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Terrestrial Habitat use by Western Pond Turtles (*Actinemys marmorata*) in the Sierra Foothills

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Abstract.—**Western Pond Turtles (*Actinemys marmorata*) are endemic to western North America and are found in a diversity of aquatic habitats. To date, few studies have examined the ecology of populations in ephemeral or intermittent ponds. Here, we studied the terrestrial habitat requirements of Western Pond Turtles in an intermittent pond that dries in years with below-average rainfall. We tracked terrestrial movements of Western Pond Turtles in an ephemeral pond at the San Joaquin Experimental Range in Madera County, California, USA, in the western foothills of the Sierra Nevada. We used radiotelemetry in 2012–13 to record their terrestrial locations and timing of departure from, and return to, the pond. Also, we examined the terrestrial microhabitat turtles selected for aestivation and overwintering. Turtles began leaving the pond as it dried in the late spring and early summer, spending an average of 235 d out of water, and their return to the pond was correlated with increasing rainfall during late winter. The majority of terrestrial locations were concealed completely in litter or duff and 95% of terrestrial locations during the study occurred within 187 m of the pond edge. Turtles in our study generally exhibited terrestrial habitat use similar to that of populations in intermittent lotic systems such as the many snow-melt and rain-fed rivers in northern California. Our results reinforce the importance of terrestrial habitat in the life history of Western Pond Turtles and the context-dependence of their habitat needs.**

Many species that rely on both aquatic and terrestrial habitats face increased risk of decline from factors that can affect either of these habitats or the linkages between them (Becker et al., 2007). For example, many aquatic snakes, turtles, alligators, and pond-breeding amphibians require both aquatic systems and core terrestrial habitat adjacent to these systems to support their populations (Burke and Gibbons, 1995; Roe et al., 2003; Rittenhouse and Semlitsch, 2007; Subalusky et al., 2009). Despite being highly aquatic, these species may live in terrestrial habitat for much of the year or they may require elements of it for nesting, overwintering, summer aestivation, or as movement corridors to reach other aquatic systems. Thus, there has been increased interest in determining the extent to which terrestrial habitat must be preserved to support functioning populations of these species (Semlitsch and Bodie, 1998, 2003).

The Western Pond Turtle (*Actinemys marmorata*) is an emydid turtle endemic to western North America. It has an extensive distribution ranging from Baja, Mexico northward to Puget Sound, Washington (Bury and Germano, 2008). It is the only one of three turtle species native to California that is distributed widely and uses freshwater habitats (Ernst and Lovich, 2009). Consequently, it exhibits a wide range of behavioral and ecological diversity that reflects its local adaptation to both perennial and ephemeral habitats in both lentic and lotic freshwater systems (Bury and Germano, 2008).

A remarkable feature of the biology of the Western Pond Turtle is its extensive use of upland terrestrial habitat adjacent to inhabited water bodies (Ernst and Lovich, 2009). The extent to which Western Pond Turtles use terrestrial habitat varies widely and depends largely on the hydrology and climate of a given area where populations occur. For example, Western Pond Turtles in intermittent water bodies may be terrestrial for a majority of the year where aquatic systems dry in the summer (Bondi and Marks, 2013; Pilliod et al., 2013). In contrast, populations in perennial water bodies may be almost entirely aquatic and only leave the water to nest, a life history more typical of many North American emydids (Lovich and Meyer, 2002; Ernst and Lovich, 2009; Bondi and Marks, 2013). Further, turtles may opt to change habitat for various reasons. Transitions between aquatic and terrestrial habitats, including those for aestivation and overwintering, can occur in response to changes in stream flow, as is typical of turtles in intermittent or seasonal streams (Rathbun et al., 2002; Bondi and Marks, 2013). In contrast, turtles in perennial rivers with little change in water availability throughout the year respond strongly to fluctuations in climate (Bondi, 2009). The variety of life histories of Western Pond Turtles (Bury and Germano, 2008; Ernst and Lovich, 2009) has made it difficult to generalize patterns of habitat use for the species. This plasticity creates challenges when determining conservation strategies, as separate populations may require different approaches.

Despite extensive study of the Western Pond Turtle in lentic habitats (Germano and Rathbun, 2008; Germano, 2010), there has been little research on its habitat use in ephemeral or intermittent ponds and marshes (but see Pilliod et al., 2013). We examined upland terrestrial habitat use by Western Pond Turtles in an ephemeral pond in the Sierra Nevada foothills in central California. Our primary objectives were to identify the extent to which this population of Western Pond Turtles requires upland habitat for aestivation or overwintering, determine the distances they travel to these sites, and characterize the type of terrestrial habitat selected by turtles when away from the pond. Our results lend important additional insights into the ecology of this highly variable species, especially for populations that inhabit ephemeral lentic systems where previous research has been scarce.

Methods

Study Site.—We studied Western Pond Turtle movements at the U.S. Forest Service's San Joaquin Experimental Range (SJER) in the western foothills of the Sierra Nevada, in Madera County, approximately 40 km north of Fresno, California. The SJER is 1,875 ha in size with an elevation range from 215–520 m. The climate is Mediterranean with cool, wet winters and hot, dry summers. Mean annual precipitation is 48.6 cm, 95% of which falls between October and April. Total precipitation from 1 April 2012 through 31 March 2013 was 34.7 cm. Vegetation consists of

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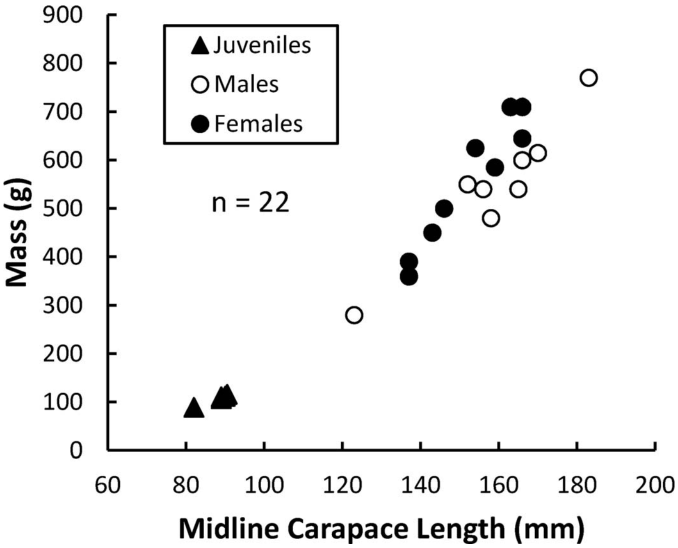

FIG. 1. Relationship between mass and length in *A. marmorata* from San Joaquin Experimental Station, Madera County, California.

an open woodland dominated by blue oak (*Quercus douglasii*), interior live oak (*Quercus wislizenii*), and foothill pine (*Pinus sabiniana*). The sparse understory includes wedgeleaf ceanothus (*Ceanothus cuneatus*), chaparral whitethorn (*Ceanothus leucodermis*), and Mariposa manzanita (*Arctostaphylos viscida* ssp. *mariposa*). Unpublished documents from the U.S. Forest Service suggest the SJER has been lightly to moderately grazed since the early 1900s.

Three reservoirs were built on SJER in the late 1930s to serve as stock ponds (Duncan et al., 1985). Anecdotal evidence suggests that Western Pond Turtles were introduced at this time, although the source population is unknown (Newman and Duncan, 1973; Duncan et al., 1985). In 2007 the population was estimated at only 10–12 individuals, all >12 yr of age, using a single, small stock pond as their primary water source (KP, pers. obs.). Juvenile turtles have been encountered each year since 2007. This pond lies within a pasture that is lightly grazed by livestock each fall. Adjacent pastures are grazed by horses irregularly (KP, pers. obs.).

Turtle Capture and Handling.—We used baited hoop nets set in shallow water to capture animals on three different sampling occasions: 23–26 March 2012, 15–16 May 2012, and 21–24 April 2013. At each capture occasion, we baited traps with sardines and checked traps each morning and again in the late evening, resulting in 14 capture periods over the course of the study. Upon capture, we measured each animal's maximum carapace length (MCL) and weighed each animal, marked them individually by notching marginal scutes, and recorded sex when animals were large enough to display obvious secondary sexual characters. Each animal was released immediately after handling unless they were large enough to carry a radiotransmitter.

Radiotelemetry.—We fitted 12 individuals with radiotransmitters (model RI-2B, Holohil Systems Ltd., Carp, Ontario, Canada) mounted to their costal carapace scutes. Only turtles with a mass ≥450 g were fitted with radiotransmitters. We secured transmitters to adults with epoxy, and the mass of the transmitter and epoxy combined was <5% of each individual's total mass. Turtles were returned to the pond and released after application of transmitters, usually within 1 h of capture. The signal of a 13th animal was lost shortly after it was released. Extensive efforts failed to recover any signal from this animal within ~2 km of the study site. This individual was omitted from our study. Two turtles were predated on separate dates but their previous known locations were included in our analyses.

We resighted turtles at least weekly using a hand-held telemetry receiver (model R-1000, Communications Specialists Inc., Orange, California) and three-element unidirectional antenna beginning 27 March 2012 and continuing through 24 April 2013. We assigned individuals as being aquatic when a signal was definitively determined to originate from the pond via triangulation. For terrestrial locations, we used standard homing techniques as opposed to triangulation. We recorded coordinates for each individual upon resighting using a Garmin Vista HCx GPS. To avoid disturbing habitat, we recorded approximate (±0.1 m) locations for turtles that were on land and buried deeply in substrate. At terrestrial sites, we noted whether the turtle was completely concealed.

Microhabitat Use.—To avoid undue disturbance to animals, all terrestrial habitat data were collected after the turtle had moved from the site. We placed a 1-m^2 PVC frame centered on each turtle's location and oriented with the cardinal directions. Inside the frame we estimated the percent ground cover of six categories (litter, grass/forb, soil, rock, log/root, and trunk) and woody plant cover within 2 m of the ground. We measured organic litter depth at four points 0.25 m from the bedding site in the four cardinal directions. We recorded the substrate type at the bedding site. We derived a variable to estimate protection from livestock, which was evaluated on a scale of 1 to 10 (1 being the least protected, 10 being the most protected). To measure canopy closure we used a spherical densiometer, averaging four readings taken at the bedding site facing the four cardinal directions. We measured percent slope with a clinometer and downhill aspect with a compass.

Analyses.—We used the Chapman estimator (Chapman, 1951) to estimate the number of turtles in the pond during each of our three sampling occasions (14 capture periods) based on the number of marked and unmarked individuals in samples. We used a chi-square (χ^2) analysis to compare the sex ratios of the sexually mature animals that were captured. We used the measuring tool in ArcMap 10.1 to calculate the distances turtles moved between each recorded location and the maximum distance moved for each individual. We measured the distance from the edge of the pond for each terrestrial location for each turtle in ArcGIS. This allowed us to calculate the average distance from the pond edge for each turtle's upland habitat use. We also calculated the distance from the edge of the pond that included 50%, 90%, and 95% of all terrestrial relocations of all turtles. We used *t*-tests to compare the sizes of male and female turtles and to compare the microhabitat variables at terrestrial locations for the two sexes. We used Rayleigh's test to examine whether aspect at terrestrial locations was nonrandom (Mardia and Jupp, 2000).

RESULTS

We captured 22 individuals during our three sampling periods (Fig. 1), and five (22.7%) of these individuals were juveniles. Average MCL of juveniles was 93.7 mm and the average MCL of sexually mature individuals was 155.5 mm. Average MCL was 159.1 mm for males and 152.3 mm for females and did not differ significantly between the two sexes ($t = 2.13$, df = 15, $P = 0.359$). The sex ratio of adults (9 females, 8 males) did not differ significantly from random ($\chi^2 = 0.59$, $P = 0.808$).

Our mark–recapture estimates of the number of turtles in the pond varied from 11.8 (95% CI 8.4–15.2) in March 2012 to 13.0

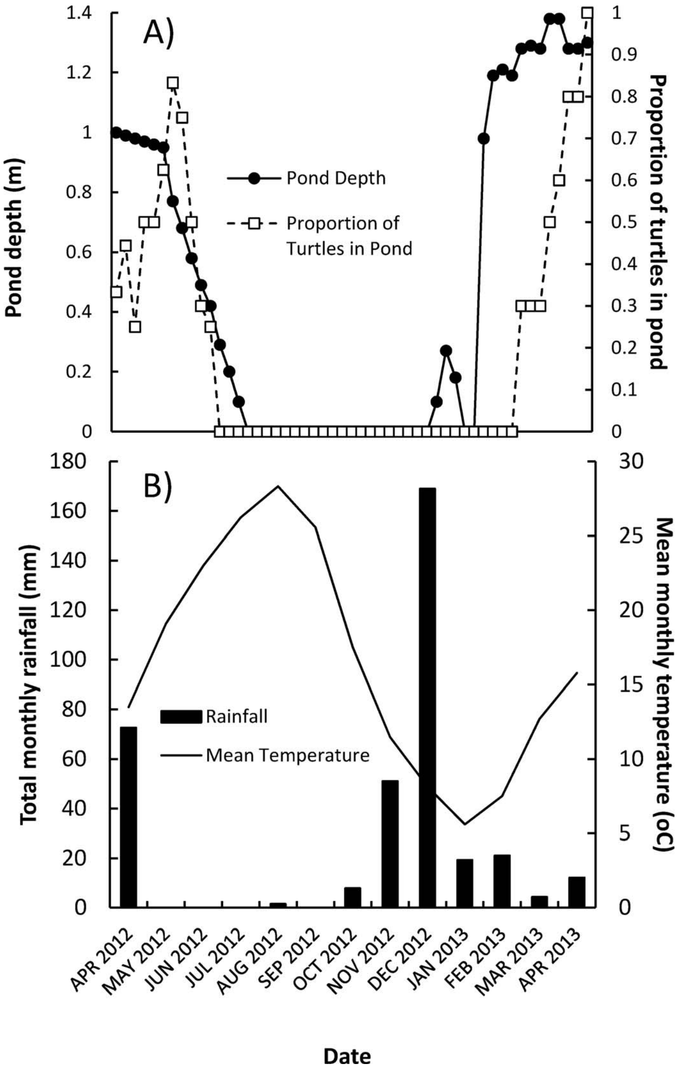

FIG. 2. Pond depth (m) and the proportion of Western Pond Turtles found in the pond over the course of the study (A), and the total monthly rainfall (mm) and mean temperatures (°C) over the course of the study (B).

(6.8–19.2) in May 2012 and 10.7 (6.1–15.2) in April 2013. Although we captured more animals than this over the entirety of the study, the greatest number that we knew was in the pond at any one time from radiotelemetry was 10, representing all individuals outfitted with radiotransmitters at that point in time. Two of the 12 animals that were tracked over the course of the study succumbed to predation, but we were unable to identify the predators responsible. One of the animals appeared to have been dug out from its terrestrial site; the other may have been predated while in transit between sites.

Although turtles remained in the pond for consistent periods of time, they shifted to terrestrial habitat use in the late spring and early summer from May to June (Fig. 2A). This coincided with a reduction in rainfall and increasing mean temperature in the area (Fig. 2B). After the pond dried completely, turtles at the study site were entirely terrestrial and spent on average more than 235 d out of water (Table 1). During this period, they were often buried just beneath the soil surface and moved infrequently, although this behavior differed among individuals, with some individuals occupying only two terrestrial sites and others moving as many as 12 times (Table 1). Females tended to move more often than males, averaging 7.0 bedding locations compared to 3.6 for males for those animals not predated during the study. However, sample sizes were too small to test for the statistical significance of this trend. Turtles were nearly always completely concealed in their bedding sites. In three instances, turtles were only partially concealed (80–90% concealment). Two of these three turtles were preyed upon. The third instance likely represents an animal that was in transit because its next sighting was in the pond. Turtles began returning to the pond from February to March as winter rains began refilling the pond (Fig. 2).

Turtles generally spent their time in the terrestrial environment an average of 80 m from the pond (Table 1; Fig. 3). However, the average maximum distance they moved between any two sightings was approximately 138 m (Table 1). Half of all terrestrial turtle locations were within 63 m of the edge of the pond. A distance of 135 m from the edge of the pond encompassed 90% of all terrestrial turtle locations, and a distance of 187 m from the edge of the pond encompassed 95% of all terrestrial turtle locations. The maximum known distance from the pond that a turtle was found was 357 m (Fig. 3).

We measured habitat characteristics of 12 turtles at 58 total locations. In a few cases, locations for the same turtle were <1 m apart. We did not record measurements at these overlapping sites. Nearly all turtles were buried in soil under litter or duff (81%). However, some were found entirely in the litter layer and a few were buried in soil lacking a litter layer. Litter depth across all sites averaged 4.1 cm (SE = 3.9, range = 0–166). Ground cover was dominated by litter (58%) followed by cover of grasses and forbs (18%) and soil (11%). Nearly three quarters of the sites had some overhead woody plant cover (42 of 58), which was predominantly interior live oak (74% of sites), but foothill pine and wedgeleaf ceanothus were present at 19% and 10% of the sites, respectively. Average canopy closure at bedding sites was 54.2%. Females tended to select sites with higher closure than did males ($t = 2.07$, df $= 56$, $P = 0.04$). There was no significant difference between the sexes in the litter depth ($t = 0.58$, df $= 55$, $P = 0.56$) or slope ($t = 0.87$, df $= 56$, $P = 0.39$) of terrestrial locations.

The sexes did not differ in the degree to which their terrestrial locations afforded protection from livestock ($t = 1.28$, df $= 56$, $P = 0.21$). Our derived variable averaged 5.5 (SE = 0.38) and ranged from 1 to 10. The slope of terrestrial locations averaged 19% and the average aspect was 74°. The average aspect at terrestrial locations differed significantly from a uniform distribution ($\bar{R} = 0.43$, $P < 0.0001$). Pond turtles tended to select bedding sites with easterly aspects (morning sun, shaded afternoons).

TABLE 1. Summary of time spent out of water, number of terrestrial locations, and movement distances for male and female Western Pond Turtles at San Joaquin Experimental Range, Madera County, California. Ranges of observed values are listed parenthetically.

Sex	Mean number of days out of pond	Mean number of terrestrial locations	Mean distance from pond in meters	Mean maximum distance moved in meters
Males	247.3 (96–332)	4.3 (2–9)	80.4 (22.6–186.8)	139.8 (26.4–186.8)
Females	237.2 (113–333)	6.8 (2–12)	76.7 (10.9–357.2)	132.2 (26.9–396.0)

FIG. 3. Aerial photograph showing all terrestrial locations of Western Pond Turtles outfitted with radiotransmitters ($N = 12$) and the various buffer distances that encompass percentages of those locations.

DISCUSSION

Turtles in our study inhabited an ephemeral pond and spent most of the year aestivating and overwintering in terrestrial habitat. Pond hydroperiod was associated strongly with timing of turtle movements between aquatic and terrestrial habitats, further demonstrating the important link between these two habitats, as suggested by some previous studies (e.g., Reese and Welsh, 1997; Rathbun et al., 2002; Pilliod et al., 2013). Western Pond Turtle populations in intermittent systems generally leave water earlier than do those in perennial systems, coinciding with the drying of water sources (Bondi and Marks, 2013). Other studies reported that turtles generally left water during the summer, from approximately July through September (Bondi and Marks, 2013; Pilliod et al., 2013). However, animals in our study began leaving the pond in late spring, from May through June 2012, earlier than that reported for other areas. This is likely because of hydroperiod differences between water bodies because the pond in our study dried earlier than ponds in comparable studies (Bondi and Marks, 2013; Pilliod et al., 2013). A return of turtles to the pond during late winter and spring coincided with increasing rainfall and pond depth from winter rains in this Mediterranean climate.

Almost half (32/67) of all terrestrial relocations occurred in a ravine south of the main pond. Compared to most of the study site, this ravine was characterized by higher densities of ground cover including litter, logs, grasses, and forbs. The results of our microhabitat analyses suggest that turtles prefer litter or duff for concealment, likely minimizing detection by predators. Two of the three individuals that lacked full concealment were later found preyed upon. Other studies in comparable terrestrial habitat reported partial exposure at all locations. (Pilliod et al., 2013; Rathbun et al., 2002). Turtles in our study exhibited a preference for terrestrial sites with an easterly aspect in contrast to previous studies which found no aspect preference (Reese, 1996; Pilliod et al., 2013). The choice of sites with an easterly aspect suggests that animals in our study may orient eastward to warm in the morning sun while avoiding hot afternoons.

The vast majority (>95%) of terrestrial turtle locations in this study were within 187 m of the edge of the pond, with a maximum distance of 357 m from the pond for one turtle. Pilliod et al. (2013) provide the most-comparable study of the terrestrial habitat use of Western Pond Turtles inhabiting nonpermanent ponds and found that turtles overwintered exclusively on land and moved, on average, 211 m and 138 m from their two study ponds, with a maximum distance moved of 345 m. Studies of Western Pond Turtles inhabiting permanent ponds often find that turtles overwinter in water (Reese, 1996; Lovich and Meyer, 2002; Sloan, 2012). Still, Reese (1996) demonstrated that turtles inhabiting permanent ponds can show a great degree of terrestrial habitat use to nest, aestivate, and overwinter, with one individual moving 235 m from a pond. Western Pond Turtle populations inhabiting streams and rivers have been studied more extensively and most individuals in this habitat overwinter terrestrially. Reese and Welsh (1997) found overwintering sites an average 203 m from the Trinity River with a maximum distance of 500 m, whereas Rathbun et al. (2002) reported much shorter movements from four creeks in Central California (mean = 49.7 m, max = 280 m), and Bondi and Marks (2013) reported intermediate results from the Mad River (mean = 95 m, max = 269 m) where both permanent and intermittent waters were examined. These results emphasize that the terrestrial habitat needs of any population of Western Pond Turtles depends on the aquatic and terrestrial conditions at that site and that we should take caution in making generalizations about the sizes of core terrestrial habitat for this species.

Our results indicate that a distance of approximately 190 m of intact core terrestrial habitat would encompass the vast majority (95%) of the turtles' terrestrial habitat use (only one location fell outside this distance). Semlitsch and Bodie (2003) recommend an additional buffer distance of 50 m around core terrestrial habitat used by semiaquatic species to minimize edge effects of surrounding land use. Adding this 50 m buffer to the 190 m that includes 95% of all turtle terrestrial locations would constitute a total distance of 240 m from the pond edge to protect terrestrial habitat. We caution, however, that the terrestrial habitat needs for Western Pond Turtles may vary depending on the population under study, the composition of upland habitat, and interannual variation in precipitation and pond hydroperiod. Nevertheless, our recommendation is similar to those of other studies of Western Pond Turtles in intermittent ponds. For example, Pilliod et al. (2013) recommended a similar distance of 250–350 m to preserve important terrestrial habitat around two intermittent study ponds in California. A distance of 240 m also lies within the range of core terrestrial habitat needed by many other semiaquatic turtles for nesting (Steen et al., 2012) and for all terrestrial activity according to recent literature reviews (Semlitsch and Bodie, 2003).

We believe our study provides a useful starting point for delineating the area necessary to protect terrestrial habitat for a population of Western Pond Turtles inhabiting an ephemeral pond, given that we radiotracked a majority of the adults in the population (12 out of <20 total according to our population estimates). If complete protection of terrestrial habitat is not feasible, and livestock are to be grazed in upland areas adjacent to water bodies inhabited by Western Pond Turtles, it may be possible to use knowledge about the hydroperiod of the focal water body to mitigate negative impacts. Limiting grazing activity to time periods when turtles are resident in the water (late winter through spring in this study) could ensure that turtles are not disturbed when they are using terrestrial habitat for nesting, aestivation, and overwintering. However, even temporally partitioned grazing may negatively affect Western Pond Turtles by altering habitat. Future studies across a gradient of aquatic systems could improve our understanding of the terrestrial needs of this species and provide more generalizable guidelines for best management practices.

Our data provide further evidence of the variability of life history traits in Western Pond Turtles. Our study also provides valuable information on terrestrial movements related to overwintering behavior, a crucial but understudied aspect of Western Pond Turtle ecology (Haws et al., 2012). Differences between the results of our study and similar studies performed in intermittent water bodies illustrate the potential range in the behavioral timing and extent of use of terrestrial habitat among isolated populations, even among ostensibly similar systems. Our study also reinforces the importance of protecting terrestrial habitat for the conservation of semiaquatic vertebrates (see Semlitsch and Bodie, 2003) and underscores the importance of knowing both the specific terrestrial and aquatic habitat requirements of a population to promote persistence.

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Literature Cited

Becker, C. G., C. R. Fonseca, C. F. B. Haddad, R. F. Batista, and P. I. Prado. 2007. Habitat split and the global decline of amphibians. Science 318:1775–1777.

Bondi, C. A. 2009. A Comparison of Western Pond Turtle (*Actinemys Marmorata*) Movements in Perennial and Intermittent Portions of a Northwestern California River System. MA. thesis, Humboldt State University, USA.

Bondi, C. A., and S. B. Marks. 2013. Differences in flow regime influence the seasonal migrations, body size, and body condition of western pond turtles (*Actinemys marmorata*) that inhabit perennial and intermittent riverine sites in Northern California. Copeia 1:142–153.

Burke, V. J., and J. W. Gibbons. 1995. Terrestrial buffer zones and wetland conservation: a case study of freshwater turtles in a Carolina bay. Conservation Biology 9:1365–1369.

Bury, R. B., and D. J. Germano. 2008. *Actinemys marmorata* (Baird and Girard 1852)—Western pond turtle, Pacific pond turtle. Pp. 001.1–001.9. in A. G. J. Rhodin, P. C. H. Pritchard, P. P. van Dijk, R. A. Saumure, K. A. Buhlmann, and J. B. Iverson, (eds.), Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs No. 5.

Chapman, D. G. 1951. Some properties of the hypergeometric distribution with applications to zoological sample censuses. University of California Publications in Statistics 1:131–160.

Duncan, D. A., L. V. Ritter, and T. F. Newman Jr. 1985. Vertebrate fauna of the San Joaquin Experimental Range, California: a 50-year checklist. California State University, Fresno. California Agricultural Technology Institute, CATI Publication 850901.

Ernst, C. H., and J. E. Lovich. 2009. Turtles of the United States and Canada. Johns Hopkins Press, Baltimore, Maryland, USA.

Germano, D. J. 2010. Ecology of western pond turtles (*Actinemys marmorata*) at sewage-treatment facilities in the San Joaquin Valley, California. Southwestern Naturalist 55:89–97.

Germano, D. J., and G. B. Rathbun. 2008. Growth, population structure, and reproduction of the western pond turtle (*Actinemys marmorata*) on the central coast of California. Chelonian Conservation and Biology 7:188–194.

Haws, C., R. Horn, K. Beal, L. Todd, S. Wray, S. Wessell-Kelly, and R. B. Bury. 2012. Conservation and restoration strategies. Pp. 69–80 in R. B. Bury, H. H. Welsh Jr., D. J. Germano, and D. T. Ashton (eds.), Western Pond Turtle: Biology, Sampling Techniques, Inventory and Monitoring, Conservation, and Management. Northwest Fauna No. 7.

Lovich, J., and K. Meyer. 2002. The western pond turtle (*Clemmys marmorata*) in the Mojave River, California, USA: highly adapted survivor or tenuous relict? Journal of Zoology, London 256:537–545.

Mardia, K. V., and P. E. Jupp. 2000. Directional Statistics. John Wiley and Sons, Ltd., New York, USA.

Newman, T. F., and D. A. Duncan. 1973. Vertebrate fauna of the San Joaquin Experimental Range: a checklist. USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, General Technical Report PSW-6, Berkeley, California, USA.

Pilliod, D. S., J. L. Welty, and R. Stafford. 2013. Terrestrial movement patterns of western pond turtles (*Actinemys marmorata*) in central California. Herpetological Conservation and Biology 8:207–221.

Rathbun, G. B., N. J. Scott, and T. G. Murphey. 2002. Terrestrial habitat use by Pacific pond turtles in a Mediterranean climate. Southwestern Naturalist 47:225–235.

Reese, D. A. 1996. Comparative Demography and Habitat Use of Western Pond Turtles in Northern California: The Effects of Damming and Related Alterations. Ph.D. diss., University of California at Berkeley, Berkeley, California, USA.

Reese, D. A., and H. H. Welsh. 1997. Use of terrestrial habitat by western pond turtles, *Clemmys marmorata*: implications for management. Pp. 352–357 in J. Van Abbema (ed.), Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles—An International Conference, Pp. 352–357. New York Turtle and Tortoise Society, USA.

Rittenhouse, T. A. G., and R. D. Semlitsch. 2007. Distribution of amphibians in terrestrial habitat surrounding wetlands. Wetlands 27: 153–161.

Roe, J. H., B. A. Kingsbury, and N. R. Herbert. 2003. Wetland and upland use patterns in semi-aquatic snakes: implications for wetlands conservation. Wetlands 23:1003–1014.

Semlitsch, R. D., and J. R. Bodie. 1998. Are small, isolated wetlands expendable? Conservation Biology 12:1129–1133.

———. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology 17:1219–1228.

Sloan, L. M. 2012. Population Structure, Life History, and Terrestrial Movements of Western Pond Turtles (*Actinemys marmorata*) in Lentic Habitats along the Trinity River, California. MS. Thesis, Humboldt State University, USA.

Steen, D. A., J. P. Gibbs, K. A. Buhlmann, J. L. Carr, B. W. Compton, J. D. Congdon, J. S. Doody, J. C. Godwin, K. L. Holcomb, D. R. Jackson, et al. 2012. Terrestrial habitat requirements of nesting freshwater turtles. Biological Conservation 150:121–128.

Subalusky, A. L., L. A. Fitzgerald, and L. L. Smith. 2009. Ontogenetic niche shifts in the American alligator establish functional connectivity between aquatic systems. Biological Conservation 142:1507–1514.

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