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**MAINTAINING LENTIC-BREEDING AMPHIBIANS IN URBANIZING LANDSCAPES:
THE CASE STUDY OF THE NORTHERN RED-LEGGED FROG (*RANA AURORA*)**

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Abstract — We used the Northern Red-legged Frog (*Rana aurora*) as a means to evaluate the efficacy of existing state and local guidelines and regulations in addressing amphibian conservation in urbanizing areas. *Rana aurora* is endemic to the North American Pacific Northwest and may serve as an umbrella species for co-occurring lentic-breeding amphibians because it requires contiguous terrestrial and aquatic habitat extending over a relatively broad area. Brief late-winter/early-spring use of lentic aquatic habitats for reproduction is the best-studied aspect of *R. aurora* seasonal life history. We know less about terrestrial habitat use in summer and even less about overwintering habitat. New data indicate that migration movements to and from breeding sites invariably extend over 300 m, frequently over 1 km in length, and occasionally up to 5 km. Guidelines and regulations for protecting habitat in developing areas within the geographic range of this frog will likely fail for two reasons. First, existing regulations requiring wetland buffers often protect breeding sites from local disturbance but not from disturbances occurring across broader landscapes that affect breeding habitat hydrology, water quality, and vegetation structure. Second, terrestrial habitat outside the wetland buffer is largely ignored, even though frogs may use this habitat for an overwhelming portion of each year. Given the nature of urbanization in the Pacific Northwest, we conclude that even if *R. aurora* can persist at sites over the short term, larger-scale habitat connectivity and perhaps interconnected habitat networks, as required to support metapopulations, may be necessary to maintain populations of *R. aurora* over the long term. If local jurisdictions seek to maintain *R. aurora* in developing areas, they need to revise their land use guidelines and regulations to protect sufficient terrestrial habitat connected to breeding habitat and consider larger-scale habitat networks to facilitate inter-population dispersal and migration.

Key words — Amphibians, Land Use, Landscape Planning, Northern Red-legged Frog, *Rana aurora*, Urban Landscapes

Awareness of increasing urbanization is nowhere greater than in the North American Pacific Northwest where the natural heritage of the area is as basic to economic viability (fishing, tourism, and timber) as it is to the quality of life. The Washington State legislature clearly understood the problem in 1990–1991 when they passed SHB 2929 and RESHB 1025, legislation collectively termed the Growth Management Act (GMA). The GMA is based on the belief that “uncoordinated

and unplanned growth, together with a lack of common goals expressing public interest in conservation and wise use of land poses a threat to the environment; sustainable economic development; and the health, safety, and high quality of life enjoyed by Washington residents.”

The GMA included the important requirement to use “best available science” (BAS) when adopting development regulations to protect critical areas. As it came to be defined in 2000,

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BAS recognized that scientific knowledge ranges from expert opinion at one end of the spectrum to scientific principle or theory at the other. Where hard data were unavailable, expert opinion was used. Local jurisdictions had two mandates if they were dissatisfied with the quality or quantity of BAS: 1) “limit development activities in critical areas until uncertainty was resolved” and 2) “use an adaptive management program in the interim” to address uncertainties (Copsey 2002). Not surprisingly, the GMA and its BAS requirement have not quelled debate over land use.

The major dispute over GMA implementation is centered on the question of what comprises the best science particularly at the “opinion end” of the BAS spectrum. In the worst case, decisions on what constitutes BAS are made only after disputes have arisen. In these instances, stakeholder positions become entrenched and BAS is used inappropriately as a way to defend positions rather than a way to reach common understanding of what we know and do not know. Entrenched positions foster argument among scientists rather than discussion among policy makers. We believe that assembling BAS and subjecting it to peer review prior to the onset of conflict can help facilitate informed decision-making. Consequently, stakeholders will better understand how to integrate protection among the growing, often confusing, lists of at-risk species and habitats, as well as the ecological processes that maintain them in urbanizing environments.

Our purpose is to suggest ways to modify approaches to lentic wetland conservation, especially for urbanizing environments in the North American Pacific Northwest, by synthesizing literature on Northern Red-legged Frog (*Rana aurora*) habitat use and movement as it relates to urban landscapes. We use a BAS approach that recognizes incomplete knowledge, integrates expert opinion, unpublished data, and existing literature, and provides a list of specific questions that should drive adaptive management. We believe that *R. aurora* can act as an umbrella species (*vide* Roberge and Angelstam 2004: a species whose conservation confers protection to many naturally co-occurring species), and thus serves to address the limited science available to guide protection of other amphibians. We show that *R. aurora* uses habitats over spatial scales larger than are currently addressed in wetland buffers for any Pacific Northwest jurisdictions in which this species may occur. Finally, we suggest ways to protect *R. aurora* by considering seasonal habitat needs and discuss knowledge gaps through which adaptive management could help refine protection measures.

MATERIALS AND METHODS

We identified gaps in existing regulations and guidelines in protecting *R. aurora* populations and their habitats by: (1) summarizing data on *R. aurora* seasonal habitat requirements, (2) identifying threats to *R. aurora* in those habitats, (3) outlining current guidelines and regulations to protect *R. aurora* habitat from those threats, and (4) contrasting existing guide-

lines and regulatory alternatives with our re-evaluation of *R. aurora* habitat needs.

We summarize the habitat requirements of and threats to *R. aurora* from diverse sources. The core data are from published literature, but we have also drawn from recently published data and literature that include recent theses and reports as well as older surveys and technical reports. Unpublished data from our continuing research are especially critical in understanding the spatial scale of *R. aurora* seasonal habitat use.

We gathered the most recent guidelines and regulations addressing wetland and other habitats from applicable state (California [CEPA 2007], Oregon [ODEQ 2008], Washington [Knutson and Naef 1997; WDOE 2004]), provincial (British Columbia [BC MMS 2008]), and federal (U.S. Environmental Protection Agency [US EPA 2008], U.S. Army Corps of Engineers [US ACOE 2005], U.S. Fish and Wildlife Service [Frayer et al. 1983; Dahl and Johnson 1991]) agencies. Our assessment of the adequacy of guidelines and regulations partly reflects a recent National Resource Council review of federal wetland regulations (NRC 2001). Land-use policies and regulations from King (King County 2004a), Pierce (Pierce County 2005) and Thurston (Thurston County 2004) counties in Washington State were also included as these represented the most protective measures among local jurisdictions. We also reviewed available guidelines and regulations focused on amphibian protection (e.g., Larsen 1997). In summary, our review reflects an amalgam of peer-reviewed and other literature, ongoing and yet unpublished studies, and professional judgment.

RESULTS

NORTHERN RED-LEGGED FROG CASE STUDY

Background — *Rana aurora* (formerly *R. a. aurora*; Shaffer et al. 2004; Fig. 1) is a moderate-sized (50–100 mm SVL) still-water-breeding frog (Storm 1960; Licht 1969a; Hayes and Miyamoto 1984) with a distribution along the Pacific coast of North America from southwestern British Columbia to northern California (Jones et al. 2005). Concerns that *R. aurora* has suffered declines or been locally extirpated (St. John 1982, 1984, 1985, 1987; Nussbaum et al. 1983; Blaustein and Wake 1990; Jennings and Hayes 1994; COSEWIC 2006) has led to the species being designated as vulnerable or sensitive in three of the four political entities across its geographic range: British Columbia (COSEWIC 2006), Oregon (Marshall et al. 1996; ODFW 1997), and California (Jennings and Hayes 1994). Collective observations of the frog’s decline are consistent with regional trends in habitat losses (Lehmkuhl and Ruggiero 1991; Noss and Peters 1995) and increases in exotic predators/competitors (e.g., introduced American Bullfrogs [*Rana catesbeiana*] and fishes; Kiesecker and Blaustein 1997, 1998; Adams 1999; Adams et al. 2003; Pearl et al. 2004).

Habitat Requirements: Aquatic Habitat — The best understood *R. aurora* habitat needs are those for aquatic habitat which are necessary for oviposition and egg development (Storm

1960; Licht 1969a, 1971, 1974; Calef 1973a; Brown 1975), larval development (Dickman 1968; Calef 1973b; Licht 1974), metamorphosis and juvenile growth before dispersal, and occasionally over-wintering (Licht 1974; Brown 1975; Hayes and Hayes 2003). Factors that determine habitat suitability for oviposition and development include water quality, hydrology, and vegetation characteristics.

Rana aurora requires fresh water (salinity > 4.5‰ kills embryos, M. Hayes unpubl. data) with circumneutral pH ($3.5 \geq \text{pH} \geq 9.0$ kills embryos; Schuyttema and Nebeker 1996; Pauli et al. 2000). Water temperatures $\geq 21^\circ\text{C}$ are lethal to early embryonic stages (Licht 1971); older developmental stages appear more tolerant of high temperatures. Eggs appear to have the lowest mortality in waters with little or no flow (Storm 1960; Nussbaum et al. 1983) or where water velocities are < 5 cm/sec (K. Richter pers. obs.). Length of larval period varies with elevation and latitude but a six-month hydroperiod appears sufficient to allow development through metamorphosis (Richter and Azous 1995). Water levels in the breeding wetland may be an important issue in developing landscapes (Richter and Azous 1995, 2001). High fluctuations during embryogeny are more likely to strand egg masses above the waterline, increasing mortality from desiccation or freezing (Reinelt et al. 1998; Ostergaard et al. 2008). Mortality of embryos may also increase with egg mass depth within the water column (K. Richter unpubl. data). Egg masses are typically attached to rooted vegetation (Storm 1960; Licht 1969a; Calef 1973a), dead branches and twigs and rarely, other stationary objects (M. Hayes pers. obs.). Sunlight appears to be important for embryonic development (Storm 1960; Licht 1969a, 1971; Calef 1973a; Brown 1975), but the basis of this apparent relationship is unclear. Observations that water molds invade excessively shaded egg masses resulting in high embryonic mortality (M. Diehl pers. comm.) imply that sunlight *per se* is important.

Biotic constraints (limits imposed by presence or absence of other species) on *R. aurora* aquatic habitat use may also exist, but to date, such constraints have been identified only in context of introduced aquatic fauna, which are discussed in the Threats section. Relatively high fecundity and long life span (8–12 yrs) suggest that *R. aurora* may be adapted to occasional reproductive failures, i.e., failure of a single cohort without incurring a large risk of local population extirpation (Licht 1969a, 1971, 1974). Resilience of *R. aurora* populations to these types of demographic events remains unquantified.

Juveniles typically disperse from their natal ponds a few weeks to two months following metamorphosis (Storm 1960; Licht 1974; Brown 1975; Hayes and Hayes 2003), and adult frogs usually disperse within eight weeks of breeding (Storm 1960; Licht 1969a; Brown 1975; Serra Shean 2002).

Postmetamorphic life stages are occasionally observed in aquatic habitats during the non-breeding season (Schuett-Hames 2004). Adults may also overwinter in aquatic habitat, especially when temperatures are colder (Ritson and Hayes 2000). Overwintering data on *R. aurora* remain sparse, but these patterns



Fig. 1. Adult female Northern Red-legged Frog (*Rana aurora*) encountered during fall pre-overwintering migration in a partly developed forested landscape, West Olympia, Washington, October 2005. (Photo: Marc Hayes)

agree with overwintering patterns known for other ranid frogs from temperate regions (Feder and Burggren 1992).

Habitat Requirements: Terrestrial Habitat — Several recent studies have augmented our understanding of terrestrial habitat use (e.g., Haggard 2000; Ritson and Hayes 2000; Hayes et al. 2001; Serra Shean 2002; Schuett-Hames 2004). These studies were limited mostly to adult female frogs since habitat use studies traditionally rely on telemetry, which requires a relatively large minimum body size (e.g., Ritson and Hayes 2000).

Adults use riparian or upland terrestrial areas during the non-breeding active season and at least some of the overwintering interval (Haggard 2000; Ritson and Hayes 2000; Hayes et al. 2001; Schuett-Hames 2004). Once reaching terrestrial habitat, adult frogs appear to be relatively sedentary, moving < 10 m daily (Haggard 2000; Ritson and Hayes 2000; Schuett-Hames 2004; Chan-McLeod and Wheeldon 2004) and up to 80 m seasonally (Schuett-Hames 2004). Although based on fewer data, juveniles also use terrestrial habitat during the active season following dispersal from their natal ponds (Licht 1986; Bury and Corn 1988a; Twedt 1993).

Despite uncertainties about the role that terrestrial habitat plays for *R. aurora*, studies indicate that *R. aurora* is strongly associated or even limited to forest habitat (e.g., Haggard 2000; Serra Shean 2002; Chan-McLeod 2003; Chan-McLeod and Wheeldon 2004; Jones et al. 2005). In addition, adult *R. aurora* seem to prefer forests with complex understory structure, often with high levels of woody debris (Aubry and Hall 1991; Haggard 2000; Ritson and Hayes 2000; Schuett-Hames 2004). When away from cover, *R. aurora* depends on crypsis and immobility to avoid detection, but rarely moves farther than 12.5 m from vegetation (Gregory 1979; Haggard 2000;

Ritson and Hayes 2000; Chan-McLeod 2003; Schuett-Hames 2004) that can serve as escape and hiding cover (Aubry and Hall 1991). Many plant species create a complex understory, but Sword Fern (*Polystichum munitum*) may create especially favorable conditions for *R. aurora* (Haggard 2000; Ritson and Hayes 2000; Schuett-Hames 2004). A complex understory likely provides appropriate moisture and temperature conditions (Schuett-Hames 2004). Forest type may also influence habitat quality. Gomez and Anthony (1996) found that *R. aurora* is more abundant in deciduous than mature coniferous forest, a pattern that may reflect richer invertebrate production in Alder (*Alnus*)-dominated deciduous forests in the Pacific Northwest (e.g., Shirley 2004). Litter depth has been positively correlated with *R. aurora* abundance (Aubry 2000). Deciduous forest with trees like Big-leaf Maple (*Acer macrophyllum*) may also provide litter structure more conducive to concealment and thermoregulation than the less structural complex litter in exclusively conifer forests (Schuett-Hames 2004).

Habitat Requirements: Landscape Complementation — Landscape complementation addresses the proximity of habitat types and the degree to which organisms can move among them (Pope et al. 2000). Adult *R. aurora* have been recaptured up to 4.8 km from their breeding sites and seasonal movements in the 1+ km range from the breeding area may be typical (Hayes et al. 2001, 2007). Studies that have examined frog movement over a fraction of the annual cycle show movement scales that exceed 150 m (Dumas 1966; Haggard 2000; Ritson and Hayes 2000; Serra Shean 2002; Schuett-Hames 2004). Movement pathways and temporary stop-over locations among seasonal habitats include upland forests, streams, riparian areas, seeps, and emergent, shrub-scrub, and forested wetlands (Haggard 2000; Ritson and Hayes 2000; Serra Shean 2002; Schuett-Hames 2004).

Threats — Washington State is expected to grow by two million people between 2000 and 2020, most of it concentrated in the Puget Sound region (WOFM 2002), which will likely result in the reduction of *R. aurora* habitat across a large portion of its geographic range. Clearing and construction activities undoubtedly kill some amphibians, but the important, long-term effect of such conversions is the loss of suitable habitat and fragmentation (Minton 1968; Knutson et al. 2000; Semlitsch 2000; Findlay et al. 2001). Loss of habitat through development and conversion represents severe and typically irreversible changes; restoration of converted lands to native vegetation almost never occurs (Minton 1968; Olson et al. 1997; Delis et al. 1996). We discuss the issue of habitat loss and its associated secondary effects in context of threats to *R. aurora* aquatic and terrestrial habitat needs.

Threats: Aquatic Habitat — Washington State had lost as much as 39% of its historical wetland area by 1988 (Lane and Taylor 1996), and 87% of wetlands were lost from Oregon's Willamette Valley by the late-1990s (Oregon Biodiversity Proj-

ect 1998). Wetland conversion began to slow around 1990 with enforcement of Sections 301(a) and 404 of the Clean Water Act and federal "No Net Loss of Wetlands" policies, but losses continued to outdistance gains (Dahl and Johnson 1991). More recently, reinterpretation of the Clean Water Act to exclude isolated wetlands from development protection has exacerbated this pattern (NRC 2001; Leibowitz 2002; Leibowitz and Nadeau 2003) in some states. However, this reinterpretation does not supercede state law in California and Washington, which have regulations that continue to protect isolated wetlands (WDOE 2001; CSWRCB 2005). Isolated wetlands may constitute some of the best breeding habitat for *R. aurora* because many of these wetlands are seasonal (Richter and Azous 1995), and thus unlikely to harbor exotic aquatic *R. aurora* predators (e.g., warmwater fishes, Adams 1999) that require permanent water.

Separating the effects of habitat loss *per se* from the effects of fragmentation on species persistence is difficult because these processes are often interdependent and difficult to study separately (Fahrig 2003). Urbanizing landscapes can negatively affect wetland function for amphibians even if the exact cause-and-effect mechanism for those declines is not known. For example, amphibian (and reptile) species richness in wetlands was negatively associated with: 1) percent of the watershed that was urbanized (Richter and Azous 1995), 2) amount of urban development within 1 km (Knutson et al. 1999), 3) the proportion of developed land within 2.5 km (Lehtinen et al. 1999), and 4) road densities within 2 km (Findlay and Houlihan 1997). These relationships may reflect the direct effects of development on wetlands through changes in hydrology or water quality. Alternatively, or perhaps in combination, declines in amphibians may be the result of alteration to terrestrial habitat (see next section). We cover four categories of threats to the aquatic habitat: water quality, hydrology, vegetation, and exotic aquatic predators.

Water quality is relatively well-studied in a general context, but data addressing *R. aurora* are limited and drawn mostly from laboratory settings. We address two types of amphibian water quality issues, problems linked to physiological ecology and problems associated with toxicology (e.g., biocides).

Rana aurora embryos have a lower critical thermal maximum than any other North American frog (Licht 1971), which suggests that this species may be vulnerable to thermal enrichment from urban runoff (see Yi and James 2004) and to warming associated with climate change. *Rana aurora* currently breeds during mid-to-late winter probably due in part to this thermal constraint. Earlier spring thaws, as have been shown by recent studies on global warming (e.g., Gibbs and Breisch 2001; Kiesecker et al. 2001), may increase risk to frogs at low elevations. At low elevations, *R. aurora* may have limited opportunities to breed earlier because the time window with appropriate temperatures available for such a shift is already short (Ovaska 1997). Thermal pollution may also lower dissolved oxygen levels, which can increase mortality of eggs and larvae. Lower oxygen levels can also increase risk to

larval stages through alteration of the competitor/predator set (Koehn and Frank 1980).

Application of fertilizers and pesticides are common practices in urban landscapes (e.g., golf courses, lawns, and yards) and in agricultural remnants within the urban matrix (Paul and Meyer 2001; Croteau et al. 2008). Ammonium nitrate (NH_3NO_3) and ammonium sulfate (NH_3SO_4), common components of many fertilizers (e.g., Matthews 1994; Akiyama et al. 2000), kill frog developmental stages at concentrations lower than typical application levels, which are lower than U.S. Environmental Protection Agency water quality criteria for either human drinking water or warmwater fishes (Marco et al. 1999). The 7-day median lethal concentration (LC50) for *R. aurora* larvae was 4.0 mg/L NH_3NO_3 , whereas the 15-day LC50 was 1.2 mg/L. In studies using *R. aurora* embryos, the 16-day LC50 for NH_3NO_3 was 71.9 mg/L, but the 16-day LC50 for sodium nitrate (NaNO_3) was 636.3 mg/L, which pointed to ammonium rather than nitrate ions producing the toxic effect (Schuytema and Nebeker 1999). Moreover, significant decreases in the length and weight of *R. aurora* embryos were observed at NH_3NO_3 concentrations ≥ 13.2 mg/L, and at concentrations of $\text{NaNO}_3 > 29.1$ mg/L (Schuytema and Nebeker 1999). In similar work, concentrations of ammonium sulfate (NH_3SO_4) ≥ 134 mg/L impaired *R. aurora* larval growth (Nebeker and Schuytema 2000). Laboratory-based studies show that low concentrations produced deleterious effects on frogs, but we do not know if typical fertilizer applications in the field produce these same effects.

In comparison to fertilizers, few studies have addressed *R. aurora* vulnerability to biocides. The herbicide diuron [3-(3,4-dichlorophenyl)-1, 1-dimethyl-urea] is commonly applied pre-emergence to control annual weeds and can persist in the soil for several months (William et al. 1993). Diuron application, which often coincides with the rainy season in the Pacific Northwest (Nebeker and Schuytema 1998), can wash into *R. aurora* breeding sites. Laboratory studies indicate that the 14-day LC50 for *R. aurora* larvae was 22 mg/L diuron and > 7.6 mg/L diuron retarded limb development (Schuytema and Nebeker 1998), but field studies have not addressed diuron application.

In the Puget Sound region of Washington and the Georgia Basin of British Columbia, atrazine, prometon, simazine, and tenthion were most frequently detected in surface water (Bortleson and Ebbert 2000). In King and Snohomish counties, Voss and Embrey (2000) found five commonly sold residential insecticides (carbaryl, clorpyrifos, diazinon, lindane, and malathion) in urban streams at concentrations exceeding maximum limits for the protection of aquatic life established by the National Academy of Sciences and National Academy of Engineering (NAS/NAE) or the Ministries of Health Canada and Environment Canada. Moreover, they found carbaryl, diazinon, and lindane exceeding chronic aquatic life criteria recommended by Norris and Dost (1992), the U.S. Environmental Protection Agency (US EPA 1998), and the State of Washington (Washington State 1992). Harmful effects of some of these chemicals on California Red-legged Frogs (*R.*

draytonii, Davidson et al. 2001) suggest that similar problems could occur for *R. aurora* in the Puget Sound lowlands.

Because endocrine disruptors are biologically active at very low concentrations, they may represent the most important class of toxic substances that humans introduce into waterways (Colburn et al. 1996). In northwestern California, adult male and subadult *R. aurora* from 9 of 13 sites were found to produce vitellogenin, a biomarker implying exposure to feminizing compounds (Bettaso et al. 2002). This problem has become increasingly apparent by three recent findings: feminization of male *Rana pipiens* in the laboratory by the widely used herbicide atrazine at concentrations far below standard application levels (Hayes et al. 2002a), the discovery of feminized male *R. pipiens* associated with areas of atrazine application in the wild (Hayes et al. 2002b), and the relationship between areas of atrazine use in the United States and *R. pipiens* declines (Hayes et al. 2003). Colburn et al. (1996) cautioned that numerous substances exist with some endocrine-disrupting action in urban effluents as yet untested for their effects on amphibians.

Urbanization can threaten *R. aurora* through changes in hydroperiod, water level, and flow rates that exceed breeding and larval rearing requirements (Holland et al. 1995; Thom et al. 2001; Kentula et al. 2004). Increasing levels of impervious surfaces can convert natural wetlands into default storm water systems with higher water level fluctuations (Horner et al. 1996). Water level fluctuations can result in stranding of amphibian eggs oviposited during high water conditions (K. Richter pers. obs.). These fluctuations may also reduce species richness of wetland plant and amphibian communities (Reinelt et al. 1998). Storm water ponds, which are designed to accommodate flows from heavy storm events, can provide new opportunities for breeding amphibians but can also act as ecological traps if *R. aurora* are attracted for breeding, but where recruitment of metamorphs is not possible (Ostergaard 2001; Ostergaard et al. 2008; K. Richter and T. Quinn pers. obs.). In some urbanizing landscapes, seasonal and semi-permanent hydrogeomorphic wetlands are transformed into permanently flooded wetlands (Kentula et al. 2004), increasing the possibility of undesirable exotics colonizing the site (Adams 1999; see subsequent paragraph on exotics). Moreover, interruption or redirection of surface flow by impervious areas of development also reduces groundwater infiltration (Arnold and Gibbons 1996; Thom et al. 2001; Booth et al. 2002), thereby diminishing wetland hydroperiods. Finally, collection and concentration of flows into wetlands may result in current velocities that discourage lentic-breeding *R. aurora* or damages or strips eggs from their oviposition sites (K. Richter and H. Roughgarden pers. obs.). In the Pacific Northwest, hydrological alterations associated with urbanization may speed or redirect the succession of wetlands to dense shrub-scrub matrices (Reinelt et al. 1998), reducing species richness of native emergent herbaceous plants (Azous and Cooke 2001).

Humans facilitate the spread of exotic wetland plant species by providing dispersal corridors, acting as agents of dispersal

(both active and passive), disturbing biological controls, and altering ecosystem processes (McKnight 1993). The effects of such exotics on *R. aurora*, however, have not been addressed. Reed Canarygrass (*Phalaris arundinacea*), a widespread invasive in Pacific Northwest wetlands (Kilbride and Paveglio 1999), had no obvious effect on *R. aurora* oviposition (Callison 2001). However, 0.5, 1.5, and 2.0% concentrations of green *P. arundinacea* extract reduced survival of Western Toad (*Bufo boreas*) larvae (A. Sullivan pers. comm.). Purple Loosestrife (*Lythrum salicaria*), a species that has only recently invaded Pacific Northwest wetlands, has also been shown to reduce growth and survival of Green Frog (*Rana clamitans*) (Blossey et al. 2001) and American Toad (*Bufo americanus*) larvae (Brown et al. 2006) in mesocosm experiments. Exotic predators are increasingly viewed as threats to amphibians in aquatic habitats. However, isolating the role of predators on amphibian communities has proven difficult because predator effects are often confounded with those resulting from habitat modification (Hayes and Jennings 1986). The American Bullfrog and several warmwater fish species, all largely limited to permanent wetlands, may hinder *R. aurora* from using or colonizing permanent aquatic habitats (Adams 1999; Ostergaard 2001; Ostergaard et al. 2008; Richter et al. 2008; see also Licht 1969b). Work in Washington State to date has been unable to identify a negative Bullfrog effect on *R. aurora*, although a negative fish effect has been documented (Adams 1999; Ostergaard 2001). When both larval and adult *R. catesbeiana* were present in enclosure experiments, *R. aurora* moved into deeper water and reduced their activity, which protracted their larval period and reduced their survival and mass at metamorphosis (Kiesecker and Blaustein 1997, 1998). Further, *R. aurora* larvae exposed to both larval *R. catesbeiana* and Smallmouth Bass (*Micropterus dolomieu*), had lower survivorship than in the presence of either alone, an effect thought to occur because *M. dolomieu* prey on *R. aurora* after *R. catesbeiana* presence causes them to shift into deeper water (Kiesecker and Blaustein 1998). How these patterns apply to free-ranging *R. aurora* larvae is unknown, but Adams et al. (2003) provided some field evidence that Bluegill (*Lepomis macrochirus*) facilitate *R. catesbeiana* survival in Oregon, which may help explain why *R. aurora* has become increasingly sparse in the Willamette Valley (Nussbaum et al. 1983; St. John 1987). *Rana catesbeiana* also prey upon *R. aurora* (Twedt 1993; Kiesecker and Blaustein 1997), but the demographic consequences on *R. aurora* are unstudied. Adults of *R. aurora* and *R. catesbeiana* display limited niche overlap (Twedt 1993) and *R. aurora* may be more able than its congener, the Oregon Spotted Frog (*Rana pretiosa*), to escape *R. catesbeiana* predation (Pearl et al. 2004). *Rana catesbeiana* are known to engage male *R. aurora* in amplexus during the breeding period (Pearl et al. 2005), which disrupts breeding.

Threats: Terrestrial Habitat — Loss of complex habitat structure (over and understory vegetation) may be the greatest threat to *R. aurora* in urbanizing areas. However, only Richter

and Azous (2001), Ostergaard (2001), and Ostergaard et al. (2008) have provided evidence that greater amounts of forest within a “broader landscape context” (within 1 km: Porej et al. 2004; within 2 km: Findlay and Houlahan 1997; and up to 2.5 km: Lehtinen et al. 1999) are positively related to wetland amphibian diversity where *R. aurora* was part of the assemblage. A recent study in a managed forest landscape suggests that canopy cover is important; clearcut-harvest patches < 12 yrs old seemed to be barriers to amphibian movement, particularly when mediating climatic conditions (e.g., rain) were lacking (Chan-McLeod 2003). Canopy cover may also explain *R. aurora*’s extended use of small patches of residual trees within clearcut blocks otherwise devoid of frogs (Chan-McLeod and Wheeldon 2004). Local alterations in microclimate due to urbanization (e.g., Eden 1985) and clearcut harvest (Chen et al. 1990, 1992a,b), and partial overstory harvest (Fritschen and Edmonds 1976; Reifsnnyder 1955) may influence the suitability of terrestrial habitat for *R. aurora* (Bury and Corn 1988b). For example, with diminished forest canopy cover, large woody debris, ground vegetation, and leaf and organic layers may experience greater fluctuations in temperatures, lower humidity, and increasing wind (Chen et al. 1990, 1992a,b). These physical changes have the potential to alter food resources (Marra and Edmonds 1998), diel refuges (Stewart and Pough 1983), and hibernacula for frogs in terrestrial habitats (Regosin et al. 2003), but such effects remain unstudied for *R. aurora*. Biocides may also affect frogs in terrestrial environments. In summer, adult *R. aurora* often absorb water from moist substrates (Schuett-Hames 2004), a behavior that could expose adults to fertilizers and pesticides.

Threats: Landscape Complementation — Reduced habitat connectivity resulting from habitat loss (With 1997) and increased numbers of roads (Gibbs 1998) are common changes in urbanizing landscapes, and are thought to negatively affect amphibian species diversity (Lehtinen et al. 1999). Fragmentation and habitat loss can inhibit movements by increasing the interspersions of suitable and unsuitable patches (Hels and Buchwald 2001; Chan-McLeod 2003) and by increasing distances among suitable patches (Gibbs 1993). Vagile species like *R. aurora*, for which the scale of seasonal habitat use is relatively large, are likely to be sensitive indicators to urbanization effects on habitat fragmentation.

The effects of roads, ranging from direct mortality to contributing to fragmentation that hinders amphibian movement, is a leading threat to biodiversity (see Andrews and Gibbons 2008). Mortality from road traffic may be critically important to *R. aurora*. Beasley (2002) found that 85% of 655 amphibians, including 138 *R. aurora*, were killed attempting to cross a coastal highway in British Columbia during spring and fall 2001. The only other information on road mortality on *R. aurora* involved observations, over a five-day period, of 15 adult frogs killed by vehicles along 0.5-km of road while frogs were moving between active season and overwintering habitat (Schuett-Hames 2004). Without demographic data,

the significance of road mortality from such studies cannot be assessed. However, factors that influence the likelihood of mortality during such crossings can be identified. Road crossing mortality rates will increase as animal movement distances and road densities increase. *Rana aurora* travel farther, cross more roads, and are thus at greater risk than most species of wetland breeding amphibians in the Pacific Northwest (Carr and Fahrig 2001). The most important factors influencing road mortality are likely traffic volume and timing of amphibian movement relative to traffic volume (Fahrig et al. 1995; Lamoureux and Madison 1999; Hels and Buchwald 2001).

An underappreciated aspect of fragmentation in general and roads in particular is the lag-time between development and species disappearance, patterns unstudied in *R. aurora*. Findlay and Bourdages (2000) reported loss of some amphibian and reptile species in < 8 yrs following road construction, but their results also suggest that measuring the full impacts of roads may require decades. Road effects can be more subtle than crossing-associated mortality. For example, roads may reduce genetic diversity (average heterozygosity and polymorphism) in local populations of amphibians without obvious demographic changes (Reh and Seitz 1990).

Guidelines and Regulations — Guidelines and regulatory measures that provide protection and maintenance for *R. aurora* habitat are diverse. We summarize these measures for each of the aquatic, terrestrial, and landscape needs of *R. aurora* (Table 1).

Guidelines and Regulations: Protection for Aquatic Habitat — Fixed-width buffers are the most common and widespread method of protecting wetlands from the detrimental impacts of adjacent land uses (NRC 2001). However, buffers applied in the range of *R. aurora* are rarely species-based, rather their application is based on wetland type, generic wetland functions (other than amphibian habitat), and adjacent land use (WDOE 2004; McMillan 2000; A. McMillan pers. comm.). Consequently, a broad range of buffer widths have been recommended for protection of wetlands (Brown et al. 1990; Castelle et al. 1992, 1994; McMillan 2000). Washington State, which has more generous buffer guidelines than other political entities across the range of *R. aurora*, recommends wetland buffers from 15.2 m to 91.4 m wide (McMillan 1998) depending on wetland quality, function, and size (Hruby 2004). However, buffer widths can be reduced if adjacent lands are relatively undisturbed and wetland function is deemed relatively good (WDOE 2004), or ignored depending on the predilections of local jurisdictions (McMillan 1998). Wetland buffer guidelines or regulations in British Columbia, California, and Oregon are uniformly less stringent.

King County, which has the most stringent regulatory protection for wetlands among local jurisdictions in Washington State, adopted the State wetland buffer recommendation in addition to allowing partial removal of vegetation for control of invasive species and other uses that enhance ecological functions (King County 2004b). Besides wetland buffers,

Table 1. Summary of adequacy of habitat protection guidelines and regulations with regard to Northern Red-legged Frog (*Rana aurora*).

Protection Category	Evaluation
1) Aquatic Habitat	<p>Physical Structure: Generally adequate when a wetland buffer consisting of native forested vegetation with well-developed understory is retained; best-case guideline recommends 91 m buffers (King County 2004a,b). Yet, buffer requirements almost never address <i>R. aurora</i> per se. Science informing buffer widths adequate to address physical disturbance to wetland habitat specifically for <i>R. aurora</i> is lacking.</p> <p>Hydrology: Generally inadequate since the hydrographic basin or area influencing wetlands is typically not addressed. The best-case scenario is a critical area ordinance to maintain 65% of rural lands in natural vegetation, but this requirement applies only to undeveloped land (King County 2004a).</p> <p>Water Quality: Unclear because the science informing selected water quality issues specific to <i>R. aurora</i> is lacking. Water quality guidelines and regulations are typically based on human or economically important fish criteria that have been shown to be harmful to some amphibians.</p>
2) Terrestrial Habitat	<p>Inadequate since even the widest buffers currently applied are small relative to the large movement scale of <i>R. aurora</i>. Some measures (e.g., geologic hazard areas, areas for aquifer recharge, and 65% vegetation retention on rural lands) provide protection beyond the broadest buffers, although the condition, extent, and location of forests in these areas may not support frog populations. Information on <i>R. aurora</i> terrestrial habitat use is lacking.</p>
3) Landscape complementation	<p>Partly adequate in the sense that buffers may meet terrestrial habitat needs for a portion of the breeding population (see Aquatic Habitat above), but inadequate in that terrestrial habitat for the wider ranging population segment are typically too small or fragmented (see Terrestrial Habitat above).</p>

King County, the most urbanized in Washington State (King County 2002), recognized that buffers might not adequately safeguard all wetland functions (Correll 1997; McMillan 2000; Thom et al. 2001). Consequently, their new critical areas ordinance now includes provisions for protecting corridors between wetland complexes and for maintaining connections to upland habitats via a wildlife network to address the issue of isolating species associated with wetlands. They also restrict the amount of rural land that can be cleared of vegetation to between 35 and 50% to help safeguard watershed hydrology and improve surface water quality, although flexibility is permitted for development and other land uses predicated on site-specific Farm and Rural Stewardship Plans that require best management practices to offset negative impacts associated with greater clearing (King County 2004b).

All jurisdictions across *R. aurora* range have regulations relating to water quality, but these are mostly based on human safety concerns or economically important fish species. For example, water quality requirements for temperature in Oregon and Washington are based largely on temperature requirements for salmonids (Hicks 2003; ODEQ 2008). Likewise, British Columbia, California, Oregon, and Washington have anti-pollution regulations for aquatic habitats aimed at minimizing risk to humans (BC MELP 1998; Seiders 2003; ODEQ 2008; CEPA 2007). However, where numeric standards exist, state-level pollution regulations revert to levels allowable by EPA (in USA) for various toxicants (see Seiders 2003; ODEQ 2008; CEPA 2007). In the few cases where an amphibian-specific endocrine disruptor (e.g., atrazine) has been identified, state jurisdictions either do not identify allowable levels, or if they do, set allowable levels for humans. These levels typically exceed the safe thresholds for the few amphibians that have been tested. Such cases are currently few, but given the number of potentially active chemicals (especially pharmaceuticals and personal care products), it is increasingly likely that regulations based on needs for human safety or endangered fish will not safeguard amphibians.

Guidelines and Regulations: Protection for Terrestrial Habitat—Aside from buffers, few guidelines and regulations provide for the terrestrial habitat needs of wetland-associated species. Within Urban Growth Boundaries (UGAs) set by local jurisdictions in California, Oregon and Washington, the protection of upland areas was typically haphazard at least until recently. The Washington State GMA, which considers areas both inside and outside of UGAs, requires local jurisdictions to designate critical areas for protection that go beyond the buffers required for most wetlands (Washington State 2005). These include geologic hazards (e.g., landslide prone), aquifer recharge areas, flood-prone areas, and fish and wildlife conservation areas. Depending on the type of critical area, these designations provide varying levels of protection from development or other human activities. While the Washington State GMA included consideration of “fish and wildlife conservation areas,” in practice these areas are often designated as specific sites (i.e.,

location of a verifiable occurrence record) with localized protection measures similar in concept to a buffer. Rarely do jurisdictions consider viability or even the broader population of the species of which such sites are a part. Except for King County, we found no critical area ordinances that specifically address terrestrial habitat needs for any amphibians.

Guidelines and Regulations: Ensuring Landscape Complementa-tion—Wetland buffers, aquifer recharge areas, geologic hazard areas, and land designated as fish and wildlife conservation areas may provide some degree of landscape complementation for *R. aurora*. In some areas like King County, wetland protection is already considered at a landscape scale even if it does not specifically address *R. aurora*. In general, however, landscape complementation for *R. aurora* (or any species) is not considered. Furthermore, even if *R. aurora* became “listed” as threatened, endangered or sensitive, the current regulatory environment within the Washington State GMA would not automatically result in protection of both aquatic and terrestrial habitat.

DISCUSSION

Humans have dramatic effects on the suitability of wetlands as *R. aurora* breeding habitat. Development can alter wetland hydrological regimes by modifying velocities, volume and timing of surface flows, reducing aquifer recharge, and lowering ground water tables. It can also result in changes to thermal (air and water) and nutrient regimes of wetlands, and facilitate the routing of toxins and spread of invasive exotic biota. Although changes in the physical processes associated with urbanization may be partly mitigated by wetland buffers, these processes typically reflect conditions across the larger watershed. Thus, maintaining wetland functions in urbanizing landscapes, including breeding habitat for *R. aurora*, requires consideration of conditions and ecological processes across the landscape in which those wetlands occur (Dodd and Cade 1998). Recent understanding of *R. aurora* movement behavior also underscores the need to consider the landscape beyond the wetland buffer.

Buffers will continue to aid conservation of *R. aurora* in urbanizing landscapes, but their role is limited. Buffers may provide habitat for a variety of species and protect wetlands from the negative influences of adjacent land uses. To maximize their usefulness, buffers must be large enough to maintain conditions important to species that rely on them (in our case *R. aurora*). Several studies have shown that microclimate within a patch is related to distance from the patch edge and conditions outside the patch (e.g., Chen et al. 1990, 1992a,b), but little work has been done to quantify microclimate as it may affect amphibian habitat (i.e., near the soil surface).

The idea that buffers alone can meet the needs of amphibians has roots in amphibian conservation literature. In a review of biologically effective recovery plans for aquatic-breeding amphibians, Semlitsch (2002) stated, “*Adult amphibians gen-*

erally remain within a few hundred meters of their home ponds or streams...survivors typically return to the same locations to breed each year.” That statement may have arisen from an earlier statement (Semlitsch 1998) made in a review of the buffer requirements for salamanders, when he stated that, “the majority of adults return to ‘home’ ponds, usually after migrating no more than 200–300 m to foraging and overwintering habitats.” Semlitsch (2002) did find support for this kind of seasonal movement scale in a review addressing European anurans (Sinsch 1990). However, his statement appears largely limited to salamanders and should not be applied to ranid frogs and bufonids, particularly species in western North America. Seasonal movement scales of ranid frogs and toads frequently exceed 500 m (see Hayes et al. 2001, 2007; Pilliod et al. 2002; Bulger et al. 2003; Bartelt et al. 2004) and movement distances up to 5 km have been recorded (Reaser and Dexter 1996; Hayes et al. 2007). The difference in movement scale between anurans and salamanders may partly reflect the greater metabolic needs of the former group (Feder and Burggren 1992).

Rana aurora will probably not persist in urbanizing environments by virtue of traditional wetland buffers, even if effects of urbanization on input processes (e.g., routing of water, sediment, heat, toxics) have been completely mitigated. Wetland buffers may provide upland habitat for a segment of the breeding population but we expect the risk of local (and likely meta-) population extirpation to increase as the proportion of forest in the landscape decreases. The nature of the extirpation risk is currently difficult to quantify, but elements of *R. aurora* ecology can shed light on relative risk. *Rana aurora* is relatively vagile and makes long migrations at least twice a year to and from the breeding site. As migration distances increase, so does mortality associated with encountering unsuitable land uses, such as non-forested areas and roads. Species that require landscape complementation, one habitat type (e.g., breeding) in close proximity to another habitat type (e.g., foraging or rearing), are especially vulnerable to local population declines (Haila et al. 1993; Gulve 1994; Sjörgen 1991; Hinsley et al. 1995; Brook et al. 2000; Lehmkühl et al. 2001; Semlitsch and Bodie 2003). Anecdotal evidence suggests that *R. aurora* use historic migration routes for travel to and from breeding sites. Development that destroys or alters these routes may negatively affect a population even though the overall landscape appears suitable.

Given the scale of movement and patchy nature of breeding habitat in time and space, *R. aurora* may typically exist as metapopulations. In urbanizing areas where *R. aurora* becomes a focus for conservation, it may be important to consider multiple wetlands across broader landscapes to avoid losing a *R. aurora* population to a single influence (Semlitsch and Bodie 1998; Fairbairn and Dinsmore 2001; Marzluff and Ewing 2001). Computer models of hypothetical species suggest that the effects of habitat loss greatly outweigh habitat fragmentation effects, which implies that protecting larger habitat blocks may be preferable to maintaining smaller blocks with corridors all else being equal (Fahrig 1997). At the most devel-

oped end of the urbanization spectrum, i.e., within the urban growth boundaries, settlement patterns and regulation result in relatively high human densities, which have precluded the protection of large blocks of forest, and perhaps *R. aurora* as well. Our greatest hope for *R. aurora* may be in those areas that are now coming under development pressure and where we may be able use the momentum of guidelines to protect human health and safety (such as those in King County) to refine protection strategies for wetland breeding amphibians. Waiting until an area is mostly developed and then trying to retrofit conservation actions for *R. aurora* is risky. Large blocks of undisturbed land rarely exist in urban areas, so the probability of encountering landowners unwilling to cooperate or voluntarily provide land for conservation increases with human density, and restoration (as opposed to conservation) is expensive and largely unproven (Minton 1968; Olson et al. 1997; Delis et al. 1996).

Signs of positive change in amphibian conservation tactics exist. Certain state and county governments in the United States have implemented more comprehensive approaches to conservation of wetland function perhaps in response to limitations of wetland buffers in dealing with storm water. For example, in Maryland (MDNR 2003), San Diego, California (SANDAG 2006), and Portland, Oregon (METRO 2002), wetlands and other resource lands were incorporated into comprehensive regional planning efforts based on principles of conservation biology and landscape ecology. King County implemented limits to the amount of land that could be cleared of vegetation mostly as a way of dealing with flooding, storm water, and other human health and safety related issues. King County regulations require that 50–65% of the undeveloped land in the county (on a parcel by parcel basis) remain vegetated unless site-specific stewardship plans provide ecological equivalency permitting tailored greater reductions (King County 2004b). This regulation may mitigate the indirect detrimental effect of human development on wetland functions and may also provide upland foraging, refuge, and hibernation habitats for *R. aurora*.

Management/Protection Recommendations — Opportunities to conserve *R. aurora* are greatest early in the urbanization process. *Rana aurora* breeding wetlands can be mapped, and corridors between nearby wetlands could be designated using landscape modeling approaches (e.g., see Ray et al. 2002). Landscape modeling suggests that retention of 50 to 80% forested habitat will have a high probability of ensuring functional habitat connectivity for species with limited vagility (With 1999), potentially providing a rule-of-thumb threshold range to assure forest connectivity within a landscape. Road density and traffic volume should be minimized especially close to breeding sites and roads can be retrofitted to provide safer crossing opportunities (van Gelder 1973).

We encourage development of regulations to protect hydrological functions of wetlands, especially those that address retention of natural vegetation and minimization of imper-

vious surfaces. Linking conservation to ongoing efforts to address human health and safety should contribute some conservation value for all wetland-dependent species. Storm water retention ponds can play a role in mitigating the hydrological effects of urbanization, but technological fixes alone will not necessarily result in conservation of relatively undisturbed land within the urban matrix, which is critical to *R. aurora*. Because *R. aurora* appear closely tied to forested habitat, wetlands (buffers) should be adjacent and connected to upland forests and nearby forested stream buffers wherever possible. Opportunistic observations on movement pathways might help to determine where to best retain upland habitat.

Many forest types (based on composition and age class) may be suitable to *R. aurora* as long as enough understory vegetation is present. Most remaining forests in the lowland Pacific Northwest are on their second or third harvest rotation (Chappell et al. 2001). Many are in the stem exclusion stage of development (Oliver and Larson 1996), characterized by dense canopies, low light levels and limited understory development. Where opportunities to conserve additional forest are limited, *R. aurora* may benefit from the creation of canopy gaps in otherwise closed canopy forests to encourage understory development. Finally, we need to expand educational outreach to reduce fertilizer and pesticide use near *R. aurora* breeding ponds and upland habitat.

Adaptive Management and Research Needs — Adaptive management has yet to become a widespread model to guide management decisions in urbanizing areas. Nevertheless, nearly everyone seems to understand the virtues of managing adaptively and governments such as Washington State have institutionalized adaptive management as part of their state-level Growth Management Act. In this section, we prioritize adaptive management research questions for the conservation of amphibians in urbanizing landscapes.

Natural patterns of development in the rapidly urbanizing Pacific Northwest provide special opportunities for a range of fruitful research agendas. One of the more important and tractable research questions is related to the quantity and distribution of forest habitat needed to support healthy populations of *R. aurora*. Even before detailed *R. aurora* habitat use patterns are described, it is necessary to understand patterns of amphibian presence or abundance across urban gradients. With more information about hydrology, invasive plants, and aquatic predators, we could better understand how native amphibian occupancy of wetlands may be related to the presence of exotic aquatic predators. This study approach could also serve as a starting point for local status and trend monitoring programs that answers the question: *Are amphibian assemblages sustaining themselves across the urban gradient through time?*

Correlative studies are relatively inexpensive, but until we begin to focus on the mechanisms that control populations, we run the risk of being wrong. New studies need to address the mechanisms by which urbanization affects life stage-specific demography, and must attempt to answer questions like:

Where do frogs go when they leave the breeding site and what route do they take to get there? What proportion of the population uses areas near the breeding site as terrestrial habitat? Used with population models, demographic data can help reveal how life stage-specific survival and natality rates affect population resilience to disturbance events (i.e., types and degree of urbanization). Demographic studies using telemetry provide further opportunities to focus management-oriented research. Telemetry studies at local scales can address urban habitat use patterns at meso- and micro-scales and can help answer questions like: *What constitutes preferred habitat?* From the few data available, roads appear to be a major mortality factor for adult frogs. While population models can help predict rates of population decline, focused studies are needed on road mortality that address various population parameters. This issue could be addressed in part by a genetic study that asks: *How does habitat quality (including roads) affect gene flow across urbanizing landscapes?* Pesticides and endocrine-disrupting chemicals continue to loom as the least-studied factors that may be of greatest importance.

Even the most elegantly designed studies may not provide enough information to protect amphibians at specific sites in developed areas. Consequently, the best approach may be conservation planning (i.e., conservation zoning) similar to that being applied by Maryland, San Diego, Pennsylvania, Tucson, and other jurisdictions that address habitat complementation of target species or overall biodiversity. Conservation planning is not a panacea since setting aside land in one area often means concentrating people into other areas. The main advantage of this type of planning is the opportunity to create “some” functional habitat that meets all life history requirements of a species even if that species cannot be supported everywhere it occurred historically.

This review underscores the fact that while wetland buffers are useful, as currently applied they do not address all the habitat needs of amphibians, like *R. aurora*, that use different habitats across broad spatial scales. Fortunately for wetland breeding amphibians, many local jurisdictions are discovering that wetland buffers also do not effectively address human health and safety issues associated with storm water. We hope this case study provides another reason to consider wetland function at landscape scales.

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