Appendix A.11

Habitat Connectivity for Tiger Salamander (*Ambystoma tigrinum*) in the Columbia Plateau Ecoregion

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Introduction

Tiger salamander, photo by Gary M. Stolz

This report describes components of tiger salamander (*Ambystoma tigrinum*) biology that are relevant to an ecoregional analysis of habitat connectivity, species-specific analysis methods and results, and suggestions for future work. The tiger salamander is one of 11 focal species that we chose for analysis in the Columbia Plateau Ecoregion. This ecoregional analysis is an extension and refinement of the *Washington Connected Landscapes Project: Statewide Analysis* (WHCWG 2010). The statewide analysis modeled connectivity for 16 focal species and landscape integrity within Washington and surrounding areas. It incorporated data that could be compiled into seamless layers across a very broad area, such as land cover/land use, elevation, slope, housing density, and roads. Resolution was at a 100-meter grid cell size. To analyze connectivity for the Columbia Plateau Ecoregion, we used additional data layers (e.g., wind power generation and transmission facilities), defined habitat quality separately from landscape resistance, and applied a finer scale of resolution (30 m grid cell). We intend this ecoregional scale analysis of habitat connectivity for the tiger salamander to inform conservation and management of this species, and other similar species, on the Columbia Plateau.

Justification for Selection

The tiger salamander was selected as a focal species to represent wetland habitat types in the Columbia Plateau Ecoregion. This amphibian species is also known to use shrubsteppe and grassland vegetation types when metamorphosed individuals disperse across upland areas. Areas with cliffs, canyons, and talus may be used during dispersal if these features are close to aquatic breeding habitat. The tiger salamander is one of few salamanders adapted to arid climates.

The group selecting focal species for the Columbia Plateau Ecoregion gave the tiger salamander an Excellent rating for all five criteria used to evaluate candidate species. Tiger salamanders and other ambystomatids are relatively well studied, including landscape genetic analyses of connectivity among populations (e.g., Spear et al. 2005; Wang et al. 2009; Cosentino et al. 2011*a*, 2011*b*). These analyses provided insights about the relative resistance of different landscape features (both natural and human related). Tiger salamanders are relatively slow moving dispersers that are susceptible to desiccation, so removal or modification of natural habitats can impede or curtail tiger salamander dispersal. Individual salamanders are known to disperse up to several kilometers, a scale of movement appropriate for analysis of habitat connectivity for the Columbia Plateau Ecoregion.

In addition to sensitivity to habitat removal and modification, the tiger salamander is susceptible to other threats to dispersal that we considered important in our connectivity analysis. In particular, residential development, roads and associated traffic, and habitat changes related to climate change are all threats that reduce habitat connectivity for salamanders (Andrews et al. 2008; Goldberg & Waits 2010; Early & Sax 2011). To the best of our knowledge, no information is available about how tiger salamanders respond to wind energy development. California tiger salamanders (*A. californiense*) are abundant around wind farms in California (P. Trenham, personal communication).

Tiger Salamanders, like most amphibians, have a biphasic life history, with an aquatic larval phase and a terrestrial adult phase (Duellman & Trueb 1994). Thus, multiple landscape features related to both aquatic and terrestrial environments are likely important for explaining their distribution, as well as the genetic structure of populations (Spear et al. 2005). Use of diverse habitats, combined with limited vagility, suggest that the tiger salamander can be an indicator of habitat connectivity for a wide range of amphibians and other low-mobility species. In addition, amphibians are in global decline (Blaustein & Kiesecker 2002; Collins & Storfer 2003), resulting in increased conservation efforts on their behalf. Information about the influence of landscape features on habitat connectivity for tiger salamanders might improve the performance of conservation and management plans developed for other amphibians (Semlitsch 2002).

Ambystomatid populations may function as metapopulations with different populations occupying various positions on a continuum ranging from completely isolated to well connected (Gamble et al. 2007). How Columbia Plateau populations of tiger salamanders are distributed across this continuum is unknown, but relatively high longevity and mobility may reduce local extinction rates, shifting these populations towards the connected end of the continuum, and away from classic metapopulations (Smith & Green 2005; P. Trenham, personal communication). Nonetheless, effective conservation strategies targeting these and similarly structured amphibian populations must address landscape-level processes that affect likelihood of successful dispersal (Gamble et al. 2007).

The Washington State status of the tiger salamander is Monitor, indicating an animal taxon of potential concern. The Washington State rank is S3, indicating the tiger salamander is rare or uncommon (Hallock & McAllister 2005). The subspecies of tiger salamander found in Washington is not listed under the federal Endangered Species Act (although other subspecies are; e.g., the Sonora tiger salamander—*Ambystoma tigrinum stebbinsi*). The tiger salamander is on the provincial Red List in British Columbia. In Canada, the southern mountain population is designated as Endangered (COSEWIC 2002). Thus, in British Columbia, the tiger salamander is protected in that it cannot be killed, collected, or held in captivity without special permits, under the provincial Wildlife Act.

Distribution

The tiger salamander is the most widely distributed salamander in North America. Its distribution extends from central Canada south throughout much of the United States and into northern Mexico. Within this wide distribution, populations are generally scattered. In more arid western locations, the sparse distribution of suitable aquatic sites that are free of predatory fish contributes to an even more widely scattered distribution of populations.

In Washington, Oregon, and Idaho, tiger salamanders are primarily found in the Columbia Plateau Ecoregion, occurring throughout this ecoregion. Early collections and descriptions from this area in Washington confirm the tiger salamander is native to the Columbia Plateau. Disjunct populations occur in the Colville area and south-central Klickitat County (Hallock 2005). The distribution of populations in Oregon is patchy, with confirmed reports in The Dalles, near Klamath Falls, and in the Moon Reservoir in Harney County (Hallock 2005). These Oregon populations may have been introduced (Hallock 2005). Tiger salamander larvae are used as fishing bait, leading to widespread introductions to areas beyond their historical native range.

In British Columbia, tiger salamanders occur in the southern Okanogan, north to Peachland; in the lower Similkameen, west to Keremeos; and in the Sidley and Kettle River valleys, east to Christina Lake (Orchard 1991; Sarell & Robertson 1994; Sarell 1996; Sarell et al. 1998). Linkages among these three drainages in British Columbia are weak, but all three drainages are joined to the more contiguous range of the tiger salamander in Washington (Sarell 2004). Tiger salamanders may also occur in the southern part of the East Kootenay Trench (Sarell 2004).

Tiger salamanders have been found from valley bottoms (300 m) up to 1250 m in British Columbia (Orchard 1991). Populations at higher elevations are usually found in areas with well-developed soils and a grasslands component (Sarell 2004). In Colorado, tiger salamanders breed in ponds over 3600 m in elevation (Smith 2003).

Factors that have a strong influence on the distribution and abundance of tiger salamanders include availability of breeding ponds free of predatory fish and availability of subterranean burrows of sufficient depth to allow salamanders to avoid desiccation during summer drought and to overwinter. Tiger salamanders can excavate their own burrows, but also use the burrow and tunnel systems of burrowing rodents. The northern distribution of the tiger salamander in North America appears to be closely linked to the distribution of pocket gophers (*Thomomys* spp.; Sarell 1996).

Periodic drought is a natural limiting factor for tiger salamander populations (Orchard 1991). Annual and seasonal variations in precipitation and ground water flows may result in some ponds or wetlands drying up completely prior to metamorphosis of larvae. Human use of water may further reduce water levels and increase the frequency of ponds drying before metamorphosis has occurred. Mass mortality due to disease has also been reported from some populations in the Pacific Northwest (Hallock 2005).

Studies of tiger salamander landscape genetics and dispersal have generally found that gene flow is reduced between populations separated by more than one kilometer. A number of factors have been proposed as supportive of gene flow, and conversely, many potential barriers have been suggested. Only a few of these hypotheses have been tested. Categories of factors that may influence dispersal and gene flow include cover types, topography, elevation, slope, temperature-moisture regime, elevation, and presence of wetlands, streams and rivers. We have included these factors in GIS layers in our analysis. Please see the section below regarding Conceptual Basis for Model Development for more details about how we parameterized these factors regarding their contributions to landscape resistance and habitat value.

Linear human developments such as roads and associated housing and commercial development, railroads, power transmission lines, and large irrigation canals may also fragment salamander habitat and subdivide populations. All of these features were included in our analysis, but the degree to which these features influence habitat quality and landscape permeability is largely a matter of professional judgment. Subsequent sections of this report examine existing evidence about the effects of these features.

Agricultural development may have the most pervasive effects on tiger salamander distribution in the Columbia Plateau Ecoregion. The spatial distribution of intensive agriculture in the ecoregion is in turn strongly influenced by the distribution of scour associated with the Missoula Floods (periodic, cataclysmic floods that swept across the Columbia Plateau at the end of the last ice age). Intense scour from these flood events removed soils from large areas, rendering them unsuitable for agricultural development. Remaining natural vegetation with ponds suitable for breeding are largely located in areas that were scoured to bedrock by these floods. These remnant sites likely are not located in the most productive habitats formerly occupied by tiger salamander populations. In contrast, agricultural development, especially widespread irrigation, has likely provided artificial habitats for tiger salamanders in many parts of the analysis area.

Water bodies containing fish are also likely to fragment or constrain the distribution of tiger salamanders. It is well documented that predatory fish limit the distribution and abundance of amphibians (see reviews by Kats & Ferrer 2003; Dunham et al. 2004). Thus, rivers, streams and lakes with predatory fish may reduce the continuity of suitable habitat across the landscape, potentially reducing or interrupting gene flow (Storfer 1999).

Because riverine travel would expose salamanders to fish predation, it is unlikely that salamanders typically would remain in moving water for extended periods. Tiger salamanders have used streams as breeding habitat (Collins 1981), but the extent of this behavior in the Columbia Plateau Ecoregion is unknown. Small, fishless pools or beaver (*Castor canadensis*) ponds that are often adjacent to streams can provide habitat or breeding sites. Periodic flooding of these off-channel habitats might introduce predatory fish and reduce the habitat quality of these pools.

Habitat Associations

Aquatic

The tiger salamander breeds in a variety of temporary and permanent aquatic habitats. In the Columbia Plateau Ecoregion many of these are currently small and alkaline, because predatory fish have been stocked into larger, permanent waterbodies, with water quality suitable for supporting game fish. Tiger salamanders typically lay their eggs in shallow, warm water that is

<1 m deep (Orchard 1991). Emergent vegetation provides cover, a supply of invertebrate prey, and substrate for attaching eggs, but is not characteristic of all breeding sites (Sarell 2004).

Aquatic habitats that retain water until late July or August provide consistent breeding sites compared to water bodies that may dry prior to larvae metamorphosing. Neotenes (extended larval morphs) and paedogens (aquatic gilled adults) require permanent water bodies that do not freeze solid during the winter and preferably lack predatory fish. These water bodies provide sustainable source populations, especially during extended droughts (Sarell 2004). For the California tiger salamander, effective population size is correlated with the size of breeding ponds, especially for natural vernal pools (Wang et al. 2011).

Ephemeral water bodies can provide extensive breeding opportunities during wet years, replenishing populations after dry years. Ephemeral ponds also permit colonization of unoccupied areas during wet years and increased connectivity among populations. Small and shallow water bodies are especially important where deeper ponds and lakes have been stocked with predatory fish.

Aquatic habitats that have physical and chemical characteristics that are suitable to tiger salamanders can be rendered unsuitable by the introduction of predatory fish. Although the relatively large body size of adult tiger salamanders may provide some protection from predation by fish, egg, larval, and juvenile salamanders are highly susceptible to predation. Thus, predatory fish can cause recruitment failure of salamanders, resulting in eventual extirpation of populations. The long lifespan of adult salamanders, however, may enable salamander populations to persist through droughts that temporarily dry out breeding ponds, extirpating populations of predatory fish. The combination of predatory fish introductions and extinctions due to drought likely leads to a highly dynamic mosaic of aquatic habitat quality through time.

Tiger salamanders are typically tolerant of relatively high water temperatures and suspended sediment levels in breeding ponds. However, if the water quality of a breeding site is high and then is abruptly degraded, mass die-offs of tiger salamanders may occur due to increases in *Acinetobacter* spp. bacteria (Worthylake & Hovingh 1989). Nutrient loading associated with livestock can also lead to dramatic increases of other pathogens or toxic levels of nitrites, especially during dry years (Worthylake & Hovingh 1989; Bishop 1992). Soil disturbances around the pond can also increase the rate of infilling and eventual loss of breeding habitat.

Breeding habitats for tiger salamanders have been unintentionally created through the development of water impoundments, especially in irrigated agricultural lands and rangelands, and waste water lagoons (Sarell 2004). Beaver may create aquatic habitat for tiger salamanders, especially at higher elevations.

Terrestrial

Within the Columbia Plateau Ecoregion, the tiger salamander primarily inhabits arid grasslands, shrubsteppe, and open forests near water bodies that do not contain predatory fish (Hallock 2005). In a British Columbia population, individuals typically occupied dry sagebrush-grassland habitat, often with greater than 30% mineral soil exposure (Richardson et al. 2000*b*). Important terrestrial habitats also include riparian habitats adjacent to aquatic breeding sites. Tiger salamanders also occur in agricultural fields, both adjacent to natural habitats and in some areas where most of the landscape has been converted to agriculture. In northeastern Washington, near the border of the Okanogan and Canadian Rocky Mountain ecoregions, tiger salamanders occupy dry, low elevation forested areas dominated by ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*; Hallock & McAllister 2005). In general, little is known about terrestrial habitat requirements in Washington, and information presented below is drawn from studies of tiger salamanders or related species or subspecies in other areas.

Tiger salamanders spend most of their lives in underground refuges, such as small mammal burrows, particularly those of the Great Basin pocket mouse (*Perognathus parvus*) and pocket gophers (*T. talpoides*; Vaughan 1961; Richardson et al. 2000*a*). Rodent burrows may be the limiting factor in terrestrial habitats (Sarell 2004). Where burrowing rodents are abundant, burrows provide plentiful opportunities for tiger salamanders to gain subterranean access. Rodent burrows typically have an abundance of prey, and provide adequate retreat depth for overwintering (Sarell 2004). Tiger salamanders also retreat under coarse woody material or dig their own burrows (Semlitsch 1983*a*). Underground refuges are used during the day or for short periods during the active season, and may be important during juvenile dispersal (e.g., Richardson et al. 2000*b*). Due to the heavy reliance of tiger salamanders on burrows throughout their terrestrial life cycle, soil with structural characteristics and depth suitable for burrowing is an essential habitat feature.

Sensitivity to Roads and Traffic

The high permeability of amphibians' skin increases their susceptibility to contaminated microhabitats near roads (Andrews et al. 2008). Substances emitted from vehicles, used for road maintenance, or applied to embankments and ditches can have toxic or endocrine disruptive effects on amphibians, reducing their reproductive success and survivorship (Andrews et al. 2008). For example, mass salamander deaths in Minnesota have been attributed to desiccation associated with exposure to dust control agents applied to roads (deMaynadier & Hunter 1995). Microhabitats near roads may also be relatively drier than surrounding areas with native vegetation, increasing desiccation risk (Rothermel & Semlitsch 2002). Microhabitat differences near roads and possibly different pavement materials (e.g., oils) may disrupt use of olfactory cues for orientation and migration (Andrews et al. 2008). Nonetheless, tiger salamanders, as well as other ambystomatid salamanders, are often found crossing over paved roads.

Like many amphibians, the biphasic life cycle of tiger salamanders may increase their susceptibility to habitat fragmentation by roads. Road-related mortality may occur as adults migrate to and from breeding ponds and as metamorphs (individuals recently transformed from the gilled larval form to a juvenile form lacking gills) emerge from ponds and disperse. As road density increases, risk of mortality during movements between aquatic and upland habitats also increases (Andrews et al. 2008). The relatively high mobility of tiger salamanders also increases the likelihood that they will encounter roads during migration and dispersal through landscapes with high road densities. In a study of the effects of landscape configuration on spotted salamander (*A. maculatum*) abundance, overall road density within 1000 m and hydroperiod were the strongest predictors of eggmass abundance (Veysey et al. 2011).

Mortalities from vehicle traffic may be one of the most significant effects on tiger salamander populations, beside outright loss of aquatic and terrestrial habitats (Seburn & Seburn 2000). Roads located between aquatic breeding and terrestrial habitats can result in increased road mortality during seasonal migrations. Richardson et al. (1998) reported up to 50 road mortalities of tiger salamanders on one day near one breeding site during September migrations. Clevenger et al. (2001) reported 180 mortalities of tiger salamanders along a 1.05 km stretch of the Trans Canada Highway during a 5-day period of heavy rain and warm temperatures. Prolonged and heavy traffic from all-terrain vehicles may also significantly reduce habitat suitability (Sarell 2004). Annual mortality rates of 10–44% occurred in a long-toed salamander (*A. macrodactylum*) population during adult migrations to and from their breeding habitat in Waterton Lakes National Park in southern Alberta (summarized in Abhat 2007). The relatively slow movement speed of salamanders increases their risk of injury or mortality while crossing roads, especially as traffic volume increases (see Hels & Buchwald 2001). This risk can be exacerbated by immobilization behavior in response to traffic (Mazerolle et al. 2005).

Little specific information is available about the relative resistance of different types of roads and different levels of traffic volume on salamander dispersal. In forested habitats, even low-use forest roads can be partial barriers to salamander movement (Marsh et al. 2005). Simple models of individual risk of mortality suggest that increasing traffic volume and road width can lead to roads being complete barriers to amphibians (Hels & Buchwald 2001). Efforts to identify "hot spots" of road mortality suggest that roads on causeways between wetlands, and roads within 100 m of wetlands had higher rates of herpetile mortality, and that hot spots of road kill overlapped for multiple taxa (Langen et al. 2007, 2009).

Tiger salamanders have been reported to display behavioral avoidance of paved roads (Madison & Farrand 1998), but this avoidance is weak and individuals frequently attempt to cross paved roads. Traffic volume, especially at night, determines rates of crossing success and the degree to which paved roads impede movement. We are not aware of any documented relationships between avoidance behavior and traffic volume. Tiger salamander behavioral responses to gravel or native surface roads are also unknown. Artificial lighting along roads may influence tiger salamander movement and foraging behavior (Wise & Buchanan 2006), but the degree to which this affects mortality risk is unknown. Salamanders also have not been reported to show attraction to roadways or a tendency to use them as travel corridors.

To date, landscape genetic studies of tiger and California tiger salamanders were conducted in areas with few roads or other anthropogenic developments. Thus, potential effects of these features on tiger salamander gene flow are currently unknown.

Sensitivity to Development

Housing—Habitat suitability for tiger salamanders is likely inversely proportional to housing density. A landscape genetic analysis of both long-toed salamanders and Columbia spotted frogs (*Rana luteiventris*) inhabiting an agricultural landscape near the eastern edge of our analysis area indicated that rural and urban developed land cover were associated with the lowest levels of gene flow (Goldberg & Waits 2010). These authors suggested their results may reflect a combination of high desiccation risk associated with traversing paved areas, traffic-related mortality, and predation by pets (Woods et al. 2003) in developed areas. Small populations in urban ponds also may produce few dispersers (Goldberg & Waits 2010). Eastern tiger salamanders (*A. t. tigrinum*) appear to avoid grassy areas, roadways, and developed areas (Madison & Farrand 1998).

Although gene flow may be constrained in developed areas, these areas are nonetheless occupied by tiger salamanders. California tiger salamanders are known to occupy landscaped areas (e.g., Stanford University Land Use and Environmental Planning Office 2009). Tiger salamanders are commonly observed in the basements of houses, suggesting opportunistic use of artificial microhabitats that meet their physiologic needs. We are not aware of any comparative studies of relative survival and productivity rates of tiger salamanders in developed areas and natural habitats.

Agriculture—We generally lack an understanding of how dispersal costs and animal movements vary among crops in agroecosystems (Cosentino et al. 2011*a*). Because water economy is a critical physiological and behavioral constraint on the life history of terrestrial amphibians (Jørgensen 1997), differences in desiccation risk likely influence the relative permeability of different crops for salamander dispersal. Risk of water loss may impose strong physiological constraints on juvenile dispersers due to their small bodies, permeable skin, and high surface area to volume ratio (Rothermel & Semlitsch 2002; Mazerolle & Desrochers 2005; Semlitsch 2008). In Illinois agroecosystems, experimental tests indicated that water loss was greater in corn and prairie than in forest and soybean, and tracked salamanders selected habitats consistent with predictions based on water loss (Cosentino et al. 2011*a*). These results suggest that estimating crop-specific dispersal costs and movement patterns may improve measures of landscape connectivity in agroecosystems (Cosentino et al. 2011*a*). Relative resistance of different crops may be proportional to desiccation risk, which can be measured experimentally by weight loss per unit time, or by temperature and humidity conditions. In Illinois agroecosystems, maps of landscape resistance that incorporated desiccation risk differed greatly from maps that used a homogeneous resistance value for all crops (Cosentino et al. 2011*a*). Connectivity maps based on desiccation risk were a better predictor of colonization than metrics representing Euclidean distance or expert opinion (Cosentino 2011). Variation in dispersal costs among crops creates the potential for the spatial distribution and temporal rotation of crops to influence population processes, especially dispersal. In a GIS study of landuse effects on landscape permeability and the presence of the alpine newt (*Trituris alpestris*), presence of this species declined with increasing area of vineyards (Ray et al. 2002).

Dispersal costs associated with desiccation risk in agricultural crops vary temporally (Mazerolle & Vos 2006). Before planting in spring, agricultural fields are open and bare in many parts of the Columbia Plateau. Thus, adult tiger salamanders may face more uniform risk of movement when migrating across agricultural fields. Field-level tillage practices, however, may moderate desiccation risk. For example, presence of old plant material in no-till fields may moderate desiccation risk by functioning as refuges, whereas tilled fields would be relatively barren at the soil surface (Cosentino et al. 2011*a*). In a forested ecosystem, Rittenhouse et al. (2008) found that the presence of coarse woody debris in clear-cuts moderated desiccation risk for anurans. In agricultural fields, desiccation risk likely declines as plant cover increases through the growing season, resulting in the potential for high variation in risk among crops late in the growing season when juveniles emigrate from ponds after metamorphosis. Finally, individuals emigrating during crop harvest may be susceptible to disturbance or harm from agricultural machinery (Saumure et al. 2007).

In arid environments like the Columbia Plateau Ecoregion, irrigation systems likely also influence relative permeability of different crops to salamander movement. Irrigation-related moderation of desiccation risk raises potential advantages and disadvantages for dispersing salamanders. By reducing desiccation risk, irrigation may extend potential dispersal distances and increase the potential for connections among populations. Alternatively, dispersing salamanders may be drawn into agricultural croplands that do not provide other essential habitat features, making them sinks for dispersing individuals. Another factor that complicates the evaluation of the effects of agriculture on salamander dispersal is that cultivated areas tend to have relatively deep soils that accommodate burrowing due to tilling. Thus, dispersing salamanders may have good access to subterranean refugia that moderate desiccation risk in some agricultural settings.

Irrigation infrastructure also may have both positive and negative effects on tiger salamanders. California tiger salamanders have been found in irrigation control boxes and drainage pipes, which may represent relatively safe artificial habitat features, as long as entry and exit are relatively easy. Tiger salamanders have also been found in irrigation ditches and ponds in the Columbia Plateau, particularly in smaller, unlined systems (L. Hallock, S. Spear, and R. Weaver, personal communication). Small irrigation ditches, with natural substrate and native vegetation nearby, may enhance dispersal opportunities in agricultural landscapes by providing microhabitats with elevated humidity (reduced desiccation risk). Ponds built to capture irrigation runoff or spill of excess water may provide breeding habitats (Collins 1981). In contrast, unscreened irrigation intakes may entrain salamanders and entrainment can increase risk of injury, entrapment in irrigation infrastructure, conveyance to unsuitable habitats, and exposure to chemicals used in agriculture and maintenance of irrigation infrastructure. Larger canals, especially concrete-lined canals, may be physical barriers to dispersal when they are not in use for irrigation, and when they are conveying water, flow velocity may displace salamanders that enter the water to unsuitable habitats.

Empirical information was not available about temperature and humidity in different crop types used in our land cover/land use layer. When assigning resistance values to different crop types, we used our professional judgment to estimate how a combination of crop structure, typical irrigation practices, and rotation practices might influence desiccation risk and ease of movement, two important components of relative resistance.

Annual and seasonal variations in precipitation and ground water flows may result in some ponds or wetlands drying up completely prior to metamorphosis of larvae. Human use of water for agricultural purposes may reduce water levels and exacerbate these impacts (Sarrel 2004).

Herbicides, fertilizers, and other chemicals used in agriculture may affect the resistance of agricultural landscapes. Contaminants may trigger avoidance responses, have direct toxic effects, or interact with pathogens to reduce physiological condition or survival (e.g., Forson & Storfer 2006). Atrazine, a commonly applied herbicide, and nitrate fertilizer resulted in decreased leukocyte levels in experimentally exposed tiger salamanders, suggesting the potential for immunosuppression (Forson & Storfer 2006). These types of chemicals are not only used in agriculture, but are also widely applied in residential areas, and along roadways, railroads, and electrical transmissions rights-of-way. We considered contaminants as a factor contributing to resistance of these landscape features, but due to uncertainty about the relative magnitude of this effect, contaminants contributed a relatively small proportion to overall resistance values.

Contaminant effects on landscape resistance warrant more in-depth consideration in connectivity analyses conducted at finer spatial scales.

Grazing—Given the apparent reproductive and survival success of tiger salamanders in many areas that are grazed, the effects of livestock grazing are less severe than many other anthropogenic effects. The extent of the effects are probably linked to the intensity and timing of grazing. Impacts that increase with the intensity of livestock grazing include soil compaction, trampling of wetland banks or edges, collapse of entrances to small mammal burrows, loss of riparian vegetation, and increased nutrient input to water (Orchard 1991; Richardson et al. 1998). If water quality is reduced at breeding sites due to livestock grazing, mass die-offs of tiger salamanders may occur due to increases in *Acinetobacter* spp. bacteria (Worthylake & Hovingh 1989). Nutrient loading can also lead to dramatic increases of other pathogens or toxic levels of nitrites, especially during dry years (Worthylake & Hovingh 1989; Bishop 1992). Soil disturbances around the pond can also increase the rate of infilling and eventual loss of breeding habitat.

It is unlikely that many tiger salamanders are trampled above ground, given that livestock do not move or forage much at night, when the salamanders are above ground.

Sensitivity to Energy Development

Most information currently available about potential impacts of energy development on salamanders focuses on potential effects to habitat, particularly degradation of aquatic habitat. Degradation risk is primarily associated with construction of access roads and the potential for runoff from these roads to deliver contaminants to aquatic habitats and to increase sedimentation rates. Installation of wind turbines can also remove upland habitat, but the footprint of turbine pads typically impacts smaller areas than access roads.

Direct impacts of energy development on salamanders are not well understood. We are unaware of any information from experiments or systematic observations describing salamander responses to energy transmission lines or wind turbine infrastructure. It seems reasonable that vibration from wind turbines could trigger avoidance responses in salamanders, and shadow flicker from rotating turbine blades could influence habitat use by burrowing rodents, thereby affecting availability of burrows for dry-season refugia. These effects, however, have not been documented. In existing impact analyses of proposed projects, direct effects of roads associated with energy developments, especially wind energy installations, are often discounted due to the expectation that traffic volumes will be too low to result in appreciable salamander mortality (e.g., USFWS 2011). California tiger salamanders remain abundant in landscapes with a long history of wind farm presence in California, suggesting that impacts may be insignificant (P. Trenham, personal communication).

Sensitivity to Climate Change

Considering the broad spectrum of habitats currently used by tiger salamanders in the Columbia Plateau, it is reasonable to hypothesize that tiger salamanders may be somewhat resilient to the effects of minor climate change. Iteroparity (having repeated reproductive cycles), a long life span (up to 25 years in captivity; Petranka 2010), and the ability to persist through droughts by using terrestrial subterranean refugia may enable tiger salamanders to “ride-out” the increasingly pronounced environmental variations expected to accompany climate change (e.g., Church et al.

2007). It is possible that higher amplitude fluctuations in temperature and precipitation could increase the frequency of extirpation of predatory fish populations when ponds dry out during droughts.

Of course, the drought resilience of tiger salamander populations also has limits, and uncertainty surrounds the question of whether the long-term effects of climate change could exceed the capacity of their life-history plasticity to buffer environmental variation (e.g., due to dramatic increases in the frequency and duration of severe droughts). Analyses of climatic niches of amphibians have generally found little change in these niches through time, suggesting that amphibians tend not to adapt to changing climatic conditions and survive in place, but rather to shift their range to find suitable climates (Kozak & Weins 2006; Vieites et al. 2009). Analysis of "climate paths" that might allow amphibian species in the western U. S. to shift their ranges in response to climate change suggested that erratic variability in climate change could cause gaps in climate paths that prevented range shifts and increased the likelihood of range contractions and extirpations (Early & Sax 2011). Ability to persist for extended periods under unfavorable climates and high dispersal capacity may improve amphibians' capacity to accomplish range shifts in spite of high temporal variation in climate change (Early & Sax 2011). Persistence under unfavorable climates may be enhanced by increasing habitat connectivity (Grant et al. 2010), and increased connectivity also diversifies opportunities to disperse successfully to locations with a suitable climate. Constraints imposed by climatic variability, dispersal capacity, and ability to persist in unfavorable climates can contribute to increased risk of endangerment (Early & Sax 2011). A combination of both high habitat connectivity and managed relocations may be needed to enable salamanders to shift their ranges in response to climate change.

Dispersal

Tiger Salamanders have complex movement patterns. They include adult migrations from terrestrial overwintering sites to aquatic breeding sites, typically in mid-March to early April, with subsequent emigration to upland foraging sites after a breeding season that can last from a couple weeks up to 3 months. In summer and fall, adults and metamorphs emigrate from breeding ponds to other ponds or to upland hibernation sites. The majority of dispersal typically occurs in the early post-metamorphic stage, when amphibians are most vulnerable to desiccation (Semlitsch 2008).

Little is known about the timing of metamorphosis or the onset of summer and fall movements in Washington. All movements typically coincide with precipitation, and occur almost entirely at night (Smith 2003). Summer and fall movements may be triggered by thunderstorms (e.g., Koch & Peterson 1995). For tiger salamanders in relatively arid environments like the Columbia Plateau, dispersal is likely dependent on rainfall (P. Trenham, personal communication). Emigration likely depends on rainfall increasing humidity sufficiently to allow movements across habitats that are relatively hostile in the absence of precipitation. Emigration from ponds may be triggered by drying, by declines in the density of preferred prey species (Whiteman et al. 1994), or by other cues.

As indicated above, desiccation risk is likely a factor that influences habitat selection by dispersing tiger salamanders, and constrains dispersal among populations. Dehydration can compromise locomotor performance (Preest & Pough 1989), and dehydrated amphibians can be subject to greater predation risk (Rohr & Madison 2003) and lower survival (Rothermel & Luhring 2005; Rittenhouse et al. 2008, 2009) than hydrated animals. Desiccation risk can vary among common upland matrix habitats, and juvenile salamanders orient movements toward low-risk habitat where dehydration may be reduced (Cosentino et al. 2011*a*). Both telemetry and landscape genetic studies have found that salamanders moving overland appear to move through all types of habitat in the landscape, and do not stay within riparian zones. Dispersal across upland areas in arid landscapes likely requires access to burrows or other features that provide suitable temperature and humidity conditions and concealment.

Available information about variation in desiccation risk among habitats focuses on daytime conditions, raising the question of the relationship between daytime temperature and humidity and nighttime conditions, when most tiger salamander dispersal occurs. It is reasonable to expect that patterns of nighttime variation parallel daytime conditions, with the overall amplitude of variation and differences among habitats being somewhat reduced at night. During the day, desiccation risk appears to be related to differences in air temperature and relative humidity levels at the soil surface (Cosentino et al. 2011*a*). These differences in microclimatic conditions may be related to canopy coverage and vegetation structure near the soil surface. Studies in forest clear-cut systems have shown that desiccation rate depends on differences in daytime air temperature among habitats, but not with relative humidity (Rothermel & Semlitsch 2002; Rothermel & Luhring 2005).

Strong philopatry is considered typical of *Ambystoma* salamanders (e.g., Gamble et al. 2007). Some studies of Eastern tiger salamanders have found very low levels of movement between breeding ponds (e.g., Church et al. 2007). Western tiger salamanders (*A. t. melanostictum*), however, may show more movement among breeding ponds, both as dispersing juveniles and among breeding seasons as adults, especially when different breeding ponds are in relatively close proximity (e.g., Trenham 2001). In California tiger salamanders, about 30% of first-time breeders moved to breeding ponds different from their natal pond, and about 30% of salamanders that bred in different years switched ponds between breeding events (Trenham et al. 2001).

Estimates of the length of tiger salamander home range movements are limited (Table A.11.1). In British Columbia, during the summer, tiger salamanders implanted with radio transmitters generally did not move far daily or even weekly, often remaining within a 5 m radius, but occasionally moving 10–100 m (Richardson et al. 2000*a*). The largest recorded movement in this study was 250 m, but no salamanders moved more than 150 m from their breeding pond. Other observations of terrestrial adults in British Columbia have found them more than 1 km from possible breeding sites (Sarell 2000). This information suggests a larger home range for at least some members of tiger salamander populations. In California tiger salamanders, relatively high probabilities of dispersal occurred between several ponds separated by 500–670 m, suggesting these salamanders are probably capable of longer distance movements (Trenham et al. 2001).

Tiger salamanders show considerable flexibility in the timing and extent of their movements. Emigration can occur in movement bouts, each being followed by local subterranean foraging (Madison & Farrand 1998). If refuges and food are abundant in habitats close to the pond, if weather is unsuitable for overland movement, if the risk of predation is extreme, or if some combination of these occur, salamanders may prolong the period of emigration or forgo emigration altogether and remain in the vicinity of the pond (Madison & Farrand 1998). Similar flexibility in movement patterns occurs in California tiger salamanders (see Table A.11.1).

Table A.11.1. Movement estimates (meters) for tiger salamanders and California tiger salamanders (CTS).

Sex and age class	*Location*	*Number of individuals*	*Mean*	*Max.*	*Range*	*Estimation method**	*Citation*
Adult	Penticton, BC	9			0–150	T	Richardson et al. 2000*a*
♂ Adult metamorph	Long Island, NY	15	92.4		0–286.5	T	Madison & Farrand 1998
♀ Adult metamorph		12	72.8		0–243.5	T	Madison & Farrand 1998
Adult (CTS)	Monterey, CA	8	94		16–248	T	Trenham 2001
Adult (CTS)	Solano Co., CA	8	171		30–600	T	P. Trenham, unpublished data
Adult (CTS)	Alameda Co., CA	5	356		Up to 510	B	Pittman 2005, USFWS 2007
♂ & ♀ Adult, subadult (CTS)	Solano Co., CA	189			10–400	P	Trenham & Shaffer 2005
Unknown				600		MR	Pechmann et al. 2001
Adult				12.4		TC	Semlitsch 1983*b*

**Telemetry (T), Burrow excavation (B), Pitfall array (P), Mark-recapture (MR), Toe clip (TC)*

The capacity of many studies of amphibian dispersal to detect maximum movement distances has been questioned, leading to the suggestion that existing information about amphibian dispersal capabilities may be biased toward low values (Smith & Green 2005). The appropriate equations to fit to limited amphibian dispersal data has also been debated (Smith & Green 2005; Gamble et al. 2007). Based on their argument that the distribution of maximum amphibian dispersal distances is better fit by a power law than other formulas, Smith and Green (2005) argued that 8–9 km was a reasonable estimate of maximum dispersal distance for salamanders.

Gamble et al. (2007) found a maximum dispersal distance of 1350 m in marbled salamanders (*A. opacum*) in unfragmented habitat, and suggested that longer distances are likely traversed, given that the maximum distance detected matched the extent of their study area. Anecdotal reports also suggest that the far tail of the dispersal distribution of salamanders may be greater than maximum distances reported in studies. For example, two Arizona tiger salamanders (*A. t. nebulosum*) were found in ponds between 1.5 and 2 km from the ponds where they were found the previous spring, and Sheridan Stone (Fort Huachuca Wildlife Office, personal communication) found 2 metamorphosed tiger salamanders (*A. t. mavortium*?) at sites 3–4 km from the nearest potential breeding site (USFWS 2002). Reed (1951) reported that newly created cattle ponds were colonized almost immediately by tiger salamanders, which he attributed to the ability of salamanders to disperse long distances.

Landscape genetic studies suggest that gene flow among tiger salamander populations diminishes at distances greater than 1 km (Spear et al. 2005). Landscape genetic studies of salamanders that we reviewed, however, did not provide estimates of maximum dispersal distances.

In marbled salamanders, experienced breeders showed a bias in their selection of destination ponds, preferring occupied ponds with large populations (Gamble et al. 2007). This apparent selectivity contrasted with movement patterns of juvenile marbled salamanders during their year of emergence (Gamble et al. 2006); these individuals were captured entering and/or traversing virtually all pond basins in the study area as they moved away from natal ponds. These observations suggest that breeding individuals are cueing to the presence of other individuals or exhibiting active selection of breeding habitats based on other physical variables (Gamble et al. 2007). If the presence of other individuals is an important cue, this behavior would tend to reinforce established breeding populations in a metapopulation context and possibly impede colonization of new sites (Gamble et al. 2007).

Conceptual Basis for Columbia Plateau Model Development

Overview

Our overall approach to assigning landscape resistance values to different features was to integrate beneficial and negative aspects of each feature (e.g., beneficial effects of mediation of desiccation risk integrated with negative impacts on ease of movement, sub-lethal physiologic effects, and mortality risk). We accomplished this integration by combining information from the literature about the resistance of different features with the judgment of local experts. For many features, specific information was not available in the literature, and we used professional judgment to select the closest analogous feature for which we had relevant information that we could use to approximate resistance. We grouped features into three general resistance categories; low resistance (values of 0–5), moderate resistance (10), and high resistance (values $\geq$100). When we found high levels of correlation among different features, we assigned values for the data layer for which we had the best background information and the most confidence in data quality. We then excluded the other correlated layers from the analysis. The following sub-sections describe our rationale for assigning resistance and habitat values to different groups of features listed in Table A.11.2.

Land cover and land use—In a landscape genetic study of tiger salamanders in the Yellowstone area, gene flow (reduced differentiation) among tiger salamander populations was positively related to open shrub habitat, and closed forest cover appeared to decrease gene flow (Spear et al. 2005). This result is consistent with other studies of tiger salamanders in the western United States: a study of *A. t. melanostictum* in British Columbia in which salamanders moved away from forested areas and used open habitats (Richardson et al. 2000*b*) and two studies of the California tiger salamander which found that they primarily dispersed through open or chaparral habitat, although individuals also were located near scattered oak (*Quercus* spp.) trees (Trenham 2001; Wang et al. 2009).

Table A.11.2. Landscape features and resistance values used to model habitat connectivity for the tiger salamander.

Spatial data layers and included factors	*Resistance value*	*Habitat value*
Landcover/Landuse		
Grassland_Basin	1	1.00
Grassland_Mountain	5	0.00
Shrubsteppe	0	1.00
Dunes	2	0.80
Shrubland_Basin	1	0.80
Shrubland_Mountain	1	0.20
Scabland	1	0.80
Introduced upland vegetation_Annual grassland	5	0.60
Cliffs_Rocks_Barren	10	0.00
Meadow	1	1.00
Herbaceous wetland	0	1.00
Riparian	0	1.00
Introduced riparian and wetland vegetation	0	0.80
Water	5	0.80
Aspen	2	0.60
Woodland	2	0.40
Forest	10	0.20
Disturbed	100	0.00
Cultivated cropland from RegapNLCD	2	0.60
Pasture Hay from CDL	1	0.80
Non-irrigated cropland from CDL	2	0.40
Irrigated cropland from CDL	2	0.60
Highly structured agriculture from CDL	2	0.20
Irrigated/Not Irrigated/Cultivated Crop Ag Buffer 0 – 250m from native habitat	2	0.80
Irrigated/Not Irrigated/Cultivated Crop Ag Buffer 250 – 500m from native habitat	2	0.60
Pasture Hay Ag Buffer 0 – 250m from native habitat	1	0.80
Pasture Hay Ag Buffer 250 – 500m from native habitat	1	0.80
Elevation (meters)		
0 – 250m	0	1.00
250 – 500m	0	1.00
500 – 750m	0	1.00
750 – 1000m	2	0.80
1000 – 1250m	5	0.60
1250 – 1500m	10	0.40
1500 – 2000m	100	0.00
2000 – 2500m	100	0.00
2500 – 3300m	100	0.00
Slope (degrees)		
Gentle slope Less than or equal 20 deg	0	1.00
Moderate slope Greater than 20 less than equal to 40 deg	1	0.60
Steep slope Greater than 40 deg	10	0.20
Soil Depth to First Restricted Layer		
0 – 20cm	5	0.40
20 – 50cm	2	0.80
50 – 100cm	0	1.00
Greater than 100cm	0	1.00
No soil	10	0.00
Landform		
Drainage	0	1.00
U-shaped valley	0	1.00
Plain (or surface water)	0	1.00

Spatial data layers and included factors	*Resistance value*	*Habitat value*
Midslope	1	0.80
Ridge or mountain top	10	0.20
Compound Topo Index		
Dry zone	1	0.80
Potential dry to moist zone	1	1.00
Potential wet zone	0	1.00
Insolation		
Very low insolation	0	1.00
Low insolation	0	1.00
Moderate insolation	0	1.00
High insolation	1	1.00
Very high insolation	2	0.80
Housing Density Census 2000		
Greater than 80 ac per dwelling unit	0	1.00
Greater than 40 and less than or equal 80 ac per dwelling unit	0	1.00
Greater than 20 and less than or equal 40 ac per dwelling unit	2	0.80
Greater than 10 and less than or equal 20 ac per dwelling unit	5	0.60
Less than or equal 10 ac per dwelling unit	100	0.40
Roads		
Freeway Centerline	400	0.00
Freeway Inner buffer 0 – 500m	1	0.20
Freeway Outer buffer 500 – 1000m	0	0.80
Major Highway Centerline	200	0.00
Major Highway Inner buffer 0 – 500m	1	0.80
Major Highway Outer buffer 500 – 1000m	0	1.00
Secondary Highway Centerline	100	0.00
Secondary Highway Inner buffer 0 – 500m	1	1.00
Secondary Highway Outer buffer 500 – 1000m	0	1.00
Local Roads Centerline	10	0.00
Local Roads Inner buffer 0 – 500m	0	1.00
Local Roads Outer buffer 500 – 1000m	0	1.00
Railroads Active		
Railroads Active Centerline	100	0.00
Railroads Active Inner buffer 0 – 500m	1	0.60
Railroads Active Outer buffer 500 – 1000m	0	1.00
Railroads Inactive		
Railroads Inactive Centerline	10	0.00
Railroads Inactive Inner buffer 0 – 500m	0	1.00
Railroads Inactive Outer buffer 500 – 1000m	0	1.00
Transmission Lines		
LessThan 230KV One Line Centerline	10	0.00
LessThan 230KV One Line Inner buffer 0– 500m	0	0.80
LessThan 230KV One Line Outer buffer 500 – 1000m	0	1.00
LessThan 230KV Two or More Lines Centerline	10	0.00
LessThan 230KV Two or More Lines Inner buffer 0 – 500m	0	0.80
LessThan 230KV Two or More Lines Outer buffer 500 – 1000m	0	1.00
Greater Than or Equal 230KV One Line Centerline	10	0.00
Greater Than or Equal 230KV One Line Inner buffer 0 – 500m	0	0.80
Greater Than or Equal 230KV One Line Outer buffer 500 – 1000m	0	1.00
Greater Than or Equal 230KV Two Lines Centerline	10	0.00
Greater Than or Equal 230KV Two Lines Inner buffer 0 – 500m	0	0.80
Greater Than or Equal 230KV Two Lines Outer buffer 500 – 1000m	0	1.00

(continued on following page)

Spatial data layers and included factors	*Resistance value*	*Habitat value*
Wind Turbine		
Wind turbine point buffer 45m radius	10	0.00
Buffer zone beyond point buffer 0 – 500m	1	0.80
Buffer zone beyond point buffer 500 – 1000m	0	1.00
Irrigation Infrastructure		
Irrigation canals	10	0.00

Studies of tiger salamanders from the eastern United States and other amphibians have suggested they tend to avoid open habitats, such as fields and road areas, and move more through forested areas (Madison & Farrand 1998; deMaynadier & Hunter 2000; Rothermel & Semlitsch 2002; Cosentino et al. 2011*a*, 2011*b*). These results are likely due to increased risks of desiccation and predation in open areas. There is some evidence that these trends in movement also translate to reduced gene flow in open areas (Hitchings & Beebee 1997; Gibbs 1998; Curtis & Taylor 2003). Western tiger salamanders, however, appear to prefer open shrubby habitat to woodlands or forests (Spear et al. 2005; Wang et al. 2009). These habitat preferences may reflect both predator avoidance and availability of rodent burrows.

In California tiger salamanders, chaparral vegetation was the cover type that predominated along least-cost paths between breeding ponds (Wang et al. 2009). Costs of traversing grassland cover types were about 2 times greater than chaparral, and woodland was 5 times more costly than chaparral, based on calibration using rates of genetic exchange (Wang et al. 2009). In their study of landscape resistance to amphibian movement, Ray et al. (2002) also used a factor of 5 to span the resistance of frequently used cover types (estimated resistance values of 5–25).

Different crops and cover types within agroecosystems may also influence rates of genetic exchange among tiger salamander populations (Cosentino et al. 2011*a*; Cosentino 2011). Crops differ in desiccation risk and salamander movements may be oriented toward crops that reduce risk. Typical agricultural practices can lead to high spatial and temporal variation in desiccation risk through time (Cosentino et al. 2011*a*). Cosentino et al. (2011*b*) used cost-distance modeling to test 3 hypotheses about effects of matrix heterogeneity on metapopulation dynamics of eastern tiger salamanders. The Euclidean distance model created a homogeneous matrix by assigning all habitats a uniform resistance of 1. The “expert opinion” model assigned all crops a homogeneously high resistance value of 500, reflecting the notion that all crops have similarly negative effects on dispersal. In this model, grasslands had a value of 200, and forests, 100. The final model used empirical information about desiccation risk to assign resistance values to different cover and crop types; forest and soybeans were assigned a value of 100, and grassland and corn were assigned a value of 500. In all models, water had a resistance of 1, assuming wetlands are stepping stones for dispersal, and roads had a value of 1000, reflecting a strong impediment to dispersal. The cost-distance model based on desiccation risk was a better predictor of colonization probability than alternative models, thereby linking isolation effects to a physiological constraint on dispersal. In contrast, initial occupancy and extinction probabilities were best explained by Euclidean connectivity (Cosentino et al. 2011*b*). The absence of matrix effects on initial occupancy and extinction for *A. tigrinum* may be related to the dynamic nature of landscape structure in agricultural systems dominated by annual row crops (Cosentino 2011).

Based on this background, we assigned resistance values to different land cover and land use categories using relatively simple rules. Because landscape genetic studies found that the differences in resistance among cover types frequently used by salamanders typically spanned a factor of 5, we assigned resistance values between 0 and 5 to all cover types we considered to be relatively conducive to tiger salamander movement. These included all agricultural cover types. Based on numerous anecdotal reports of tiger salamanders occupying agricultural landscapes in the Columbia Plateau, we assigned relatively low resistance (values of 1 or 2) to agricultural cover types. These values were meant to reflect the balance between the features conducive to movement associated with agriculture such as increased humidity due to irrigation and deep soils, in contrast with resistive features such as increased concentrations of contaminants and risk associated with agricultural machinery. Other cover types that we considered moderately resistant (e.g., forest) or highly resistant (commercial sites or mines), were assigned resistance values of 10 and 100, respectively. We chose 10 as the value for moderately resistant cover types to reflect the finding that salamanders disperse across a variety of cover types and that they typically move when weather conditions reduce the humidity-related differences among cover types, "flattening" the level of resistance in the landscape. We considered only one cover type to have high resistance, the Disturbed category which includes mines and commercial sites.

The high resistance category included mostly topographic and anthropogenic features. Our choice of 100 as the value for highly resistant features is subjective. We intended this value to reflect habitats that have a combination of physical impediments to movement, as well as high injury or mortality risks. The value of 100 was also selected to result in features that were more than one grid cell wide creating a nearly complete impediment to salamander movement.

Our assignment of habitat values was largely subjective and was based on narrative descriptions of habitats typically occupied by tiger salamanders in the Columbia Plateau and elsewhere. We relied on the professional judgment of local experts with extensive field experience to review and refine these assignments. For both habitat resistance values and habitat quality values, several iterations of assignment and review were needed before resulting ecoregional maps conformed reasonably well with expert opinion about the distribution of tiger salamander populations and features resistant to salamander movement. We also used the distribution of known sites of tiger salamander populations as a primary indicator of accuracy of our habitat value assignments. Because tiger salamander habitat is highly variable and dynamic in this arid landscape, we expected our habitat quality modeling to capture the majority of known sites, but also expected our habitat modeling might not encompass some known sites in marginal habitat.

Topography (elevation, slope, landform, compound topographic index and insolation)—Spear et al. (2005) used GIS analyses to investigate the influence of landscape features on population genetics of tiger salamanders in the northern range of Yellowstone National Park. Gene flow among tiger salamander populations was highly restricted, especially at distances greater than 1 km, with significant isolation by distance (Spear et al. 2005). Topographic distance was the most consistent predictor of F_{ST} (an index of the reduction in heterozygosity of a subpopulation due to genetic drift), and elevation difference was also positively related. High levels of amphibian population subdivision have been reported among populations separated by mountains compared to low subdivision within basins (Tallmon et al. 2000; Funk et al. 2005). Slope was a poor predictor of differentiation among populations (Spear et al. 2005). Rivers and streams had a positive effect on gene flow, contrary to the expectation that they might be barriers (Spear et al. 2005).

Because tiger salamanders occur only below 1250 m in elevation on the Columbia Plateau, we assigned progressively increasing values of resistance to elevation categories above this level. Modification of this elevation constraint to investigate opportunities for accommodating climate change could be enlightening.

We considered steep slopes and ridges to have about 10 times the resistance of flat ground. We felt this range of values balanced the results of landscape genetic studies, which suggest ridges can subdivide amphibian populations, with many observational reports of salamanders which describe their capacity and willingness to traverse steep terrain.

Due to high correlation between slope and our Ruggedness categories, we did not include ruggedness in our analysis. Insolation is also highly correlated with slope. However, we felt that the combination of steep slope and high insolation needed to be captured because these features have a higher likelihood of reducing salamander movement relative to each feature alone.

Soils—We expected soil texture to be an important variable for both landscape resistance and habitat value because we believed it would reflect the availability of small mammal burrows or other subterranean refugia. We found, however, that our soil texture layer had a disturbing frequency of abrupt discontinuities that corresponded with county lines, suggesting differences among observers might be responsible for differences in values. Consequently, we did not include soil texture in our analysis.

Our soil depth layer was not as strongly affected by apparent observer-related differences. We included soil depth as a measure of potential availability of subterranean refugia. We did not have information about burrow densities or population densities of burrowing mammals. In general, we considered areas with deeper soils to have lower resistance, and areas with no soil to be somewhat resistant to movement (resistance value of 10).

Housing development, roads, and other infrastructure—In keeping with landscape genetic studies of other salamander species, we assigned high resistance (value of 100) to housing density of less than 10 ac per dwelling unit, which includes both suburban and urban settings. In this agricultural landscape, we considered the resistance of areas with lower housing densities to be dominated by other features, such as cover type.

We considered roadways to be among the most resistant features on the landscape, especially freeways (value of 400 for the centerline), major highways (200), and secondary highways (100). These values were meant to reflect the combination of high mortality risk, behavioral avoidance of pavement and stimuli from traffic, and contaminants associated with management of roadside vegetation and winter maintenance. We felt that the impact of these features, however, was largely confined to the 30 m grid cells containing roadway center lines. We assigned very little added resistance to the road-effect zones adjacent to the roadways. This pattern of assigning resistance reflected both our sense that 30 m captured most road effects, and that buffers around roads occupied a large proportion of the landscape, and high resistance values or low habitat values in these buffers would render many known sites of tiger salamander populations to be unsuitable habitat.

In the absence of specific information about resistance of railroads and energy generation and transmission infrastructure, we assigned values that paralleled those of roadways that we considered to be reasonable analogs. We considered railways to be similar to secondary highways (resistance of 100 for the centerline), and the resistance of energy transmission lines to be analogous to that of local roadways. These values were intended to incorporate the effects of access roads with official and recreational traffic, and the application of herbicides to manage vegetation in rights-of-way.

We also lacked specific information about the resistance of major irrigation canals. Again, we considered these features to be analogous to local roads. We feel that overall resistance of these canals was a combination of effects from their access roads, the canal itself, and maintenance activities that could include herbicide applications. Most large canals have adjacent, native-surface access roads. These roads typically have very low traffic volumes, suggesting that the resistance of the access road component is probably lower than that of typical local roads. Considering the canals alone, during the irrigation season, high water velocity in these canals would increase landscape resistance by exposing salamanders to harm from water diversion infrastructure and by displacing salamanders that entered the canal to locations where low habitat values could reduce survival. When irrigation was not occurring, these steep-sided concrete chutes would likely impede movement, and could increase predation risk.

Movement Distance

One of the central objectives of our analysis was to explore connectivity opportunities across the very broad geographic area encompassed by the Columbia Plateau Ecoregion. In this context, we consistently chose options that were more inclusive when we were confronted with different options about how to proceed with our analysis; i.e., we sought to avoid constraining connectivity opportunities unless we had a strong rationale based on research or repeated observation. We applied this general approach to our consideration of tiger salamander movement distance.

We selected 10 km as the maximum Euclidean distance between habitat concentration areas (HCAs) for which we would model habitat linkages. This choice implies we thought that exchange of individuals could occur between populations separated by up to 10 km. This distance is well beyond any movement distances recorded in studies of tiger salamanders (Table A.11.1), but is consistent with some analyses of potential dispersal capabilities of salamanders (Smith & Green 2005). Our rationale for this choice is based on: (1) HCAs were focused on the best habitat patches, likely excluding many patches of suitable habitat that could serve as stepping stones between HCAs; (2) tiger salamanders have demonstrated a capacity to find and opportunistically exploit stepping stone habitats in ways that would enable them to pursue a "linkage dweller" approach to long-distance movements, essentially spreading movements across years or even generations; and (3) limited anecdotal and conceptual support for rare, but realistic long distance dispersal by salamanders. We acknowledge that this approach may be perceived as providing an optimistic view of habitat connectivity for tiger salamanders, which is consistent with our objectives.

We did not specify a maximum cost-weighted distance beyond which linkages between HCAs would not be displayed. This approach allowed us to identify promising opportunities for connectivity restoration.

Habitat Concentration Areas

Tiger Salamanders use both aquatic and terrestrial habitats, requiring our approach to modeling HCAs to include consideration of both habitat types within our estimated home range radius of 0.5 km. We integrated habitat types by following a general approach in which patches of suitable aquatic habitat served as foci around which we aggregated suitable terrestrial habitat.

We used a modeling approach to define HCAs rather than rely only on known sites. Conversations with local experts led us to believe that the coverage of survey effort for tiger salamanders on the Columbia Plateau was patchy, and that the existing database of known sites was likely incomplete. We recognize that all approaches to identifying habitat have limitations, and we felt the limitations of modeling approaches were most consistent with our overall objectives (see HCA Modeling Limitations sub-section below).

Aquatic habitat—We used the Herbaceous Wetland category of the land cover/land use layer as the basis for identifying potential aquatic habitats. In our land cover/land use layer, wetland and riparian systems were grouped into three classes. The Riparian class includes those ecological systems where woody species (trees or shrubs) were a defining characteristic of the system. Systems without woody species were categorized into two separate classes: Herbaceous Wetland includes systems where soil saturation—either permanent or seasonal—is a driver of the structure and composition of the vegetation, while Meadow captures systems with characteristics similar to grassland classes, but where greater availability of water allows more mesic species to grow (See Appendix D). We eliminated the Riparian class from consideration as aquatic foci for HCAs because tiger salamanders in the Columbia Plateau typically do not use forested wetlands for breeding and most areas in the Riparian class were associated with flowing water. We excluded the Meadow category because it contained primarily moist areas, but not locations with surface water.

The Wetland class in our land cover/land use layer was derived from a base layer from the Northwest Gap Analysis Program overlaid with the National Wetland Inventory (see Appendix D). The Gap layer included a combination of vernal pools, closed depressions, playas, and emergent marshes. The National Wetland Inventory overlay included freshwater emergent wetlands and freshwater ponds. Some shrubby and partially forested wetlands were included in this class.

We considered predatory fish presence to be a key variable determining the quality of aquatic habitat and sought to include this factor in our approach to delineating HCAs. We did not have good information, however, about the distribution of fish across water bodies and wetlands in the study area, prompting a search for useful surrogate information. Of course, wetlands with hydroperiods long enough to support metamorphosis of salamanders, but that dried annually, would preclude fish occupancy while retaining high habitat value for salamanders. Thus, wetland hydroperiod would have been a good criterion for identifying aquatic habitats that were the best candidates for HCA development. However, reliable hydroperiod information was not available across the study area, either. We gave extensive consideration to using water body or wetland size as a surrogate indicator of the likelihood of fish presence, assuming that larger water bodies and wetlands were generally more likely to have year-round water, across multiple years, making them more likely to get and sustain fish populations. We found it problematic, however, to select an appropriate size cutoff above which patches of aquatic habitat would be excluded from HCA consideration due to high likelihood of fish presence. Ultimately, we included all wetlands in our land use/land cover layer as potential aquatic habitat foci for the development of HCAs, consistent with our overall approach of erring on the side of inclusiveness. In contrast, we excluded the Open Water class (a separate class in our land cover/land use layer that captured major water bodies) from consideration as a potential focus for HCA development. We believed water bodies in this class had too high a likelihood of containing predatory fish to function as foci for HCA development.

We overlaid resulting maps of aquatic habitats that were candidates for HCA development with satellite imagery to examine the physical characteristics of candidate water bodies and to compare them to sites known to be occupied by tiger salamanders. Based on this inspection, we concluded that the "Wetland" land cover/land use class was likely to identify the majority of suitable aquatic habitats for tiger salamanders in the study area (see HCA Modeling Limitations sub-section below).

Terrestrial habitat—In an effort to reflect typical patterns of tiger salamander habitat use around breeding ponds and to include only the highest quality habitat in HCAs, terrestrial habitat within 0.5 km of wetland grid cells in the land cover/land use layer received full habitat value as assigned through habitat quality parameterization (Table A.11.2). To reflect the well-reported relationship of declining terrestrial habitat use at distances greater than 0.5 km from breeding ponds, we made habitat values for grid cells from 0.5 to 1 km away from wetlands decay to zero as a linear function of distance from a focal wetland.

We attempted to create HCAs that met our minimum size requirement of 12.5 km^2 (for low-mobility focal species) in which the average habitat value of a home range (circle with a radius of 0.5 km) was 0.75. We found this stringent criterion for average home range value, however, yielded a distribution of HCAs in the study area that was not representative of the known distribution of tiger salamander sites, and also did not create HCAs in the vicinity of many known sites. We explored less stringent thresholds for average habitat value of a home range following the rationale that tiger salamander populations can thrive in areas with relatively high variation in habitat quality, as long as a reasonable amount of very high quality habitat is present. We found that using 0.67 as the average habitat value of the home range allowed HCAs to form that met the minimum size criterion, were well distributed across the study area, and captured a large proportion of known tiger salamander sites.

Our overall approach to HCA delineation had the effect of favoring the creation of HCAs in locations that had clusters of small wetlands surrounded by high quality terrestrial habitat. These conditions occurred in some portions of the Columbia Plateau that had no historical or current records of tiger salamander occurrence (namely Kittitas, Yakima, Benton, and Klickitat counties). These counties are separated from the main body of tiger salamander distribution by the Columbia River, which is a reasonable barrier to salamander dispersal. Although we considered survey effort on the Columbia Plateau insufficient to be used as the sole basis of HCA delineation, we felt survey effort was sufficient to consider these counties outside the range of the species. Consequently, we manually deleted HCAs that formed in these counties. Confirmed records of tiger salamanders in the Oregon portion of our analysis area are confined to the area near The Dalles. Our HCA delineation procedure produced numerous HCAs in Oregon, including a cluster near the Columbia River east of The Dalles. We considered manually deleting all Oregon HCAs, but in keeping with our approach of favoring inclusiveness, retained the cluster of HCAs east of The Dalles in order to explore the degree of habitat connectivity present in this area. We have no evidence, however, that this area is currently occupied by tiger salamanders.

Habitat concentration areas did not form in the Methow Valley and in the Palouse region, two areas known to contain tiger salamander populations. We believe this result reflects a combination of low terrestrial habitat quality and high levels of terrestrial habitat fragmentation in these areas. Both of these areas are disjunct from the main distribution of tiger salamanders in the Columbia Plateau. We added "extra-model" HCAs to both these disjunct areas in order to explore the level of habitat connectivity present within them. We created these HCAs by using the coordinates of known sites as foci for HCA development. We developed HCAs by adding grid cells with habitat quality values $\geq$0.75 that were within a cost-weighted distance equivalent to 2 km of Euclidean distance (the radius necessary to create an HCA that met our minimum size criterion of 12.5 km^2). We used a cost-weighted distance radius to avoid having HCAs include features with high resistance. If HCAs created using this approach overlapped, they were merged. This approach led to the addition of 4 "extra-model" HCAs in the Methow Valley, and 2 HCAs in the Palouse region.

HCA modeling limitations—Our evaluation criteria for candidate spatial models of HCAs included: (1) conformance with known occupied sites of tiger salamanders on the Columbia Plateau, (2) concordance between our proposed HCAs and areas found to be high quality habitat in previous modeling efforts, and (3) the degree to which our proposed HCA models were focused on the highest quality habitat. Given our objective of exploring connectivity opportunities, we sought to create efficient HCAs that provided space for linkage models to run (i.e., oversized HCAs may overestimate habitat contiguity while also reducing opportunities to identify least-cost linkages). During the process of HCA model development, we explored numerous iterations of habitat value parameters and approaches for integrating aquatic and terrestrial habitat quality. Peer review was instrumental in improving our models through this process. The model we present here performed well on all three of our evaluation criteria, though not all known sites were captured. We believe it produced efficient HCAs that capture the majority of sites most likely to be occupied by tiger salamanders.

We acknowledge, however, that these modeled HCAs have limitations. Some larger wetlands we included are undoubtedly perennial and may contain predatory fish. In contrast, by excluding Open Water we likely erroneously excluded some fish-free water bodies that were suitable aquatic habitat, particularly if those water bodies were not fringed by, or classified as Wetlands. For example, we are aware of a group of small, fish-free, ponds in the Telford area west of Davenport that are occupied by tiger salamanders, but were not captured in our modeled HCAs (J. Lowe, personal communication; see Fig. A.11.1). Ponds in this area fill shallow bedrock depressions and have limited development of emergent wetland vegetation (J. Lowe, personal communication). This combination of aquatic habitat features along with surrounding shallow soils that reduce terrestrial habitat quality, likely prevented our HCA modeling approach from identifying this area as an HCA. We suspect other similar omissions occurred.

We think alternative approaches to HCA delineation are worthy of future exploration. In particular, an approach that combines forcing development of HCAs around known sites with modeling of HCAs based on wetland foci could yield a more complete representation of high quality habitats across the Columbia Plateau. Time limitations, however, prevented us from exploring this approach.

Resistance and Habitat Values for Landscape Features

The parameterized spatial data layers and the corresponding resistance values and habitat values used to develop the connectivity models are given in Table A.11.2.

Modeling Results

Resistance Modeling

Our assignment of resistance values to different landscape features generated a resistance surface in which much of the undeveloped landscape had low resistance for tiger salamander dispersal (Fig. A.11.2). Densely developed areas, roadways, large irrigation canals, and railroads were the human-related features to which we assigned the highest resistance values, reflecting that these features simultaneously increase difficulty of movement, impose sub-lethal physiologic costs, and increase mortality risk. I-90, Highway 395, and Route 2 are high-resistance linear features that have a strong effect of subdividing tiger salamander habitats. Natural features with high resistance included high-elevation areas, forests, cliffs and ridges, and large expanses of open water.

This assignment of resistance values to features resulted in patterns of resistance that were associated with topographic relief and the legacy of the Missoula Floods. In relatively flat areas of the Columbia Plateau, the symmetric grid of roadways subdivided low-resistance areas with natural land covers and agriculture. In areas with more topographic relief, less housing, and less agricultural development, areas of low resistance tended to follow valley bottoms and drainages with natural vegetation. Cliffs and scoured plateaus of the channeled scablands had higher resistance to dispersal. Higher elevation areas surrounding the Columbia Plateau also had higher resistance that may limit opportunities for immigration of tiger salamanders from adjoining ecoregions.

Although we assigned relatively low resistance values to all classes of agriculture, the intensity of agricultural conversion of landscapes in some areas nonetheless led to fragmentation; not in the form of acute barriers, but in the form of cumulative resistance that builds across long expanses of converted cover types. This pattern of resistance was especially apparent in the Palouse region.

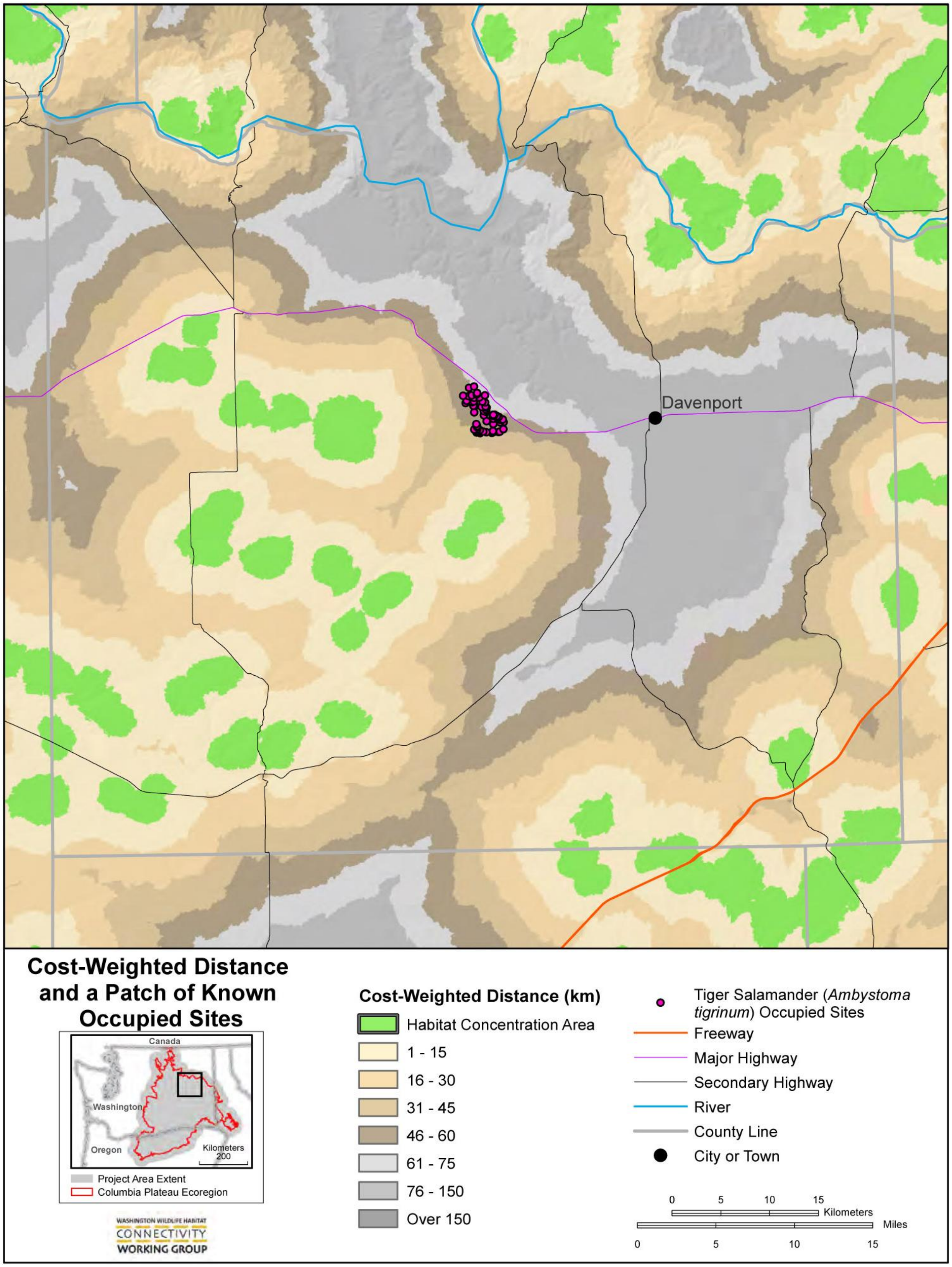


Figure A.11.1. Detail of the Telford area showing red points for known sites south of Route 2.

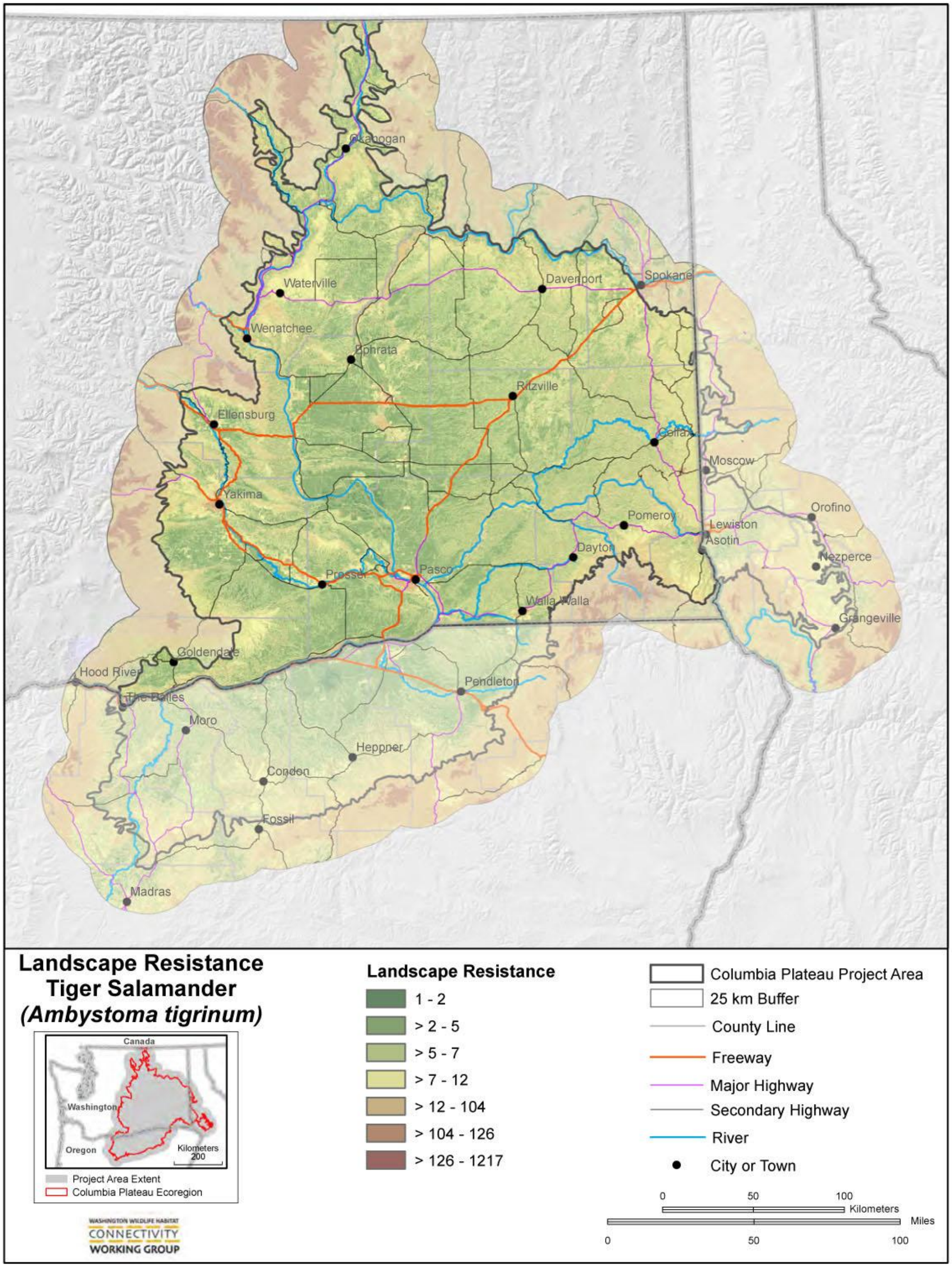


Figure A.11.2. Resistance map for tiger salamander in the Columbia Plateau Ecoregion.

Habitat Modeling and Habitat Concentration Areas

Our approach to modeling HCAs yielded a total of 115 across the Columbia Plateau Ecoregion and buffer. Our modeled HCAs show a high level of correspondence with tiger salamander habitat mapped in the Washington State Gap Analysis Project (Dvornich et al. 1997; Fig. A.11.3). Most HCAs were located in Gap core zones, consistent with our intent that HCAs represent the best quality habitat areas.

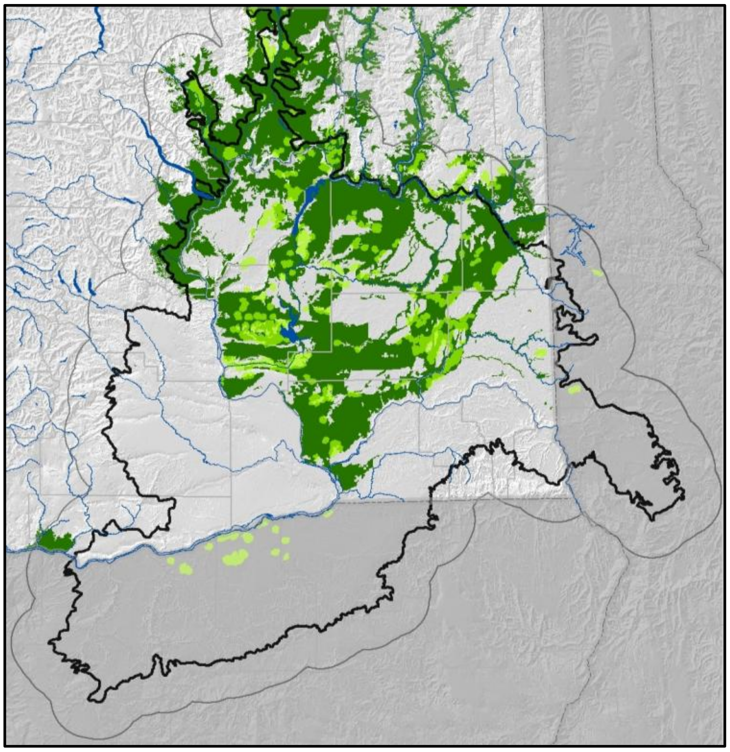


Figure A.11.3. Tiger salamander HCAs (light green) and GAP distribution (dark green) in the Columbia Plateau Ecoregion.

Within the Columbia Plateau Ecoregion, moderate quality habitat (coefficients of 0.5–0.75) is well distributed, overall (Fig. A.11.4). High quality habitat (coefficients $\geq$0.75), however, is sparsely distributed and frequently associated with patches of public land that retains relatively natural cover types. Higher levels of habitat fragmentation associated with increased interspersion of low quality habitat (coefficients of 0–0.5) are apparent in Spokane County, northern and eastern Lincoln County, western Douglas County, central Adams County, and throughout the Palouse (Fig. A.11.4). Multiple factors contributed to this apparent increase in habitat fragmentation, and contributing factors varied by location, but agricultural development generally played a central role.

Our assignment of habitat quality coefficients led to a pattern in which most of the buffer surrounding the Columbia Plateau Ecoregion has low habitat value, suggesting that opportunities for immigration from surrounding ecoregions are limited (Fig. A.11.4). This habitat result is consistent with the result of our resistance estimates.

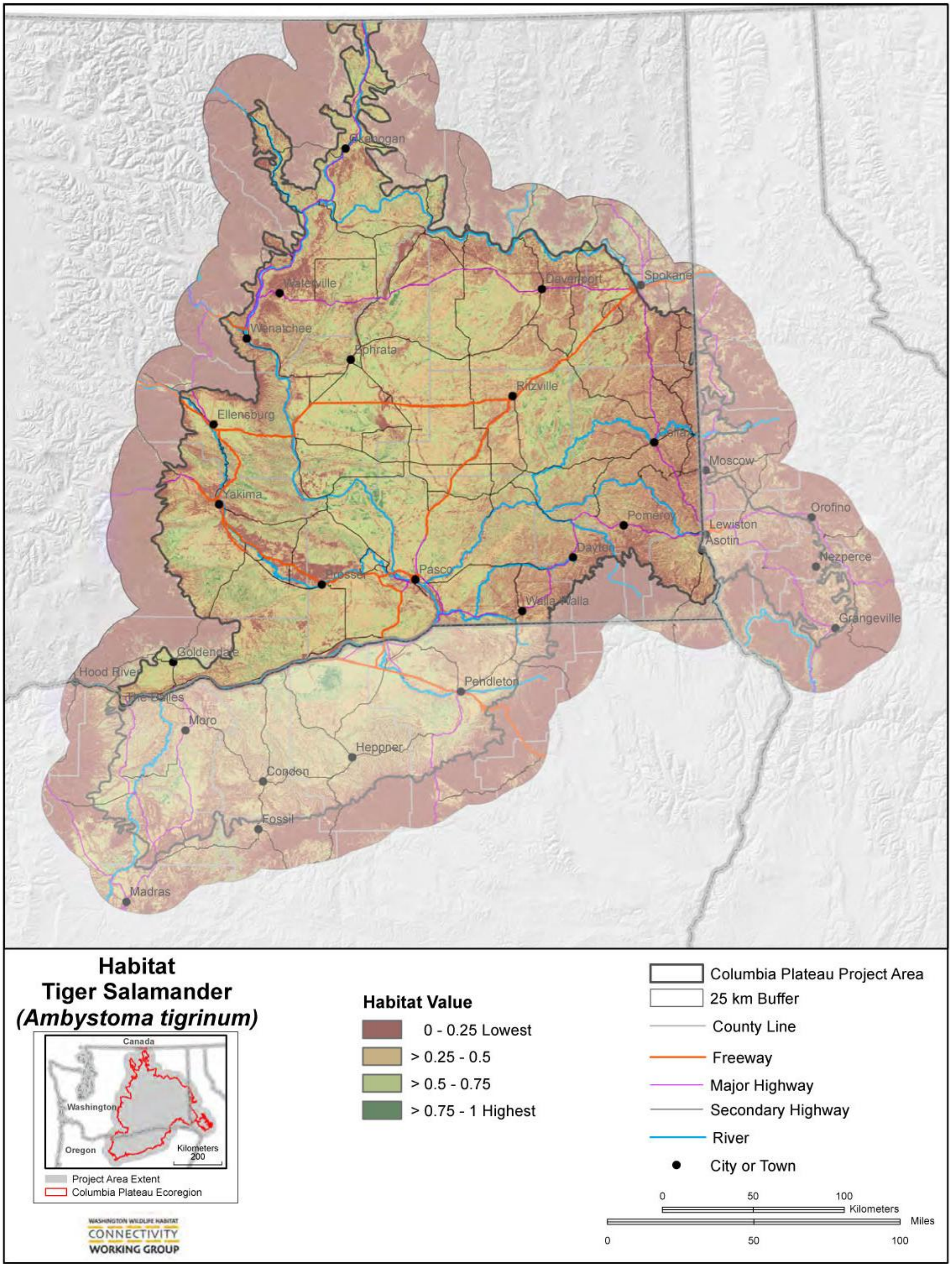


Figure A.11.4. Habitat map for tiger salamander in the Columbia Plateau Ecoregion.

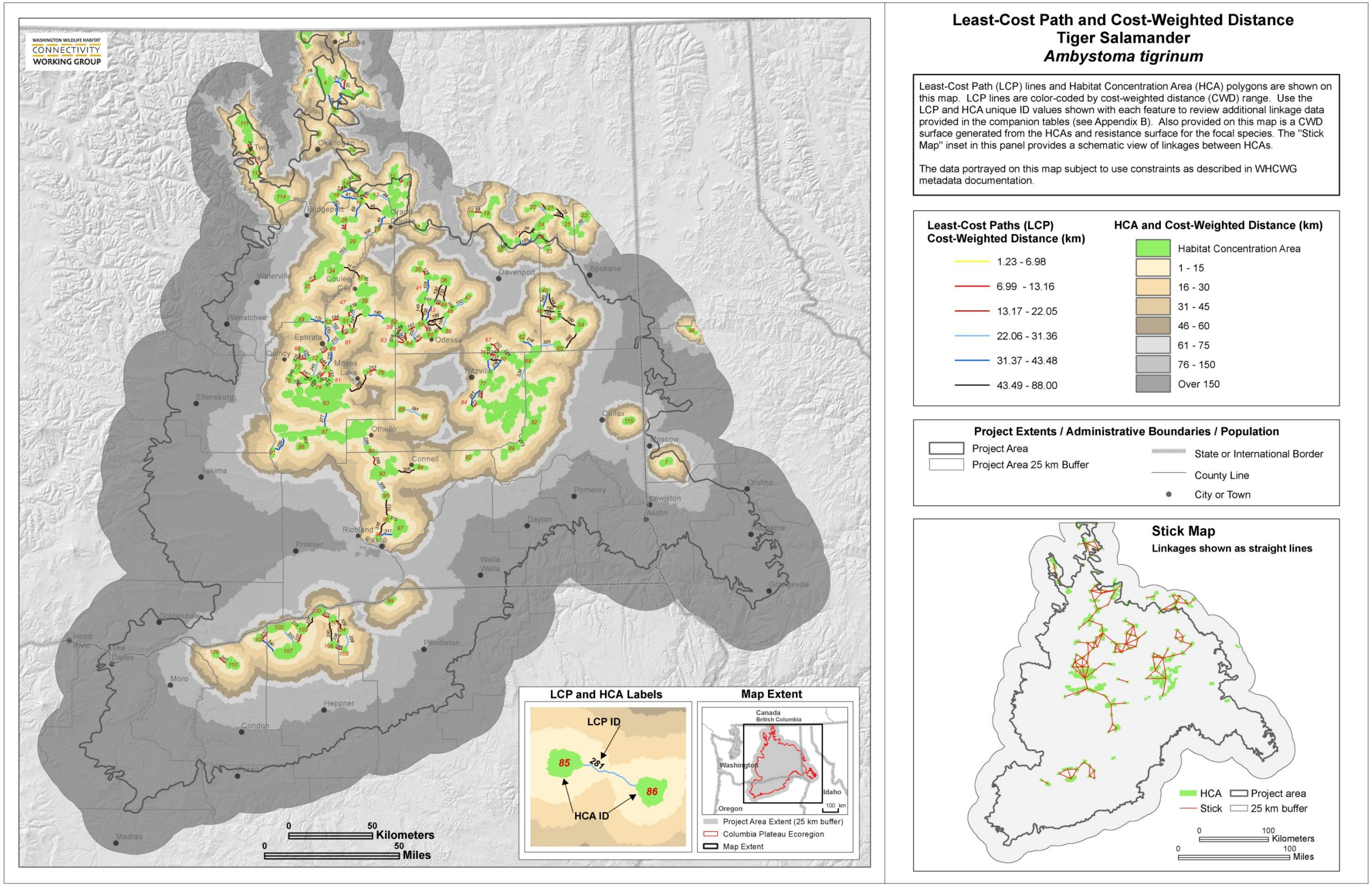
As suggested by the distribution of habitat patches with high quality coefficients, HCA modeling yielded a distribution of HCAs that is closely tied to areas of public lands. These patches of high quality habitat can be described as consisting of 10 groupings or clusters of HCAs (See Fig. A.11.5 for HCA identification). We identified these clusters by visual inspection of the relative proximity of HCAs, and based on results of cost-weighted distance (Fig. A.11.6) and linkage (Fig. A.11.7) modeling, rather than by statistical analysis. Starting in the north and working south, we identified the following HCA Clusters (see Fig. A.11.8):

1) Upper Okanogan Valley (4–8)
2) Lower Methow Valley (111–113)
3) Northeast Douglas County and adjoining areas of Okanogan County (11–17, 19, 26–29, 34, 38)
4) Southern Stevens County (20, 21, 23 to 25, 30–33)
5) Southwestern Lincoln County (35, 36, 41 to 44, 48, 52, 55, 58, 59, 60, 63, 64)
6) Cheney to Washtucna (40, 45, 46, 50, 54, 62, 65, 67, 69, 70, 71, 77, 82, 84, 89)
7) Northern Grant County (37, 39, 47, 49, 51, 53, 57, 61, 66, 68, 72, 73, 74, 78–81)
8) Central Grant County (75, 76, 83)
9) Southern Grant and Franklin counties (87, 88, 90, 91, 93–98)
10) Morrow County (OR) (100–108)

The remaining HCAs, a total of 16, were isolated as singles or pairs (1, 2, 3, 9, 10, 18, 22, 56, 85, 86, 92, 99, 109, 110, 114, 115). Many of these isolated HCAs were small in size.

This coarse clustering of HCAs suggests subdivision of populations in the Columbia Plateau into sub-units, with roughly 14% of HCAs being isolated or nearly so.

The size distribution of the HCAs had a median of about 27 km^2 with a range from 12.6 km^2 to 678 km^2. The distribution is positively skewed toward smaller HCAs. A subset of 12 HCAs were larger than 100 km^2. Most clusters had at least one of these large HCAs, except southern Stevens County (Cluster 4) and southwestern Lincoln County (Cluster 5). We assume that increasing size of suitable habitat patches likely increases the conservation value of these patches. Probability of occupancy and persistence of resident populations may be related to both patch size and proximity to other suitable patches.



Least-Cost Path and Cost-Weighted Distance
Tiger Salamander
Ambystoma tigrinum

Least-Cost Path (LCP) lines and Habitat Concentration Area (HCA) polygons are shown on this map. LCP lines are color-coded by cost-weighted distance (CWD) range. Use the LCP and HCA unique ID values shown with each feature to review additional linkage data provided in the companion tables (see Appendix B). Also provided on this map is a CWD surface generated from the HCAs and resistance surface for the focal species. The "Stick Map" inset in this panel provides a schematic view of linkages between HCAs.

The data portrayed on this map subject to use constraints as described in WHCWG metadata documentation.

Figure A.11.5. Cost-weighted distance map with numbered HCAs (green polygons labeled with red numerals) and least-cost paths (lines labeled with black numerals) for the tiger salamander. Linkage modeling statistics provided in Appendix B.

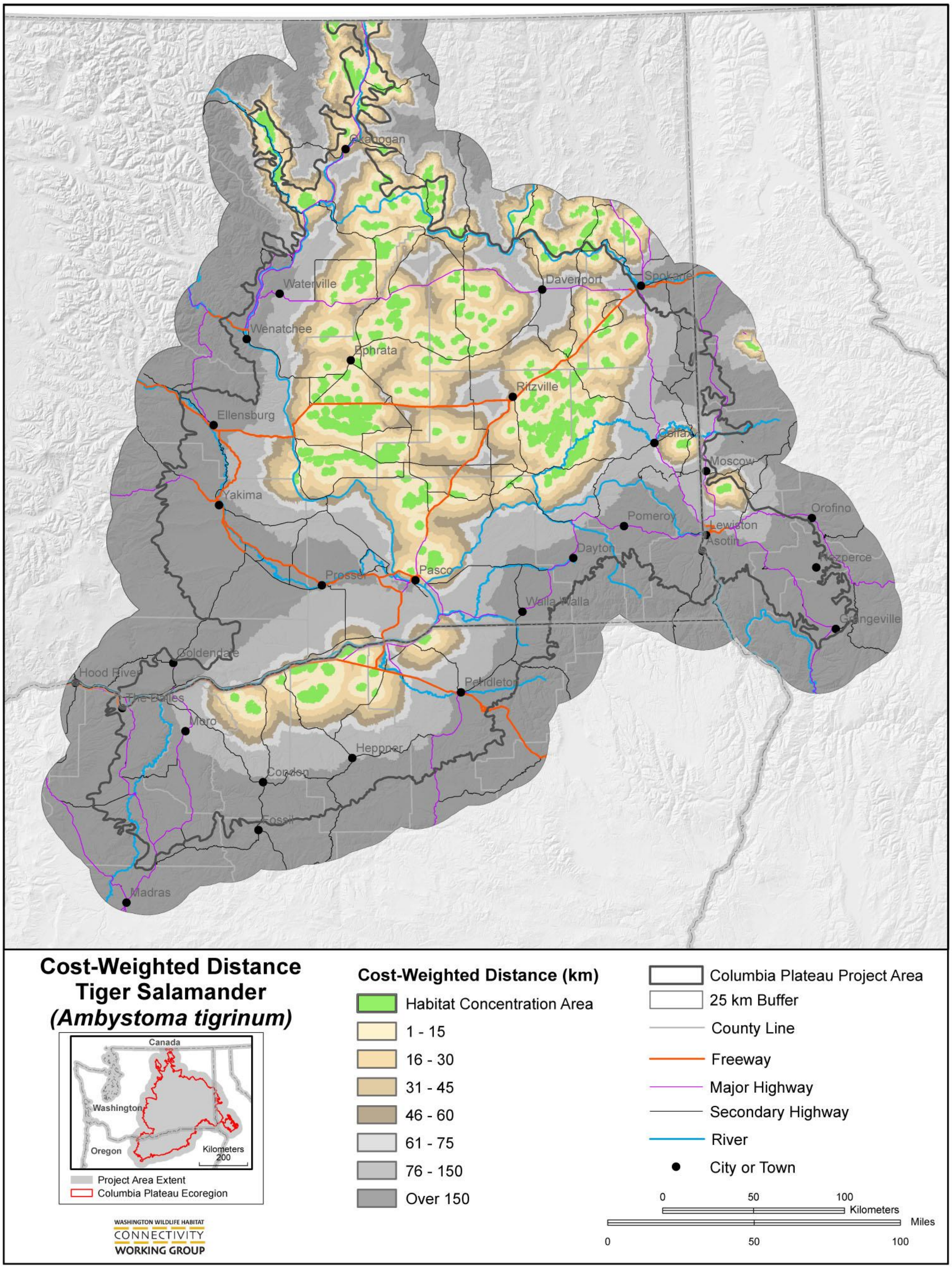


Figure A.11.6. Cost-weighted distance map for tiger salamander in the Columbia Plateau Ecoregion.

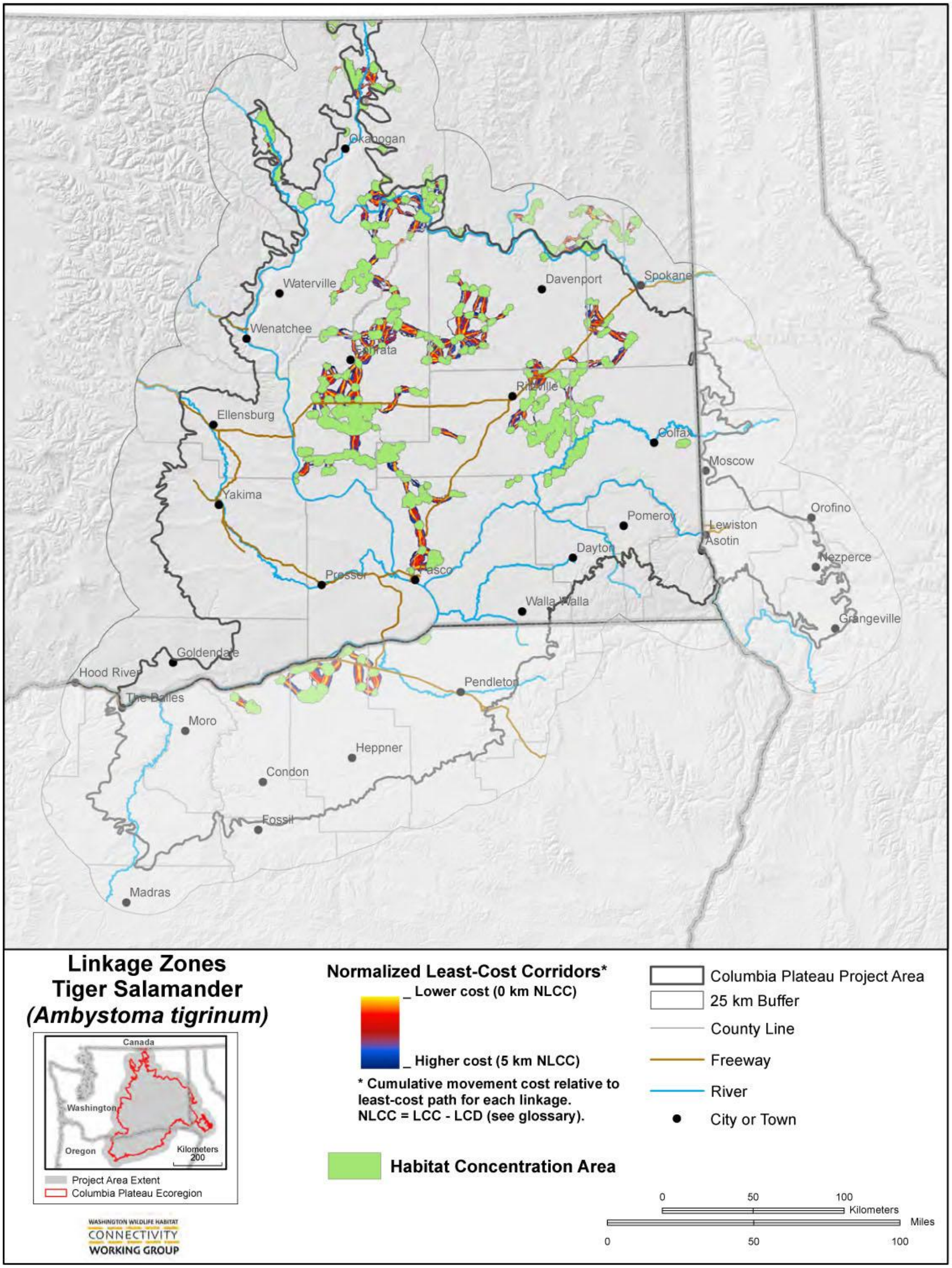


Figure A.11.7. Linkage map for tiger salamander in the Columbia Plateau Ecoregion.

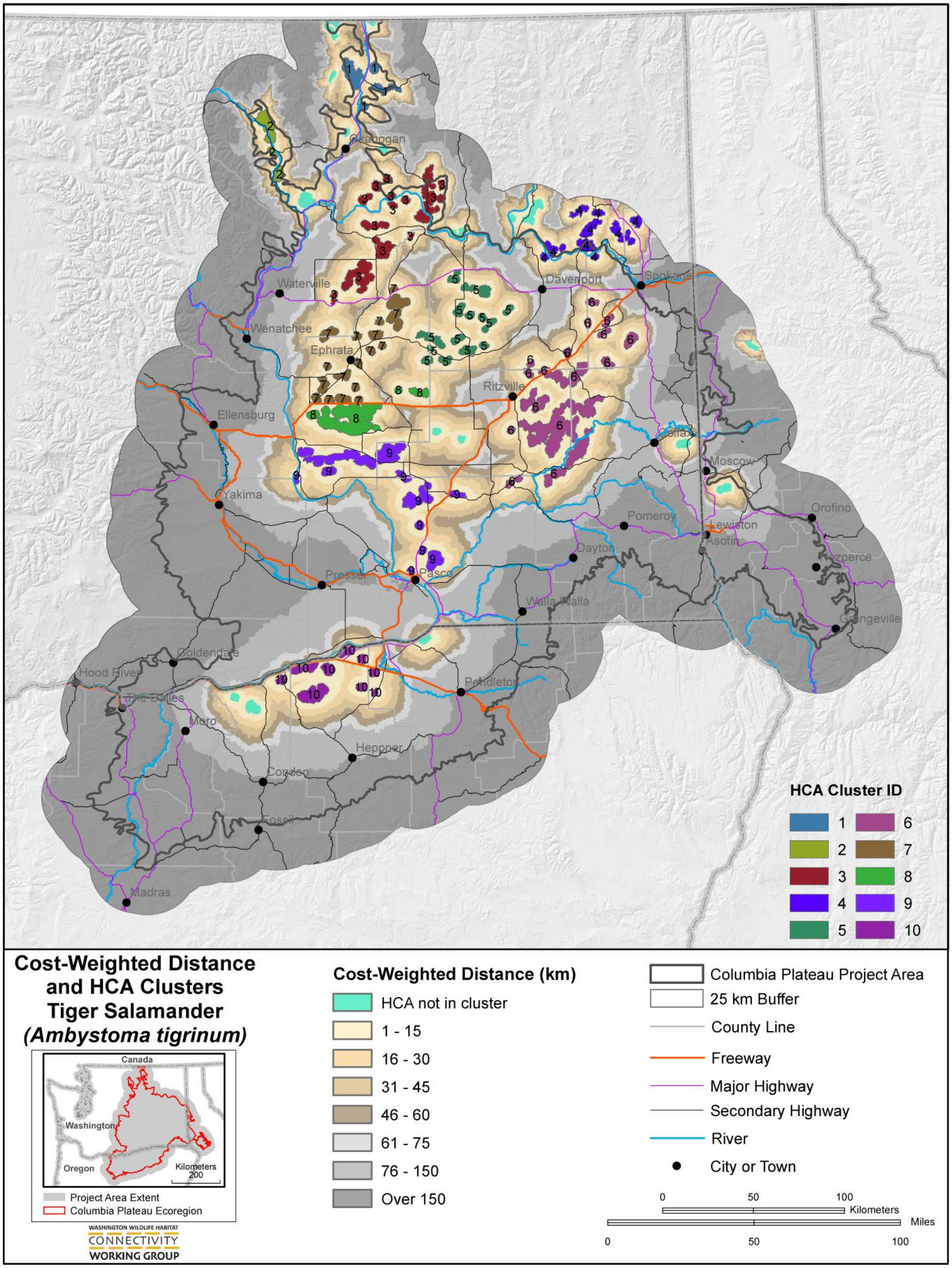


Figure A.11.8. Cost-weighted distance map with tiger salamander habitat concentration areas (HCAs).

Cost-Weighted Distance Modeling

This modeling step enabled us to identify what portions of the study area were accessible to tiger salamanders, what features presented the greatest impediments to connectivity, and also provided insights about the potential for structuring of populations within the study area. To determine what areas had a reasonable likelihood of being accessible to tiger salamanders moving out from our modeled HCAs, considering landscape resistance, we needed to estimate the highly variable relationship between Euclidean distance and cost-weighted distance (CWD). Linkage modeling produced 22 linkages ≥8 km in Euclidean distance. This subset of linkages reflects the high range of Euclidean distances we expected tiger salamanders to move in this landscape. The mean cost-weighted distance of this subset was 49.2 km. This mean provided an index of the CWD within which tiger salamanders were likely to access habitat areas outside HCAs, (recognizing that linkages formed along the least-cost paths represent the lowest possible cost accrued while traversing the landscape). We suggest that areas within a CWD of about 45 to 50 km from HCAs may be accessible to tiger salamanders, assuming use of patches of temporary, stepping stone, and sub-optimal habitat. Applying this threshold to Figure A.11.6 revealed that tiger salamanders may have relatively contiguous access to habitat in the west-central portions of the Columbia Plateau (clusters 3, 7, 8, and 9). In the remaining clusters, salamanders have relatively contiguous access to habitat within each cluster, but each cluster is relatively discrete; i.e., with limited access to habitats shared with other clusters.

The CWD analysis shows the clear impact of I-90, Highway 395, and Route 2 as linear anthropogenic features that limit tiger salamander access to habitat (Fig.A.11.6). Agricultural development does not form a sharp-edged boundary like highways, but limits habitat access due to its extent, especially in western and central Adams County and in the Palouse (Fig. A.11.6). The CWD analysis also shows the combined influence of highways, railroads, reservoirs, and residential, commercial, and agricultural development in valley bottoms, causing rapid accumulation of cost-weighted distance and constraining habitat access. These features contribute to the barrier effect of the Columbia, Snake, and lower Okanogan rivers.

The CWD analysis also suggests that opportunities for connectivity with other ecoregions are very limited. Connections to British Columbia via Cluster 1 and the upper Okanogan River drainage, and to the Okanogan Ecoregion via Cluster 4 and the Colville River drainage may be the most likely opportunities for movement of tiger salamanders between ecoregions.

Linkage Modeling

We used a 10 km maximum Euclidean distance as the cutoff for linkage modeling. Applying this cutoff to our distribution of modeled HCAs yielded a total of 144 linkages among HCAs (Fig. A.11.7; see also Fig. A.11.5 for HCA identification). We divided the total of 144 linkages into those between clusters (7 linkages) and those within clusters (137 linkages; Table A.11.3). Surprisingly, the mean Euclidean distance of linkages between clusters (4.2 km) was less than the mean for linkages within clusters (4.5 km; Table A.11.3). This pattern reflects that 4 of the 7 between-cluster linkages cross I-90 between HCAs in clusters 7 and 8. These short linkages across the Interstate reduce the mean Euclidean distance, but the high resistance of the Interstate led these linkages to have a high mean cost-weighted distance (32.7 km) compared to the within-cluster mean (24.8 km; Table A.11.3). Our two indices of linkage quality reflected this pattern with linkages between clusters having mean index values that were three to four times as high as mean index values for linkages within clusters (Table A.11.3).

Table A.11.3. Statistics and qualitative evaluation for linkages between and within clusters of tiger salamander HCAs.

Linkage group	*n*	*Euclidean length (km)*		*Cost-weighted distance (km)*		*Least-cost path length (km)*		*Ratio CWD to Euclidean*		*Ratio CWD to LCPL*		*Qualitative connectivity rating*
		Mean	*SD*	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*	
Between	7	4.2	4.2	32.9	25.5	5.2	4.8	24.4	28.3	12.2	10.7	Poor
Within	137	4.5	2.8	24.8	16.8	5.6	3.4	7.1	11.7	4.8	2.7	N/A
Cluster 1	6	5.2	1.5	32.7	8.6	6.8	1.8	6.6	2.0	4.8	0.9	Moderate
2	2	3.1	2.5	15.0	10.0	3.8	2.6	5.2	0.9	4.0	0.1	Moderate
3	18	4.5	2.9	22.8	15.7	5.6	3.4	5.7	3.8	4.4	2.5	Moderate
4	11	3.4	3.0	26.2	21.7	4.7	4.0	10.2	6.9	6.6	3.3	Poor
5	24	4.6	2.9	23.7	15.5	5.4	3.4	5.2	0.9	4.3	0.5	Moderate
6	21	4.8	3.1	30.1	18.1	5.9	3.6	14.3	28.6	6.6	5.3	Poor
7	28	3.6	2.5	17.5	12.2	4.2	3.0	5.0	1.2	4.2	1.0	Good
8	2	6.3	4.2	51.2	52.0	10.7	9.6	6.9	3.6	4.4	0.9	Poor
9	10	5.6	2.8	28.8	16.0	7.0	3.5	5.3	1.3	4.0	0.8	Moderate
10	12	5.1	2.3	26.6	18.2	6.3	2.8	5.1	2.6	4.0	1.8	Moderate
Pairs	3	5.1	2.9	20.4	7.2	6.1	2.9	4.4	1.7	3.6	1.2	Moderate

Between-cluster linkages—Linkages between clusters may be considered particularly important for maintaining connectivity among populations in the Columbia Plateau Ecoregion. Single between-cluster linkages occurred between clusters 3 and 7, 5 and 7, and 8 and 9. Another group of four between-cluster linkages occurred between clusters 7 and 8.

The single linkage between clusters 3 and 7 connected the northern clusters to the eastern and central portions of the distribution in the Columbia Plateau. This linkage was nearly 10 km in Euclidean distance, with a cost-weighted distance of nearly 88 km, yielding linkage quality index values of near 9 and 7 (See Appendix B). These values suggest that this important linkage passes through habitat with moderate resistance, suggesting that habitat restoration in this linkage could be effective. This linkage passes through state lands, including Sun Lakes – Dry Falls State Park, suggesting opportunities for maintaining and improving this linkage may be good. Natural ruggedness of the terrain in this linkage along with the intersection of Highways 2 and 17 may be the features contributing most to resistance in this linkage.

The single linkage between clusters 5 and 7 connected an extensive area of relatively high quality habitat in central and western Lincoln County to the western tier of clusters. This linkage between HCAs 39 and 52 had a Euclidean length of 8.7 km and a cost-weighted distance of about 36, yielding index values of 4.1 and 3.4 (See Appendix B). These values suggest a linkage through good quality habitat (i.e., the average resistance is less than 5). This linkage passes through primarily private lands near Wilson Creek, east of Billy Clapp Lake. Highway 28, a major railway, and agricultural development were the primary sources of resistance near this linkage.

The single linkage between clusters 8 and 9 connected the large and diffuse Cluster 9 to the remainder of the western tier of clusters. This linkage between HCAs 83 and 87 had a Euclidean length of 7.2 km and a cost-weighted distance of about 33 km, yielding index values of 4.6 and 4, again suggesting that this linkage passed through primarily good quality habitat (See Appendix B). This linkage extended primarily across private lands in the Frenchman Hills, from the Desert Wildlife Area southward toward the Lower Crab Creek Wildlife area. Primary sources of resistance in this area were relatively steep natural topography, agricultural developments, including irrigation canals, and Highway 26. Like the other between-cluster linkages described here, this linkage may provide good opportunities for connectivity maintenance and restoration for salamanders.

Finally, we modeled four linkages that crossed the I-90 corridor between HCA 83 in Cluster 8 to the south, and four small HCAs (78 to 81) in cluster 7 to the north. These linkages were essential for maintaining connections between the northern and southern portions of the distribution in the study area. We have not obtained detailed information about the relative permeability of I-90 in this vicinity between Potholes Reservoir Wildlife Area and the Winchester Reservoir Wildlife Area. Our modeled linkages in this area ranged in Euclidean length from 0.2 km to 2.4 km, suggesting that the total distance is within the dispersal capabilities of tiger salamanders. Due to resistance from the highway and associated development, cost-weighted distances for these linkages ranged from 14.4 to 22.4 km (See Appendix B). Corresponding linkage quality indices were highly variable, ranging from 8 to 80. The linkage with the longest Euclidean distance had the best linkage quality indices, suggesting this linkage has reasonable restoration potential. This area warrants more detailed local connectivity analysis to find the best options for restoration or enhancement.

Within-cluster linkages—In this sub-section, we describe the status of connectivity for each cluster we identified by comparing it to mean values derived from all within-cluster linkages combined (*n* = 137 linkages; see also Table A.11.3). We used mean values as the basis for comparison for all characteristics. Comparison of mean and median values indicated that the frequency distributions for cost-weighted distance and the linkage quality indices were positively skewed by very large values. We found, however, that use of median values did not change our qualitative assessments based on mean values. We conclude each of these cluster-specific descriptions with a qualitative assignment of clusters to categories of good, moderate, or poor internal connectivity.

Cluster 1, in the upper Okanogan Valley included 4 HCAs connected by 6 modeled linkages. This cluster was isolated from other clusters. Both mean Euclidean distance and mean cost-weighted distance for linkages in this cluster were well above ecoregional mean values (Table A.11.3). Linkage quality indices, however, were not particularly elevated, suggesting that the relatively long expanses between HCAs contained relatively good habitat. Relatively rugged natural terrain, the Okanogan River, highways 97 and 20, and residential and agricultural developments were landscape features that reduced habitat connectivity for salamanders in this cluster. We interpreted this combination of factors as indicating that this cluster had a moderate level of internal connectivity.

Cluster 2 in the lower Methow Valley also was isolated from other clusters. This cluster included 3 "extra-model" HCAs (added to explore potential internal linkages) connected by 2 linkages. This small sample of linkages within this cluster had low Euclidean lengths and cost-weighted distances, leading to corresponding linkage quality indices that suggest good habitat quality in the linkages (Table A.11.3). Like Cluster 1, factors that influenced habitat connectivity in Cluster 2 included relatively rugged natural terrain, the Methow River, highways 153 and 20, and residential and agricultural developments. We interpreted this pattern as suggesting that Cluster 2 also had a moderate level of internal connectivity.

Cluster 3 in northeast Douglas County and adjacent Okanogan County was a larger and more spatially complex cluster containing 13 HCAs connected by 18 internal linkages. In contrast to the previous clusters, many HCAs in this cluster were linked to more than one other HCA. HCAs 11 and 34 were both large HCAs (>100 km^2), anchoring the northeast and southwest portions of this cluster, respectively. Linkage statistics for linkages in this cluster generally had values near the ecoregional mean values (Table A.11.3). Highways 17, 172, and 174, and agricultural developments were the primary landscape factors influencing habitat connectivity. We considered this cluster also to have a moderate level of internal connectivity.

Cluster 4 in southern Stevens County contained 9 HCAs connected by 11internal linkages. This cluster was isolated from other clusters and did not contain any HCAs greater than 100 km^2 in size. Although linkages in this cluster had a low mean Euclidean length, they had above average cost-weighted distances, leading to linkage quality statistics that indicated habitat between HCAs was generally moderate to low quality. Relatively rugged natural terrain, the Spokane River and associated development, agricultural development, and Highway 231 were among the key landscape features limiting connectivity for salamanders in this cluster. We considered this cluster to have a poor level of internal connectivity.

Cluster 5 in southwestern Lincoln County was linked only to Cluster 7, despite its central location in the study area. Cluster 5 had a total of 14 HCAs connected by 24 modeled linkages, and no large HCAs. Like clusters 3 and 7, Cluster 5 had many HCAs that were linked to more than one other HCA. HCA 55 had particularly high centrality, linking to 7 other HCAs. Mean values for linkage statistics for this cluster were very similar to ecoregional means for all statistics (Table A.11.3). Agricultural development and Highway 21 were the primary sources of landscape resistance affecting habitat connectivity within this cluster. Despite the high number of internal linkages, we felt Cluster 5 had a moderate level of internal connectivity, mostly due to these linkages generally having near average values for linkage quality indices.

Cluster 6 was a relatively loose aggregation of HCAs that spans a broad area in the eastern portion of the study area, roughly from Cheney to Washtucna. This cluster is not connected to any other clusters. This cluster contains 15 HCAs, including three large HCAs (69, 77, and 82—the largest HCA in the study area at about 678 km^2). This cluster was connected by 21 internal linkages, with several HCAs connected to only one other HCA. The mean Euclidean length of these linkages was near the mean for the study area, but mean cost-weighted distance was well above the mean. Consequently, linkage quality indices were also well above the study area means. The mean ratio of cost-weighted distance to Euclidean distance was nearly two times the study area mean (Table A.11.3). Interstate 90 was a significant contributor to resistance along with agricultural developments. Despite the presence of three large HCAs, we felt that high values of the linkage quality indices suggested that this cluster had poor internal connectivity.

Cluster 7 was located in northern Grant County. It was linked by single linkages to clusters 3 and 5, and by multiple linkages to Cluster 8. Due to these linkages to three other clusters, Cluster 7 has the highest among-cluster centrality in the study area. Cluster 7 contains 17 HCAs, including one large HCA (39) near the northern end of the cluster. Cluster 7 had a total of 28 internal linkages, so all but two HCAs were connected to more than one other HCA. HCAs 55 and 72 had high centrality, both linking to five other HCAs. Mean values for all linkage measures were well below the ecoregional mean values (Table A.11.3). Agricultural development and Highways 17 and 28 were the major factors contributing resistance to this cluster. Based on this pattern, we considered this cluster to be the only cluster in the analysis area that warranted a rating of “good” for internal connectivity.

Cluster 8 contained one large and two small HCAs in central Grant County, south of I-90. As described above in the section on between-cluster linkages, large HCA 83 in Cluster 8 has four linkages to small HCAs in Cluster 7, and one linkage to HCA 87 in cluster 9. Within-cluster linkages are limited to two linkages. The Euclidean length of one of these linkages is below the mean for the study area, but the other is 9.3 km long, near the upper limit of allowable linkage lengths. The long linkage crossed I-90, resulting in the highest cost-weighted distance of any linkage (88 km). Interstate 90, highways 17 and 262, Potholes Reservoir, Moses Lake, residential and commercial development, and agricultural development, including major irrigation canals all were important contributors to resistance in this cluster. This collection of factors led us to rate Cluster 8 as having poor internal connectivity.

Cluster 9 consisted of 10 HCAs, including two large HCAs (87 and 93). This cluster was connected only to Cluster 8. Cluster 9 contained 10 internal linkages, meaning three HCAs were connected to only one other HCA. Mean values of most linkage statistics for this cluster were above the mean values for the study area, but only by relatively small amounts (Table A.11.3). Agricultural development, the Saddle Mountains, and Highway 24 were important landscape features contributing to resistance in this cluster. We considered this cluster also to have a moderate level of internal connectivity.

Cluster 10 was located in Morrow County, Oregon, and contained 9 HCAs, including one large HCA (107). We have no evidence to indicate that this cluster is occupied by tiger salamanders, but we retained HCAs and modeled linkages to explore connectivity opportunities in this area. Mean values for linkage statistics for this cluster were very similar to ecoregional means for all statistics (Table A.11.3). Several highways, including interstates 82 and 84, residential, commercial, and agricultural developments and the Columbia River all constrain connectivity in this cluster. Our exploration of connectivity opportunities in this area suggested a moderate level of internal connectivity was present.

Finally, six HCAs were distributed as isolated pairs across the study area. Statistics and quality indices for linkages between these pairs generally were similar to or lower than ecoregional means (Table A.11.3). Because of their relative isolation, and because none of these pairs included a large HCA, we considered these pairs to have moderate internal connectivity.

Linkage modeling summary—Linkages for tiger salamanders show a pattern of generally moderate quality connectivity within HCA clusters, but tenuous linkages among clusters. As described in the Cost-Weighted Distance Modeling section above, linkages among clusters in the west-central portion of the Columbia Plateau are marginally better than in other portions of the study area. Clusters 1, 2, 4, 6, and 10 are likely disconnected from other clusters in the ecoregion. Clusters 1 and 4 may be connected to populations outside the study area, but the existence of these connections is speculative and the quality of these potential connections is unknown. Populations outside our study area in British Columbia and the Colville River drainage are likely to be either small, isolated, or both.

Our overall interpretation of the linkage patterns we modeled for the tiger salamander was that the spatial architecture of populations in the Columbia Plateau may not be conducive to long-term persistence. Columbia Plateau populations may reflect a relictual, post-glacial, distribution that was largely or entirely isolated from populations in other ecoregions. Within this relictual distribution, tiger salamander populations primarily occupy fragmented remnant habitats associated with areas that were less suitable for agriculture. It is possible that even the best quality habitats that are currently occupied are toward the low end of the historical spectrum of habitat quality. At least half of all clusters we identified were isolated, with a very low likelihood of successful immigration or recolonization if extirpation occurred. These disconnected clusters, especially those without large HCAs, likely have a reduced probability of long term persistence, assuming they are likely to support relatively small populations. Linkages between clusters were limited, with most clusters linked to only one other cluster. Fortunately, remaining between-cluster linkages appear to be in relatively good condition or to provide reasonable opportunities for enhancement or restoration. About 14% of all the HCAs we modeled were completely isolated or connected to only a single other HCA, also indicating limited opportunities for demographic and genetic exchange. Within clusters, a disturbing number of HCAs were linked to only one other HCA. Clusters in the west-central portion of the analysis area appeared to be the best connected. Nonetheless, we only considered one cluster in this area to have good internal connectivity. The pattern of connectivity suggested by our modeling implies a relatively high risk of local extirpations without replacement, resulting in greater fragmentation, and even greater risk for remaining populations. Genetic analysis (see Opportunities for Model Validation section, below) could provide insights about levels of inbreeding within clusters and drift among clusters, providing a better understanding of current levels of genetic and demographic risk.

One of the most encouraging aspects of our analysis was strong anecdotal evidence of tiger salamander populations persisting within agricultural landscapes. More information is needed about the specific conditions that enable or promote persistence in agricultural landscapes and the status and resilience of these populations. This information could provide important clues about techniques for restoring connectivity and locations where these techniques might have the greatest conservation benefits.

Based on our results, we think the most pressing connectivity implementation need is to bolster connectivity among clusters. Our analysis highlights several specific opportunities:

- Along I-90 in Central Grant County (between clusters 7 and 8),
- From central Grant County (Cluster 8) to southern Grant/Franklin counties (Cluster 9),

- From Lincoln County (Cluster 5) to northern Grant County (Cluster 7), and
- From northern Grant County (Cluster 7) to Douglas County.

All of these areas, especially the first listed, warrant more detailed local analysis to find the best locations for maintaining or restoring connectivity.

Key Patterns and Insights

- Our approach to modeling habitat suitable for supporting tiger salamander populations suggested remaining habitats were concentrated in areas less suitable to agriculture (i.e., scoured by the Missoula floods; periodic, cataclysmic floods that swept across the Columbia Plateau at the end of the last ice age).
- Anthropogenic features contributed most to landscape resistance in relatively flat areas of the Columbia Plateau. In areas with more topographic relief, areas of low resistance tended to follow valley bottoms and drainages with natural vegetation. Cliffs and scoured plateaus of the channeled scablands had higher resistance to dispersal.
- Higher elevation areas surrounding the Columbia Plateau also had higher resistance which may limit opportunities for immigration of tiger salamanders from adjoining ecoregions.
- Moderate quality habitat was well distributed, but high quality habitat was sparsely distributed and frequently associated with patches of public land that retain relatively natural cover types.
- Most of the buffer surrounding the Columbia Plateau Ecoregion had low habitat value, reinforcing the pattern suggested by resistance values that opportunities for immigration from surrounding ecoregions were limited.
- The distribution of modeled HCAs (115 total) suggested they could be subdivided into 10 clusters, 5 of which are isolated from other clusters. Sixteen HCAs were either completely isolated or found in pairs.
- Areas within a CWD of about 45 to 50 km from HCAs may be accessible to tiger salamanders, assuming use of patches of temporary, stepping stone, and sub-optimal habitat. Tiger salamanders may have relatively contiguous access to habitat in the west-central portions of the Columbia Plateau (clusters 3, 7, 8, and 9). In the remaining clusters, salamanders have relatively contiguous access to habitat within each cluster, but limited access to habitats shared with other clusters.
- Highways limit tiger salamander access to habitat. Agricultural development does not form sharp-edged boundaries like highways, but limits habitat access due to its extent, especially in western and central Adams County and in the Palouse. The combined influence of highways, railroads, reservoirs, and residential, commercial, and agricultural development in valley bottoms caused rapid accumulation of cost-weighted distance and constrained habitat access. These features contribute to the barrier effect of the Columbia, Snake, and lower Okanogan rivers.

- We modeled a total of 144 linkages among HCAs and divided this total into those between clusters (7 linkages) and those within clusters (137 linkages).
- Linkages show a pattern of generally moderate quality connectivity within HCA clusters, but tenuous linkages among clusters. Linkages among clusters in the west-central portion of the Columbia Plateau were marginally better than in other portions of the study area.
- The spatial distribution and relative connectivity of populations in the Columbia Plateau may not be conducive to long-term persistence of tiger salamanders.

Considerations and Needs for Future Modeling

Several types of information could improve future connectivity modeling for tiger salamanders, other amphibians, and species with relatively low-mobility in this ecoregion.

- Better information about salamander use of agricultural landscapes would greatly improve connectivity modeling. The ability to incorporate more detail about the relative resistance of different crop types, and how typical crop rotation sequences could influence this pattern through time would also improve modeling.
- As described above, delineation of HCAs presented us with many challenges. Information about the spatial distribution of predatory fish or a surrogate variable that accurately reflects their distribution would enhance delineation of HCAs. We think there are many alternative approaches to HCA delineation that warrant further investigation.
- Considerable uncertainty surrounds the effects of contaminants on relative landscape resistance. Better information about how chemicals that are typically used in road and railroad maintenance, agriculture, and residential settings could affect landscape resistance would allow refinement of resistance values. Our review of current literature suggested contaminants could be important factors in landscape resistance, but we did not include contaminant effects in an explicit, quantitative way in our assignment of resistance values.
- The relative resistance of wind energy developments also was a source of considerable uncertainty. We felt both turbines and transmission lines could influence landscape resistance, but could not find any published information that could help us refine our estimates of their relative effects.
- The apparent relationship we observed between the Missoula Floods and the current distribution of tiger salamander populations led us to wonder if other aspects of geologic history (e.g., rock types) might influence the quality and distribution of salamander habitats and opportunities for habitat connectivity. We are relatively confident that better information about the soil types preferred by tiger salamanders as well as information about the spatial distribution of burrowing mammals that produce suitable subterranean refugia for salamanders could improve connectivity models.

Finally, landscape genetic analysis of populations, including comparative analysis of different connectivity models to determine which landscape features have the greatest influence on connectivity at different spatial scales, would be a profitable avenue for further research on tiger salamander habitat connectivity on the Columbia Plateau.

Opportunities for Model Validation

Our models and resulting maps of potential HCAs for tiger salamanders and linkages between them are best viewed as hypotheses to be tested. In particular, our products are hypotheses about population structure and the likelihood of gene flow among populations. Tiger salamanders on the Columbia Plateau provide an outstanding opportunity for testing these sorts of hypotheses. Landscape genetic techniques have been used successfully to explore patterns of gene flow in many salamander populations. In the field, metamorphs and adult salamanders are relatively easy to capture as they migrate to or from breeding ponds, and tissue sampling for genetic analysis is also relatively straightforward, using buccal swabs or toe clips. In the laboratory, techniques for DNA extraction and amplification of micro-satellites from ambystomatid salamanders are well established. We are hopeful that this combination of facilitating factors will encourage genetic tests of our connectivity hypotheses. Such studies could provide critical insights about how changes in land cover affect the population structure of pond-breeding amphibians. These tests would also provide valuable information about calibration of parameter values for different landscape features that could be used to improve subsequent connectivity analyses.

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