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A LITERATURE REVIEW

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OREGON SPOTTED FROG (*RANA PRETIOSA*):
A LITERATURE REVIEW

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ABSTRACT

The Oregon spotted frog (OSF; *Rana pretiosa*) is presumed extirpated from ca. 70% of historic habitat in the Pacific Northwest. Successful conservation of the species will likely depend on a more detailed understanding of OSF habitat associations and life history requirements that drive those use patterns. Among the more prominent factors limiting knowledge of OSF habitat requirements has been an incomplete knowledge of the species' life history, extirpations asymmetrically concentrated in the lowland Pacific Northwest, and hydrological alterations in both unoccupied historic sites and sites where OSF is still present.

Data from historic and occupied OSF sites suggest a strong relationship between upper elevation limit and latitude, such that OSF at their northern range limits are unlikely to occur above 200 m. Oregon spotted frogs are generally associated with wetland complexes > 4 ha in size with extensive emergent marsh coverage that warms substantially during seasons when OSF are active at the surface. The expanse of inundation in wetlands where OSF are extant often varies greatly between spring and fall, but sites always include some permanent water juxtaposed to seasonally inundated habitat. Wetland complexes that include diverse hydrological regimes (based on National Wetland Inventory classification) may also be favored, and this pattern may be indicative of juxtaposed seasonal use habitats. Occupied OSF sites that are larger in spatial coverage tend to have larger populations. Current understanding of OSF demographic patterns suggests the species demonstrates more rapid population turnover than other ranid frogs in the Pacific Northwest, and larger populations may be less susceptible to high predation and stochastic events. Many remaining OSF populations appear isolated from the nearest known OSF site by extensive uplands, but how site isolation relates to population persistence is unclear.

Field observations and recent telemetry data suggest OSF utilize different wetland microhabitats for breeding, the non-breeding active season (summer and portions of spring and fall), and overwintering. Breeding sites are generally associated with seasonally flooded, shallowly sloping benches that are vegetated with the previous year's emergent vegetation and are relatively unshaded. Attributes of OSF oviposition behavior (apparently locally philopatric, communal, and selecting for shallow water that is likely to decline as spring progresses) may contribute to relatively frequent stranding of egg masses and substantial egg mortality. Limited data suggest that OSF adults may move little during the non-breeding active season, and may prefer microhabitats of moderate vegetation density that are near aquatic refuges. Oregon spotted frogs make at least occasional underwater movements during winter, and may make extensive use of streams or springs at higher elevation sites. Movements during winter may be associated with dissolved oxygen gradients, but this needs further corroboration. More broadly, OSF movements between seasonal use areas appear to be more extensive than movements within a seasonal use area, and appear focused on aquatic connections.

We recommend additional research in the following areas of OSF habitat associations: 1) Minimum site size and habitat complexity necessary to support an OSF population even when isolated; 2) Habitat characteristics and types of corridors that may reduce isolation between extant OSF breeding sites; 3) Overwintering habitat use and quality (especially for selected water quality parameters) at low and high elevation sites; 4) Attributes of OSF movements and utilized pathways between seasonal use areas; 5)

Importance of vegetation change (both invasion by non-native species such as reed canarygrass and encroachment by woody vegetation in fire-suppressed areas) in affecting habitat suitability, and OSF response to vegetation management alternatives; 6) OSF habitat responses to management practices such as livestock grazing and hydrological alterations (anthropogenic, beaver and others); and 7) Habitat attributes that relate to coexistence or increased risk of extirpation when OSF occur with non-native fish and bullfrogs.

SECTION I. BACKGROUND

The Oregon spotted frog (OSF: *Rana pretiosa*) occupies wetland habitats across a wide geographic and elevation range in the Pacific Northwest. Aspects of the species' autecology and behavior appear to make only a subset of available aquatic sites suitable. Understanding these habitat requirements and their link to OSF natural history is crucial to conserving the limited number of populations known to persist. The precariousness of the OSF situation, a species currently only a federal candidate for listing, is underscored by the fact that it has less than one third the extant populations possessed by the federally threatened California red-legged frog.

Several important factors confound our understanding of OSF habitat associations. Resurveys of historic sites across its geographic range (California, Oregon, Washington and British Columbia) over the last decade suggest that the OSF is currently found in < 30% of its original distribution (McAllister *et al.* 1993, Hayes 1997, Hayes *et al.* 1997). Extirpation of the OSF has also been more severe in its intensively altered lowland range, and probably includes wholesale loss from Oregon's Willamette Valley (Nussbaum *et al.* 1983, McAllister *et al.* 1993, Hayes 1994, Hayes *et al.* 1997). Loss from the Willamette Valley (potentially > 40% of OSF historic range in the western lowlands) combined with the low number of extant lowland populations (N = 5 in WA and BC) and extensive alteration of hydrology and vegation in now-unoccupied historic sites greatly constrains our ability to understand habitat associations in its lowland range. Further, the recent and widespread establishment of non-native predators and competitors across much of the species' historical range has potential to affect OSF habitat occupancy asymmetrically across habitat types.

Heightened concern over the species' status has generated increased attention to OSF ecology and habitat needs over the last 10 years. Until very recently, little had been done to specifically address OSF habitat associations and requirements. A synthetic review of existing data has not yet been conducted, and will be useful for evaluating the potential of unsurveyed wetlands to harbor OSF. We provide the following review of literature on OSF habitat associations to summarize current understanding, identify knowledge gaps, and provide resource managers with a basis for investigating potential

OSF habitats. Throughout the review, we relate what is known of habitat associations to aspects of OSF ecology that may form the basis for those associations. We begin with a brief review of early literature on OSF, most of which provides only general information on habitat associations. We then focus on more recent work related to OSF habitat associations at a broader landscape scale (Section II: Landscape-scale habitat patterns) and within-wetland scale (Section III: Within-wetland and seasonal habitat associations). These latter sections are intertwined, and a fuller understanding of OSF habitat associations will incorporate information that is relevant at both these scales. We conclude with recommendations for further research on OSF habitat use (Section IV).

Early Descriptions

Any review of historical attention to the habitat affinities of spotted frogs is complicated by the inclusion of two now-recognized species within the taxon formerly named *Rana pretiosa*. Under that nomenclature, the Oregon spotted frog frequently fell within *R. p. pretiosa* (*e.g*. Dunlap 1959, Dumas 1966). These relationships were clarified only recently with the elevation of *Rana pretiosa* (*sensu stricto*) to full species (Green *et al.* 1996, 1997)[1]. Historical observations attributable to the OSF were made by a variety of herpetologists and natural historians scattered across the 1900s (Jewett 1936, Graf *et al*. 1939, Slater 1939, Slipp 1940, Dunlap 1959, Dumas 1966 and others). Slipp (1940) associated OSFs in the Puget Lowlands with wetlands that were proximal to "prairie" habitats. Information from the Portland area and southern Willamette Valley in Oregon (assembled in Hayes 1994a) suggest that OSF historically made extensive use of off-channel wetlands associated with riverine meanderings. For example, Jewett (1936), in a study of amphibians near Portland, Oregon, commented that the taxon attributable to OSF was "common along the sloughs of the Willamette and Columbia rivers". Graf (1939) noted that OSF (discussed as spotted frogs) were common in the Willamette Valley south of Salem. This large flat expanse of valley was historically characterized by an abundance of sloughs and off-channel wetland habitats as well as extensive seasonally

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[1] The current *Rana pretiosa* (*sensu stricto*), which applies only to the western populations of the former *Rana pretiosa* (*sensu lato*), retains the same scientific name because the type specimen came from within the range of the western complex now called *Rana pretiosa*.

flooded emergent wetland (see Sedell and Froggatt 1984, Benner and Sedell 1997). Hayes (1994a) notes that the reduction in numbers of OSF in museum collections from the Willamette Valley coincided with the construction of large dams in the Willamette Basin that drastically reduced the extent and frequency of flooding in the region, which strongly influenced the formation and extent of off-channel wetland habitats (Benner and Sedell 1997).

Among the first researchers to investigate the ecology of OSF was L. E. Licht (1969b; 1971b; 1974; 1986a,b), who studied one population along the Little Campbell River in the Lower Fraser valley of southwestern British Columbia. He described that study site as a flat 7-ac [2.8 ha] field near sea level, dominated by rushes (*Juncus effusus*), sedges (*Carex* sp.), and buttercups (*Ranunculus repens*). The site was bordered on two sides by alder and coniferous forest. The Little Campbell River, a permanent, low-gradient stream, flowed through the field, and varied in width between 5 and 100 ft [1.5 – 30.3 m] depending on season. Vegetation along the river included rushes, sedges, pondweeds (*Potamogeton* sp.) and cattail (*Typha* sp.). A well-vegetated (with at least *Juncus* sp.) temporary pond ca. 40×200 ft [12.1×60.5 m] and 0.5 to 3.0 ft [0.2 – 0.9 m] deep was intermittently connected to the river by floodwaters. It generally held water until July. Other smaller pools occurred in the complex, but were generally dry by June. Oregon spotted frogs (and northern red-legged frogs; *Rana a. aurora*) used both the river and the pond for breeding, rearing and feeding after metamorphosis.

Work on the OSF shifted focus toward the species' conservation status in the early and mid-1990s. Inspection of sites where OSF had been documented from museum collections provided a quantitative assessment of the species' range contraction across the Pacific Northwest (McAllister *et al.* 1993; Hayes 1994a, b; Hayes 1997). A general model of OSF habitat was developed through this evaluation. Based on work in Oregon, Hayes (1994a, b) described the OSF as a warmwater marsh specialist generally associated with larger wetlands. McAllister and Leonard (1997) described the species as associated with emergent wetlands within forested landscapes. Habitat changes, such as hydrological alterations, successional and anthropogenic vegetation shifts, and introduction of a variety of non-native predators, have been qualitatively evaluated for their importance in OSF population risk (Hayes 1997, Pearl 1999, Haycock 1999).

Comparisons between historical and current habitat occupancy have resulted in increased concern of OSF conservation status, and have led to designations in Oregon (Sensitive-Vulnerable; Oregon Natural Heritage Program 1995), Washington (State Endangered; WDFW 2000) and British Columbia (Endangered; COSEWIC 1999). These elevated concerns for the species' status have generated study of specific segments of life history and ecology that are the functional basis for OSF habitat associations. While this recent work has advanced our understanding of OSF habitat associations, many aspects of the species' life history and ecology remain incompletely understood.

SECTION II. LANDSCAPE-SCALE HABITAT PATTERNS

Elevation and Latitude

Compilation of location data on historic and extant sites led Hayes (1994a, 1997) to posit that a latitudinal gradient of OSF upper elevation limits exists across the species' range. Additional OSF populations have been detected since the hypothesis was framed. Here, we examine this hypothesis including the expanded list of OSF occurrences and historic sites thought to be unoccupied (N = 73 sites). We generated elevation and latitude (in meters) from US Geological Survey topographic maps and from GPS measurements taken on site. We adjusted latitude by subtracting the UTM Northing of each site from that of the northernmost record (Seabird Island) in British Columbia. To assess whether maximum elevations of OSF across its range are related to latitude, we divided the entire range (ca. 930 km) into 9 equal segments of ca. 104 km. We used the mean elevation of the two highest OSF sites (extant or unoccupied) within each 104-km band as the response, and ordered the bands 1 (north) to 9 (south). We used this adjusted UTM Northing as the dependent variable and the ordered latitudinal bands as the independent variable in a linear regression analysis (S-Plus, Student Edition 4.5, 1999).

We found that maximum elevation of OSF sites within bands was strongly linked

to latitude (Multiple $R^2 = 0.89$; $F_{1,6} = 48.52$, $P < 0.001$; Figure 1). [2] We did not treat the data as a quadratic, since available wetland sites are disproportionately rare in middle elevations in the southern portion of OSF range. This pattern has strong implications for survey efforts across the range of the species, but particularly in northern segments of this range. These data suggest it is unlikely to find OSF above 200m above MSL in northern Washington and British Columbia. Moreover, anthropogenic impacts such as agricultural and urban development are generally most intensive within these lowest elevations, and surveys in the Willamette Valley (Oregon) and Puget Lowlands (Washington) suggest OSF populations have been disproportionately lost in these lower elevations (McAllister *et al.* 1993, Hayes 1994a, b; Hayes 1997; Figure 1). Conversely, surveys in southern Oregon and northeastern California cannot reasonably dismiss sites up to 1700 m as without potential to harbor OSF.

Physiological or ecological mechanisms underpinning this distribution pattern for OSF are currently not fully understood. However, much evidence exists to suggest that OSF are adapted to warmwater marsh conditions (summer shallow water exceeding 20° C), which sets the species apart from other *Rana* in the Pacific Northwest (Licht 1971, Hayes 1994a). Such warmwater habitats are likely to be less available toward the northern ends of this range, particularly at mid- and high elevations. Supporting the hypothesis of an association between OSF and warmwater wetlands are a lack of occurrence records from montane sites lacking extensive shallows and from coastal regions of comparable latitudes in Washington, Oregon and California, where mean and summer temperatures are relatively cool (Hayes 1994a). Autecological evidence of the OSF link to warmwater habitats include high critical thermal minima and slow developmental rates in egg stages compared with other pond-breeding *Rana* in the west (Licht 1971), as well as increased surface activity in adult OSF as water temperatures exceed 20°C (Hayes 1994a, b). Particularly at higher elevations and in varied topography,

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[2] Historic and extant sites come from McAllister *et al.* 1993, Hayes 1994, Hayes 1997, Pearl 1999, Haycock 1999, and unpublished data from J. Bowerman (Sunriver Nature Center), M. Blouin (Oregon State University), R. Hardy and D. Ross (US Fish and Wildlife Service, Klamath Basin Field Office). We used only the specifically identifiable sites from multiple records in Seattle (N = 2) and Vancouver, Washington areas (N = 2). The historic Sweet Home, Oregon site was not included since location information was not specific enough to generate latitude and elevation data. We do not include unverifiable records such as Dunlap's (1959) Paulina Lake and observations from the Warner Lakes basin, which are likely the westernmost extent of Columbia spotted frog (*Rana luteiventris*) (Hayes 1997).

it is likely that larger sites may be necessary to generate open habitat, greater insolation and warmer temperatures (Hayes 1997, Pearl 1999).
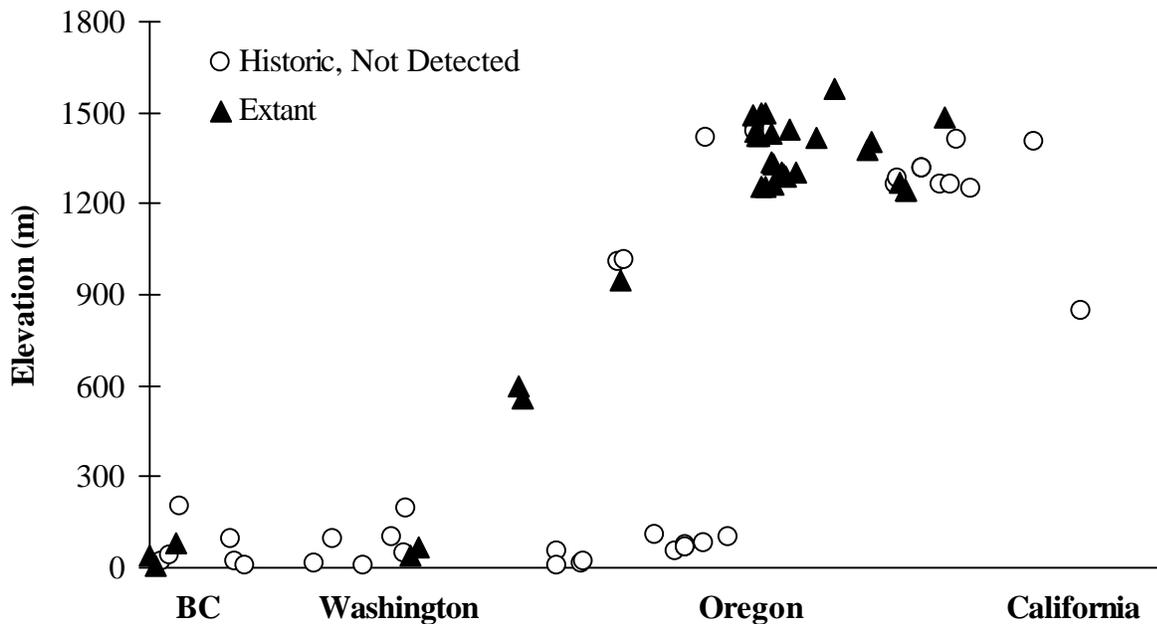

Figure 1. Elevation (meters above MSL) of historic and extant Oregon spotted frog sites across the species' latitudinal range.

Site Size and Isolation

After examining historical sites in the Willamette Basin in Oregon, Hayes (1994b) concluded that OSF required wetland sites where $\geq$ 4 ha (10 ac) of suitable habitat exist. Pearl (1999) found that 80% (4 of 5) of OSF breeding sites in the Three Sisters Wilderness Area of the Oregon Cascades exceeded 5 ha, while only 40% (10 of 25) of unoccupied sites in the study area exceeded that size. All 4 known OSF sites in Washington exceed 4 ha (Beaver Creek ca. 12 ha; Dempsey Creek 16 ha; Trout Lake 453 ha; Conboy Lake NWR 1989 ha.). More recent surveys have detected OSF populations at several Oregon sites at or below that threshold (*e.g.* Muskrat Lake, Unnamed Marsh,

Wickiup Reservoir ditch; C. Pearl, unpublished data). Historically, however, these sites probably functioned within a larger group of interacting habitats, and the latter 2 are notably small in breeding population size (<15 egg masses; Pearl and Bury 2000, J. Bowerman and C. Pearl, unpubl. data). Smaller, isolated populations are generally more likely to be extirpated by stochastic events and genetic drift (Lande 1988), and a variety of demographic attributes of OSF suggests they may be vulnerable to stochastic and chronic sources of mortality (M. Hayes and C. Pearl, unpubl. data). Modeling across a variety of amphibian taxa suggests pond-breeding frogs have high population variance and high local extinction rates relative to other groups, and that smaller frog populations experience disproportionately large population fluctuations (Green 2003). If small populations of OSF are particularly susceptible to chronic and stochastic mortality as a result of their demography (see Hayes 1997), larger sites may be favored for OSF persistence if they support larger populations.

We sought to examine this specific relationship between site size and OSF population size for sites where directed breeding surveys afford a reasonable estimate of effective population size (N = 14 sites; Appendix 1). For sites where multiple years of egg mass counts were available, we averaged across years. We adjusted egg mass counts to reflect the total portion of the site that was included in the egg mass surveys. For example, the egg mass tally for Conboy Lake NWR was divided by the 60% of suitable habitat surveyed to arrive at an estimate across the entire breeding site. For Conboy Lake NWR, we averaged counts of 1998 and 1999 data. We did not include data from very recent searches since anthropogenic hydrological changes are thought to have reduced population size (M. Hayes and J. Engler, pers. obs.). Estimated OSF egg mass production ranged from 10 (Wickiup ditch, Oregon; 2000-2001) to 9753 (Conboy Lake NWR, Washington; 1998, 1999). We used size estimates (extent of total habitat available during the spring freshet) from other reports and USGS topographic maps. Sizes of these sites ranged from 1-1989 hectares, and 13 of 14 sites considered were above the proposed 4 ha threshold (Figure 2).

We used a Spearman-rank correlation analysis (StatView 5.0.1, SAS Institute, Inc. 1998) since it provides a conservative assessment of the relationship between the two variables. This is appropriate because accuracy of counts, as well as number of years

during which surveys were conducted, varied across sites. For example, only one year of egg mass counts was available for 5 sites, and it is not well known how well single years reflect mean breeding population size. Thus, this analysis must be considered preliminary. Egg mass count data suggest there is a significant link between site size and OSF breeding population size (correlation coefficient: $\rho = 0.766$, $z_{\text{tie-adjusted}} = 2.762$, $P = 0.0057$). Data depicted in Figure 2 are natural log transformed only to fit onto one figure; the Spearman-rank analysis was on untransformed data.

Hayes (1994 a, b) proposed that two ecological attributes of OSF contribute to their association with larger wetlands: a reliance on warmwater habitats and the potential that the species has high mortality and population turnover rates compared with other western ranid frogs. Data supporting high mortality rates that may be unique to the OSF are briefly reviewed below, and if this is true, it may partially explain the lack of OSF persistence in smaller populations at smaller sites. Aspects of OSF ecology that may pre-dispose them to elevated mortality risks include vulnerability of egg masses to fluctuating water levels (Licht 1974, Hayes *et al.* 2000, Pearl and Bury 2000) and high vulnerability of post-metamorphic stages of OSF to predation (Hayes 1994a). For example, Licht (1974) found that eggs and post-metamorphic OSF had lower survivorship than related northern red-legged frogs (*R. a. aurora*) in a 2-yr field study. Juvenile OSF also appear to be more susceptible to bullfrog predation than equally sized northern red-legged frogs (Pearl *et al.* unpubl. data). Evidence suggesting high predation pressure on most OSF life stages includes cryptic behavior in larvae (Hayes 1995) and adult males (R. Haycock, pers. comm., C. Pearl, pers obs.), scarring on transmittered and field-caught adults, and observed predation by snakes and mink on transmittered and free-ranging adults (Hayes 1995, 1997; Haycock 1999, Hallock and Pearson 2001, Hayes *et al.* 2001, Pearl and Hayes 2002). Other sources of mortality, such as low overwintering survival, also have potential to contribute to relatively rapid population turnover in OSF (Hallock and Pearson 2001, Hayes *et al.* 2001, Risenhoover *et al.* 2001).

Information to specifically test our hypothesized reduced probability of persistence in smaller OSF populations at smaller sites is limited. Only one population extirpation has been cursorily observed. At that site in British Columbia, Licht (1969) reported 30 (1968) and 54 (1969) egg masses in the 7-ac [2.8 ha] emergent wetland and stream complex.

Repeated surveys have failed to detect OSF at that site (Haycock 1999, R. Haycock, pers. comm. 2003). Interpretation of causes of this extirpation is difficult since this OSF habitat experienced several potential stressors, including but not limited to, changes in vegetation, cattle grazing, and subsequent invasion by bullfrogs (Licht 1974).
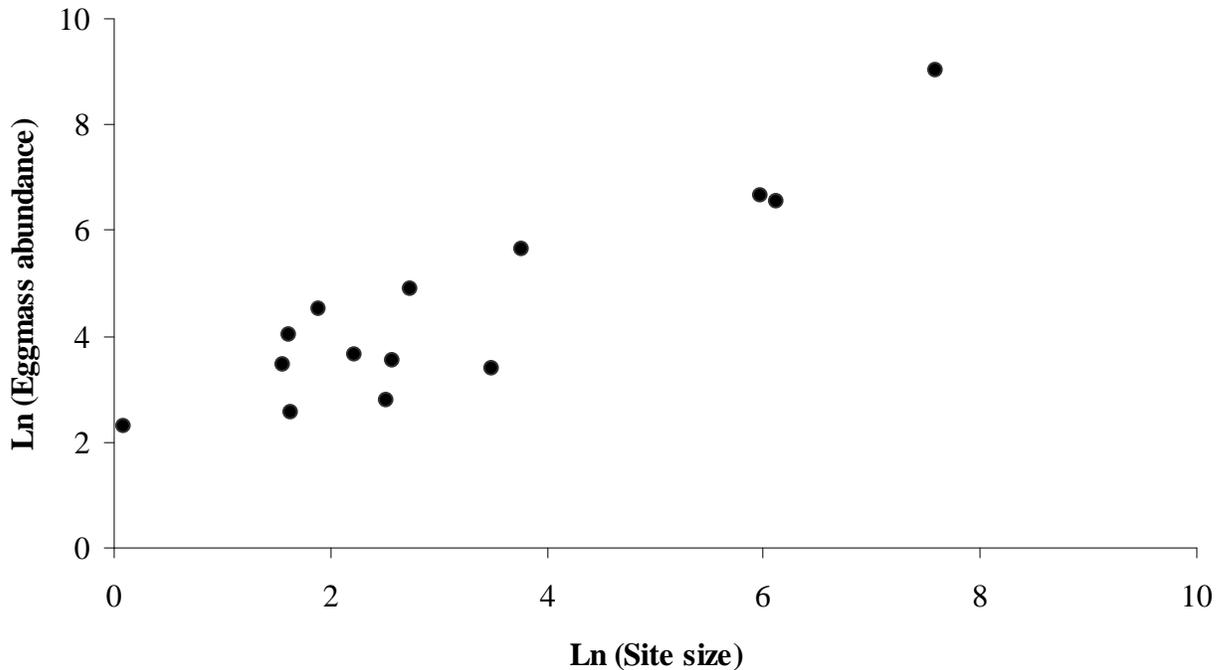

Figure 2. Relationship between site size and estimated breeding population size (mean egg mass counts of Oregon spotted frogs. Axes are natural log-transformed for display, not for Spearman-rank analysis.

Benefits of larger sites appear to be of aforementioned indirect nature (correlates of site size such as likelihood of a wetland containing warmwater habitats or of having multiple seasonal use habitats) than due to the size of the site *per se*. For example, available information does not suggest individual OSF make regular use of large ranges within or between sites. Rather, summer active season ranges may be particularly small, with adults commonly moving < 100 m between summer recaptures (Hayes 1998b, Pearl and Bury 2000, Watson *et al.* 2003; see Section III). Between-season OSF movements

may also be limited in habitat complexes where required seasonal microhabitat requirements are available within confined areas. Estimates of OSF home range size (N = 4 adult females) across a whole year at Dempsey Creek averaged 2.2 hectares (range 1.3 − 5.0 ha) in a lowland habitat complex that covers ca. 28.3 ha (15.6 ha wetland). Seasonal home ranges that included other tracked OSF were all smaller than the 2.2 estimate (discussed in Section III). At Trout Lake, all tracked OSF (N = 12) moved less than 400 m from their original capture location in fall and early winter (Hallock and Pearson 2001). Oregon spotted frogs have been able to persist in some smaller sites in Oregon (Long Prairie, Unnamed Marsh, Muskrat Lake, Wickiup ditch; Appendix 1) suggesting that small populations can persist at some sites near the lower end of the hypothesized range, but we believe this condition to be atypical. As previously mentioned, it is likely that these habitats were historically sub-populations within an interacting complex of breeding sites, and they may still today interact to a lesser extent with other Deschutes Basin OSF sites. Limited data suggests that OSF populations may be sustainable in contexts where sites interact or where seasonal habitat needs are present in relatively close juxtaposition.

Specific inquiry into other potential benefits (*e.g.* direct importance of insolation and elevated temperatures on larval rearing and adult basking areas) is needed to fully address the importance of site size on OSF population persistence. Larger sites are probably more likely to include multiple wetland types, and thus be more likely to provide for seasonal microhabitat use by OSF, more likely to have a temporally reliable prey base, or more likely to include suitable overwintering sites. Larger sites may also be more likely to be recolonized by dispersing individuals in the event of a localized extinction when functioning as part of a metapopulation (*sensu* Pulliam 1998).

Site Isolation

Limited attention has so far been paid to inter-wetland movements, and such data are needed to better understand potential influences of site isolation. Recent movement studies suggest that OSF are limited in their overland dispersal and potential to recolonize sites. Larger movements (> 1 km) have been documented within large wetland complexes

(Dempsey Creek, WA; Watson *et al.* 2003) and linear riparian systems (Jack Creek, OR; J. Oertley, pers. comm.), but they may be rare. Existing data suggest a large portion of OSF movements are associated with aquatic connections (Watson *et al.* 2003; M. Hayes, J. Bowerman, unpubl. data), and this limitation has potential to influence dispersal ability and underscore the importance of site isolation. At Dempsey Creek, transmittered adult OSF were tightly linked to aquatic habitats throughout the year, and only one of 645 frog locations may have represented an overland move (Watson *et al.* 2003).

Dispersal attempts between sites separated by uplands have only been studied at cursory levels, and functional dispersal (founding individuals that are able to breed successfully in new sites) is essentially unknown. The importance of potential inter-site movements in OSF is underscored by Hayes' (1997) finding that 13 of the 24 sites known in 1997 were isolated by at least 16 km (10 mi) from their nearest known population. In many of these cases, the intervening habitat lacks substantial hydrological connections (Hayes 1997). Moreover, due to current levels of isolation in extant populations and alteration of historical hydrological connections, limited opportunities exist to gather data about movements between discrete habitats that may be suitable for OSF.

In a study in an area of the Oregon Cascades populated with lentic habitats, dispersal from known breeding sites to nearby sites appears limited (Pearl and Bury 2000; C. Pearl, unpubl. data.). In surveys of 25 sites within that study basin, occurrence of post-metamorphic OSF was best predicted by distance to known breeding site (Pearl 1999, Pearl and Bury 2000). Over 4+ years of monitoring, post-metamorphic OSF have been found at 8 sites that have not been observed to support OSF breeding. Since the OSF captured at these 'satellite' sites were not marked, their site of origin remains unknown. All of these satellite sites were within 1200 m straight-line distance of a known breeding site, with a mean of ca. 560 m. The most direct predominately-riparian paths between satellites and known breeding sites were considerably longer than the direct upland routes (mean ca. 975 m; range 87 − 2660 m). Data from this study in the Oregon Cascades and from the telemetry studies in Washington (Hayes *et al.* 2001, Hallock and Pearson 2001, Risenhoover *et al.* 2001, Watson *et al.* 2003) suggest that wetland sites within 2 − 3 km of historic, known or suspected OSF breeding sites should be surveyed with particular attention and be considered to have increased potential for harboring adult

OSF. Resolving dispersal moves and gaining additional information on movement habitat will require fairly intensive telemetry or mark-recapture efforts, but will be necessary to better understand isolation and planning conservation networks at a landscape scale. The population level significance of apparent dispersal moves also requires more detailed attention, and whether adult OSF leave or remain at a satellite site could be based upon some set of habitat characteristics.

Wetland Complexity

Data from Dempsey Creek in lowland Washington (Watson *et al.* 2003), the Sunriver complex in central Oregon (J. Bowerman, pers. comm.) and accumulated work at Conboy Lake NWR (Hayes *et al.* 2000, Hayes *et al.* 2001) have begun to elucidate seasonal use patterns within wetland complexes (Section III). Wetland complexity may be a useful predictor of OSF habitat suitability since it potentially reflects the range of habitats used by OSF across seasons. For example, Munger *et al.* (1998) found that wetland characterization provided in National Wetland Inventory (NWI) mapping had some predictive value for occurrence of Columbia spotted frogs (*R. luteiventris*). Major differences exist between spotted frog species and habitat types within the 2 species' ranges, so specific extrapolation from that study to OSF is not advised. However, that general habitat modeling approach is likely to have predictive value for OSF occurrence.

To date the only study to assess associations of OSF with NWI indicators in unsurveyed lentic sites was conducted in the central Oregon Cascade range (Pearl 1999, Pearl and Bury 2000). In that study, Pearl (1999) posited that sites with higher richness of NWI hydrological modifiers may be more likely to possess conditions that meet the season-specific habitat affinities of OSF. The number of hydrologic modifiers was generally higher in OSF breeding sites (60% of breeding sites had >2 hydrologic modifiers) compared to non-breeding sites (5% of non-breeding sites had > 2 hydrological modifiers) (Pearl 1999). The sample size was small in the Oregon study, but data on NWI classifications for the 4 known OSF wetland complexes in Washington are generally supportive of this pattern. We found that Washington OSF sites averaged 4.75 hydrological modifiers, which is a higher average count than occupied sites in the Oregon

Cascades study (Pearl 1999). We did not compare these to unoccupied sites in Washington, which would be helpful in confirming the apparent relationship between OSF breeding complexes and high richness of hydrological modifiers. The patterns in the Oregon Cascades study are potentially revealing, and the seasonally varying habitat uses by OSF are consistent with hydrologically complex wetlands.

In the Oregon Cascades study, OSF adults were found at a variety of NWI wetland types, whereas OSF breeding was associated with wetlands dominated by palustrine aquatic bed and emergent vegetation (Pearl 1999). Wetlands where OSF reproduction was detected (N = 5) averaged 82% of areal extent in palustrine emergent wetland classes, whereas sites lacking OSF reproduction (N = 20) averaged 34% in palustrine emergent classes. Extant OSF sites in Washington appear to follow a similar pattern of high coverage in emergent wetland classes. We used NWI maps to estimate that the 4 OSF sites average ca. 55% of coverage in palustrine emergent wetland classes (range 40 – 80%).

Pearl (1999) considered the OSF breeding sites in the Oregon Cascade study a specific successional subset of the regional population of lentic sites, which range from oligotrophic lakes (lacustrine unconsolidated bed) to wet meadows with shrub-scrub components. Wetlands of these intermediate successional states (*e. g*. shallow lakes or oxbows with extensive emergent and/or submergent vegetation) may provide quality OSF habitat, but may also be susceptible to encroachment by woody vegetation, which has potential to reduce site suitability for OSF (Hayes 1997, Pearl 1999). Moreover, the floodplain dynamics involved in creation or renovation of such sites has been degraded or lost in many lowland areas of the Pacific Northwest (e.g. Benner and Sedell 1997), and may place some sites where OSF is extant at risk.

SECTION III. WITHIN-SITE AND SEASONAL HABITAT ASSOCIATIONS

While linked tightly to aquatic habitats throughout its life history, OSF shift use of microhabitats based upon seasonally varying behaviors. Existing data suggest that OSF make differential use of wetland environments for three major segments of their life history: breeding, the non-breeding active season, and overwintering. A detailed understanding of the range of microhabitats required by this species should allow more effective predictive modeling as well as help identify potential wetlands for repatriation or restoration, should those management options become acceptable.

Breeding and Oviposition Habitat

Recent efforts to quantify breeding population size at extant sites across the species' range have substantially increased understanding of OSF breeding habitat requirements, and this may be the best understood of the species seasonal habitat associations. This segment of the species' life history and habitat requirements may also play an important role in limiting the species distribution. Oregon spotted frog breeding sites are generally temporarily inundated shallows that are hydrologically related to permanent waters (Licht 1971, Hayes *et al.* 2000, Pearl and Bury 2000, Hallock and Pearson 2001, Risenhoover *et al*. 2001, Watson *et al.* 2003). Breeding habitats often do not retain water beyond mid-summer, and may dry as early as June in some lowland sites. Breeding shallows with high solar exposure (and potential to reach high daytime water temperatures) appear to be favored (Hayes *et al.* 2000, Pearl and Bury 2000). Oregon spotted frog breeding use of seasonally flooded fringes associated with permanent water bodies also suggests that certain types of wetland complexes may be favored (Hayes 1997, Pearl 1999; see Wetland Complexity). Seasonally flooded habitats of this type have undergone extensive alteration throughout the range of the OSF, particularly in the Klamath basin, Puget Trough, and Willamette Valley. The latter western lowlands now exhibit dramatically altered hydrology due to dams, channel simplification, and the rise to dominance of agricultural and urban land uses in the last 150 years (Sedell and Froggatt 1984, Hayes 1994a, 1997; Hulse *et al.* 2002).

Water temperature and day-length are common cues for breeding in many temperate ranid frogs (Duellman and Trueb 1986). Physical features such as insolation and wind exposure may interact with other habitat features such as substrate slope, distance from shore and form of vegetation to influence water temperatures and locations of breeding (Hayes *et al.* 2000; Pearl and Bury, unpubl. data). These same physical habitat variables relate to the significant risks posed by desiccation and freezing, which are potentially selective forces acting on breeding site selection and philopatry. Below we review data pertaining to OSF breeding habitat selection. We also caution that social factors in the communal-breeding OSF may also influence their selection of breeding sites and are currently largely unknown.

Water depth

Oregon spotted frogs use shallow oviposition sites consistently across their range, with average depths per site ranging from 5.9 to 25.6 cm (Table 1). At the largest breeding population site surveyed (Conboy Lake NWR), Hayes *et al.* (2000) reported that 99% of 5430 egg masses measured were in water < 25 cm in depth. Some evidence exists to suggest OSF deposited egg masses in deeper microsites within 1 x 1 m use plots at Trout Lake (Lewis *et al.* 2001). However, this pattern was not observed at Beaver Creek during the same year (McAllister and White 2001). Of potential importance is that the 2 sites where shallowest depth at egg masses were reported (Dempsey and Beaver Creeks, WA; Table 1) are located in shallow floodplains where reed canarygrass (*Phalaris arundinacea*) is dominant or subdominant (McAllister and White 2001, Risenhoover *et al*. 2001). Whether establishment of reed canarygrass can reduce water depths available for oviposition, and thus potential for stranding in receding water levels, merits further investigation. Moreover, little attention has been paid to water level variation and its relationship with oviposition dates and timing of egg mass surveys. Such data are needed to better understand OSF depth selection and the factors that may alter water depth in OSF breeding habitats.

Distance from shoreline and substrate slope

   Oregon spotted frogs appear to prefer oviposition microhabitats that are gradually sloped and relatively close to shorelines (Hayes *et al.* 2000, Pearl and Bury 2000, C. Pearl and M. Hayes, unpubl. data). Sites with egg masses in one 5-hectare Oregon Cascade lake averaged 11.2 ± 4.2 m from the nearest land-water interface, and egg masses are deposited closer to shorelines at other sites (Pearl and Bury 2000, C. Pearl, M. Hayes, pers. obs.; J. Bowerman, pers. comm.). Protection from strong winds may contribute to oviposition near shorelines in expansive sites such as Conboy

Table 1. Water depths at Oregon spotted frog breeding locations within selected study sites.

Water depth in cm (Mean ± SD)	Range (cm)	Site	Reference
Not provided	5 –12	Little Campbell River, BC	Licht 1971
14.5 ± 2.3	7 – 40	Conboy Lake NWR, WA	Hayes *et al.* 2000
10.6 ± 2.9	Not provided	Trout Lake, WA	Lewis *et al.* 2001
7.1 (mean)	3 – 10	Dempsey Creek, WA	Risenhoover *et al.* 2001
5.9 ± 2.3	Not provided	Beaver Creek, WA	McAllister and White 2001
11.2 ± 3.0 15.4 ± 5.8	6.5 –15.5	Penn Lake, OR	Pearl and Bury, unpubl. data (2000 and 2001)
25.6 ± 7.9	7 –31	Muskrat Lake, OR	Pearl and Bury, unpubl. data

Lake NWR, where < 10% of OSF egg masses were in areas exposed to the predominate open windward exposure (Hayes *et al*. 2000). Data on substrate slopes at OSF oviposition sites are available from two breeding populations in the Oregon Cascade range. At those two lakes, oviposition sites were above substrates sloped between 1.1 – 1.4 % and 1.4 – 3.0 % (measured perpendicular to shoreline; Pearl and Bury, unpubl. data.). The apparent preference of OSF for ovipositing relatively near shorelines and over shallowly sloped

terraces likely also contributes to the risk of mass embryonic mortality if waters recede (see 'Importance of philopatry and communal breeding' discussion below).

Vegetation

Oregon spotted frog oviposition sites are generally characterized by low canopy coverage and a substrate at least partially covered with the previous year's emergent herbaceous vegetation (Licht 1971, Leonard 1997, Hayes *et al.* 2000, Pearl and Bury 2000, Lewis *et al.* 2001, Risenhoover *et al.* 2001). Egg masses are not affixed to a vegetation brace, as in the related northern red-legged frog (*R. a. aurora*; Licht 1971). At Conboy Lake NWR, OSF sometimes deposit egg masses nested in submerged vegetation, which Hayes *et al.* (2000) suggest could represent a response to windier conditions in large, open sites. However, similar oviposition microenvironments have been observed near Wickiup Reservoir (OR), Dempsey Creek and Trout Lake (WA), where wind is likely not pronounced (C. A. Pearl, pers.obs.; W. P. Leonard, pers. comm.).

Recent OSF breeding surveys have begun to examine potential selection or avoidance of vegetation species and forms in oviposition sites. Vegetation coverage beneath egg masses is generally high and OSF egg masses are rarely found over open soil or rock substrates (Hayes *et al.* 2000, Pearl and Bury 2000, Lewis *et al.* 2001, Risenhoover *et al.* 2001). Composition of this coverage varies among sites, and is one suggestion that OSF may respond more to physical attributes of breeding sites (*e.g.* water temperature, slope, distance from shoreline, wind exposure) than to plant species. However, certain sedges (*Carex* sp.) and grasses that are tightly linked with specific hydrological regimes may provide indicators of potentially favored OSF breeding microhabitats. Furthermore, plants of that growth form generally offer an open canopy and high insolation during the temporal windows (early spring in lowland Washington, early summer in montane Oregon sites) when OSF breed. At one site in the Oregon Cascades, 20 of 21 egg masses were above the previous year's sedge vegetation (Pearl and Bury, unpubl. data). Risenhoover *et al.* (2001) reported that Dempsey Creek OSF selected oviposition sites that were generally dominated by sedges, reed canarygrass and algae. At Trout Lake, grasses dominated 62% of OSF oviposition use plots, while sedges (21%) and rushes (17%) also were common substrates (Lewis *et al.* 2001). Plants in

submerged forms dominated 90% of use plots at Trout Lake (Lewis *et al.* 2001). The mean height of vegetation was lower at OSF oviposition sites than at random points at Dempsey Creek (Risenhoover *et al.* 2001), which is consistent with an influence of increased insolation.

Telemetry data during breeding season at Dempsey Creek also suggests adult OSF make more use of sedge-dominated microhabitats than would be expected by the distribution of the cover type (Watson *et al.* 2003). Selection of sedge habitats during the breeding season was the strongest difference between use and availability of any cover type in any season, and sedge habitats were not strongly selected in other seasons (Watson *et al.* 2003). Adult OSF at Dempsey Creek also were observed to use areas of reed canarygrass less frequently than would be expected by its coverage (Watson *et al.* 2003). Notably, sedge microhabitats in the lowland Pacific Northwest also may be particularly vulnerable to invasion and dominance by reed canarygrass, and OSF apparent avoidance of canarygrass suggests these vegetation shifts could impact OSF behavior during breeding.

Experimental approaches will help separate the importance of vegetation type from its correlates (*e.g.* slope, distance from land-water interface, etc.) in predicting OSF oviposition sites. One field manipulation at Beaver Creek investigated the influence of vegetation height on OSF oviposition site selection (McAllister and White 2001, White 2002). In that study, White (2002) concluded that reducing the height of the previous years' emergent vegetation (largely reed canarygrass) improved oviposition site quality for OSF. Their conclusions were limited by a small number of samples, but are consistent with observations at the same site in the previous spring, when 59% of egg masses occurred in areas of tire tracks or vegetation removal. Reduced canopy coverage resulted in warmer water temperatures than untreated controls, and access of newly opened sites amidst dense mats of canarygrass also may attract breeding use (McAllister and White 2001, White 2002).

A somewhat similar vegetation manipulation in potential OSF breeding habitat was conducted at Conboy Lake NWR in 1999-2000 and 2000-2001 (M. Hayes, unpubl. data). In the fall of the earlier of each pair of years, 15-m wide swaths that were perpendicular to the Conboy Lake shoreline were mowed of their reed canarygrass-

dominated vegetation. In the latter spring of each year, egg mass counts in these areas revealed a mean of 63% of the egg masses occurred in the mowed vegetation swaths over both years combined. Moreover, in the second pair of years, the mowed and unmowed swaths were alternated, but the higher proportion of egg masses recorded in mowed swaths did not change significantly between years. As water temperatures were warmer in the mowed swaths, these differences may also be attributable to temperature.

Juxtaposition and connection to overwintering sites

Connections and distances between overwintering sites and breeding sites may also be habitat features that influence overall quality of wetland sites for OSF. Evidence of predation on OSF that may have been moving toward breeding sites has been observed (M. Hayes, J. Engler, pers. obs.), and could underscore the importance of relatively direct aquatic connections between these two seasonal use areas. Hayes *et al.* (2000) described OSF oviposition at Conboy Lake NWR as consistently 'relatively near permanent channels or springs', averaging ca. 45 m from springs or permanent stream sites that other work suggests are used as overwintering habitat (Hayes *et al.* 2001). A similar pattern of proximity between breeding areas and groundwater springs has been observed at 3 sites in the Oregon Cascades (C. Pearl, pers. obs.). However, this pattern may not be universal, and OSF may be capable of longer moves if conditions are favorable. For example, OSF located in mid-winter at Trout Lake were >1000 m from the nearest known breeding site (Hallock and Pearson 2001) and large numbers of OSF at the Sunriver complex in central Oregon are known to make substantial moves (> 100 m) between an overwintering pond and breeding marsh via a direct aquatic connection (J. Bowerman, pers. comm.). Further investigation into pathways of movement in this critical temporal window, as well as into habitat and environmental conditions associated with this movement, will allow more thorough understanding of the relationship between these seasonal uses.

Importance of philopatry and communal breeding

Extensive egg mass stranding associated with receding water levels has been quantified at Trout Lake (estimated 27% of egg masses; Lewis *et al.* 2001), Conboy Lake

NWR (ca. 65 % in 1999, and 47.2% in 1998; Hayes *et al.* 2000) and one site in the Oregon Cascades (100% stranding in 2001; C. Pearl, unpubl. data). Extant OSF sites vary in rapidity and frequency of water level changes, and anthropogenic alterations to site hydrology may alter frequency and severity of water level fluctuations during the breeding window. At Conboy Lake NWR, removal of beaver impoundments in segments of the outflow may have contributed to rapid water level reductions and large-scale stranding of OSF egg masses (M. Hayes and J. Engler, unpubl. data). The effects of low water years on OSF breeding microhabitat selection and probabilities of stranding are incompletely understood, but merit further inquiry. For example, both McAllister and White (2001) and Lewis *et al.* (2001) suggested that reduced spring freshets may force oviposition nearer permanent water and actually result in reduced likelihood of stranding.

Two attributes of OSF breeding ecology (communal breeding and oviposition site philopatry) may contribute to an increased likelihood of large-scale egg mortality, and have potential to influence the probability a wetland can sustain an OSF breeding population. First, OSF focus a large proportion of their breeding effort in relatively few locations (Licht 1971, Leonard 1997, Hayes *et al.* 2000, Pearl and Bury 2000, McAllister and White 2001, Risenhoover *et al.* 2001). At Conboy Lake NWR, Hayes *et al.* (2000) found that 2% of breeding sites accounted for 19% of OSF egg masses. Similar breeding concentrations have been documented at Trout Lake (3% of breeding sites accounting for 26% of egg masses; Lewis *et al.* 2001) and Beaver Creek (27% of breeding sites accounting for 71 % of egg masses; McAllister and White 2001).

Second, OSF appear to consistently use similar locations within sites for oviposition (Pearl and Bury 2000; C. Pearl, pers. obs.). For example, over the last 4+ years at Penn and Muskrat Lakes in the Oregon Cascades, OSF have deposited >75% of their egg masses in very similar locations ($\pm$ 5 m) within each wetland complex (Pearl and Bury, unpubl. data). How much this represents the same adults returning to specific sites or physical habitat attributes consistently attracting frogs is unknown. Still, detailed monitoring of OSF breeding over the last 5+ years at Conboy Lake NWR has revealed repeated use of management units where large-scale desiccation occurred over a sequence of years (1999-2001; Hayes *et al.* 2000; M. Hayes and J. Engler, unpubl. data). A more detailed understanding of habitat and environmental conditions that attract

oviposition, are associated with deposits of large numbers of egg masses, and the degree of breeding site philopatry in adult OSF should allow improved management and minimization of large scale egg mortality in managed sites.

Summer Active Season Habitat

Field data from Oregon and Washington suggest adult OSF can move relatively little during the summer active season compared to early (movements to oviposition areas) and late (movements to and among overwintering positions) in the year (Hayes 1998b, Pearl and Bury 2000, Watson *et al.* 2003, J. Bowerman, pers. comm.). Estimated home range sizes of 9 OSF at Dempsey Creek were ca. 0.2 ha during the dry season (June-August; Watson *et al.* 2003). This figure represents between 10% and 28% of the estimated home range size of OSF during the breeding season (February-May) and winter (September-January), respectively. Daily movement rates of OSF in summer were ca. 50% of those during breeding and winter seasons (Watson *et al.* 2003). Recaptures of individual frogs within the same pool or habitats < 50 m away were found across summers.

Restricted habitat use might be expected at sites like Dempsey Creek where summer aquatic habitats are confined to in-channel pools as water levels recede. However, two mark-recapture studies in the Oregon Cascades also suggest limited summer movements of adult OSF in more isolated montane habitat conditions. At one complex in the southern Oregon Cascades, Hayes (1998b) found 11 OSF adults were recaptured in summer an average of ca. 70 m from original capture location (temporal window from 1 to 746 days; 8 were across consecutive summers). Excluding one recaptured juvenile OSF that was found ca. 450 m from its original site, the average distance between captures is < 30 m (N = 10 frogs). Moreover, 7 OSF were recaptured within ca. 25 m of original captures, and 6 of these were across two summers, suggesting some degree of site fidelity among individual OSF (Hayes 1998b). This is consistent with other within- and between-summer recapture observations at two sites in the Oregon Cascades. At Penn Lake in the central Cascades, zero of 10 adult recaptures within one

summer were found > 100 m from original point of capture, and 6 of those 10 were estimated to have moved < 25 m from original capture location (Pearl and Bury 2000).

Scattered data suggest that summer habitat use by OSF may be influenced by behaviors and ecological demands related to feeding and predator avoidance. The relative importance of these two pressures on adult OSF may differ with respect to gender. Field observations from British Columbia, Washington and Oregon suggest that OSF juveniles and adult males may be particularly susceptible to predation (Licht 1974; Haycock, 1999; M. Hayes and C. Pearl, pers. obs.). Male OSF are markedly smaller than females and thus may be more vulnerable to gape-limited predators (Watson *et al*. 2000). For example, at sites in the central Oregon Cascades, male OSF attain a maximum snout-vent length (SVL) of ca. 78 mm, whereas females attain ca. 98 mm (C. Pearl, unpubl. data). At Conboy Lake NWR, males attain a maximum of 83 mm SVL, whereas females attain 103 mm SVL (M. Hayes and J. Engler, unpubl. data).

Male OSF get increasingly more difficult to observe at sites in the Oregon Cascades as summer progresses, which could reflect high predation rates, increased crypsis, or some combination of the two (Pearl and Bury, unpubl. data; M. Hayes, pers. comm.). During the summer, microhabitats with some standing water but concealing cover may be particularly important for OSF adults (Watson *et al.* 2003; C. Pearl, pers. obs.). Proximity to escape cover such as flocculant organic substrates also may be particularly important for OSF to successfully evade predators (Licht 1986b, Hallock and Pearson 2001, C. Pearl and M. Hayes, pers. obs.). Telemetry data from Dempsey Creek suggest that OSF increase their use of shallowly-ponded *Spiraea* thickets during the dry season (Watson *et al.* 2003), which may be consistent with this hypothesis. While no use-versus-availability analysis has been performed, OSF adults at 2 sites in the Oregon Cascade range appear to select microhabitats that offer aspects of both openness and cover (Pearl and Bury, unpubl. data; M. Hayes, pers. obs.). Similarly, Watson *et al*. (2003) report that adult OSF tend to select canopies of intermediate densities (51-75%) at Dempsey Creek across all seasons. Hallock and Pearson (2001) report that OSF adults selected emergent vegetation habitats during late-summer (mid-September to late-November) at Trout Lake. In contrast to the Dempsey Creek telemetry data, OSF at Trout Lake did not utilize shrub-scrub wetlands during this period (Hallock and Pearson 2001).

The collective body of movement data appear to imply that the densest vegetation types may be avoided during summer in particular. Given our observations of adult OSF hunting behavior (see Pearl and Hayes 2002), as well as observations of crypsis before surveyors, these positions of intermediate 'architecture' may offer prey ambush sites with relatively high insolation and water temperatures, as well as some proximal escape refuge from predators (M. Hayes and C. Pearl, pers. obs.). Additional research is needed on OSF movement and foraging responses to increasing vegetation densities within emergent wetlands, such as is occurring at many Puget Trough and Willamette Valley sites (K. McAllister, pers. comm.; C. Pearl and M. Hayes, pers. obs.).

At other sites, basking habitat that affords some protection from predators such as dense beds of floating vegetation [including species such as pondweeds (*Potamogeton*), common bladderwort (*Utricularia vulgaris*), water buttercup (*Ranunculus aquatilis*)] has been documented. At Conboy Lake NWR, dense mixed beds of *Potamogeton natans* and *Utricularia vulgaris* that dominate in the channels in this altered wetland complex during spring and summer maintain the warmer surface water temperatures that OSFs seem to favor (i.e. $> 20^o$ C [68° F]) and are the refuge into which individuals escape when disturbed (M. Hayes and J. Engler, unpubl. data).

Female OSF can make extensive use of amphibian prey, as well as feed aquatically (Licht 1986a, Pearl and Hayes 2002). At several sites in Oregon, OSF can demonstrate fairly sophisticated cryptic ambush behaviors during this hunting, which may serve to lessen their detection by potential OSF prey and predators (Pearl and Hayes 2002). Hayes (1997) reported that OSF were associated with sites of higher amphibian richness in higher elevations sites in Oregon, and this association may partially be one of quality food supply for female OSF in abbreviated growing seasons. A parallel relationship between mountain yellow legged frog (*Rana muscosa*) and prey amphibians (especially *Hyla regilla*) has been documented in high elevations of the Sierra Nevada in California (Pope and Matthews 2002). Nutritious or abundant prey may facilitate increased fecundity and growth of female OSF, and allow size refuge from some gape-limited predators.

These two ecological factors, potentially in tandem with distances from breeding and overwintering habitats, are likely to influence summer habitat use. No analysis has

yet quantified the benefits of different summer cover habitats to OSF, but such information may provide insights on how OSF persist with high predator abundances, particularly as non-native predators increase their distribution (Hayes 1997, Pearl and Bury 2000). Available movement and home range data imply that if quality habitat is present, individual adult OSF may need relatively little space to meet summer metabolic and refuge demands. The apparent tendency for OSF to have small summer active season home ranges, along with their potential vulnerability to predators during this season, suggests that sites that have degraded summer cover have potential to exacerbate interactions with predators and potentially affect OSF persistence.

Overwintering Habitat

Oregon spotted frogs at the Washington sites appear to be almost exclusively aquatic during winter, and are known to at least sporadically exhibit underwater movement , including during periods of ice formation (Leonard *et al.* 1997, Hallock and Pearson 2001, Hayes *et al.* 2001, Risenhoover *et al.* 2001, Watson *et al.* 2003). Hallock and Pearson (2001) also report little or no loss in mass among a small sample of adults over this period, suggesting that they may continue feeding or have exceptionally low metabolic demands in coldwater conditions. Habitat associations during this period are perhaps the most incompletely known of all seasonal uses, and parallel overwintering studies remain needed in Oregon to better understand behavior and habitat selection in the higher elevation core of the species' range.

Water depth, vegetation and distance to land-water interface

An almost universal finding among 3 studies of Washington OSF overwintering ecology was that OSF made little or no use of upland terrestrial habitats (Hallock and Pearson 2001, Hayes *et al.* 2001, Risenhoover *et al.* 2001, Watson 2003). The closest observations to a departure from the model of OSF utilizing aquatic wintering sites were detections of OSF using beaver structures at Conboy Lake NWR (Hayes *et al.* 2001). Even in this case, Hayes *et al.* (2001) concluded that frog locations were in aquatic

positions within those structures, and suggested that they may be favored due to additional protection from potential predators.

Movement and microhabitat data from 3 sites in Washington suggest there may exist important differences in OSF overwintering behavior between lowland and higher elevation sites. These differences in habitat use appear to be focused during the colder portions of the winter and center around use of stream and spring microhabitats. Habitat use during the warmer periods of late fall and early winter does not appear to differ markedly among the 3 study sites. At Dempsey Creek in the Puget Lowlands [elev. 43 m (140 ft)], winters are relatively mild and ice formation rarely lasted for > 3 days during the overwintering studies (Risenhoover *et al.* 2001, Watson *et al.* 2003). Risenhoover *et al.* (2001) found that wintering OSF most strongly selected habitat types of open water with submerged vegetation and shrub-scrub, which often was *Spiraea* with some emergent vegetation in the understory. Watson *et al.* (2003) also reported that Dempsey Creek OSF used *Spiraea* with reed canarygrass understory more frequently than would be predicted by its coverage. Moreover, this was the only habitat type of the 5 prominent habitat types in the wetland (reed canarygrass, sedge, alder-willow, *Spiraea*-reed canarygrass, *Spiraea* alone) for which there was evidence of selection by OSF (Watson *et al.* 2003). Whether OSF were selecting sites based on vegetation is unclear from these data, and Risenhoover *et al.* (2001) suggest that OSF may have been responding to areas of shallower water that were less dense than the mats of reed canarygrass that occur in other portions of the wetland. Watson *et al.* (2003) also found that OSF used reed canarygrass dominated habitats less than would be expected by its coverage during winter. Both studies at Dempsey Creek documented frequent use of relatively shallow areas within the wetland, and Risenhoover *et al.* (2001) reported that most overwintering positions were relatively close to shore (Table 2).

These findings at Dempsey Creek contrast with OSF overwintering data from two higher elevation sites. Trout Lake (597 m [1960 ft]) and Conboy Lake NWR (555 m [1821 ft]) are situated in the southern Washington Cascades, and normal winters at these sites can include extended periods of cap ice and temperatures below 20° F. Overwintering telemetry studies at both these montane sites suggest OSF shift locations to flowing water and springs during the coldest periods of winter (Hallock and Pearson

2001, Hayes *et al*. 2001). For example, Hallock and Pearson (2001) reported that OSF

used emergent wetland more than other available habitat types (aquatic bed/open water,

Table 2. Water depth and distance to land-water interface at OSF overwintering positions. Distances are in cm. * = Data are means of OSF at 4 sites on Conboy Lake NWR.

Mean water depth in cm (range)	Mean distance from shoreline in cm (range)	Temporal Interval	Site	Reference
22 (0 – 120)	9 (0-68)	Oct-March	Dempsey Creek, WA	Risenhoover *et al.* 2001
17.4 (Not provided)	Not provided	"coldest weather"	Dempsey Creek, WA	Watson *et al.* 2003
26.2 (1 – 88)	130 80 20	Oct-Nov Dec Jan	Trout Lake, WA	Hallock and Pearson 2001
62, 49, 34, 29 * (6 – 111)	180 50 30	Pre-Ice Ice Post-Ice	Conboy Lake NWR, WA	Hayes *et al.* 2001

riverine, and scrub-shrub) in fall and early winter at Trout Lake. As ice covered the

emergent and aquatic bed habitats in early winter (mid-November), OSF moved closer to

habitats with some flow. By mid-winter (January), four transmittered OSF had relocated

to undercut banks in Trout Lake Creek (Hallock and Pearson 2001). A fifth OSF made a

long move (2nd longest of the study) to a spring in shrub-scrub habitat (Hallock and

Pearson 2001). Overall, however, OSF moved less than 450 m from original point of

capture (Hallock and Pearson 2001), implying that OSF may move relatively little when

requisite fall and winter habitats occur in proximity to each other.

A similar pattern has been reported from Conboy Lake NWR, where

transmittered OSF moved to lotic habitats during a late-fall air temperature decline

preceding thick ice formation (Hayes *et al*. 2001). In that study, 3 of 4 OSF from lentic

habitats moved to lotic sites (channelized ditches, in some cases with areas of

groundwater upwelling), and all 6 OSF that were released in lotic habitats remained

there. No OSF moved from lotic to lentic habitats (Hayes *et al.* 2001). At Conboy, OSF tended to use microhabitats with simpler, more open vegetation compared to that which was locally available (Hayes *et al.* 2001). This apparent selection for less dense vegetation may be consistent with OSF avoiding microenvironments that could become oxygen depleted due to winter respiration (see below; Hayes *et al.* 2001).

Potential influence of dissolved oxygen

Water temperature and dissolved oxygen (DO) are highly spatially and temporally variable, and studies of their influence on OSF overwintering habitat use are made difficult by the need for fine spatial and temporal resolution. Nonetheless, the apparent association of extant OSF populations with wetlands that include springs or lotic environments (Hayes 1997), as well as supportive data from other North American *Rana* species (Lamoureux and Madison 1999, Ultsch *et al.* 2000, Bull and Hayes 2001) suggest specific research attention to this relationship is warranted. Particularly in montane areas, flowing streams and springs may offer consistently non-frozen habitats with moderated thermal regimes, stable DO, or a combination of these two qualities. Thermal data from springs in OSF lakes in the Oregon Cascades suggests that many of these microenvironments do not achieve the near-freezing minima of adjacent areas that lack groundwater upwelling (Pearl and Bury, unpubl. data).

Additional resolution of temperature, DO, and their interaction is needed for a clearer understanding of factors driving OSF movements during winter, and data from overwintering studies at the more montane Washington sites are suggestive but not conclusive (Hallock and Pearson 2001, Hayes *et al.* 2001, Risenhoover *et al.* 2001). Oregon spotted frogs from at least some populations can survive in low oxygen conditions for at least a short time (Risenhoover *et al.* 2001, J. Bowerman, pers. comm.). Risenhoover *et al.* (2001) measured low dissolved oxygen concentrations (0.4 and 0.87, 1.01, 1.15, 1.30, 1.37 mg/L) near locations of 2 overwintering OSF at Dempsey Creek in the Puget Lowlands and concluded that their data 'do not support the hypothesis that frogs avoided areas having low dissolved oxygen'. However, spatial variation in dissolved oxygen was quantified generally (range available across winter study period of 0.4 – 12.75 mg/L) and OSF could respond on temporal scales shorter than would be

detected by weekly visits, so firm conclusions about preference or avoidance are difficult to make. At higher elevations in central Oregon, tolerance of low winter dissolved oxygen concentrations has been proposed as allowing OSF to persist in ponds where non-native bullfrogs (*Rana catesbeiana*) suffer some winterkill (J. Bowerman, pers. comm.).

Field studies at higher elevation sites offer countervailing evidence that low DO may be important for initiation of OSF movements, and may be associated with mortality of some individuals. For example, Hallock and Pearson (2001) reported from Trout Lake that overall DO was higher in the OSF overwintering stream (mean ca. 10.3 mg/L) than the emergent (mean ca. 5.0 mg/L) and aquatic-bed wetlands (mean ca. 5.2 mg/L) from whence they came. Two transmitted OSF that did not move to stream or spring when the other frogs moved perished in the emergent wetland (Hallock and Pearson 2001). Dissolved oxygen concentrations of 1.10 and 1.71 mg/L were measured at the locations where those 2 mortalities were recovered. Still, clear conclusions cannot be drawn since spatial gradients of DO and water temperature were not quantified and average dissolved oxygen in an OSF overwintering spring was comparable (mean ca. 4.8 mg/L) to values in the emergent and aquatic-bed wetlands (Hallock and Pearson 2001).

Telemetry data from Conboy Lake NWR may also suggest a relationship between dissolved oxygen and OSF movement and microhabitat in winter conditions. During ice-cover in mid-winter when overall DO was lowest, Hayes *et al*. (2001) reported significantly more OSF movements from areas of low DO than from areas of higher DO. In addition, OSF movement distances were correlated with the difference in DO between current and previous locations. Transmittered OSF also made more frequent use of shallower areas near shorelines in the period of cap ice than either before or after cap ice (Hayes *et al*. 2001). A similar pattern of appearance of OSF in shallower pond perimeter areas under ice has been observed at Sunriver in central Oregon (J. Bowerman, unpubl. data). Hayes *et al*. (2001) also posited that 3 of the 5 located OSF overwinter mortalities lacked signs of predation and may have been related to low DO.

Even though OSF may be able to survive at least pulses of low dissolved oxygen, laboratory experimentation is necessary to address lethal and sub-lethal concentrations, movement induction thresholds, and interactions with water temperatures. In lowland habitats such as Dempsey Creek, where cap ice is normally short in duration, shallow

flooding allows exchange between water and air, and substantial flow-through is the norm, dissolved oxygen may not be the primary driver of winter OSF microhabitat selection. There, OSF may select vegetation types that reduce predation risk. Oregon spotted frog use of lotic and spring overwintering sites for at least segments of the winter may be the norm for montane sites which regularly experience heavy ice cover and low temperatures. Most extant OSF populations are in Oregon at high elevations in and along the Cascades (Hayes 1997, Pearl 1999), and many of these sites are associated with spring habitats. Studies of OSF overwintering are needed in Oregon to further elucidate the importance of these habitats to OSF in the core of their extant range.

SECTION IV: RECOMMENDATIONS FOR FURTHER RESEARCH

There remain many aspects of OSF habitat use and behavioral ecology that are poorly understood. Among the outstanding questions, we recommend additional research in the following areas:

1. *Minimum site size and level of habitat complexity necessary to support an OSF population even when isolated*. These factors may be elucidated by the development of a predictive OSF habitat suitability model based upon historically and currently occupied sites in Washington.

2. *Habitat characteristics and types of corridors that may reduce functional isolation between extant OSF breeding sites*. Improved understanding of movement corridors between isolated sites is critical for landscape scale conservation planning.

3. *Attributes of OSF movements and utilized pathways between seasonal use areas.* Additional resolution of connective habitats between seasonal use areas and reliance on aquatic pathways is needed.

4. *Importance of vegetation change in affecting habitat suitability.* Little is known about how OSF habitat is affected by invasion by nonnative species such as reed canarygrass and successional encroachment by woody vegetation

in fire-suppressed areas. In addition, [comma] information is needed regarding OSF response to vegetation management alternatives that are used to address the aforementioned conditions.

5. *Habitat responses to management practices such as livestock grazing and hydrological alterations (anthropogenic, beaver and others).* Limited attention has been paid to grazing effects on OSF habitat features and utilization (but see Watson *et al*. 2003), and effects are likely to be complex and habitat-specific. Additional studies at higher elevations are needed. Of potential importance are data from laboratory studies suggesting larval stages of OSF may be susceptible to nitrogenous compounds associated with fertilization (Marco *et al*. 1999). However, certain habitat conditions may reduce the potential for field sites to experience the high nitrogen concentrations that lab results suggest are detrimental (K. McAllister, C. Pearl, unpubl. data), so verification of lethal concentrations under field conditions are needed.

6. *Overwintering habitat use and quality (especially for selected water quality parameters) at low and high elevation sites*. Limited data suggest overwintering habitats may differ with elevation and winter severity, and that overwintering mortality can be severe in other ranid frogs, particularly at higher elevations. Little is known about which habitat components determine quality of overwintering sites.

7. *Habitat attributes that relate to coexistence or increased risk of extirpation when OSF occur with nonnative fish and bullfrogs.* Structural complexity has potential to mediate interactions between OSF life stages and native and non-native predators. Such an ameliorative effect may also be more important for some seasonal use habitats (for example, breeding and larval rearing) than others, but details of these interactions are currently unavailable. Also, it may be possible to identify habitat conditions that reduce potential for OSF sites to be colonized by non-native fish or bullfrogs; further research will be necessary to identify these factors.

ACKNOWLEDGMENTS

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Appendix 1. Oregon spotted frog egg mass counts and site sizes.

Site	State or Prov	# Years	Mean # Egg Masses	Site Area (ha)	Ln (Counts)	Ln (Area)	Reference
Wickiup Ditch	OR	2	10.0	1.1	2.3	0.1	J. Bowerman and C. Pearl, unpubl. data
Penn Lake	OR	4	34.3	13.0	3.5	2.6	Pearl and Bury, in prep.
Unnamed Marsh	OR	4	12.8	5.1	2.5	1.6	Pearl and Bury, in prep.
Muskrat Lake	OR	2	31.5	4.8	3.4	1.6	Pearl and Bury, in prep.
Big Marsh	OR	1	780.0	390.0	6.7	6.0	J. Kitrell (USFS), pers. comm.
Camas Prairie	OR	1	30.0	33.0	3.4	3.5	M. Blouin,(OSU), C. Corkran, pers. comm.
Jack Creek	OR	4	282.0	43.3	5.6	3.8	J. Oertley (USFS), M. Hayes, unpubl. data
Long Prairie	OR	2	56.0	5.0	4.0	1.6	M. Hayes, R. Demmer (BLM), unpubl. data
Dempsey Cr	WA	4	132.5	15.6	4.9	2.7	McAllister and Leonard 1997, Risenhoover et al. 2001
Conboy Lake NWR	WA	2	8360.0	1989.0	9.0	7.6	M. Hayes et al. 2000, unpubl. data
Trout Lake	WA	6	689.0	453.0	6.5	6.1	Leonard 1997, Lewis et al. 2001, L. Hallock, pers. comm.
NRS Aldergrove	BC	1	90.0	6.6	4.5	1.9	Haycock 1999
Mountain Slough	BC	1	16.0	12.3	2.8	2.5	Haycock 1999
Seabird Island	BC	1	38	9.2	3.6	2.2	Haycock 1999