Herpetological Conservation and Biology 8(1):207–221.
Submitted: 13 November 2011; Accepted: 16 February 2013; Published: 30 April 2013.

TERRESTRIAL MOVEMENT PATTERNS OF WESTERN POND TURTLES (*ACTINEMYS MARMORATA*) IN CENTRAL CALIFORNIA

DAVID S. PILLIOD[1,2], JUSTIN L. WELTY[1], AND ROBERT STAFFORD[3]

[1]*U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, 970 Lusk Street, Boise, Idaho 83706 USA*
[2]*Corresponding author e-mail:* dpilliod@usgs.gov
[3]*California Department of Fish and Wildlife, P.O. Box 6360, Los Osos, California 93412 USA*

***Abstract.*—We used radio telemetry to track the terrestrial movements and seasonal habitat use patterns of Western Pond Turtles (*Actinemys marmorata*) near two ponds in the Carrizo Plain Ecological Reserve, California, USA. We captured 93 turtles in September 2005 and, of these, we tagged three males and six females (weighing > 300 g) with external transmitters. Tagged turtles traveled from 255–1,096 m over the 448-day study, and we found none further than 343 m from ponds. All turtles moved away from the ponds as water levels receded in the fall, resulting in periods of terrestrial overwintering ranging from 10–30 weeks (74–202 d). We found no evidence for group migrations as turtles departed ponds over 2–8 week periods, moved in different directions from their ponds, and used different habitats. Turtles overwintered mainly in oak and chaparral vegetation communities, which constituted most of the local vegetation. We found overwintering turtles in a variety of microhabitats, but all turtles were on the surface with their carapace just visible amongst the duff layer. Turtles returned to ponds over several weeks, sometimes months after they refilled with winter rains. In the winter of 2006–2007, no turtles returned to terrestrial overwintering sites used the previous year. Most of the turtles we tracked spent over half of each year on land, demonstrating the importance of terrestrial habitats around these seasonal ponds. This pattern is similar to pond turtles living in streams (overwinter on land), as compared to permanent ponds (turtles often remain in water).**

Key Words.—Carrizo Plain Ecological Reserve; Chelonians; *Emys marmorata*; GIS; radio telemetry

INTRODUCTION

The Western Pond Turtle (*Actinemys marmorata*) is widely distributed along western North America, living in both lentic and lotic habitats. The species has experienced population declines associated with habitat degradation in parts of its range (Garber and Burger 1995; Jennings 2004; Bury and Germano 2008), but is capable of exploiting a wide range of freshwater habitats including reservoirs, water treatment ponds, agricultural ponds, rivers, and seasonal creeks. The distribution of the species may have been larger during wetter periods of the Pleistocene and some populations are now isolated in arid environments, such as in the Mojave Desert, where rivers and ponds dry each year (Lovich and Meyer 2002). This wide distribution and use of diverse habitats has resulted in considerable variability in demography, morphology, and behavior among populations (Bury and Germano 2008).

One of the most striking behavioral differences among populations is the use of upland habitats throughout the year (i.e., not just for nesting), a behavior rarely observed among freshwater turtles (Ultsch 2006). Like other freshwater turtle species, some pond turtle populations remain in water year-round, with females moving onto land only for short periods (hours to days, up to 4 d maximum) to lay eggs (Reese 1996; Holte 1998; Lovich and Meyer 2002; Rathbun et al. 2002). This behavior appears to be particularly prevalent in populations living in permanent ponds (Table 1). In some populations, however, particularly those living in streams and rivers, males and females leave the water for months each year and travel 100s of meters into upland habitats (Reese and Welsh 1997; Bury and Germano 2008). This terrestrial behavior often spans winter, but is not solely associated with overwintering or hibernating.

Radio telemetry studies have demonstrated that the timing of departure from and return to water, distances traveled over land, and habitats used during terrestrial movements are highly variable among individuals, even from the same population. Some turtles travel 300–500 m from water into surrounding uplands, while others remain a few meters from water in riparian habitats (Table 1). Movement of pond turtles away from streams and rivers in late fall has been attributed to avoidance of high flow of winter and spring runoff (Goodman 1994; Reese 1996; Rathbun et al. 2002). Propensity for terrestrial overwintering in populations living in permanent ponds appears to be much lower than stream and river populations (Reese 1996). For example, in telemetered individuals across the range of the species (Table 1), 20% of 109 turtles in permanent ponds overwintered terrestrially (n = 6 studies) compared with 97% of 71 turtles in streams and rivers (n = 6 studies).

TABLE 1. Summary of published and unpublished literature on Western Pond Turtle (*Actinemys marmorata*) movements outside of the nesting season and usually associated with winter.

Water body type	No. turtles overwinter in water	No. turtles overwinter on land	Time on land (d)	Max distance from water (m)	Location	Citation
Stream	0	7	n.r.	15–187	Streams, California / Oregon	Dan Holland, unpubl. report
Stream	0	6	66–234	77–260	Trinity River, Northern California	Reese 1996[1]
Stream	2	10	210	65–500	Trinity River, Northern California	Reese and Welsh 1997[2]
Stream	0	17	34–191	8–280	4 Creeks, Central California	Rathbun et al. 2002[3]
Stream	0	28	121–310	23–269	Mad River, Northern California	Bondi 2009
Stream	0	1	n.r.	55	Trinity River, Northern California	Sloan 2012
Permanent Pond	29	3	n.r.	n.r.	Ponds, California / Oregon	Dan Holland, unpubl. report[4]
Permanent Pond	12	3	57–122	80–235	Santa Rosa Ponds, Northern California	Reese 1996[1]
Permanent Pond	3	9	88–115	n.r.	Fern Ridge Reservoir, Central Oregon	Holte 1998[5]
Permanent Pond	7	0	0	0	Afton Canyon Ponds, Southern California	Lovich and Meyer 2002
Permanent Pond	6	6	34–191	8–280	Pico Creek-Pico Pond, Central California	Rathbun et al. 2002[3]
Permanent Pond	30	1	n.r.	10	Lowden Ranch Ponds, Northern California	Sloan 2012[6]
Seasonal Pond	0	9	48–217	80–345	Gillam and Taylor Ponds, Central California	Current Study

n.r. = not reported. [1]Reese 1996: The thesis contained additional data from the Trinity River but this was published in Reese and Welsh 1997 and therefore is not included here. [2]Reese and Welsh 1997: The paper states "All of the radio-equipped turtles spent seven months of the year away from the river at overwintering sites," no range was provided. [3]Rathbun et al. 2002: Distance and time on land were not separated between the stream and pond turtles and are therefore duplicated in both records. [4]Dan Holland, unpubl. report: No distance could be determined for two of the turtles that moved into terrestrial habitats and one turtle stayed in the stream system but did not move when the stream dried out. [5]Holte 1998: Eight turtles overwintered terrestrially or semi-terrestrially but the semi-terrestrial turtles were along the pond's edge and submerged in water after precipitation events. [6]Sloan 2012: During the winter of 2010–2011, 22 of 23 turtles overwintered in ponds and in the following winter, 15 of 16 did (some were the same turtles from the previous year). Most turtles moved from their summer pond to a different winter pond.

Factors influencing the selection of terrestrial habitats for traveling, resting, or overwintering are unclear. Telemetry studies have found high variability in terrestrial habitats used by turtles, including coniferous forest, oak woodland, and chaparral (Reese and Welsh 1997; Rathbun et al. 2002). Turtles are consistently found resting in shallow surface depressions within, and sometimes covered, by litter and duff (Reese and Welsh 1997), but little is known about why turtles select different micro- and macrohabitats. Even the thermal biology of this species, likely an important factor in overwintering, is poorly studied. The dearth of information on terrestrial habitat selection and use patterns presents a challenge for the development of species conservation and habitat management plans.

The goal of our study was to characterize the terrestrial movements and upland habitat use patterns of Western Pond Turtles at the Carrizo Plain Ecological Reserve in central California, USA and identify areas or habitats around ponds that may need protection from cattle and other human-associated disturbances. We focused our research on two populations that lived in seasonal ponds, an aquatic habitat that has not been well documented for this species. We hypothesized that turtles would move away from ponds in the late summer and fall as the ponds dried and return as soon as they refilled with winter rains. We also hypothesized that turtles would over winter in terrestrial habitats with higher cover (to avoid predation) and more frequently on south-facing slopes (to allow for basking).

MATERIALS AND METHODS

Study area.—We studied terrestrial turtle movements at Gillam and Taylor ponds located in the Chimineas Unit of the Carrizo Plain Ecological Reserve, San Luis Obispo County, California, USA (Fig. 1). Both ponds were constructed over 50 y ago to provide water for cattle. The California Department of Fish and Wildlife owns the 12,140 ha (30,000 ac) Chimineas Reserve, which is intended to protect over 50 sensitive species in the area. Cattle production on the reserve continues through private leasing and, during this study, cattle had access to the ponds during the summer as a water source. Public recreation on the site is restricted most of the year. Vegetation around both ponds consists mainly of Blue Oak (*Quercus douglasii*), Chamise (*Adenostoma fasciculatum*), California Buckwheat (*Eriogonum fasciculatum*), Juniper (*Juniperus californica*), Big Berry

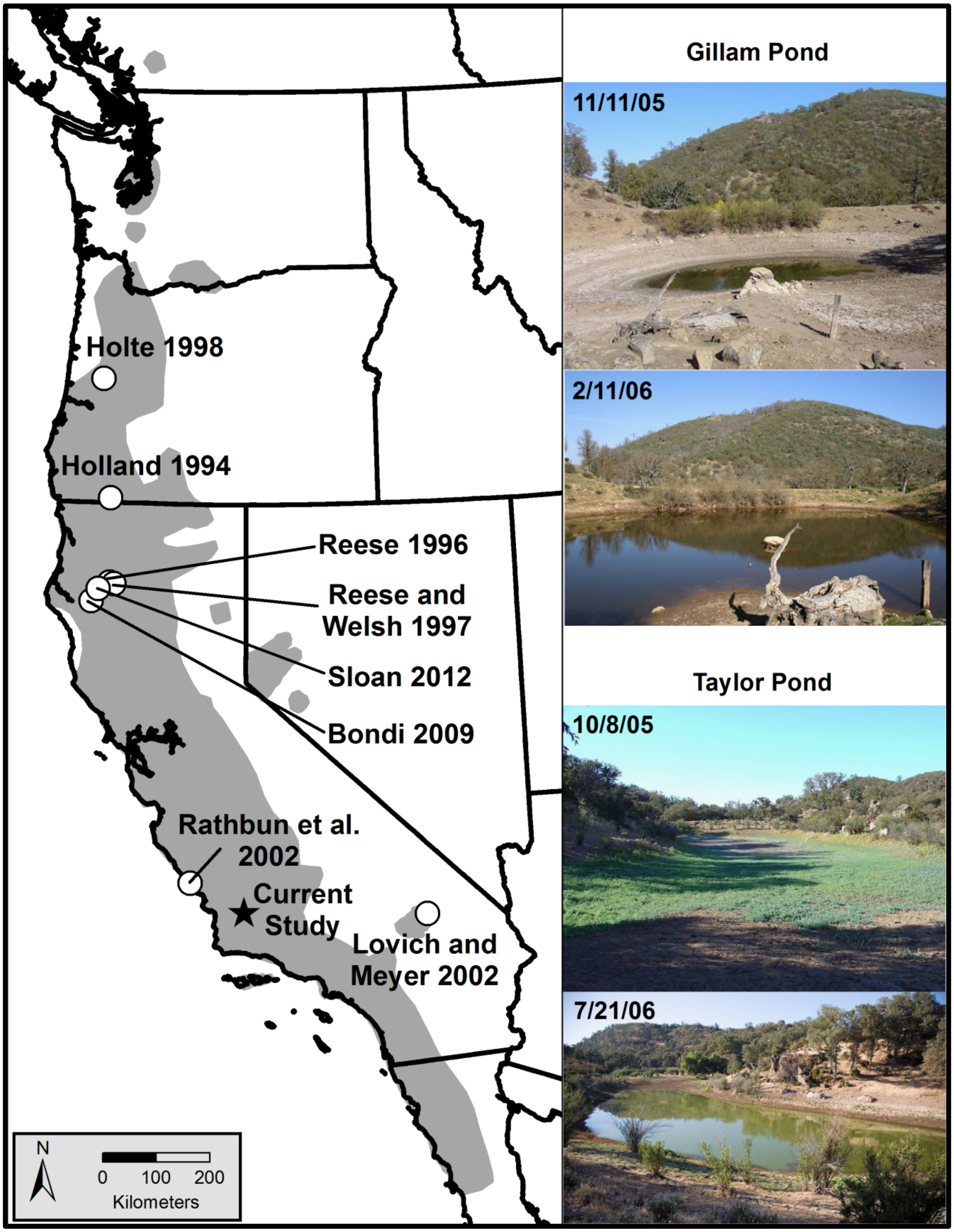

FIGURE 1. Location of the current study and previous studies that reported data on Western Pond Turtle (*Actinemys marmorata*) movements. The range of the Western Pond Turtle is shown in grey (NatureServe 2011). Photographs of Gillam and Taylor ponds at low and high water are shown with date of photograph. (Photographed by David Pilliod).

Manzanita (*Arctostaphylos glauca*), Ceanothus (*Ceanothus cuneatus*), and Yucca (*Yucca whipplei*). Also, there are patches of annual grassland and emergent wetland. The reserve is located on the eastern edge of the Santa Lucia Mountains in central California, which is characterized by a Mediterranean climate with hot, dry summers and cool, relatively wet winters. Most precipitation falls as rain from November to April and measurable rain is rare throughout the summer months (Fig. 2). Average rainfall for the study area is 26.9 cm but annual rainfall is highly variable (range 6–64 cm during the past 20 years; La Panza and Branch Mountain U.S. Department of Agriculture Remote Area Weather Stations [RAWS]). Temperatures fluctuate by season, reaching a high of 35° C in August and dropping below 0° C periodically between November and March; the annual freeze-free period is 200 days (La Panza RAWS).

Gillam Pond is a seasonally inundated, semi-permanent lentic water body that is fed by groundwater and overflow from a nearby spring. It fills with winter rains and usually dries by July, but occasionally holds water year-round (see Fig. 1). When full, Gillam Pond measures approximately 53 m × 42 m and is about 3.5 m deep. The shorelines are usually muddy and willows (*Salix* spp.) occur along the eastern shore. Taylor Pond, located 2.75 km north of Gillam Pond, also dries seasonally and refills with winter rains. Taylor Pond, however, is fed by groundwater only and dries completely each year, usually before Gillam Pond. It is a shallow pond that measures roughly 100 m × 30 m and is about 2 m deep when full. The gently sloping shores are covered with sedges and grasses.

Radio telemetry.—In September 2005, we trapped 93 turtles (81 at Gillam Pond and 12 at Taylor Pond) by hand and in floating wire traps (60 cm diameter × 100 cm long) baited with sardines. For each turtle, we measured carapace length (nearest mm) with calipers and mass (nearest g) with a digital scale (Table 2). We selected nine turtles (four from Gillam Pond and five from Taylor Pond) for radio attachment from the 16 that weighed more than 300 g (Fig. 3). This weight criterion was intended to reduce risk of hindering turtle movements (Rowe 2003). Selected turtles were fitted with 10 g radio transmitters (Advanced Telemetry Solutions Model R1860, frequency range 159.3–159.5). We attached transmitters to the external dorsal carapace with Loctite Gel® epoxy and Aquamend® epoxy. We embedded the 20 cm external antenna in epoxy along the marginal scutes (Rowe 2003). To increase field

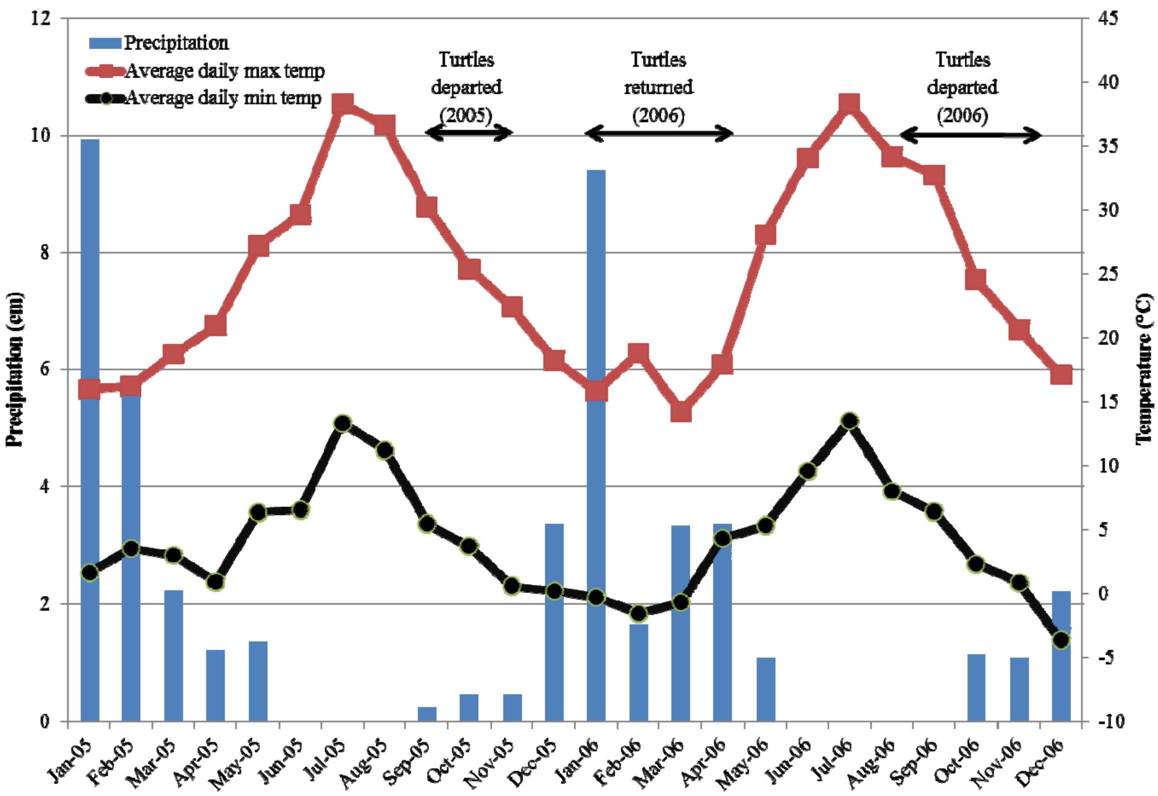

FIGURE 2. Average monthly daily maximum and minimum air temperature and total precipitation recorded at La Ponza Weather Station, located 28 km from the study ponds, from January 2005–December 2006.

TABLE 2. Characteristics of telemetered Western Pond Turtles (*Actinemys marmorata*) and duration of radio telemetry at the Carrizo Plain Ecological Reserve, CA from September 2005–December 2006. Turtles are identified using a five character symbol. For example, G310F signifies a turtle from Gillam Pond (G), frequency 310, female (F). Eight turtles had transmitters removed in December 2006 while T440M's transmitter fell off prematurely during the summer of 2006.

Turtle	Sex	Mass (g)	Carapace Length (mm)	Points Recorded	Days Tracked
G310F	F	370	135	74	446
G350F	F	360	132	74	446
G367F	F	310	131	73	446
G450M	M	300	126	74	446
T328M	M	330	133	75	446
T339F	F	340	136	76	446
T400F	F	660	163	75	446
T440M	M	370	142	49	345
T461F	F	455	147	76	446

identification of the turtles, we colored each transmitter either solid white, solid green, white base with green parallel lines, or white base with green crosshatch (e.g., Fig. 6). We released turtles at the capture site the next day after the epoxy had dried.

We radio-tracked turtles with both Telonics TR2 and Communications Specialist R1000 receivers and Telonics two-element (H-style) receiving antenna at least once a week except during the winter. Winter road conditions hampered our ability to travel to the site resulting in three extended periods of 30, 31, and 57 consecutive days where turtles were not located. We verified visually the exact location of each turtle whenever possible. We recorded a GPS location (Garmin 12XL™, accurate to 3 m) for each turtle that was visible (basking at pond or in uplands) for use in GIS analyses. Turtles that were underwater and thus not visible were recorded as "in pond" and their location recorded as pond centroid.

We radio-tracked turtles from September 2005 to December 2006. Eight turtles wore their transmitters for 446 days and were monitored through the entire winter of 2005–2006 and only partially through the winter of 2006–2007. One turtle (T440M) lost its transmitter after 345 days and thus was monitored only through summer 2006. During the study period, we located each turtle between 73 and 76 times (49 times for T440M; Table 2).

Habitat characterization.—Small sample sizes inhibited our ability to perform statistical analyses with useful inference, so we instead summarized habitat associations relative to available habitat at both macrohabitat and microhabitat scales. We found that some turtles occasionally made short movements (< 10 m) within their overwintering locations, a behavior reported in other studies (Rathbun et al. 2002). Therefore, we defined an overwinter site as a cluster of points within a 20 m diameter circle where a turtle stayed for more than a week. We characterized habitat

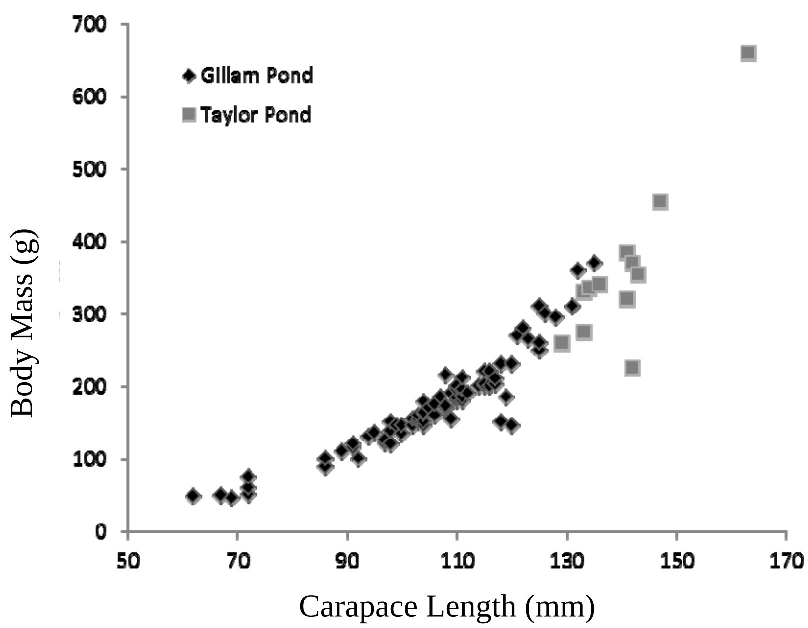

FIGURE 3. Size distribution of 93 Western Pond Turtles (*Actinemys marmorata*) captured in Gillam and Taylor ponds in September 2005. Nine of 16 turtles weighing more than 300 g were fitted with radio transmitters.

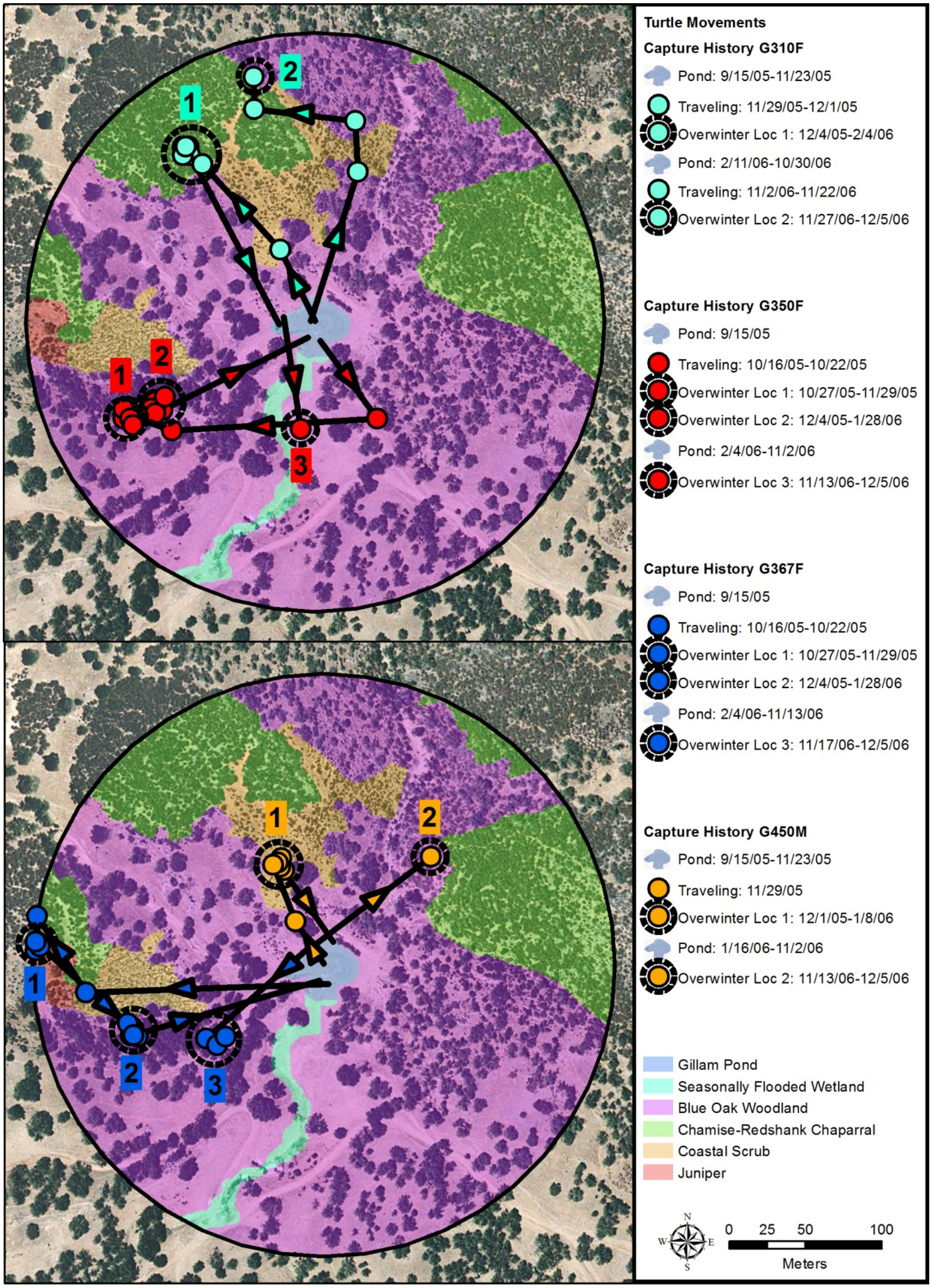

FIGURE 4. Terrestrial movements based on telemetry locations of Western Pond Turtles (*Actinemys marmorata*) associated with Gillam Pond at the Chimineas Unit of the Carrizo Plain Ecological Reserve, California from 15 September 2005 through 5 December 2006. Turtle T440M lost his transmitter by 26 august 2006. The top panel shows G310F and G350F. The bottom panel shows G367F and G450M.

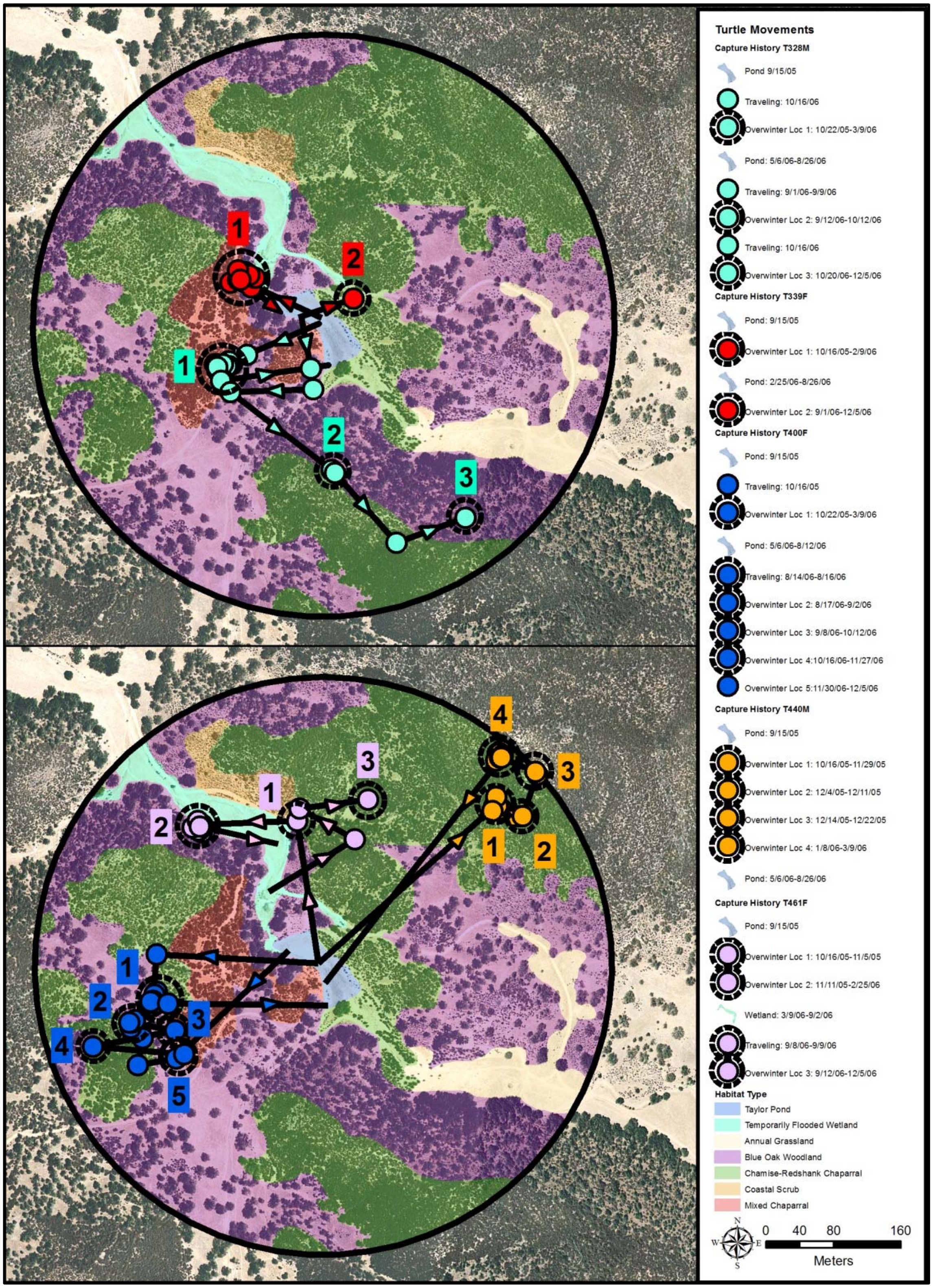

FIGURE 5. Terrestrial movements based on telemetry locations of Western Pond Turtles **(***Actinemys marmorata***)** associated with Taylor Pond at the Chimineas Unit of the Carrizo Plain Ecological Reserve, California from 15 September 2005 through 5 December 2006. Turtle T440M lost his transmitter by 26 august 2006. The top panel shows T328M and T339F. The bottom panel shows T400F, T440M, and T461F.

associations within these overwintering sites as averages (e.g., slope) or percentages (e.g., percent of days in each habitat type) using actual turtle locations.

To examine macrohabitat use patterns, we first calculated the furthest point from each pond any turtle traveled. In GIS, we placed a circle of this radius (188 m for Gillam Pond and 345 m for Taylor Pond) around each pond and used this polygon as the focal habitat within the turtles' traversable distance around the pond. We created a detailed plant community map of this focal habitat using the California Carrizo Vegetation layer and California Department of Fish and Wildlife 1-ft resolution aerial photography (California Department of Fish and Game 2010). Plant communities were verified by botanists in the field and classified as Annual Grassland, Blue Oak Woodland, Chamise-Red Shank Chaparral, Coastal Scrub, Juniper, and Mixed Chaparral. Using XTools Pro's Identity tool (DeLaune 2009) in ArcMap (ESRI 2009), we identified the vegetation type for each turtle location and calculated the number of days spent in each plant community at each overwintering site. For movements between consecutive locations, we assumed the turtle had moved to the new location on the day the new point was recorded. For the three periods of time when > 30 d passed between consecutive locations, we used the median day between the two consecutive locations as the date when the turtle moved. For example, we estimated the date of pond departure in the fall of 2005 as 1 October for G350F, G367F, T328M, T339F, T400F, T440M and T461F by using the midpoint between consecutive observations that were approximately one month apart. We estimated the date of return to the pond as 7 April for T328M and T400F using a similar approach.

We calculated elevation, slope, and aspect using a 1/3 Arc second digital elevation model (U.S. Geological Survey, Earth Resources Observation and Science Center, Sioux Falls, SD. Available from http://seamless.usgs.gov [Accessed 25 March 2011]) in ArcMap. Slope was calculated as percent slope (0–10%, 10–20%, 20–30%, and > 30%), with 0% as flat and 100% as 45 degrees from flat. We grouped aspect as North: 337.6–22.5; North East: 22.6–67.5; East: 67.6–112.5; South East: 112.6–157.5; South: 157.6–202.5; South West: 202.6–247.5; West: 247.6–292.5; and North West: 292.6–337.5. We calculated the number of days that turtles spent at each elevation, slope, and aspect.

We characterized microhabitat associations for each

FIGURE 6. Western Pond Turtle (*Actinemys marmorata*) G350F photographed on 11 November 2005 in a Blue Oak Woodland near a fallen branch. The turtle was buried within dry grass and oak leaves about 3 cm into loamy soil. Inset photo: Biologist Michael Pierce points at turtle's location. (Photographed by David Pilliod).

turtle located in a terrestrial habitat. We recorded dominant plants (defined as species with > 20% cover) within a 5 m radius of turtles. We estimated canopy cover of vegetation above each turtle using a curved densiometer for 0–1 m (understory) and > 1 m (overstory). We recorded fine wood (percentage cover of wood with < 1 cm diameter), coarse wood (percentage cover of wood with > 1 cm diameter), dominant substrate, and maximum duff depth (cm) within a 0.7 m^2 quadrat centered on each turtle. Substrate included rock, soil, moss, grass, leaf litter, woody debris, and shrubs. Unless otherwise noted, we reported all data summaries either as averages and standard deviations, or as percentages (e.g., 52% of days, or 26% of observations).

RESULTS

The mean mass of radio-tagged turtles was 388.3 ± 111.5 g; whereas, carapace lengths were 138.3 ± 11.1 mm (Table 2). The mean mass and carapace length for all other captured turtles was 183.9 ± 71.1 g and 108.3 ± 16.8 mm, respectively (Fig. 3). All radio-tracked turtles left their respective ponds as water levels began to lower during the summer and fall and they returned to the ponds weeks or months after they filled with water from winter rains. We did not record water depth at each pond, but movements away from ponds occurred three months after last measurable rainfall and when air temperatures were decreasing, approximately 1–2 months after reaching an annual maximum in July (Fig. 2). We did not detect any other movements away from the ponds, such as for nesting or dispersal.

Terrestrial movements.**—**During fall 2005, all but two turtles left their ponds between 15 September and 16 October; two turtles in Gillam Pond moved onto land on 29 November (Figs. 4 and 5; Table 3). Taylor Pond was completely dry by 25 September, while Gillam Pond held some water through the fall. During the 2005–2006 overwinter period, turtles spent a mean of 148 ± 62 d on land (range = 48–217 d). Turtles traveled further from Taylor Pond (mean = 211 ± 90 m) than from Gillam Pond (mean = 138 ± 45 m; Table 3). Turtles did not appear to move away from ponds in a particular direction nor select routes based on vegetation community or riparian corridors (Figs. 4 and 5).

We did not observe any mass migration behavior and turtle travel routes and patterns appeared independent of each other. As turtles moved from ponds into terrestrial habitats, they gained elevation (mean = 13 m; max = 35 m), although one turtle (T461F) traveled down the drainage system below the pond and lost 7 m elevation (Fig. 5). Total movements through the 2005–2006 winter ranged from 157–873 m (Table 3).

In the spring of 2006, turtles returned to Gillam Pond from 8 January to 11 February and Taylor Pond from 9 February to 7 April. Turtles remained in ponds for about 215 ± 79 days (Table 3). In general, turtles moved away from ponds 18 days earlier in fall 2006 than in fall 2005 (Table 3). Turtles G350F and G367F were exceptions, leaving Gillam Pond 45 and 47 days later in fall 2006 than in fall 2005. Turtles left Gillam Pond over a two week period in November 2006 (from 2–17 November; Fig. 4) and Taylor Pond 2–3 months earlier (from 12 August–8 September; Fig. 5).

All turtles moved uphill upon leaving their ponds in the fall of 2006, overwintering 1–57 m higher than the elevation of the ponds when full. Until we removed the radio transmitters in December 2006, we located turtles 154 ± 89 m (range = 68–307 m) away from their ponds (Table 3). On average these distances were comparable between the winters of 2005–2006 and 2006–2007 (Table 3), but individual turtles behaved differently between winters. Individual turtles varied widely in distances traveled and locations in the winter of 2005–2006 compared with 2006–2007 (Figs. 4 and 5; Table 3). Turtles selected different overwintering sites (mean = 110 ± 59 m apart; range = 44–207 m) from the sites used the previous winter. Three of the nine turtles used more than one terrestrial overwintering site during the winter of 2005–2006 and three different turtles (relative to the winter of 2005–2006) used more than one site during the winter of 2006–2007. Overwintering sites used within the same year ranged from 22 to 168 m apart mean = 88 ± 53 m).

Macrohabitat characteristics of overwintering sites.**—**Most terrestrial overwintering sites were located on fairly moderate slopes, but this varied widely (mean = 26 ± 17%; 1–59%). Turtles overwintered approximately equally on slopes with northeast (337–112°) facing aspects (n = 11 overwintering sites) as southwest (157–292°) facing aspects (n = 14 overwintering sites; Appendix 1 Table S1). Vegetation was associated with aspect and we found turtles on northeast slopes were generally in Blue Oak Woodlands and those on southwest slopes were mostly in Chaparral.

At Gillam Pond, turtles overwintered in vegetation communities approximately proportional to their availability. Vegetation communities within a 188 m buffer around Gillam Pond consisted of Blue Oak Woodland (70%), Chamise-Red Shank Chaparral (20%), Coastal Scrub (7%), and Juniper (3%). Turtles were found mostly in Blue Oak Woodland (68% of days), followed by Chamise-Red Shank Chaparral (14%), Coastal Scrub (10%), and Juniper (8%).

In contrast, turtles at Taylor Pond demonstrated some preference for certain vegetation communities over others. For example, Taylor turtles were found overwintering predominantly in Chamise-Red Shank

TABLE 3. Summary of Western Pond Turtle movements at the Carrizo Plain Ecological Reserve, California from September 2005 - December 2006. Distance traveled is a minimum cumulative distance estimated by summing line lengths between consecutive locations. Maximum distance from pond is a straight-line distance from pond edge to furthest observed turtle location. Transmitters were removed prior to the end of the 2006–2007 winter period and thus distances and days on land reported for this period are underestimates.

	2005- 2006 Winter Period						2006 - 2007 Winter Period			
Turtle	Departed pond	Distance traveled (m)	Max. distance from pond (m)	Days on land	Returned to pond	Days in water 2006	Departed pond	Distance traveled (m)	Max. Distance from pond (m)	Days on land
G328F	29-Nov	312	144	74	11-Feb	264	2-Nov	225	166	33
G350F	1-Oct	435	141	126	28-Jan	282	13-Nov	75	75	22
G367F	1-Oct	488	190	126	28-Jan	286	17-Nov	109	93	18
G451M	29-Nov	157	80	48	8-Jan	301	13-Nov	98	98	22
T328M	1-Oct	353	136	217	7-Apr	118	1-Sep	539	307	95
T339F	1-Oct	304	122	147	9-Feb	188	1-Sep	68	68	95
T400F	1-Oct	530	215	217	7-Apr	100	14-Aug	566	260	113
T440M	1-Oct	873	345	217	7-Apr	.	.	.	.	.
T461F	1-Oct	458	235	159	9-Mar	183	12-Sep	279	162	88
Average	14-Oct	434	179	148	25-Feb	215	5-Oct	245	154	61
St. dev.	26	200	79	62	34	79	40	204	89	40

Chaparral (52% of days) and Mixed Chaparral (20%) habitats, but these habitats represented only 40% and 5% of available habitats around the pond. Similarly, turtles were found only 21% of the time in Blue Oak Woodlands, yet this habitat represented 48% of the vegetation around the pond. No turtles were found in Annual Grasslands, a vegetation community representing 6% of available vegetation.

Microhabitat characteristics of overwintering sites.— We recorded the microhabitat characteristics of 15 overwintering sites, all in the 2005–2006 overwintering season. The dominant plant species within 5 m of overwintering turtles was most often Chamise (27%), but Blue Oak, Manzanita, and Yucca were also frequently present (Appendix 1 Table S2). Turtles tended to overwinter within some form of low vegetative cover (mean canopy cover = 40%, 12–90%, from 0–1 m above turtles), but not areas of dense overstory vegetation (mean canopy cover 24% above 1 m). Overwintering turtles were found nestled within a variety of substrates, including grass (26% of observations), low shrub ground cover (22%), leaves (22%), bare mineral soil (12%), and occasionally other substrates including downed wood, Yucca leaves, moss, and rocks. Duff was fairly shallow where turtles were found (range = 12–66 mm) and the carapace of all turtles was visible at overwintering sites (e.g., Fig. 6).

DISCUSSION

Although the inference of our data is limited to larger Western Pond Turtles living in these seasonal ponds, our findings provide further evidence that terrestrial overwintering behavior in pond turtles is highly variable and may be more common in seasonally inundated ponds than permanent ponds. This information has important implications for the biology and conservation of pond turtles living in Mediterranean climates (long dry summers) or in areas where hydroperiods of lentic habitats are changing (i.e., shortening or shifting temporally) as a result of climatic changes in precipitation patterns. Our data suggest that multiple factors may be influencing turtle movements around these two seasonally inundated ponds. In support of our hypothesis, hydroperiod of the ponds (i.e., when ponds fill and dry) appears to be one of the strongest determinants of the timing of terrestrial migrations and thus the duration of terrestrial activities for these turtles. In one of the only other Western Pond Turtle studies conducted in non-permanent waters, turtles in intermittent sections of the Mad River in northwestern California departed earlier than those in perennial sections (Bondi 2009). We found somewhat similar patterns where turtles departed Taylor Pond earlier than Gillam Pond each year, coincident with an earlier drying date. However, in contrast to the findings from Mad River where turtles that departed earlier also returned

earlier (Bondi 2009), we found that turtles from Taylor Pond returned months later than turtles from Gillam Pond even though the ponds refilled around the same time. Further evidence that factors other than hydroperiod influence the timing and length of terrestrial activities, we found that radio-tagged turtles in Gillam Pond departed over a two-month period in 2005–2006 and turtles in Taylor Pond departed over a one month period in 2006–2007, when water still remained in the pond.

Turtles from Taylor Pond traveled greater distances from the pond, both in terms of maximum distance from the pond and total distance traveled, and were more likely to use multiple overwintering sites, than turtles from Gillam Pond. We are uncertain why turtles from Taylor Pond travel further and move more often, but one explanation is that they simply have more time to move around because they spend more days on land. Gillam Pond is in a relatively steep area and thus it is also plausible that the energetic demands of climbing steeper slopes may limit the distances traveled by these turtles.

The minimum and maximum distance from the pond where we found overwintering turtles (75–345 m) was comparable to other studies (8–500 m; Table 1). Similar to other studies, we found no obvious relationship between sex or size of individuals and distances traveled (Reese and Welsh 1997; Rathbun et al. 2002). However, we had limited ability to address these questions because we only studied larger turtles in these populations and our sample size was small.

Radio-tracked turtles did not move along riparian corridors and their direction and distance of travel did not follow any obvious pattern. The propensity to travel through a variety of habitats and overwinter in different vegetation communities is consistent with other studies (Reese and Welsh 1997; Rathbun et al. 2002). A telemetry study conducted in the lower portion of four creeks in the Coast Range of central California found that the majority of turtles overwintered at the ecotone between dense woody vegetation and more open habitats (Rathbun et al. 2002). Most (64%) of the turtles (n = 28) overwintered in riparian vegetation; whereas, 18% each overwintered in oak or pine woodlands and in coastal sage scrub. We rarely found turtles in riparian areas, but otherwise found similar variability in macrohabitats used. The only obvious pattern was that turtles overwintered primarily within moderate to high cover provided by woody plants, a pattern consistent with our original hypothesis and other studies (Reese and Welsh 1997; Rathbun et al. 2002; Bondi 2009). We also found that turtles tended to use terrestrial habitats based on their availability, but some turtles seemed to prefer particular vegetation communities over others. Turtles may be choosing these areas as cover from predators, to aid thermoregulation, or because of the soil and moisture properties within these microhabitats. However, we found more generality in macrohabitat associations than microhabitat ground conditions, suggesting that thermal and protective cover may be more important than soil, litter, and duff properties.

Similar to other studies (Reese and Welsh 1997), we found that turtles overwintered on fairly moderate slopes but not with a particular aspect. Turtles overwintered equally on northeast (337–112°) and southwest (157–292°) slopes, each with different thermal and moisture characteristics. This finding was contrary to our original hypothesis that turtles would select south-facing slopes to allow for basking. Northeast slopes are generally cooler than southwest slopes and thus it is possible that turtles were choosing slopes to thermoregulate for their health or reproductive state. However, we are uncertain whether aspect or vegetation community, which covaried, were being selected. Blue Oaks retain their leaves through January, which may further complicate this relationship because solar radiation could increase slightly in February and March in this habitat type.

Turtles overwintering in terrestrial habitats periodically make short movements during the winter, possibly to bask or thermoregulate (Reese and Welsh 1997; Rathbun et al. 2002). We found that turtles made two types of movements among terrestrial sites, short movements (< 10 m) within a vegetation patch and longer movements (approx. 100 m) to new habitat patches with different macrohabitat characteristics. All turtles made these short intra-patch movements, but only four of nine turtles (44%) moved among patches in the first winter and three of eight turtles (38%) moved among patches in the second winter. This variability among individuals was also observed by Rathbun et al. (2002), who found that turtles could use between one to nine refuge sites during the winter. These differences may depend on the heterogeneity of habitats and changes in thermal conditions throughout the winter; some locations may vary less over a winter than others.

We did not observe overwintering site fidelity among the eight turtles monitored over two winters. Only one of the eight turtles returned to within 50 m of their overwintering site used the previous year. In contrast, evidence of upland site fidelity has been observed in the Coast Range of central California where 70% (16 of 23) of turtles returned to within 100 m and 52% returned to within 50 m of their previous season's overwintering site (Rathbun et al. 2002). Other studies have also reported individuals returning to the same overwintering location each year and generally using only one habitat type (Reese 1996; Goodman 1997; Bondi 2009).

We did not detect female movements on land during the breeding and egg laying stages (May–July) as have been described in other studies (Reese and Welsh 1997; Rathbun et al. 1992, 2002), but this is likely due to our weekly visits that were insufficient to detect this movement. Lovich and Meyer (2002) checked turtles at

least daily and found that females may only spend 0.83–86 h on land for nesting purposes, thus making detection of nesting activities difficult.

For terrestrial habitat protection, we suggest that a minimum buffer zone around these seasonally inundated ponds of at least 250–350 m would be sufficient, with a special emphasis on preserving moderately dense, woody vegetation (e.g., understory canopy cover about 40% and overstory canopy cover around 24%). Human activities within this buffer may need to be restricted, especially from September (or when ponds begin to dry) until March, corresponding to the period of active migration and overwintering. This buffer zone would be similar to that of Western Pond Turtles in other portions of the range (Reese and Welsh 1997; Rathbun et al. 2002) and other turtle species as well (Burke and Gibbons 1995). However, there is variation in terrestrial activities of Western Pond Turtles across its range and we suggest that the terrestrial protection provided for each population may need to be assessed at each area.

Acknowledgments.—We thank Patricia Anderson, Carolyn Rech, and the California Department of Fish and Wildlife for initiating and supporting this project. Funding was provided by the California Department of Fish and Wildlife (formerly California Department of Fish and Game), Resource Assessment Program through a federal State Wildlife Grant. Morgan Ball, Jared Bigler, Craig Fiehler, Jennifer Moonjian, Michael Pierce, and Martha Schauss assisted with field work and other logistics of the project. Hart Welsh provided helpful comments on an earlier version of the manuscript. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. government.

Literature Cited

Bondi, C.A. 2009. A comparison of Western Pond Turtle (*Actinemys marmorata*) movements in perennial and intermittent portions of a Northwestern California river system. M.A. Thesis, Humboldt State University, Arcata, California, USA. 87 p.

Burke, V.J., and J.W. Gibbons. 1995. Terrestrial buffer zones and wetland conservation: a case study of freshwater turtles in 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. Chelonian Research Monographs 5:001.1–001.9.

California Department of Fish and Game. 2010. Meta data and mapping report: Vegetation of the California Department of Fish and Game Carrizo Plain Ecological Reserve, including the Chimineas, American, Panorama, and Elkhorn Units, San Luis Obispo County, California. Internal report prepared by Vegetation Classification and Mapping Program. 58 p.

DeLaune, M.G. 2009. XTools ArcView Extension (Version 6.0.0). Oregon Department of Forestry, Oregon.

ESRI (Environmental Systems Resource Institute). 2009. ArcMap 9.3. ESRI, Redlands, California.

Garber, S.D., and J. Burger. 1995. A 20-yr study documenting the relationship between turtle decline and human recreation. Ecological Applications 5:1151–1162.

Goodman R.H., Jr. 1997. The biology of the Southwestern Pond Turtle (*Clemmys marmorata pallida*) in the Chino Hills State Park and the west fork of the San Gabriel River. M.S. Thesis, California State Polytechnic University, Pomona, California, USA. 81 p.

Holland, D.C. 1994. The Western Pond Turtle: Habitat and history. Final Report DOE/BP-62137 Bonneville Power Administration, U.S. Department of Energy and Wildlife Diversity Program, Oregon Department of Fish and Wildlife, Portland, Oregon, USA. 302 p.

Holte, D.L. 1998. Nest site characteristics of the Western Pond Turtle, *Clemmys marmorata*, at Fern Ridge Reservoir, in West Central Oregon. M.S. Thesis, Oregon State University, Corvallis, OR, USA. 119 p.

Jennings, M.R. 2004. An annotated check list of the amphibians and reptiles of California and adjacent waters. California Fish and Game 90:161–213.

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 256:537–545.

NatureServe. 2011. NatureServe Explorer: An online encyclopedia of life [web application]. Version 7.1. NatureServe, Arlington, Virginia. Available http://www.natureserve.org/explorer. (Accessed: November 7, 2011).

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

Rathbun, G.B., N. Siepel, and D. Holland. 1992. Nesting behavior and movements of Western Pond Turtles, *Clemmys marmorata*. Southwestern Naturalist 37:319–324.

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. Dissertation, University of California, Berkeley, California, USA. 253 p.

Reese, D.A., and H.H. Welsh, Jr. 1997. Use of terrestrial habitat by Western Pond Turtles, *Clemmys marmorata*: implications for management. Pp. 352–357 *In* Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles – An

International Conference. J. Van Abbema (Ed.). New York Turtle and Tortoise Society, New York, New York.

Rowe, J.W. 2003. Activity and movements of Midland Painted Turtles (*Chrysemys picta marginata*) living in a small marsh system on Beaver Island, Michigan. Journal of Herpetology 37:342–353.

Sloan, L.M. 2012. Populating structure, life history, and terrestrial movements of Western Pond Turtles (*Actinemys marmorata*) in lentic habitats along the Trinity River, California. M.S. Thesis, Humboldt State University, Arcata, California, USA. 111 p.

Ultsch, G.R. 2006. The ecology of overwintering among turtles: where turtles overwinter and its consequences. Biological Reviews 81:339–367.

David S. Pilliod is a Research Ecologist with the US Geological Survey at the Snake River Field Station, Forest and Rangeland Ecosystem Science Center in Boise, Idaho, USA. After graduating from the University of California Santa Cruz, he worked as a seasonal biologist on a variety of projects studying a variety of mammals and birds. His interest in amphibians and reptiles grew during his graduate experience at Idaho State University, where he received his PhD. His research on amphibians has focused on the effects of fire, forest management, disease and invasive species. He began studying Western Pond Turtles while working as an Assistant Professor in the Department of Biological Sciences at California Polytechnic State University, San Luis Obispo. His current research focuses on wildlife-habitat relationships and the factors influencing wildlife population dynamics, community structure, and species distributions. David is particularly interested in applications of long-term monitoring data to improve ecological understanding and management of shrubland and forested ecosystems. (Photographed by Elena Velasquez)

Justin L. Welty is an Ecologist with the US Geological Survey at the Snake River Field Station, Forest and Rangeland Ecosystem Science Center in Boise, Idaho, USA. He began his career in biology working as an undergraduate at the Merry Lea Environmental Learning Center in Wolf Lake, Indiana where he performed wetland surveys, identified insects, banded songbirds, trapped and tagged salamanders, and taught students of all ages about biology and the environment. In 2010, he received his M.S. from Boise State University in Raptor Biology studying the costs and benefits of variable nesting density in Burrowing Owls (*Athene cunicularia*). He also has a Graduate Certificate in Geographic Information Systems from Boise State which was earned in 2008. His research interests include avian ecology, predators, and using GIS information to analyze data and results. (Photographed by Corey Riding)

Robert Stafford has a worked on a wide array of wildlife species in central California for over 25 y. He received his Bachelors of Science in Biology from California State University, Bakersfield. His primary expertise is the vertebrate ecology of the Carrizo Plains region where he is working with colleagues to refine aerial monitoring techniques for detecting large scale population trends in Giant Kangaroo Rats (*Dipodomys ingens*). He is currently employed as an Environmental Scientist with the California Department of Fish and Wildlife (CDFW) and is the reserve manager for a number of CDFW properties including the Chimineas Unit of the Carrizo Plain Ecological Reserve. (Photographed by Karen Stafford)

APPENDIX 1. Macrohabitat associations of radio-located Western Pond Turtles at the Carrizo Plain Ecological Reserve, California, USA during winter. Data were calculated for all overwintering sites throughout the winter of 2005–2006 and part of the winter of 2006–2007. Weighted means adjust for the number of days.

							Vegetation Community (% of days within while on land)					
Turtle	**Overwinter site**	**No. points**	**No. days**	**Slope (%)**	**Aspect**	**Elevation difference from pond (m)**	**Annual grassland**	**Blue oak woodland**	**Chamise - redshank chaparral**	**Coastal scrub**	**Juniper**	**Mixed chaparral**
G310F												
	1	12	74	23	S	31	0	0	97	3	0	0
	2	8	33	43	SE	33	0	79	21	0	0	0
G350F	1	10	49	13	N	8	0	100	0	0	0	0
	2	9	62	7	NE	7	0	100	0	0	0	0
	3	7	22	6	N	4	0	100	0	0	0	0
G367F	1	8	38	40	SW	27	0	0	21	0	79	0
	2	9	62	2	S	6	0	100	0	0	0	0
	3	6	18	6	E	5	0	100	0	0	0	0
G450M	1	7	46	21	S	12	0	0	0	100	0	0
	2	7	22	59	W	1	0	100	0	0	0	0
T328M	1	23	173	1	NE	16	0	3	0	0	0	97
	2	8	34	46	NE	33	0	100	0	0	0	0
	3	12	46	42	NE	41	0	100	0	0	0	0
T339F	1	21	132	25	E	7	0	49	0	0	0	51
	2	27	95	2	NE	1	0	0	100	0	0	0
T400F	1	22	167	21	W	15	0	0	100	0	0	0
	2	11	22	29	N	15	0	9	91	0	0	0
	3	11	38	10	W	15	0	0	0	0	0	100
	4	11	45	45	NW	25	0	0	100	0	0	0
	5	2	5	8	W	15	0	0	0	0	0	100
T440M	1	10	49	34	SW	35	0	0	100	0	0	0
	2	3	10	41	W	39	0	0	100	0	0	0
	3	2	25	45	W	57	0	0	100	0	0	0
	4	8	89	43	W	51	0	0	100	0	0	0
T461F	1	5	26	11	SW	0	0	0	0	100	0	0
	2	17	118	46	N	-7	0	100	0	0	0	0
	3	23	84	21	W	3	0	0	100	0	0	0
Mean				**26**		**18**	**0**	**39**	**38**	**8**	**3**	**13**
St. Dev.				**17**		**17**	**0**	**47**	**48**	**27**	**15**	**32**
Wt. Mean				**23**		**16**	**0**	**34**	**42**	**5**	**2**	**18**

APPENDIX 2. Microhabitat observations of radio-located Western Pond Turtles at the Carrizo Plain Ecological Reserve, California during the winter of 2005–2006. The weighted mean accounts for number of observations. Missing values are indicated by a dot.

			Dominant plants within 5 m of turtle (% of observations)									Percent cover within 0.7 m quadrat (%)				Substrate where turtle found (% of observations)						
Turtle	**Overwinter site**	**No. observations**	**Buckwheat**	**Blue oak**	**Chamise**	**Grass**	**Juniper**	**Manzanita**	**Yucca**	**Mixed[1]**	**Other[2]**	**Understory canopy**	**Overstory canopy**	**Fine wood**	**Coarse wood**	**Soil**	**Leaves**	**Down woody debris**	**Grass**	**Shrubs**	**Other[3]**	**Duff depth (mm)**
G310F	1	8	0	0	100	0	0	0	0	0	0	12	47	50	12	0	10	10	50	30	0	45
G350F	1	8	0	38	0	50	0	12	0	0	0	.	.	.	.	38	25	25	12	0	0	.
	2	7	0	78	0	22	0	0	0	0	0	12	36	13	41	0	67	0	11	0	22	37
G367F	1	10	10	0	10	0	0	0	80	0	0	.	.	.	.	0	0	0	10	0	90	.
	2	7	0	33	0	0	33	0	0	0	33	66	12	11	5	0	44	11	11	11	22	46
G450M	1	5	86	14	0	0	0	0	0	0	0	90	3	20	0	0	29	0	29	43	0	20
T328M	1	18	0	0	26	4	0	22	0	48	0	27	34	7	14	17	22	4	43	13	0	51
T339F	1	18	0	0	14	0	0	86	0	0	0	65	48	10	4	0	71	5	14	5	5	66
T400F	1	18	0	0	64	0	0	0	0	36	0	29	17	27	9	9	27	14	45	5	0	39
T440M	1	10	0	0	10	0	0	0	0	90	0	.	.	.	.	0	30	10	30	30	0	.
	2	3	0	0	67	0	0	0	0	33	0	.	.	.	.	0	0	0	67	33	0	.
	3	2	0	0	50	0	0	0	0	50	0	25	8	10	25	0	0	0	50	0	50	30
	4	8	0	0	63	0	0	0	0	25	12	58	13	27	19	50	0	0	12	38	0	26
T461F	1	5	0	0	0	0	0	0	100	0	0	.	.	.	.	0	0	0	0	100	0	.
	2	15	0	11	0	44	0	39	0	0	6	18	20	8	4	67	11	0	0	22	0	12
Mean			**6**	**12**	**27**	**8**	**2**	**11**	**12**	**19**	**3**	**40**	**24**	**18**	**13**	**12**	**22**	**5**	**26**	**22**	**13**	**37**
St. Dev.			**25**	**10**	**28**	**13**	**10**	**26**	**35**	**29**	**10**	**26**	**15**	**8**	**9**	**23**	**22**	**5**	**22**	**28**	**28**	**18**
Wt. Mean			**4**	**9**	**26**	**9**	**2**	**18**	**9**	**20**	**3**	**28**	**21**	**13**	**8**	**15**	**22**	**6**	**24**	**17**	**4**	**30**