 (1.7)	1.8 (1.8)	3.0 (1.7)
Duration of stage 3	2.1 (1.0)	1.7 (1.7)	1.7 (1.7)	3.0 (1.1)
Duration of stage 4	2.0 (1.2)	1.9 (1.0)	2.4 (1.9)	1.4 (1.4)
Duration of stage 5	1.8 (1.5)	3.1 (1.7)	3.3 (2.4)	2.2 (1.6)
Weeks to hatching	9.7 (2.8)	7.5 (2.1)	9.6 (1.9)	9.1 (2.8)

masses that were eventually lost was consistent with predation by Rough-skinned Newts. About one half of egg masses had at least one embryo hatch, although hatch rate varied by 9-15% among years (Table 4). The average number of weeks to hatching varied from 7.5 to 9.7.

The regression tree based on the total number of egg masses/m³ explained 57% of the variation in the data and was optimally sized at four terminal nodes. The explanatory variables in this model were the number of partially submerged shrub stems, Rough-skinned Newts, and larval Northwestern Salamanders (Fig. 5a). Ponds with few shrubs averaged 175% more egg masses than ponds with more shrubs. Ponds with few shrubs and low numbers of Rough-skinned Newts averaged 6-times more egg masses than those with more Rough-skinned newts. Ponds with few shrubs, few Rough-skinned Newts, and more larval Northwestern Salamanders averaged 220% more egg masses than ponds with similar amounts of shrubs and Rough-skinned Newts, but fewer larval Northwestern Salamanders.

The tree based on the percentage of egg masses that completed hatching explained 25% of the variation and also had four terminal nodes. The explanatory variables in this model were pond volume and number of overhanging shrub stems. Hatching success was 72% greater in ponds ≤ 3.3 m³ than in larger ponds (Fig. 5b). Furthermore, in ponds > 3.3 m³, the percentage of egg masses hatching was 1.5-fold greater where shrubs were more abundant. In addition, in ponds > 3.3 m³ with more overhanging shrubs, hatching success was 4.5-times greater in ponds ≤ 71.4 m³ than in ponds > 71.4 m³ (Fig. 5b).

DISCUSSION

The importance of oviposition site selection on reproductive success in amphibians has long been recognized. However, most studies have focused on anurans, and the effects of timing, predators, and competitors on the number and rate of eggs laid, or larvae performance (Crump 1991; Howard 1978; Resetarits et al. 2004; Spieler and Linsenmair 1997; Wilbur and Alford 1985). I did not find any studies that quantified habitat characteristics at oviposition sites of Northwestern Salamanders. Most publications had broad descriptions of

the months that egg masses were first observed, weeks to hatching, generic descriptions of attachment substrates, and ranges of depths below the surface (Snyder 1956; Knudsen 1960; Licht 1975; Taylor 1983; Hoffman et al. 2003). Several authors have noted egg mass attachment substrates similar to those found in this study (Slater 1936; Henry and Twitty 1940; Watney 1941; Knudsen 1960; Licht 1975). Only Hoffman et al. (2003) noted that limbs and branches were used more than other substrates. In addition, the range of egg mass depths reported in other studies was similar to this

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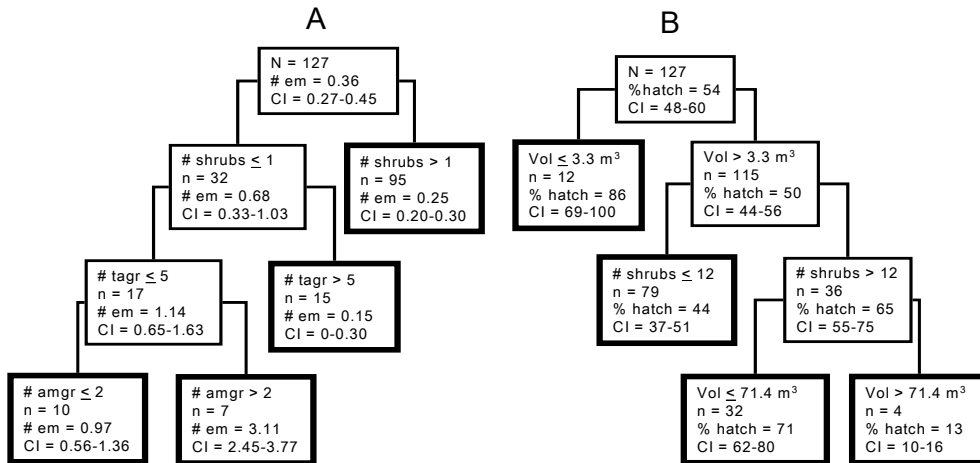


FIGURE 5. Regression trees for; “A” the number of egg masses/m³, and “B” the percentage of egg masses hatched/pond. Each rectangle is a node of the tree and terminal nodes have thicker frames. Within each node is the sample size (N or n), the explanatory variable producing the split, the value associated with the split, and the mean and 95% confidence interval (CI) of the response variable (# em is the mean number of egg masses/m³ and % hatch is the mean percentage of egg masses hatching) for each tree. # shrubs is the mean number of overhanging shrub stems, # tagr is the mean number of Rough-skinned Newts (*Taricha granulosa*), # amgr is the mean number of larval Northwestern Salamanders (*Ambystoma gracile*), and Vol is the mean pond volume.

study (Slater 1936; Henry and Twitty 1940; Licht 1975).

Of the studies that quantified other characteristics of Northwestern Salamander oviposition sites and embryonic development, most results were similar to this one; including egg mass depths (Licht 1975), timing of breeding in relation to water temperature (Licht 1975; Eagleson 1976), and embryonic development (Brown 1976). However, Licht (1975), Slater (1936), and Watney (1941) reported time to hatching of about one-third of what I found. Water temperature may explain this discrepancy as both Licht (1975) and Slater (1936) reported higher average water temperatures. Watney (1941) did not measure water temperature, but her observations were from a lake at sea level.

Regression tree models indicated that three biotic characteristics interacted to influence oviposition by Northwestern Salamanders. The variable producing the greatest difference in the number of egg masses deposited in ponds was the maximum number of Rough-skinned Newts in a pond. I observed Rough-skinned Newts tear through egg mass jelly with their forearms, as well as bite off pieces, to access embryos. In addition, about 58% of the egg masses that were lost appeared to have been dismantled by Rough-skinned Newts. Experiments with anurans indicate that females can detect the presence of predators in artificial ponds and either avoid, or abort oviposition (Resetarits and Wilbur 1989; Rieger et al. 2004).

Brook Trout likely prey on Northwestern Salamander larvae (Efford and Mathias 1969; Tyler et al. 1998a), and occurred in 30% of the ponds in my study area. The effects of introduced trout on the ecology of ambystomatid salamanders, including Northwestern Salamanders, have

been documented. All studies have found fewer animals in the presence of trout (Taylor 1984; Larson and Hoffman 2002; Hoffman et al. 2004). Hoffman et al. (2004) also reported fewer egg masses in one lake with trout than another adjacent lake without trout. Nonetheless, Northwestern Salamanders inhabit lakes with trout and coexist through behavioral adjustments, such as nocturnal activity and use of shallow water habitats (Efford and Mathias 1969; Tyler et al. 1998b; Hoffman et al. 2004). The fact that presence of trout in a pond was not important in either regression tree supports the observations of coexistence and the primacy of the other factors measured in this study in the breeding ecology of Northwestern Salamanders.

The second most important factor in pond use by Northwestern Salamanders was the number of larval conspecifics in ponds with relatively few Rough-skinned Newts. Most Northwestern Salamander larvae over-winter in natal ponds at least once before metamorphosis and the presence of larvae may provide females with a highly reliable mechanism for assessing pond quality through chemical cues (e.g., Petranka et al. 1987; Resetarits 1996). Mesocosm experiments similar to those of Resetarits and Wilbur (1989) and Rieger et al. (2004) could be used to test the relative influence of predators and larval conspecifics on pond use for oviposition by Northwestern Salamanders.

Hatching success was influenced by both physical and biological characteristics of the ponds. The initial and final split in the regression tree was based on pond volume with smaller ponds averaging 1.7 to 5-fold greater hatching success. Smaller ponds tended to have fewer Rough-skinned Newts and less surface area in emergent

vegetation, i.e., shallow water. As noted, more egg masses were laid in deep water portions of ponds.

The number of partially submerged shrubs was also an important variable in both trees. However, the number of overhanging shrubs in a pond had contrasting effects as ponds with few shrubs had more egg masses, but ponds with more shrubs, greater hatching success. When two or more explanatory variables are very close in their effectiveness in splitting a node, the nature of the cross-validation procedure results in a random selection of one of the variables, and examining the relationships between the selected variable and other “competing or surrogate” explanatory variables at a node can be useful in tree interpretation (Breiman et al. 1998). The best competing variable for overhanging shrubs in the analysis of pond use was the presence of trout, and as noted above, there were 9-times more egg masses in ponds without trout than ponds with trout. In addition, there were more shrub stems in ponds without trout than in ponds with trout. The best competing variable for shrubs in the hatching success model was maximum water temperature. Egg masses deposited on overhanging shrub stems were closer to the surface than egg masses deposited on other substrates and ponds in the study area developed water temperature strata over the summer with surface strata 3-4°C warmer than at greater depths (MacCracken unpubl. data). Overhanging shrub stems may provide higher quality attachment substrates. They are stronger than Sitka Sedge stems, about the same diameter, and water temperatures may favor accelerated embryo development, reducing exposure to Rough-skinned Newts and the chance of desiccation as water levels progressively declined over the summer.

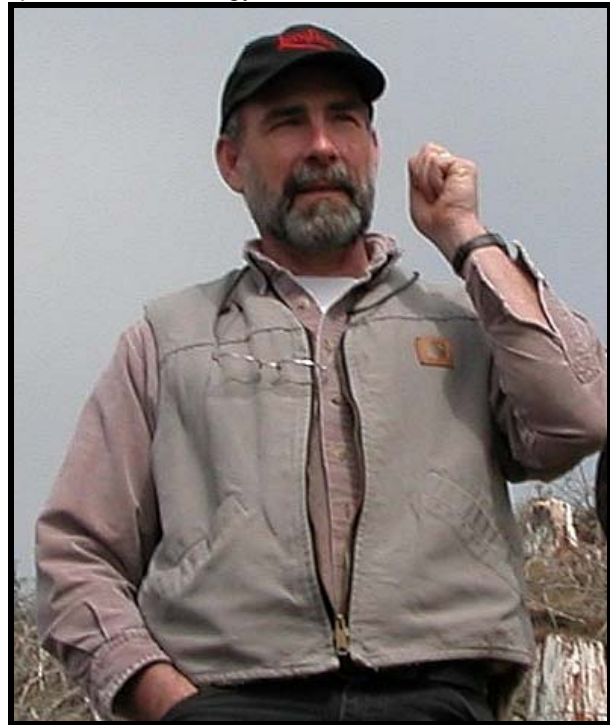
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MacCracken—*Ambystoma gracile* reproduction

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JAMES G. MACCRACKEN is a Wildlife Biologist with Longview Timberlands LCC. He received his B.S. and M.S. from Colorado State University in Wildlife Biology and Range Ecology, respectively, and Ph.D. in Forestry, Wildlife, and Range Resources from the University of Idaho. His current research program is focused on estimating the effects of timber harvest on amphibians and small mammals. In addition, he provides technical assistance to company tree farm operations and state and federal forest policy makers (Photographed by Kenneth L. Risenhoover).

