

WESTERN POND TURTLE (*ACTINEMYS MARMORATA*) CONSERVATION:
FUTURE DIRECTIONS FOR RESEARCH

By
DANIEL OHRN

A Thesis

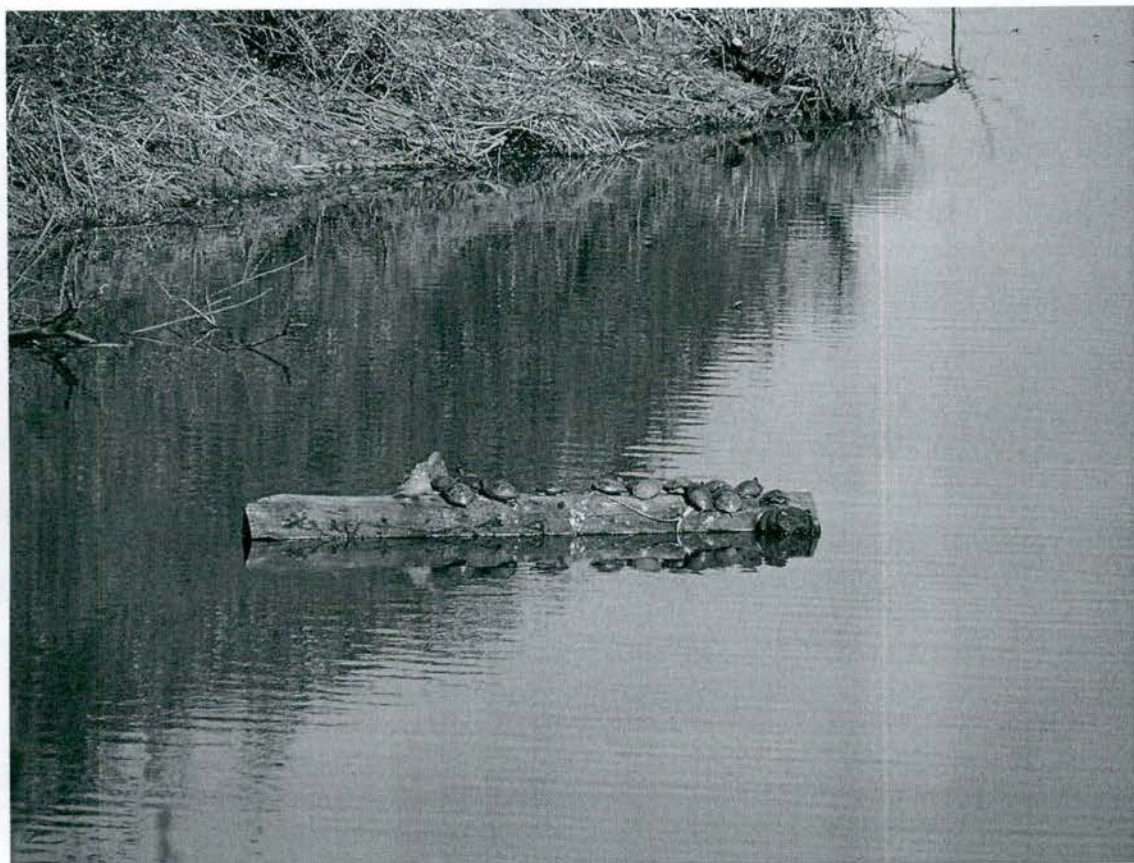
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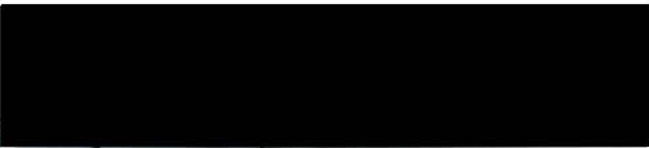
An Abstract of the Thesis of

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Title: WESTERN POND TURTLE (*ACTINEMYS MARMORATA*) CONSERVATION:
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Approved


Professor Brendan Bohannon

The western pond turtle (*Actinemys marmorata*) has suffered a significant decline coinciding with Euro-American occupation of the western United States. Threats to the species' persistence include habitat loss, competition from invasive species, predation, and road mortality. The species was petitioned for listing as 'threatened' under the Endangered Species Act in 1992, but denied listed status in 1993 due to a lack of credible science. Since then, western pond turtle conservation research has made great progress, but the field still operates on a deficient knowledge base. This thesis aggregates influential western pond turtle research to date in order to suggest future directions for research and approaches to management. Further research is required in the areas of dispersal, population stability, the severity of threats posed by invasive species, artificial discharge from river impoundments, and nest locating methodologies.

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Introduction

Western pond turtle (*Actinemys marmorata*) populations historically inhabited river valleys and coastal wetlands from Baja California to southern British Columbia, supported by an extensive network of rivers, lakes, streams, oxbows, and wetlands (Holland 1994). The species was abundant, providing economic stimulation through commercial harvest beginning in 1860 (Lockington 1879). San Franciscans bought 18,000 individuals per year, the harvest peaking in 1890 and dwindling soon after (Smith 1895; Lockington 1879).

Although the species is now protected by law, its habitat is not. Since the early 1800s, urban and agricultural development as well as river impoundment has led to a loss of the landscape heterogeneity afforded by riparian and backwater areas (Benner and Sedel 1997; Taft and Haig 2003; Grosslinger et al. 2007; Holland 1994). California's Central Valley was estimated to contain 787,000 ha of rivers, lakes, streams, wetlands, and backwater areas before human settlement, more than half of which have disappeared (Bury and Germano 2008).

As a result, western pond turtle populations have declined. While the severity of the decline is arguable, a number of conservationists describe the species' status as dire. Holland (1994) estimates that the Willamette River Drainage historically supported 90,000 individuals but currently contains only 1500 to 2400 individuals. In southern California, pond turtle populations have been reduced to small, isolated patches separated by cities and roads (Brattstrom 1988). The species was effectively extirpated from

Washington and remains uncommon in the region (Bury 1995; Milner 1986). Western pond turtles do not face the same set of threats across their range, and different regions exhibit differing overall threat levels. Contrasting with Puget Sound populations, many in southwestern Oregon, for example, are relatively stable (B.R. Bury pers. comm.). Bury and Germano (2008) describe three geographic areas showing the most marked decline: 1) southern California from Baja to Ventura, 2) California's Central Valley, and 3) the northernmost portion of their range, particularly populations in Washington. In these areas, habitat loss and degradation are the greatest threats to the species (Bury and Germano 2008).

The decline of the western pond turtle is disconcerting; it is one of only two extant freshwater turtle species native to the western United States and the only species of its genus (Holte 1998; Patrick and Weins 2004). Of equal concern is that the decline of the western pond turtle indicates poor functioning of west coast lowland ecosystems, where the species once made up a significant percentage of animal biomass (R.B Bury pers comm.). In addition to western pond turtles, a host of other less visible species with obligate ties to the historic landscape are likely facing decline. While it is arguable that biodiversity has inherent value, it has been shown to have utilitarian value, providing necessary ecosystem services (Constanza 1997).

State agencies in Washington, Oregon and California afford the western pond turtle some protection. In Washington, the species is listed as State Endangered.¹ Oregon

¹ State Endangered is defined (under WAC 232-12-297 section 2.4) as "any wildlife species native to the state of Washington that is seriously threatened with extinction throughout all or a significant portion of its range within the state."

lists it as Sensitive – Critical.² In California, the western pond turtle is a Species of Special Concern.³ The western pond turtle is a federal species of concern⁴ and was proposed for federal listing as a threatened species⁵ in 1992, but the species was denied listed status due to a lack of evidence for listing (USFWS 1993).

This thesis aggregates influential western pond turtle research to date in order to suggest future directions for research and approaches to management. The western pond turtle research base is dominated by observational studies attempting to generally describe western pond turtle behavior. These are comparatively cheap and provide a basis for experimental design, but have approached, and in some cases exceeded, the limit of their utility. Disunity among research groups has led to high redundancy in observational research and a lack of funding hinders the much-needed shift to hypothesis-driven, experimental research. The thesis is divided into three major sections: the life history of the western pond turtle, current management strategies, and recommendations for further research.

² Sensitive – Critical denotes that “listing as threatened or endangered is pending or may be appropriate if immediate conservation actions are not taken.”

³ A Species of Special Concern is a species, subspecies, or distinct population native to California that currently satisfies one or more of the following criteria: 1) is extirpated from the State or, in the case of birds, in its primary seasonal or breeding role; 2) is listed as Federally-, but not State-, threatened or endangered; 3) meets the State definition of threatened or endangered but has not formally been listed; 4) is experiencing, or formerly experienced, serious (noncyclical) population declines or range retractions (not reversed) that, if continued or resumed, could qualify it for State threatened or endangered status; 5) has naturally small populations exhibiting high susceptibility to risk from any factor(s), that if realized, could lead to declines that would qualify it for State threatened or endangered status.

⁴ Species of Concern is an informal term that refers to those species that might be in need of concentrated conservation actions. Species of concern receive no legal protection and the use of the term does not necessarily mean that the species will eventually be proposed for listing as a threatened or endangered species.

⁵ Threatened Species are those likely to become endangered within the foreseeable future throughout all or a significant portion of its range.

1. Life History

Morphology

Actinemys marmorata is a small to medium-sized turtle, with a carapace length ranging from 160 to 190 mm, rarely exceeding 200 mm (Bury 1970; Ashton et al. 2001). Plastron coloration among adults is variable, consisting of pale yellow covered to varying degrees with dark green and brown blotches (Seeliger, 1945). The carapace is olive, with dark brown or black markings. Head and neck coloration vary considerably and can contain olive, brown, yellow, and black hues (Seeliger, 1945). The limb undersides are yellow with brown and black blotches or spots. Adult tail length to carapace length ratio is 0.3 to 0.6 (Seeliger, 1945). The feet are webbed and populations in fast moving water may have elongated carapaces (Ernst et al., 1994; Lubcke and Wilson, 2007). Western pond turtle morphology can vary greatly between sites. Lubcke and Wilson (2007) found that turtles at three different sites along the Trinity River in Northern California displayed a high degree of variation in plastron length, shell height, and shell width.

Juveniles are much less morphologically variable than adults, probably due to their greater need for camouflage (Seeliger, 1945). The plastron of nearly all juveniles is gray or grayish brown in the center and yellow on the outside. The carapace of juveniles is brown. Many display yellow around the edge and some have small black spots. The carapace darkens and elongates with age, gaining more black spots and becoming oblong rather than circular. Head, neck, and limb coloration can vary considerably in juveniles, but is generally lighter and contains fewer dark spots than adults. Juveniles have a tail length to carapace length ratio of 0.75 to 1.0 (Seeliger, 1945).

Nearly all morphological features vary by sex (Holland, 1992). Male plastrons are slightly to prominently concave, whereas flat plastrons characterize females. In the Seeliger 1945 study, 59 % of males had thick tail bases accompanied by anuses protruding beyond the posterior margin of the carapace. All others had a thinner tail and an anus that remained within the posterior margin of the carapace. Females tend to have taller carapaces than males, as well as smaller heads in similarly sized specimens (Seeliger, 1945; Holland, 1994). The head and neck of females are more heavily mottled than in males; the throat is darker yellow and displays more spots than in males (Holland, 1994). In the Seeliger 1945 study, 62 % of all males had very few or no throat spots while 71 % of females had many. The male snout is long and 10 to 15 degrees from vertical. Females have snouts that are short and 5 degrees or less from vertical (Holland, 1994). Bury and Germano 2008 report that males are generally larger than females, while Seeliger 1945 and Buskirk 2002 report no sexual dimorphism in carapace length. Lubcke and Wilson (2007) found that males in two of three sites along the Trinity River in Northern California had a significantly longer mean carapace length than that in females. At the third site, there was no significant size difference between males and females. This indicates phenotypic plasticity regarding size sexual dimorphism. The ratio of females to males also varies significantly from site to site, from 0.43 to 1.43 in the Lubcke and Wilson (2007) study. Only 1-2 % of turtles exhibit intermediate sexual characteristics (Holland, 1994).

Taxonomic Classification

Baird and Girard (1852) first described the western pond turtle, as *Emys marmorata*,

based on its morphological resemblance to other members of *Emys*. The species name, *marmorata*, stems from the Latin root *marmor*, meaning marbled, a reference to the turtle's marbled carapace (Bettelheim 2004). The other members of *Emys*, *Emys blandingii* and *Emys orbicularis*, are morphologically similar to the western pond turtle, but have a plastral hinge, a trait lacking in the western pond turtle. As a result, *Emys marmorata* would be the only member of the *Emys* genus unable to perform plastral kinesis (Feldman and Parham 2002).

Strauch (1862) erected the genus *Clemmys* to contain species with the plastron fused to the carapace, reclassifying the western pond turtle as *Clemmys marmorata*, a taxonomic arrangement that was maintained for over 100 years. Bickham et al. (1996) used molecular phylogenetic analysis of mitochondrial DNA (mtDNA) sequence data to indicate that *Clemmys* is paraphyletic and that *Clemmys marmorata* is more closely related to *Emys blandingii* and *Emys orbicularis*.

Feldman and Parham (2002) confirmed this result with additional mtDNA sequence data, formally placing *Clemmys marmorata* in the genus *Emys* and suggesting that the western pond turtle once had and subsequently lost the plastral hinge. All cladograms resulting from molecular phylogenetic analysis show that the western pond turtle is more closely related to taxa that exhibit plastral kinesis than those that do not, confirming a clade that includes *Emys marmorata*, *Emys blandingii*, and *Emys orbicularis* (Holman and Fritz 2001).

Most recently, Stephens and Wiens (2003) use morphology and mtDNA sequence data to show that despite *Emys marmorata*'s close relation to other *Emys*, it is the most genetically dissimilar within the clade. In anticipation of further divisions of both *Emys*

marmorata and *Emys orbicularis*, Stephens and Wiens (2003) reassign *Emys marmorata* to the monotypic genus *Actinemys*. The authors' assumption that *Actinemys marmorata* will likely be divided in the future is supported by a history of subspecies classification.

Subspecies and Future Taxonomic Divisions

Seeliger (1945) first described two subspecies of *Clemmys marmorata* based on coloration, size, and the presence or absence of inguinal plates: *C. m. marmorata*, the northwestern pond turtle, and *C. m. pallida*, the southwestern pond turtle. Approximately 89 % of *C. m. marmorata* have large triangular inguinal plates, whereas 94 % of *C. m. pallida* have extremely small or absent inguinals (Seeliger, 1945). *C. m. marmorata* is slightly larger and darker in color than *C. m. pallida*. Specimens from Southern California rarely exceed 160 mm, whereas specimens of 190 mm are common in Northern Oregon (Holland, 1994). The ranges of the subspecies were said to overlap from the San Joaquin Valley to San Francisco Bay in central California.

Although *Clemmys* has been shown to be paraphyletic, and subspecies of *Actinemys marmorata* are no longer recognized, genetic data support a latitudinal distinction (Gray 1995; Spinks and Shaffer 2005). A recent phylogeographic analysis of *Actinemys marmorata* using mtDNA data supports four geographically distinct clades within the species (Spinks and Shaffer 2005). The northernmost clade is consistent with *Clemmys marmorata marmorata* described by Seeliger (1945), while *Clemmys marmorata pallida* is broken into three unnamed clades. Spinks and Shaffer are

continuing their research to support the division of *Actinemys marmorata* into four distinct species.

Historical Range

The western pond turtle historically ranges from Southern British Columbia to Northern Baja California, between the Cascade-Sierra Nevada crest and the Pacific Ocean, although several isolated populations exist as far east as the Snake River (Holland 1994; Bury and Germano, 2008). Typically found below 500 m, western pond turtles exist at elevations up to 2,000 m but rarely occur above 1,500 m (Holland, 1994; Stebbins, 2003). The western pond turtle is the only extant freshwater turtle species native to the geographic region spanning northern Baja California through the central Willamette Valley (Reese and Welsh 1997; Bury and Germano, 2008).

Growth and Demographics

A secure understanding of western pond turtle growth and demographics is essential for any comprehensive conservation strategy. Demographic data can diagnose problems and prescribe management actions at the population level. Undersized populations, for instance, can be caused by a variety of problems (skewed sex ratios, juvenile mortality, adult mortality, a lack of nesting habitat, etc.)

Age-class is estimated by carapace length or scute ring analysis. Ashton et al. (2001) provides the following size/age-class categories:

Hatchlings: carapace length 25 to 69 mm

Juveniles: carapace length 70 to 125 mm

Adults: carapace length greater than 125 mm.

Western pond turtles add an average of one annulus per year to the plastron and carapace until age 10 when growth rate slows and annuli become less obvious, but deposition of multiple annuli per year is common (Bury and Germano, 1998; Holland, 1994). Age-demographics can indicate overall population health. Holland (1994) asserts that healthy populations are comprised of 70 % adults and 30 % juveniles, but these percentages are still a matter of debate due to the difficulty of accurately censusing juveniles (Germano and Bury 2001).

Upon hatching, juveniles are small and slow, weighing 3 to 7 g (Holland 1994). Juveniles most often overwinter in the nest and emerge in March or April, although some emerge immediately after hatching (Holte 1998; Holland 1985). Survivorship is very low in neonates, hatchlings, and juveniles, as low as 10 to 15 % per year in the first three years (Holland 1994). Of 122 nest sites at Fern Ridge Reservoir surveyed between 1993 and 1997, only 10 were fully successful (all eggs hatched) and 13 were partially successful (Holte 1998). Hatchlings emerging from the nest weigh an average of 5.7 g and travel a mean distance of 3.3 meters per day, and sometimes lie motionless for several days (Holte 1998). The small size and slow movement of hatchlings make them highly susceptible to predation by striped skunk, coyote, red fox, raccoon, black bear, osprey, bald eagle, river otter, mink, and bullfrogs after they leave the nest (Holland 1994).

High predation rates mandate rapid growth in hatchlings. Holland (1985) found that hatchlings in the central coast of California grew an average of 3.29 millimeters per

month (mm/mo) in the first season, 1.95 mm/mo during the second season, declining to 0.4 mm/mo by the fourth season; growth remained steady for the remainder of the study after the fourth season.

The average lifespan of western pond turtles is not known, but specimens of up to 40 years in age are common (Bury and Germano, 2008). Some individuals may exceed 60 years of age (B.R. Bury pers. comm.). The age of sexual maturity ranges from four to 10 years and varies geographically, with individuals in the southern part of the range reaching sexual maturity more quickly than those in the north (Bury and Germano, 2008).

General Habitat Requirements

Western pond turtles are habitat generalists found in ephemeral and perennial streams, wetlands, oxbows, lakes, ponds, reservoirs, sewage treatment plants, and abandoned gravel pits (Buskirk 2002). Even heavily urbanized environments sustain western pond turtle populations (Spinks et al. 2003). Despite its adaptability, the species requires a heterogeneous landscape to persist. Aquatic habitat facilitates feeding and thermoregulation, whereas upland habitat provides for overwintering and nesting. Heterogeneity within aquatic and upland sites is an essential feature of viable habitat (Reese and Welsh 1998b).

Aquatic Habitat

Aquatic habitat serves the primary function of protection from predators. With well-developed eyesight and a passable sense of hearing, western pond turtles are extremely cautious. They often retreat when a perceived threat approaches to within 100 m away

(Hays et al. 1999). Because of their wariness, western pond turtles will seek out slow-moving water of a shallow to moderate depth (<1-10m) that allows for quick escape to refugia consisting of undercut banks, large rocks, and aquatic plants (Bettelheim 2004; Reese and Welsh 1998b). The turtles' linear adult home range can be from 32 to over 4,000 m depending on food and habitat availability (Goodman and Stewart 2000). Juveniles have a much smaller home range, sometimes only 16 m in length (Bury 1972). While adults tolerate a wide range of water temperatures and a moderate range of water velocities, juveniles require warm, slow water (Reese and Welsh 1998a). The combination of small home ranges and specific water temperature and velocity requirements make juveniles particularly susceptible to aquatic habitat alteration (Reese and Welsh 1998b).

Feeding

Suitable aquatic habitat contains a variety of food sources. Western pond turtles are omnivorous dietary generalists; they readily consume algae, aquatic vascular plants, aquatic invertebrates, terrestrial invertebrates, tadpoles, egg masses, and weakened or dead fish, but they show a preference for animal tissues over plant material (Bury and Germano, 2008; Bettelheim, 2004; Bury, 1986). Western pond turtles can locate food items via sight or smell and employ a variety of foraging tactics (Holland, 1994).

Lacustrine turtles commonly paddle along the surface with necks outstretched, moving their heads from side to side. When a food item is located, the turtle snaps at it with a quick biting motion and submerges to consume it. Riverine turtles lie in wait along riffles for food items to drift into their outstretched mouths (Bury, 1986). Although they are

most commonly foragers and scavengers, there are instances of turtles actively pursuing prey. Bury (1986) observed a western pond turtle that unsuccessfully pursued a small fish for several minutes, as well as an individual that successfully pursued several grasshoppers on land. Each time a grasshopper was caught, the turtle returned to the water to swallow it.

Several sex and age-based dietary differences exist. The male diet includes a higher percentage of large food items and animal tissues than that of females, which contains a higher percentage of plant tissues. Juveniles consume much smaller prey than adults, and favor insect larvae. Age-based dietary differences may serve to reduce intraspecific competition (Bury 1986).

Thermoregulation and Basking

An ectotherm's relationship with temperature pervades every aspect of its life. For western pond turtles, ectothermy requires an aquatic habitat that offers basking structures of sufficient size and sun exposure. Activity increases as water temperatures exceed 15 degrees C (Bury and Germano, 2008). Western pond turtles bask on rocks, logs, plant masses, or sandbars and stretch their necks toward the sun to maintain a body temperature of 32 degrees C, returning to water if they overheat (Bury 1972). Basking occurs most frequently in the spring to midsummer when air temperatures exceed water temperatures, although turtles have been observed basking in February (Bury and Germano, 2008).

Preferred basking structures are adjacent to refugia, easily accessible from the water, and large enough to keep the entire turtle out of the water (Bury and Wolfheim,

1973). Riparian forests of intermediate seral stages are necessary to provide sufficient basking sites (Cook and Martini-Lamb 2004; Reese and Welsh 1998). These forests provide logs with intact branches and leaves, providing refugia and shade directly adjacent to basking areas. A scarcity of basking structures forces turtles to congregate on any available structure. Spinks et al. (2003) once noted 13 western pond turtles on a structure 5 m in length.

When basking space is scarce, turtles may exhibit aggressive behavior such as ramming, pushing, or biting, acts that are usually preceded by an open-mouthed gesture (Bury and Wolfheim, 1973). Bury and Wolfheim (1973) report that, in 70 % of aggressive incidents, an openmouthed gesture elicited a defensive maneuver such as flight or withdrawal into the shell. Aggressive turtles did not pursue one another after eliciting defensive maneuvers. During 37 hours of observation at Hayfork Creek, Trinity County, during July, August, and September of 1970 and 1971, Bury and Wolfheim (1973) recorded 111 openmouthed gestures, 11 biting attacks, and 23 pushing or ramming attacks, but no serious injuries. Aggressive behavior is not unique to western pond turtles. The Eastern painted turtle (*Chrysemys picta picta*) and the gopher tortoise (*Gopherus polyphemus*) exhibit similar aggressive basking behavior (Lovich, 1988; Bury and Wolfheim, 1973).

Upland Habitat

In the past, western pond turtle habitat restoration efforts have focused almost exclusively on protection and restoration of aquatic habitat. The species was believed to be entirely aquatic aside from nesting (Pritchard 1979). However, pond turtle conservationists now

consider upland habitat equally essential for the survival of the species. This change in tone comes with the increased use of radio telemetry in the late 1990s to track individual turtles. Reese and Welsh (1997) used radio-telemetry to observe the terrestrial movements of western pond turtles throughout the year. They observed that both males and females utilize upland habitat during a much greater portion of the year than previously thought, and found that males use upland habitat during every month of the year except July and August. Females rely even more heavily on these areas, making use of upland habitat in every month of the year. Western pond turtles use upland habitat primarily for over-wintering and nesting, but there are additional uses of upland habitat such as overland dispersal and terrestrial basking. Behavioral patterns of upland habitat use vary heavily from site to site and between individuals from the same site (Rathbun et al. 2002; Holte 1998; Reese and Welsh 1997; Holland 1994).

Overwintering

Overwintering is common among emydine turtles. It is a life stage by which the individual goes into a dormant state during months that are cold enough to severely restrict activity. In western pond turtles, activity dramatically decreases when water temperatures drop below 15 degrees Celsius (Bury and Germano 2008). If the temperature drops too low, finding food and shelter becomes difficult, leaving the turtle undernourished and vulnerable to predators. As temperatures fall in autumn, turtles avoid exposure during cold temperatures by seeking out shelter for the winter. The overwintering behavior of western pond turtles varies significantly by latitude, site conditions, and among individuals.

Turtles typically bury themselves in 5 to 10 cm of leaf litter or loose soil, pre-existing holes, or other secluded locations that enable them to lie motionless for months without the threat of freezing or disturbance (Holland 1994; Rathbun et al. 2002).

Lacustrine turtles often spend the winter in muddy benthic areas of slow-moving water (Holland 1994). Overwintering individuals sometimes congregate in the same benthic area. Holland (1994) recorded 43 turtles overwintering on the muddy bottom of a pond in an area less than 1 m². Overwintering turtles are non-responsive when disturbed and their eyes are sealed with dried fluid (Rathbun et al. 2002).

Climactic variation throughout the species' range means that turtles from different latitudes begin and end dormancy at different times of the year. In the Southern portion of their range, western pond turtles may remain active year-round, whereas turtles of the Willamette Valley often lie dormant for more than 8 months due to the long Pacific Northwest cold season (Holland 1994).

Both males and females travel between 0 and 500 m from water in search of suitable overwintering sites, although the distance traveled varies among populations (Reese and Welsh 1998b; Cook and Martini-Lamb 2004). Reese and Welsh (1997) found that one population along the Trinity River in Northern California overwintered a mean distance of 203 m from the aquatic habitat. Rathbun et al. (2002) found that distance to be significantly lower (49.7 m) in a Central Californian population, and some populations are entirely aquatic aside from nesting trips (Cook and Martini-Lamb 2004).

Some turtles remain in one location for the duration of the winter, whereas others may change locations up to nine times in one season (Reese and Welsh 1997; Rathbun et al. 2002). Slightly more than half of turtles followed in the Rathbun et al. (2002) study

changed overwintering sites mid-season. The motive for relocation is not known, but Rathbun et al. (2002) observed turtles basking on upland features during the coldest months of the year, their eyes open and necks outstretched, exposed to direct sunlight. The authors also noted that all overwintering sites were located adjacent to areas that receive direct sunlight during part of the day. This indicates that relocation may be for purposes of thermoregulation and that upland basking areas are important for thermoregulation during the winter. In addition, 70 % of turtles return to within 100 m of a site visited in the previous year (Rathbun et al. 2002).

In short, overwintering is a necessary seasonal stage for the western pond turtle, and the timing, substrate, and distance from aquatic features varies by latitude, site-conditions, and individual.

Nesting

Nearly all species of freshwater turtles use upland nesting in their life cycles. Eggs deposited on land are buried in sunlit soil for incubation where they are afforded some protection from natural disturbances and predators. Survival rates within the nest can be as high as 70 % in western pond turtles, but are often very low depending on the influence of predators (Holland 1994). Of 122 Fern Ridge Reservoir nest sites studied between 1993 and 1997, 10 were fully successful and 13 were partially successful (Holte 1998).

In western pond turtles, mating and oviposition occur in spring and mid to late summer, respectively, but the timing of these activities varies with latitude (Holland 1985). Populations in central California mate in April and May and oviposit between two

and 12 eggs from June through August (Holland 1985). The eggs then incubate for 80 to 100 or more days (Holland 1994). Hatchlings overwinter in the nest and emerge the following spring (Holte 1998). Some females nest twice in one season, once in mid summer and once in late summer, sometimes choosing nest sites 500 m apart (Rathbun et al. 2002). Females often make several trips (from two to 11) to nesting sites before deposition of eggs, spending up to 3 days buried in leaf litter and basking periodically (Reese and Welsh 1997, Rathbun et al 1992). These trips may be an attempt to increase body temperature and metabolism before nesting (Reese and Welsh 1997). A female will typically spend 2 to 10 hours digging a nest 90 to 120 mm deep, depositing her eggs, and plugging the nest with humus (Holland 1994). According to Rathbun et al. (2002), 30 % of females dug out a nest only to abandon it for another location. Holland (1994) suggests that poor soil workability or perceived predatory threats cause females to abandon nest sites. Females become extremely cautious during nesting trips. Sudden sounds, lights, or movements cause females in search of nesting sites to return to aquatic habitat immediately (Rathbun et al. 2002).

Characteristics of desirable nest sites include moderately compact soil made up of silt and clay rather than sand, high sun exposure on gentle slopes (0 to 40 degrees), and little vegetative cover (Holland 1994; Holte 1998). It is not known why western pond turtles prefer soils containing a high percentage of silt or clay, but only an estimated 1 % of nests are created in soils containing a significant percentage of sand (Holland 1994). Temperature-dependent sex determination is likely the reason turtles seek out nest sites with high sun exposure. Higher nest temperatures result in a greater percentage female offspring, which is advantageous because the vast majority of western pond turtle

populations are male-biased (Ewert et al. 1994; Germano and Rathbun 2008; Cook and Martini-Lamb 2004; Bury 1972; Holte 1998). While the species prefers nesting sites with little vegetative cover, presumably for soil workability, nests with low vegetative cover are less successful than nests in high vegetative cover (Holte 1998). Raccoons, a significant predator of turtle nests in human-altered environments, locate nests primarily by ground surface disturbance and secondarily by olfactory cues (Spinks et al. 2003; Strickland and Janzen 2008; Burke et al. 2005). Mammalian predators likely have a more difficult time locating nests by soil disturbance within dense ground cover. Rain also decreases nest predation, presumably by washing turtle scents away (Bowen and Janzen 2005).

Western pond turtles nest up to 400 m linearly and 90 m vertically from aquatic habitat (Storer 1930). Even females that double clutch move up to 500 m between nest sites (Rathbun et al. 2002). The distance traveled to nesting varies significantly among populations and between individuals of the same site (Storer 1930; Holte 1998; Rathbun 2002; Rathbun et al. 1992; Reese and Welsh 1997). Rathbun et al. (2002) found that the distance of nesting sites from aquatic habitat ranged from 9.5 to 80 m in several central Californian arroyos, whereas Holte (1998) found that nest sites at Fern Ridge Reservoir range from 0.80 to 215 m from aquatic habitat.

Rathbun et al. (1992) poses several hypotheses to explain why some females travel such great distances to nest. Riparian areas may be too shady to allow for successful incubation or to produce a satisfactory sex ratio. Nesting further from aquatic habitat also reduces the threat of nest inundation during flooding, a threat known to increase egg mortality (Feldman 1982). Despite these advantages, the majority of females

nest within 100 m of aquatic features, often within shady riparian areas and the floodplain. It has been suggested that turtles nesting near aquatic habitat attract nest predators, acting as a decoy to protect nests further away, but studies on the painted turtle (*Chrysemys picta*) suggest that spatial orientation distribution and nest-site density do not predict nest success (Burke et al. 1998; Kolbe and Janzen 2002).

Other Uses of Upland Habitat

Overwintering and nesting are the most well-documented uses of upland habitat, but western pond turtles also venture upland for terrestrial basking and aestivation, as well as movement within a home range. In rare cases, populations can be entirely aquatic aside from nesting trips (Lovich and Meyer 2002).

During the spring and summer, western pond turtles often leave aquatic habitat for unknown reasons, sometimes appearing to wander aimlessly (Reese 1996; Chris Rombough pers comm.). These trips are accompanied by terrestrial basking on rocks or sandbars or sometimes under vegetative cover with high sun exposure, usually less than 12 m from aquatic areas. (Rathbun et al. 2002). While turtles basking on aquatic structures are easily disturbed, individuals basking terrestrially do not respond when disturbed, spending one to five days on land (Rathbun et al. 2002). These trips sometimes last for months, even blending into overwintering, and can be considered aestivation (Slavens 1995). Juveniles may aestivate more frequently than adults, perhaps due to their vulnerability to predation (Sue Bielke pers. comm.).

Western pond turtles frequently make short one-way and two-way terrestrial trips between aquatic features within a home range. Reese (1996) used radio telemetry to track

44 western pond turtles for 4 years (1991-1995). Over the course of the study, 18 turtles traveled between water bodies at a mean distance of 237 m per trip, and one male visited eight ponds during the study. Western pond turtle populations occupying ponds and rivers tend to have larger home ranges than those in small streams (Bury 1979; Goodman and Stewart 2000). Where small streams provide a host of microhabitats in a small area, turtles living in ponds and rivers cover a larger area to exploit these habitats. Western pond turtles occasionally make longer trips of at least 1500 m, but the dispersal capabilities of the species are largely unknown (Bury 1972).

Western pond turtles often engage in terrestrial excursions for unknown reasons and travel between water bodies more frequently than exotic turtles sharing the same habitats (Reese 1996; Patterson 1996). The western pond turtle is the only extant freshwater turtle species throughout the majority of its range; frequent overland movements between water bodies were likely a major factor in the species' survival in the stochastic and dry environments of the mid to late Pliocene (Holland 1992; Hutchison 1982). Movement between drying ponds may have enabled the species to persist when more sedentary species could not. Even in more recent times, braided river valleys supported continuous cycles of disturbance (caused by flooding and sedimentation) and seral succession. These cycles were severely diminished with the installation of river impoundments for flood control, navigation, and electricity production, and have negatively impacted western pond turtle populations (Reese and Welsh 1998a).

Habitat Fragmentation

Species exhibiting frequent overland movements require a high degree of habitat connectivity. Human activities have fragmented western pond turtle habitat by erecting physical barriers, and by increasing that causes of mortality that surround aquatic habitat. The effect of these barriers is increased genetic isolation of populations.

Known physical barriers to migration include fencing, thick vegetation, and steep riparian slopes caused by river channelization (Reese and Welsh 1998b). The ability of the western pond turtle to traverse other physical obstacles such as culverts, boulders, and train tracks, is unknown. Suitable habitats are engulfed by development, leaving intact populations increasingly distant from one another. As is the case in several other turtle species, this process may isolate western pond turtle populations by distance regardless of other deleterious effects of urbanization (Edwards et al. 2004).

Urban centers also significantly increase mortality for turtles venturing onto land. Mammalian predators such as raccoons and rats feed on trash, and are positively correlated with human population density (Spinks et al. 2003). Raccoons can cause significant losses of adult turtles. More than 23 % of pond turtles radio-tagged by Rathbun et al. (2002) between 1991 and 1998 were recovered, dead, with obvious signs of mammalian predation. This study was carried out in San Luis Obispo County in close proximity to suburban development.

Roadways also pose a significant threat to many semi-aquatic and terrestrial turtle species (Ashley and Robinson 1996). A single trip across a busy highway can confer a 68 % chance of mortality (Aresco 2004). Even so, turtles do not typically avoid roadways, which act as barriers to migration through increased mortality (Sue Bielke pers comm.).

Well-meaning citizens sometimes pick up turtles crossing roads, either keeping them as pets or releasing them at another location (Edwards et al. 2004). In an extreme case, a 2005 flash flood in urban southern California forced overwintering pond turtles into the streets where concerned citizens mistook a number of them for sea turtles and released them into the ocean.

Owing to naturally high juvenile mortality and low adult mortality, the removal of adults (either by mortality or by humans for pets) can have devastating impacts on long-lived turtle populations (Heppell et al. 1996). Road mortality has also been shown to selectively target nesting females, further skewing already male-biased sex ratios (Steen et al. 2006).

Whether individuals are physically walled into a given area, killed, or taken for pets, the result is genetic isolation among populations. Gray (1995) used genetic fingerprinting to show that Washington populations of western pond turtles exhibit little genetic variation within populations and a large amount between populations. In southern California, pond turtle populations have been reduced to small, isolated patches separated by cities and roads (Brattstrom 1988). Spinks and Shaffer used mtDNA sequencing to show that moderate to large genetic fragmentation exists throughout the species' range. Southern populations, however, exhibit more genetic diversity within and among populations, relative to those in the north (Janzen et al. 1997).

2. Current Management Strategies

Management strategies for western pond turtle conservation have been focused on reducing juvenile mortality, removing invasive species, and restoring habitat. A number

of visual surveys report adult-biased populations across much of the species' range (Holland 1991; Holland 1994; Brattstrom and Messer 1988). Populations in which demographic data show low juvenile recruitment may benefit from management strategies aimed at protecting neonates, hatchlings, and juveniles. These strategies include nest enclosure, captive breeding, and headstarting. A great deal of effort has also been expended trapping and removing invasive species by hand. While habitat degradation is widely accepted as the most significant threat facing the western pond turtle, habitat restoration is expensive. All current management strategies require ongoing treatments, making restoration feasible only on a small scale.

Nest Enclosure

One of the most common causes of mortality is mammalian nest predation. A survey of Kirk Ponds (Eugene, OR) between 1992 and 1993 revealed 120 predated nests, an estimated 99 % (Holland 1994). Nest enclosure is a relatively cheap method to prevent nest predation. The technique involves placing a metal enclosure around the nest and securing it to the ground. These enclosures were placed over turtle nests at Kirk Ponds between 1993 and 1997. Predator excavation was reduced to 12 % of nests during this time (Holte 1998).

Enclosures are effective, but western pond turtle nests are very difficult to locate and many go undetected by land managers. The most common method for locating turtle nests is visual inspection of suspected nesting areas. Turtle nests are scattered almost randomly across a wide area, are difficult to see, and nesting turtles rarely leave tracks. Nest predation sometimes begins within hours of oviposition, and enclosures must be

installed quickly (Marchland and Litvaitis 2004). Western pond turtles nest in the late afternoon and evening, adding to the difficulty of timely discovery (Sue Beilke pers. comm.).

Captive Breeding

When extirpation is imminent, conservation organizations are forced to capture individuals from the wild and breed them in captivity. It is a last resort and there is only one such breeding program for western pond turtles, located in the Puget Sound area (Hays et al. 1999). For example, Washington pond turtles suffered a severe decline in the late 1800s due to commercial exploitation and have not recovered since (Hays et al. 1999). By the 1980s, the species was effectively extirpated from Washington (Milner 1986). Western pond turtles of unknown origin were again sighted in the early 1990s, and the USFWS began a captive breeding program in 1991. Despite these efforts, Puget Sound pond turtle populations are rare, small, isolated, and have required assistance through captive breeding (David Sheperdson pers. comm.).

Captive breeding is a useful tool, but it can generate problematic side effects. Captive breeding programs are notorious for genetic bottlenecks. The Washington captive breeding program is using outcrossing to reduce the potential for inbreeding, but southern populations still harbor much more overall genetic diversity than northern populations (Janzen et al. 1997). Behavioral differences between captive-bred and wild hatchlings have not been studied in western pond turtles, but are known to occur in other turtle species. Captive-bred green turtles (*Chelonia mydas*), for instance, are an average of 12 % slower in the water than turtles not kept in a hatchery (Pilcher and Enderby

2001). Despite these issues, Puget Sound populations require the captive breeding program to persist.

Headstarting

Pre-existing populations in which demographic data show low juvenile recruitment may benefit from a headstarting program. Headstarting is a management technique in which individuals mate and oviposit in the wild. Eggs are collected from the nest, then incubated, hatched, and reared in captivity. Alternatively, eggs can be collected directly from gravid females. Subadults are released into the wild when their size no longer leaves them vulnerable to predators.

The headstart strategy has been used since the 1950s to conserve sea turtle populations and is an effective means of building up populations of many long-lived turtle species, but only if adult mortality is very low (Huff 1989; Heppell et al. 1996). Haskell et al. (1996) found that headstarting is an effective means for increasing the population size of redbelly turtles (*Pseudemys rubriventris*) in Massachusetts, where juvenile mortality from invasive bullfrogs is the primary threat. The strategy has more recently proven effective for increasing the size of previously established populations of western pond turtles (Hays et al. 1999). Under Washington State's recovery plan, 64 % of the 296 western pond turtles headstarted and released to Klickitat County in 1991 were recaptured in 2003 (Van Leuven et al. 2004).

Headstarting is less effective for establishing western pond turtle populations. Van Leuven et al. (2003-2006) established a western pond turtle population of 59 individuals at the Pierce Northwest Reserve in 2002. Another 51 headstarted turtles were

added to the population in 2003, 62 were added in 2004, 83 were added in 2005, and 19 were added in 2006. The population was estimated to contain 92 individuals in 2006 (Van Leuven 2006). Such low survival rates indicate a low carrying capacity.

Headstarting may increase turtle numbers, but it does not deal with the root causes of population decline — namely habitat loss and degradation — and has therefore been referred to as a halfway technology (Frazer 1992). If habitat loss and degradation are not addressed, population establishment will likely fail, and may negatively impact other species of concern. Additionally, some have suggested that headstarted individuals behave differently than wild individuals (Bolten et al. 1990). There are few data regarding potential unintended consequences of headstarting, and the technique should be used only where necessary to sustain declining populations.

Invasive Species Removal

Habitat restoration projects for the western pond turtle commonly include the removal of invasive species. Invasive ground cover removal is a high priority; Armenian blackberry (*Rubus armeniacus*) and a variety of dense grasses inhibit a turtle's overland movement and make soil impenetrable for gravid females. Blackberry species can be removed by mowing, which must be repeated three to five times per year for several years to prevent regrowth (Jones 2007). Mowing should occur during seasons when turtles are not present and exotic plant seeds have not yet dehisced, in order to avoid further seed dispersal.

Another method of removing blackberries is to apply a fungal biocontrol (*Phragmidium violaceum*). This method is still under scientific scrutiny (the first case of *Phragmidium*

violaceum affecting *Rubus armenicus* was observed in 2004) (Osterbauer et al. 2005; Charudattan and Dinor 2000).

Thick grasses are either manually pulled or sprayed with herbicides. Due to the overwhelming abundance of these grasses, complete eradication from the restoration site is not usually feasible. Instead, land managers focus their attention on clearing nesting sites, but turtles are unreliable in their use of even the best artificial nesting sites (Chris Rombough pers. comm.). Complete eradication of invasive ground cover species from a restoration site is rarely possible, and ongoing monitoring and treatment is essential to prevent their encroachment and re-establishment (Jones 2007).

Largemouth bass (*Micropterus salmoides*) are a growing concern for many western pond turtle conservationists, but the economic significance of bass as a sport fish precludes removal efforts. The species is a predatory generalist and is often cited as a significant predator of juvenile western pond turtles, but no studies have verified the severity of bass predation on western pond turtles (Holland 1994; Buskirk 2002; Bettelheim 2004). Largemouth bass removal is extremely difficult and few measures have been taken to eradicate the species. It is a prized warm water sport fish and state agencies actively introduce the species to water bodies within the range of the western pond turtle (Oregon Department of Fish and Wildlife 2009a; California Fish and Game Commission 2009). These agencies also maintain robust bass fisheries by providing legal protection to juveniles (ODFW 2009b).

A number of restoration programs involve the removal of bullfrogs (*Rana catesbeiana*), but the extreme quantity of individuals at many sites and high reproductive output of females renders these efforts ineffective. Govindarajulu et al. (2005) used

demographic data and computer models to show that the most common strategy for bullfrog eradication - removal of breeding adults and tadpoles - may serve to reduce competition between tadpoles and decrease cannibalism by adults on subadults. An initial reduction in bullfrog numbers is soon followed by a population increase. Bullfrogs have good dispersal capabilities, and habitats created for western pond turtles often become havens for bullfrogs (Bury and Germano 2008). This can be mitigated by focusing restoration efforts on ephemeral wetlands, as the species is associated with permanent water bodies (Adams 1999). Bullfrog predation on juvenile western pond turtles is well-documented and, because of the extremely high number of bullfrogs in the majority of warm water habitats, is assumed to be a very significant threat (Hays et al. 1999; Holland 1994).

More than 17 exotic species of semi-aquatic freshwater turtles inhabit all or part of the western pond turtle's range (Holland 1994). The red-eared slider, a common pet turtle native to the Mississippi Valley, is the most widespread exotic and threatens a variety of turtles around the world, including the western pond turtle and its closest extant relative, *Emys orbicularis* (Kovacs et al. 2004). Hatcheries routinely ship live individuals to and from the United States. Between 1989 and 1997, 5,252,173 red-eared sliders were imported to the United States (out of 5,708,972 turtles and tortoises imported) and 52,122,389 were exported (out of 53,751,521 turtles and tortoises exported) (Telecky 2001).

Red-eared sliders are sold as small pets (at carapace lengths of 5-6 inches) but grow to carapace lengths greater than 12 inches and many are released by their owners at this stage (Susan Barnes pers. comm.). Red-eared sliders nests up to 5 times per year,

oviposit a maximum of 30 eggs per clutch, tend to have equal sex ratios, grow rapidly, and reaches a final size up to twice that of the western pond turtle (Ernst et al. 1994; Tucker 1996; Patterson 1996; Stebbins 1985). Many of these animals are bred in dirty environments and harbor diseases such as shell rot, which they can spread to western pond turtles (Susan Barnes pers. comm.). Red-eared sliders compete with western pond turtles for both basking and nesting sites as well as food. Spinks et al. (2003) notes several instances of red-eared sliders making open-mouthed gestures towards western pond turtles on basking structures. In every instance, the smaller and less aggressive western pond turtles retreated to the water.

Land managers commonly trap or manually capture red-eared sliders. Anecdotal observations suggest that turtle traps baited with dead fish attract western pond turtles whereas traps baited with hot dogs predominantly attract red-eared sliders (Lauri Mullen pers comm.). Trapping is very effective; red-eared sliders require an adult annual survival rate greater than 80 % to maintain population sizes (Tucker and Moll 1997; Frazer et al. 1990).

Wetland Mitigation Banking

The majority of habitat restoration projects are small in scale. Simply adding artificial basking structures can greatly increase habitat suitability (Alvarez 2006). On the other end of the spectrum, some projects involve adjusting the underlying hydrology of a site, removing invasive plant species, and building nesting areas from scratch (Jones 2007). Few projects receive enough funding to accomplish this. Wetland mitigation banking is a

way to fund large-scale restoration projects, providing habitat for western pond turtles and other wetland species.

Wetland mitigation banking is a process by which developers that build over wetlands are required to pay for the creation of wetland habitats elsewhere. Wetland mitigation banks can accrue large amounts of very high quality habitat that would otherwise be prohibitively expensive. For geographically fragmented species such as the western pond turtle, the large, contiguous tracts of land afforded by mitigation banks offer higher quality habitat than a landscape of fragments connected by travel corridors (Harrison and Bruna 1999). The allure of high quality habitat has led some to suggest that conservation organizations should rely more heavily on wetland mitigation banking for western pond turtle conservation.

Turtles inhabiting wetland mitigation banks are continuously managed to ensure their survival, and large tracts of land are ideal for research projects. However, wetland mitigation banks pose problems for the western pond turtle. In genetically fragmented species, there exists a high level of genetic variation between populations relative to variation within any given population. Wetland mitigation banking requires a sacrifice of many existing population fragments that constitute much of the among-population variation present in the species. This process would permanently diminish the western pond turtle's total genetic diversity. Some freshwater turtle species have inherently low genetic diversity and resist inbreeding depression (Rosenbaum et al. 2007). This is not likely to be the case for western pond turtles because intact (i.e. unfragmented) populations have relatively high levels of genetic diversity within populations (Spinks and Shaffer 2005).

3. Recommendations for Further Research

Current management strategies are effective on a small scale, but require continuous inputs of time and money. Despite a large body of research regarding western pond turtle conservation, the requisite knowledge for creating long-term, scalable solutions is lacking. Gaps in the knowledge-base are a major obstacle to continued progress. The following subsections identify these gaps and suggest ways to fill them.

Support for Existing High-risk Populations

A conservation plan for the western pond turtle must begin with the conservation of existing populations. All future research on the species depends on the maintenance of existing genetic variation. To avoid losing this variation, conservationists should seek to support the largest possible number of existing populations rather than creating a few large populations with wetland mitigation banks. In addition, effective population sizes must be maintained, and in some cases increased, in order to minimize random fixation of alleles by genetic drift.

Habitat restoration should be the first step in supporting high-risk populations. Habitat restoration should consist of adding basking structures, clearing potential nesting areas of thick ground cover, removing obstacles to overland travel such as dense vegetation, removing invasive animals, and maintaining or creating a spatially diverse habitat to support diversified food sources for males, females, and juveniles. Home range data show that a single site can include several water bodies up to 1500 m apart connected by travel corridors (Bury 1972; Reese 1996). Nests may be protected with

cages, and fencing can separate turtles from roads or other physical hazards and keep mammalian predators out. Habitat creation is expensive and this time and energy should be directed toward restoration projects, which have a higher probability of success and conserving genetic variation.

Some populations require captive breeding or headstarting programs in tandem with habitat restoration efforts. Although the practice of captive breeding is dubious in some regards, the northernmost populations require such a program in order to persist. Special care must be taken, however, to implement these strategies only when necessary to maintain pre-existing populations at high risk of decline and extirpation. Captive breeding and headstarting should not be utilized in low-risk populations, or to establish new populations, because of the high cost involved, the low establishment success rate, and possible unintended effects such as the introduction of behavioral differences exhibited by captive-reared turtles (Pilcher and Enderby 2001).

Assessment of Dispersal Capabilities and Barriers to Gene Flow

The restoration of heterogeneous microhabitats within sites is a priority, but a recovery plan for the western pond turtle should include the restoration of connectivity between sites to ensure the long-term viability of populations. Knowledge of pond turtle dispersal is required to achieve appropriate connectivity between sites.

Previous studies of western pond turtle movement have been confined to home-range size, and long-distance aquatic and terrestrial dispersal ability is unknown. Freshwater turtles are difficult and expensive to track beyond their home range, but this research is necessary to achieve the long-term goal of habitat connectivity. Long-distance

tracking has been used to assess the dispersal capabilities of other turtle species, notably for the desert tortoise (*Gopherus agassizii*). Edwards et al. (2004) compared several microsatellite loci between populations and tracked tortoises over long-distances in order to determine historical rates of gene flow as well as human-imposed obstacles to gene flow. One female made a 34 km journey from a population in the Rincon mountain range to another population in the Santa Rita mountain range. The researchers retrieved the tortoise several times from private citizens who had taken her as a pet, and helped her over train tracks, fences, canals, and an interstate freeway. This study was extremely valuable, revealing dispersal capabilities, historic dispersal routes, and obstacles to dispersal. A tempting, inexpensive alternative is to translocate turtles between populations to provide necessary gene flow. Translocated turtles, however, most often attempt to return to their site of origin and die in the process (Dodd and Seigel 1991; Barrett et al. 1990).

Connectivity restoration also requires an assessment of the species' ability to traverse obstacles. Bog turtles (*Clemmys muhlenbergii*) have been shown to traverse small barriers such as thick vegetation and rocky ground (Morrow et al. 2001). The Oregon Wildlife Institute will soon publish similar data for the western pond turtle (Dave Vesely pers. comm.). This information is especially important because pond turtles must increasingly contend with a fragmented landscape. Passageways such as culverts, bridges, or aquatic and terrestrial corridors must be created for western pond turtles to overcome obstacles to dispersal.

Assessment of the Stability of Western Pond Turtle Populations

Many western pond turtle populations contain significantly fewer turtles than existed before Euro-American settlement, but the stability of these populations remains a matter of debate (Smith 1895). Demographic data should be the starting point for determining the stability of remaining populations, and will provide a basis for prioritization of restoration sites. Those sites projected to decline should receive more funding than stable sites, provided the cause of the decline can be addressed. A great deal of demographic data exists, but previous surveys have underrepresented juveniles and have not been designed to demonstrate population stability or instability.

Holland (1992; 1994) provided an inventory of demographic data for a very large number of western pond turtle sites throughout the species' range. The majority of these data were collected using visual surveys, and juveniles were reported at very few sites. Visual surveys under-represent juveniles, which are small, rare, indistinctly colored, utilize different habitats than adults, and rarely bask (Germano and Bury 2001, Jennings and Hayes 1994; Lovich and Meyer 2002). Although traditional survey methods overlook juveniles, these methods are often used to report a lack of recruitment (B.R. Bury pers comm.).

A sampling methodology specifically designed to detect juveniles should be developed. Development of an accurate sampling methodology requires experimental, hypothesis-driven research. An accurate count of a juvenile population could be obtained by intensive mark-recapture. These same juvenile populations could then be censused with less intensive and less accurate sampling methods such as visual surveys or trapping. Comparing the estimates from the intensive versus the less intensive sampling provides

an index for correcting juvenile population estimates for other populations that were derived using less intensive sampling. Research of this kind will produce a sampling methodology that can be used to develop accurate life tables. In addition to identifying causes of mortality in declining populations, life-table analyses can reveal source and sink populations. The latter application will be necessary for designing travel corridors needed for the long-term viability of the western pond turtle.

The U.S. Fish and Wildlife Service denied a petition to list the western pond turtle as threatened under the Endangered Species Act in 1993 because of a lack of credible science showing instability (USFWS 1993). Upon listing, the federal government is required to develop and initiate a recovery plan, and additional grant funding becomes available. Credible science showing the species' instability could contribute to listing the western pond turtle as threatened under the Endangered Species Act and remains a priority for conservation. The wealth of visual survey data collected in the early 1990s provides a reference for comparison with future adult census data to show whether or not the species has declined across this time period (Holland 1994). Effective population sizes should be re-estimated using the same methods as in the previous census. Overall trends may be used as evidence to petition for listed status under the Endangered Species Act. Visual surveys should be completed on a periodic basis to confirm the efficacy of conservation activities.

Determination of the Threat Level of Invasive Species

Despite the prevalence and possible competitive advantages of red-eared sliders, their removal is not a high priority for pond turtle conservation. Spinks et al. (2003) estimated

that a population of pond turtles continued to decline by 40 % following trapping and removal of red-eared sliders. Patterson (1996) recorded a slight increase in the population size of a Central Valley population of pond turtles over two years despite the presence of a red-eared slider population that was 15-fold larger than the pond turtle population.

These studies indicate that the western pond turtle likely faces more severe threats from habitat loss, road mortality, and mammalian predation. Nevertheless, competition with sliders has been shown to cause weight loss and increased mortality in *Emys orbicularis* under experimental conditions, and the increasingly ubiquitous nature of the red-eared slider necessitates research designed to define the threat level of this exotic species on western pond turtles (Cadi and Joly 2004).

A commonly cited explanation for the success of red-eared sliders relative to western pond turtles is that eggs of the former are more moisture-tolerant than eggs of the latter, but the available data do not support this claim (Holland 1991; Holland 1994). Feldman (1982) found that western pond turtle eggs crack and die when placed in saturated substrate in a laboratory environment, but this has not been the case *in situ*. The median period of inundation for successful nest sites at Fern Ridge Reservoir between 1995 and 1996 was 76 days (range: 0-120 mean: 64 days), indicating that western pond turtle eggs can tolerate moisture to some degree (Holte 1998). During this time, the most common cause of mortality was mammalian nest predation rather than water damage (Holte 1998). Red-eared slider eggs are no more moisture-tolerant than western pond turtle eggs in a laboratory environment. Tucker et al. (1997) found 100 % mortality in red-eared slider eggs exposed to saturated substrates for 24 hours, even when saturated

gradually. This indicates that moisture tolerance is not a significant factor in determining the relative success of the two species.

A more likely explanation is that human alterations to habitat favor the red-eared slider over the western pond turtle. Western pond turtles are adapted to the stochastic environment that has been present during the majority of their evolutionary history (Hutchison 1982). Human activities such as damming, fire suppression, and invasive plant introductions serve to stabilize these environments, reducing the advantage of traits such as small body size and frequent terrestrial activity. In human-impacted environments, these traits have become disadvantageous. Western pond turtles are very terrestrially active - risking predation, road mortality, and non-navigable terrain - whereas red-eared sliders venture upland less frequently (Chris Rombough pers. comm.). Indeed, western pond turtles are negatively correlated with sites heavily impacted by human activities, whereas sliders are not (Madden-Smith et al. 2005; Smith et al. 2006). The abundance of turtle species historically present in the Mississippi Valley applies selection pressure on traits such as rapid growth, increased size, and aggression (Cadi and Joly 2003; Madden-Smith et al. 2005). These traits allow the red-eared slider to flourish in stable environments and remain relatively unfazed by habitat fragmentation. Further research is needed to determine whether projects designed to increase stochasticity and connectivity between sites will reduce red-eared slider numbers or merely spread the species to sites not previously inhabited by sliders.

Pet owners continue to release adult red-eared sliders into the wild, effectively headstarting them. Patterson (1996) described a sizeable population of red-eared sliders that did not have sufficient recruitment to persist. Nevertheless, the population increased

over the course of two years due to an influx of adult sliders. The red-eared slider might die off without a continued influx of pet turtles. Efforts to illegalize red-eared slider possession should continue. The species is currently illegal in Oregon, but legal in both Washington and California (ODFW 2008; Washington Department of Fish and Wildlife 2009; Chrisman and McCamman 2008). Like the western pond turtle, red-eared sliders are a long-lived species able to persist for decades without recruitment. While illegalizing possession of red-eared sliders in Washington and California will certainly reduce the species' prevalence, the effects of this legislation may not be seen for decades.

As with the red-eared slider, the threat level of largemouth bass has not yet been determined. There is evidence that some small freshwater turtle species can defend against largemouth bass attacks. Britson and Gutzke (1993) presented captive largemouth bass with six forms each of red-eared slider and western painted turtle: ground internal organs and meat, ground shell and skin, ground whole turtle, dead hatchlings, anesthetized hatchlings, and active hatchlings. The bass consumed all treatments except the active hatchlings of both species. These were partially ingested and then ejected from the bass' mouth after intense scratching and biting. The bass avoided active hatchlings during subsequent treatments. Britson (1998) determined that bass are less likely to avoid cryptically colored turtle species. These results are not transferable to western pond turtles because they are less aggressive than either red-eared sliders or western painted turtles, and more cryptically colored (Sue Beilke pers. comm.). Research specifically related to interactions between largemouth bass and western pond turtles is needed to assess the severity of the threat.

Although bullfrogs are known to eat western pond turtles, there has been no attempt to quantify impact of bullfrogs on western pond turtles. The severity of the threat posed by bullfrogs has been assessed for several ranid frog species. Hayes and Jennings (1986) applied statistical tests to pre-existing data on ranid frog mortality and found that bullfrogs were not likely a major culprit in the decline of ranid frog species in western North America. Adams (1999) also used statistical methods to show that habitat structure and the presence of exotic fish were a greater factor in the decline of red-legged frogs (*Rana aurora*) than the presence of bullfrogs. Studies such as these should be completed to specifically assess the impact of bullfrogs on the western pond turtle. This knowledge will be useful in determining the risk of additional bullfrog introductions caused by connecting habitat fragments as well as the importance of restoring ephemeral habitats over permanent ones, as bullfrogs require permanent water bodies due to their two-year larval stage (Freeman 1998).

Assessment of Artificial High Flows for Habitat Heterogeneity

A heterogeneous landscape is vitally important for a number of fauna, and western pond turtles are no exception. The list of necessary habitat components is long; it includes upland areas with both high and low levels of canopy-cover, basking structures with nearby shade opportunities, shallow and warm as well as deep and cool water, and abundant refugia. While these components were commonplace before major river impoundments, sites containing all of these features are rare today (Holland 1994). One solution that merits additional research is the practice of discharging pulses of water from river impoundments. This process mimics natural flooding, but is controlled to avoid

human displacement. Flooding alters the watercourse and deposits patches of sediment, which varies water depth and resets the process of seral succession. Sedimentation is patchy, providing upland areas of varying seral stages. In areas of low rainfall, the magnitude of flooding is the primary regulator of riparian vegetation (Stromberg 2006). Areas recently disturbed by sedimentation provide nesting habitat, whereas later seral stages provide overwintering habitat. Intermediate-stage riparian forests provide basking structures with nearby shade opportunities and refugia in the form of fallen logs with intact foliage (Cook and Martini-Lamb 2004). Periodic flooding also provides temporally variable landscapes that favor western pond turtles over exotics. The key elements of discharge frequency, discharge rate, magnitude, timing, and temperature, along with their potential impacts on native species and human activities, should be assessed individually for each watershed (Poff et al. 1997). Less sophisticated water impoundments may not have the capacity to regulate discharge temperature, and may do more harm than good.

Artificial high flows mimicking the timing of natural high flows, with partial mimicry of the amplitude, volume, and duration of natural high flows, can be beneficial. High flows have increased the density of native fishes in the San Juan River by 10 times (Propst and Gido 2004). Natural flow regime discharges have also proven effective for native bird conservation (Rood et al. 2003). This technique has not been used explicitly for western pond turtle conservation, but has been suggested as a management technique for western pond turtles on the Trinity River (Reese 1996; Reese and Welsh 1998b).

Development of an Efficient and Accurate Nest Locating Methodology

Nest predation is the primary source of juvenile mortality at many sites, and should be addressed, but nests are very difficult to locate for protection, and mammalian predators remain an issue. The Oregon Wildlife Institute uses trained detector dogs to locate turtle nests by olfactory cues. The dogs approach 100 % accuracy during testing, but there are difficulties applying this method (Dave Vesely pers. comm.). Nests must be located very quickly after oviposition (within 24 hours) in order for the smell to be strong enough for dogs to detect. Rain shortens this period of time. The dogs must also be in the vicinity of the nests to detect a smell. Lastly, dogs must go through a long training period before becoming proficient at locating nests. Despite these limitations, detector dogs are a promising technology for locating turtle nests. More field tests are needed to determine the viability of this method.

Synthesis and Prioritization

The western pond turtle is one of only two extant freshwater turtle species native to the western United States, and once made up a significant percentage of animal biomass within its range (Holte 1998; B.R. Bury pers. comm.). The species' numbers have declined considerably since Euro-American settlement in the mid 1800s (Holland 1994). This decline is primarily the result of human development that has reduced the heterogeneity, stochasticity, and connectivity of the landscape. But the species faces several proximate threats layered over these primary threats. Invasive species, mammalian predators, and road mortality have become significant contributors to the

western pond turtle's decline. Balancing efforts to combat short and long-term threats with limited funding will be the goal of future conservation efforts for the western pond turtle.

This thesis has aggregated influential western pond turtle research to date and suggested future directions for research, but the implementation of this research requires a prioritization system. While all of the threats mentioned above are significant, few sites can support research addressing them all, and each site will have a different priority structure. Several categories of risk are outlined below (high-risk, moderate risk, low risk, and stable), and priorities for research and management will be presented for each.

High-risk populations are those under imminent threat of extirpation. This may be due to extremely low effective population sizes or a rapid decline in numbers. The most pressing priority at high-risk sites is the conservation of genetic variation within the population. First, a headstarting program should be initiated to ensure the population's existence in the near future. A second goal for management is habitat restoration in order to promote recruitment. This restoration should include additions of basking structures, removal of dense vegetative cover from nesting areas, removal of invasive species, and construction of fencing near hazards. Research should be restricted to inexpensive projects that do not interfere with management of the population, such as describing an efficient nest location methodology.

Populations are moderate-risk when the effective population size is low, or if it is high but markedly declining, and may warrant concerns regarding random fixation of alleles and inbreeding depression. Here, the highest priority for conservation remains the preservation of genetic variation. Unlike high-risk populations, however, this can likely

be achieved with habitat restoration alone. Because moderate-risk populations are not under an imminent threat, they may support increased research intensity.

Low-risk populations are defined as those with moderate effective population sizes that do not show a downward trend. Like the previous categories, preservation of genetic variation through habitat restoration is the first priority, but there is also a great deal of room for all facets of research. These could include anything from research regarding the severity of the threat posed by invasive species to the development of a juvenile census methodology. The types of research conducted will be dictated by site conditions.

Stable populations have higher effective population sizes than low-risk populations and show no signs of declining. These sites should be dedicated to future research that answers broad questions such as those related to dispersal capabilities of the western pond turtle and whether restoration of vegetative succession is scalable in its effects.

Prioritization of research and management actions based on population level risk of extirpation is more useful when guided by a more general set of priorities. Research and management actions required for successful conservation of the species have been divided by their mitigation of short and long-term threats, with priority given to research addressing short-term threats.

Short-term threats to western pond turtle conservation efforts include a loss of genetic diversity and a lack of funding. Because all future conservation research depends on the maintenance of genetic diversity present in western pond turtle populations, management practices supporting high-risk populations are therefore the highest priority.

The vast majority of funding allocated for western pond turtle conservation is already being spent in this category, and this should continue until additional funding opportunities arise. The development of an efficient nest location methodology is also included in this category because it will aid in the protection of juveniles and can be developed quickly.

Research providing credible science for listing under the Endangered Species Act is a second conservation priority. Upon listing, federal funding must be allocated for the development of a recovery plan, and additional grants will become available. This funding is necessary to continue expensive research and management. The western pond turtle was denied listed status in 1993 due to a lack of credible science showing that the species is threatened in all or part of its range. While many populations have been reduced in size since the mid 1800s, too little evidence has been collected to show that these populations are unstable and require listed status. In addition to population stability assessments, taxonomic revisions will likely be necessary to list the western pond turtle as threatened under the Endangered Species Act. Spinks and Shaffer (2005) have proposed four distinct clades, two of which coincide regions showing a very marked decline (California's central valley and southern California from Baja to ventura). Taxonomic distinctions between high and low-risk regions have been used successfully to list both the desert tortoise and the bog turtle, among others. Further work on these revisions is warranted for the western pond turtle.

Long-term threats to western pond turtle conservation involve habitat alteration and the spread of invasive species, especially during restoration activities. The first long-term priority for future research includes studies aimed at restoring habitat stochasticity,

heterogeneity, and connectivity. Damming has stabilized and homogenized the landscape by reducing flooding and sedimentation, resulting in a loss of backwater habitats and creating overgrown riparian zones due to continued vegetative succession. To date, land managers engage in de-succession by applying herbicides, mowing, and manually weeding. These methods require a great deal of time and money, and cannot be scaled to the majority of the western pond turtle's range. Artificial discharges from dams are a potential scalable solution, but more research is needed in order to show its level of effectiveness.

At the same time that habitats have been stabilized and homogenized, they have also been fragmented by the development of roads, as well as urban and agricultural areas. Fragmentation increases mortality from mammalian predators and motor vehicles, and results in genetic isolation. Additional research regarding the western pond turtle's dispersal capabilities is required in order to alleviate problems associated with habitat fragmentation.

A second long-term conservation priority consists of research that reduces the possibility of spreading harmful invasive species through restorative actions. There are insufficient data to conclude whether invasive species such as largemouth bass, bullfrogs, and red-eared sliders are a severe threat to the western pond turtle. Assessments of the severity of threats posed by invasive species should be completed in order to make certain that future conservation efforts are not jeopardized. Bullfrogs, in particular, often colonize habitat after restorative activity. Before floodplain restoration spreads bullfrogs across the landscape, managers must have some knowledge of the severity of the bullfrog threat. Likewise, restoring habitat connectivity may spread red-eared sliders to additional

sites. Before the severity of these threats is known, conservation organizations should use their judgment to reduce the spread of invasive species in restoration projects.

A successful conservation program is one that coordinates efforts across the species' range, and no single conservation group is large enough to take on this project alone. This is especially true for species covering a wide range of habitats and jurisdictions such as the western pond turtle. Research at one site should inform the management activities at other sites. This requires that researchers publish their data, or at a minimum, distribute it to fellow conservationists. Of 16 Ph.D. dissertations and M.A. theses on the subject of western pond turtle conservation, only four have been published (B.R. Bury pers. comm.). All of the priorities outlined above are essential to western pond turtle conservation, but a lack of coordination will waste time and money, and put the species' future in jeopardy.

Glossary

Aestivation

A state of dormancy much like hibernation, but during the summer months.

Annulus

One of many concentric circles found on the shell of many turtle species.

Carapace

The dorsal section of a turtle's shell.

Ectotherm

An organism that regulates its body temperature by seeking out hot and cold environments.

Effective Population Size

The number of breeding individuals in an ideal population exhibiting the same level of genetic drift as the population in question. It is sometimes referred to as the number of individuals within a population that contribute genes to future generations.

Genetic Drift

A process by which alleles are randomly fixed and lost due to a population's small effective population size.

Inguinal Plates

Small plate-like protrusions formed around the edges of a turtle's carapace.

Interspecific Competition

A struggle for resources between members of different species.

Intraspecific Competition

A struggle for resources between members of the same species.

Linear Adult Home Range

The furthest distance traveled by a western pond turtle within a definable region said to be its home range.

Microsatellite Loci

Specific locations on a gene that are commonly used to compare the overall genetic similarity between populations of pond turtles.

Mitochondrial DNA

Nucleic acids found in organelles known as 'mitochondria' that code for protein formation.

Molecular Phylogenetic Analysis

Any of many methods of using DNA to illuminate evolutionary relationships between taxa.

Oviposition

The act of depositing eggs.

Paraphyletic

A taxonomic group composed of some but not all members descended from a common ancestor.

Phenotypic Plasticity

The ability of an organism to alter character traits in response to its environment.

Phylogeographic Analysis

The study of the phylogeny of a species as it relates to the current geographical distribution of that species.

Plastral Hinge

A flexible joint located on the ventral side of some freshwater turtle species.

Plastral Kinesis

The act flexing the plastral hinge (see above).

Plastron

The ventral side of a turtle's shell.

Riparian

The area immediately adjacent to a water body.

Seral Succession

The growth of plant communities after a disturbance until a climax community composition.

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