TERRESTRIAL HABITAT USE BY PACIFIC POND TURTLES IN A MEDITERRANEAN CLIMATE

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ABSTRACT—The Pacific pond turtle (*Clemmys marmorata*) is a widespread aquatic turtle in the Pacific states, yet relatively little is known about its ecology. We radio-tracked 34 individuals during an 8 year period in 4 small coastal creeks in central California to determine their use of terrestrial upland habitats. Most of our turtles left the drying arroyos during late summer and returned after winter floods. Turtles spent an average of 111 days at these land refuges, which were located in woodland and coastal sage scrub habitats an average of 50 m from arroyos. Most gravid females left the creeks during June to oviposit in sunny upland habitats with low vegetation structure, such as grazed pastures. Nest sites were an average of 28 m from creeks. Terrestrial basking sites averaged 4.5 m from streams, but were only used for a few days. We believe the use of terrestrial upland sites was related to the Mediterranean climate and the resulting unique hydrodynamics of the small coastal arroyos (dry in summer and flooding in winter).

RESUMEN—La tortuga *Clemmys marmorata* es una tortuga acuática ampliamente dispersa en los estados del Pacífico, sin embargo, se sabe muy poco acerca de su ecología. Equipamos a 34 individuos con radios durante un período de 8 años en 4 pequeños riachuelos costaneros en el centro de California para determinar el uso de hábitats terrestres tierra arriba. La mayoría de las tortugas abandonó los arroyos casi secos a fines de verano y regresaron después de las inundaciones de invierno. Las tortugas pasaron un promedio de 111 días en estos refugios terrestres, los cuales estaban localizados en hábitats como bosques y matorrales de artemisa costaneros a un promedio de 50 metros de los arroyos. Las hembras grávidas dejaron los arroyos durante junio para desovar en hábitats asoleados tierra arriba con poca vegetación tales como pastos cortos. Los nidos estuvieron a un promedio de 28 metros de los arroyos. Los sitios terrestres para asolearse promediaron 4.5 metros de los arroyos, pero fueron usados solamente por pocos días. Creemos que el uso de hábitats terrestres tierra arriba se relaciona al clima mediterráneo y a la peculiar hidrodinámica resultante de los pequeños arroyos costaneros (secos en el verano e inundados en el invierno).

The Pacific pond turtle (*Clemmys marmorata*) is distributed along the Pacific coast of North America west of the Cascade Mountains and Sierra Nevada, from Washington south to Baja California Norte (Stebbins, 1985). The major portion of the distribution is in California, in a climate characterized by long, warm, dry summers and short, mild, wet winters (Dallman, 1998). The predictable yearly wet-dry cycle is further characterized by large variations in the amount of rainfall within and between winters (Gasith and Resh, 1999) that can be rigorous for an aquatic vertebrate. Indeed, climatic adversity may partially explain why the Pacific pond turtle is the only native freshwater chelonian in this Mediterranean region (Stebbins, 1985).

These features of *C. marmorata* offer unique research opportunities. Early accounts (e.g., Storer, 1930) were followed by ecological field studies in northern California (Bury, 1972, 1986) and central California (Holland, 1985, 1994). When the Pacific pond turtle became a candidate for federal listing as threatened or endangered, resource managers and biologists realized how little information was available on

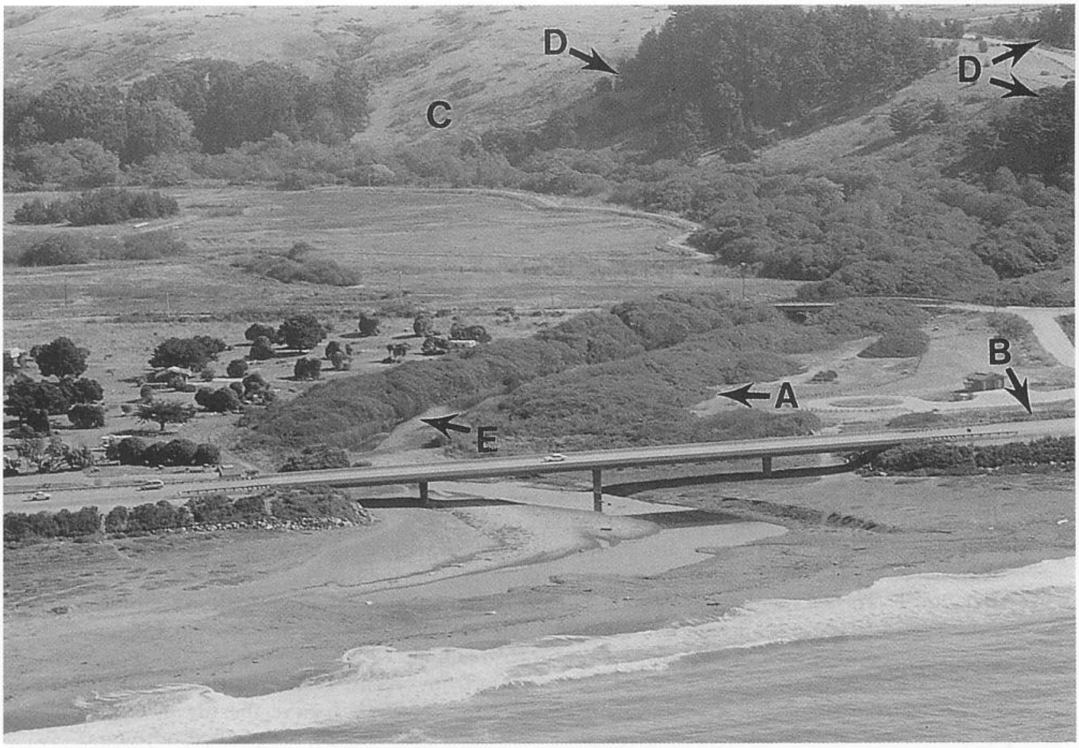

FIG. 1—Aerial photograph (November 1993) of the mouth, lagoon, and lower riparian corridor of San Simeon Creek. Riparian vegetation is dominated by willows. The northern (left) side of the riparian corridor has been highly modified by a public campground (foreground) and the Cambria wastewater spray field. The southern side is a relatively undisturbed mosaic of grassland, coastal sage scrub, and Monterey pine woodland. Terrestrial refuges of Pacific pond turtles were located at ecotones between grassland and willow thickets (site A), and grasslands and Monterey pine woodlands (D). Nesting sites were located in open grasslands (C) and in coastal sage scrub on the shoulder of State Highway 1 (B). Terrestrial basking sites were located on sandbanks on each side of the creek and lagoon (E).

this species (United States Fish and Wildlife Service, 1989, 1993). We initiated our studies in the coastal creeks and lagoons of central California in 1991 with the objective of learning more about the ecology of the Pacific pond turtle. Here, we report the results on the use of terrestrial habitats by radio-tagged *C. marmorata*.

METHODS—*Study Area*—Our research was done in the lower portions of 4 creeks along a 12 km stretch of coast north of the town of Cambria (35°32′N, 121°04′W) in northern San Luis Obispo Co., California. Arroyo Laguna–Oak Knoll Creek, Little Pico Creek, Pico Creek, and San Simeon Creek (north to south) drain the Santa Lucia Mountains, which are part of the Coast Range. These mountains rise from a 2 to 3 km wide coastal terrace to 3,264 m, about 12 km inland from the coast. As is typical of streams in regions with a Mediterranean climate, the riparian corridors are well defined (Gasith and Resh, 1999) by thickets dominated by willows (*Salix*), alder (*Alnus rhombifolia*), and blackberry (*Rubus*). A mosaic of annual exotic grasslands, oak (*Quercus agrifolia*) or pine (*Pinus radiata*) woodlands, and coastal sage scrub (Fig. 1) dominate the surrounding uplands. Near the mouths of the creeks, the woody riparian vegetation changes to herbaceous wetland plants dominated by bulrushes (*Scirpus*), cattails (*Typhus*), sedges (*Juncus*), pickleweed (*Salicornia virginica*), saltgrass (*Distichlis spicata*), and cinquefoil (*Potentilla*) that are associated with lagoon-estuary systems.

Pico Creek is unique among the 4 streams in that it has a permanent 0.16–0.25 ha man-made, freshwater pond in the flood plain next to the lagoon at the mouth. The pond is 2 to 3 m deep with a margin dominated by bulrushes. Our study focused on the

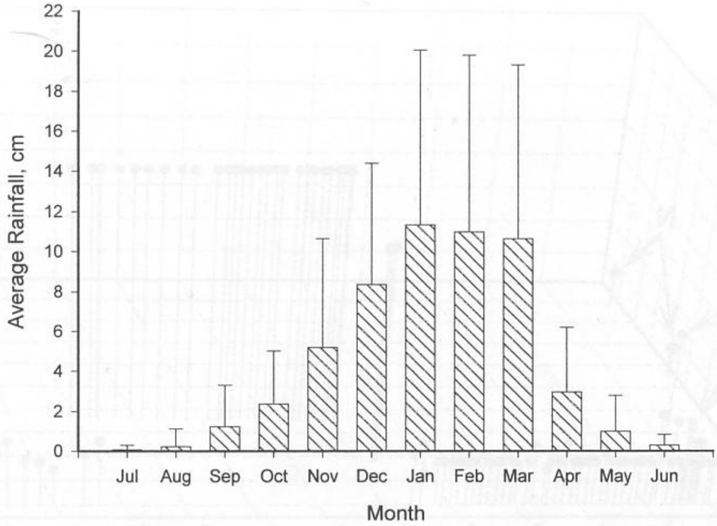

FIG. 2—Mean (bars) and standard deviation (lines) rainfall at the mouth of Santa Rosa Creek (3.5 km south of San Simeon Creek) for 25 years (1973–1997). Yearly mean = 55.52 ± 22.76 cm. Data courtesy of the Cambria Community Services District.

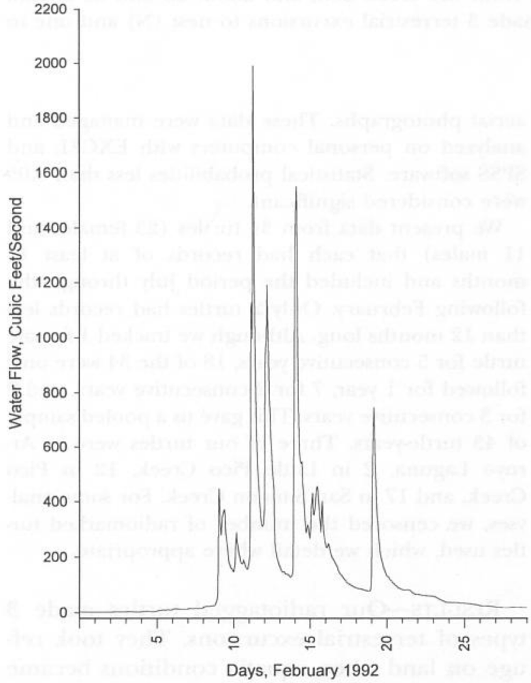

FIG. 3—Instantaneous hourly water flows (cubic ft/sec) in San Simeon Creek during February 1992. Measurements were recorded at a gauging station (#22) 1.8 km upstream from the mouth. Data courtesy of the San Luis Obispo Co. Department of Engineering.

lower parts of the 4 streams, including the lagoons and Pico Pond, and spanned 8 years (1991–1998).

Average annual precipitation in the area is nearly 56 cm (22.0 in), with 75% of this falling from December through March (Fig. 2). This pattern, typical of Mediterranean climates (Gasith and Resh, 1999), results in highly seasonal creek flows. By October, our creeks often stopped flowing and only scattered pools remained until the winter runoff, which usually started in December. During consecutive years of below average precipitation, even isolated pools in the creeks disappeared. Another characteristic of these streams was winter flow prone to unpredictable and abrupt change. Often, flows would jump 2 orders of magnitude within several hours (Fig. 3) when strong Pacific storms moved through the region. Air temperatures in our area were also typical of a Mediterranean climate, with the buffering effects of nearshore ocean upwellings and currents maintaining air temperatures between freezing and 20°C year around (Dallman, 1998).

Capture and Radiotagging—We set commercial turtle traps baited with canned sardines each spring and fall in likely turtle habitat in each creek during 4 consecutive days. We also opportunistically captured by hand any turtles seen in the creeks or on land. The sex of all turtles was determined based on morphological traits, and during the breeding season from late April through June, all females were palpated for shelled eggs, and those that were gravid were X-rayed. We marked each turtle for individual identification with a passive integrated transponder (PIT) tag injected intra-abdominally (Elbin and Bur-

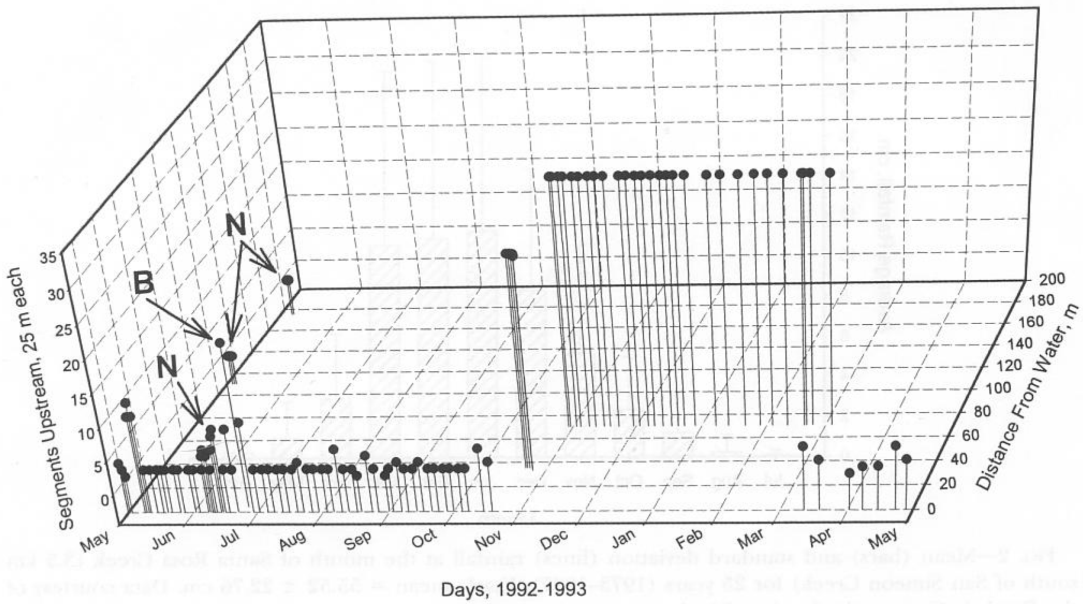

FIG. 4—Three dimensional plot of the spatial and temporal locations of radio-tagged female Pacific Pond Turtle # 93D20 in San Simeon Creek from May 1992 through April 1993. Each black dot, with a drop-line to the X-axis, represents a single radiolocation. From mid-October 1992 through early March 1993 the turtle occupied 2 terrestrial refuges, about 35 m and 75 m from the creek bed, and about 25 and 35 stream segments (1 segment = 25 m) upstream. The turtle made 3 terrestrial excursions to nest (N) and one to bask (B).

ger, 1994). All animals with PIT tags were notched on the left femoral scale of the plastron. Some individuals also were marked with unique patterns of notches on the marginal scales of the carapace.

We attached radio transmitters to some adult turtles (carapace lengths > 14 cm). The transmitters measured 4.5 cm by 2.0 cm by 1.0 cm, weighed about 15.0 g and had an internal helical antenna. Predicted battery life was about 175 days. Radio packages were glued onto the middle of the carapace with Devcon 5-min epoxy, and then contoured to the shell with dental acrylic colored black with copy machine toner. We used a receiving system composed of a directional "H-style" antenna attached to a 164 MHz wildlife radio receiver. Under good field conditions the transmission range was at least 1.0 km.

We divided each creek into 25-m-long segments, starting from the mouth, and each side within a segment was further divided into quarters. We used standard homing techniques (as opposed to triangulation; Kenward, 1987) to locate our radiotagged turtles about every 2 weeks, although many, including some gravid females, were followed more intensively—sometimes nearly continuously. We recorded turtle identity, date, time, location to the nearest quarter segment (e.g., within ca. 6 m), and associated habitat on field data sheets and maps based on aerial photographs. These data were managed and analyzed on personal computers with EXCEL and SPSS software. Statistical probabilities less than 0.05 were considered significant.

We present data from 34 turtles (23 females and 11 males) that each had records of at least 11 months and included the period July through the following February. Only 2 turtles had records less than 12 months long. Although we tracked 1 female turtle for 5 consecutive years, 18 of the 34 were only followed for 1 year, 7 for 2 consecutive years, and 2 for 3 consecutive years. This gave us a pooled sample of 43 turtle-years. Three of our turtles were in Arroyo Laguna, 2 in Little Pico Creek, 12 in Pico Creek, and 17 in San Simeon Creek. For some analyses, we censored the number of radiomarked turtles used, which we detail where appropriate.

RESULTS—Our radiotagged turtles made 3 types of terrestrial excursions. They took refuge on land when aquatic conditions became particularly adverse (e.g., flooding), they nested on land, and they sometimes rested on land well away from water. These 3 patterns were distinct from each other, as illustrated by the spatio-temporal data over a year for a female in San Simeon Creek (Fig. 4). Details of the

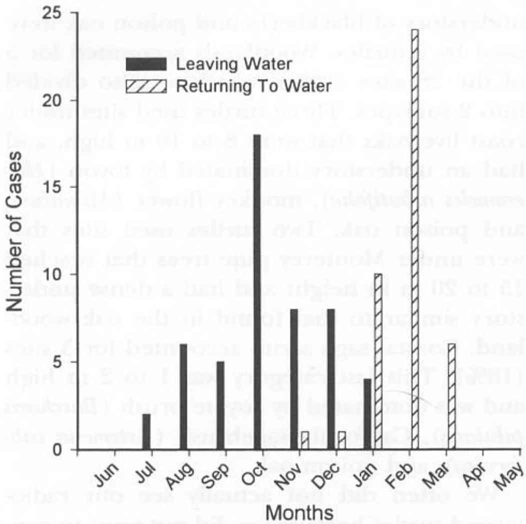

FIG. 5—Frequency distribution of Pacific Pond Turtles leaving water for, and returning from, terrestrial refuges along coastal creeks of central California, 1991–1998. The number of turtles leaving and returning are different because of predation while on land (see text).

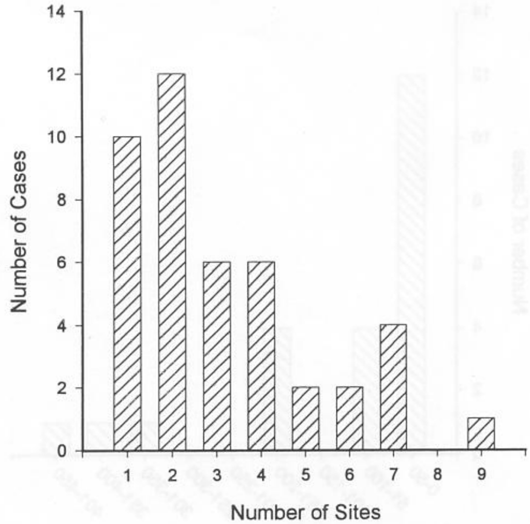

FIG. 6—Frequency distribution of the number of multiple terrestrial refuges used by Pacific pond turtles within a season in coastal creeks of central California, 1991–1998.

characteristics of each of these patterns of land use follow:

Refuge Sites—Turtles did not show any pattern from year to year on the dates they started or finished using terrestrial refuges. For example, the female (# 21B38) that we radiotracked for 5 consecutive years left creek water as early as 31 October and as late as 9 January, and the range of her land-use was 34–133 days. The pooled average duration of terrestrial refuging for 28 individuals (43 turtle-years) was 111 days ($SD = \pm 44.3$ days, range = 34 to 191 days), with no significant difference between the sexes (*t*-test, $P > 0.3$). The distribution of the number of turtles leaving and returning by month (Fig. 5) shows that October was the modal month for leaving water, and February was the modal month for returning. The pooled average exit day was 25 October ($SD = \pm 52$ days), and the mean return day was 21 February ($SD = \pm 25$ days). Although the distribution by month for leaving water spans 7 months from July through the following January, the spread for returning is tighter, ranging 5 months from November through March (Fig. 5).

The difference in the sample size (Fig. 5) for leaving turtles ($n = 51$) and returning turtles ($n = 43$) is due to deaths while on land. For example, of the 34 radio-tagged turtles, 13 were found dead on land and of these, 8 showed obvious signs of predation, probably by raccoons (*Procyon lotor*). We lost track of 9 radio-tagged turtles, most likely because of predation and radio failure. We believe it is unlikely that any of the missing turtles moved outside of our search area. We removed the transmitters from 10 *Clemmys,* and 2 were still radiotagged at the end of 1998.

The mean perpendicular distance from the edge of creek beds to the furthest refuge site for the 43 turtle-year cases was 49.7 m ($SD = \pm 54.8$ m, range = 8 to 280 m). There was no difference between the sexes (*t*-test, $P < 0.5$). Although we did not routinely determine elevation of land sites above creek beds, all sites were outside of areas that would be expected to flood during normal winter rains and many were in upland habitats. The maximum elevation of a refuge site was about 38 m above the creek bed.

Turtles did not always remain at the same refuge site during the same excursion. For example, 22 of the 43 cases (51%) involved only 1 or 2 sites. At the other extreme, one turtle used 9 different sites (Fig. 6). The 23 turtles that we tracked for 2 or more consecutive years showed some season-to-season site fidelity. Six-

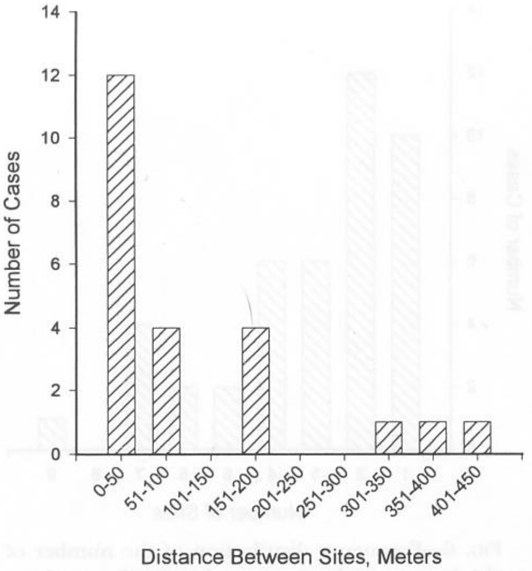

FIG. 7—Frequency distribution of the distances (in 50 meter increments) between terrestrial refuges used by Pacific pond turtles in consecutive seasons in coastal creeks of central California, 1991–1998.

teen (70%) returned to within 100 m of their previous season's first land site, and 12 of these (52%) within 50 m (Fig. 7). In several cases, turtles returned to within centimeters of a previous location. At the other extreme, 425 m separated land sites between consecutive seasons for 1 turtle (Fig. 7).

Not all of the radio-tagged turtles left their aquatic habitats for terrestrial refuges. Only 6 of 12 turtles in the Pico Pond–Pico Creek system left water, but at San Simeon Creek, which has no permanent pond, all 17 turtles used terrestrial refuges ($P = 0.004$, Fisher Exact Test).

The ground at refuges was typically covered with dense leaf litter produced by an overstory of woody vegetation. For the vegetation type at refuges, we used only the first land site per year for each turtle ($n = 28$) to avoid auto correlation biases. Riparian areas accounted for 18 of the 28 sites (64%). We subdivided these into 2 subtypes. Dense riparian thickets of willow that were about 5 to 7 m high and supported a dense understory of blackberry, poison oak (*Toxicodendron diversilobum*), and Cape ivy (*Delaria odorata*), were used by 16 turtles. Riparian vegetation dominated by large, widely spaced sycamore (*Platanus racemosa*) and alder trees that were 10 to 15 m high and had a sparse understory of blackberry and poison oak were used by 2 turtles. Woodlands accounted for 5 of the 28 sites (18%), which we also divided into 2 subtypes. Three turtles used sites under coast live oaks that were 8 to 10 m high, and had an understory dominated by toyon (*Heteromeles arbutifolia*), monkey flower (*Mimulus*), and poison oak. Two turtles used sites that were under Monterey pine trees that reached 15 to 20 m in height and had a dense understory similar to that found in the oak woodland. Coastal sage scrub accounted for 5 sites (18%). This last category was 1 to 2 m high and was dominated by coyote brush (*Baccharis pilularis*), California sagebrush (*Artemesia californica*), and poison oak.

We often did not actually see our radio-tagged turtles because we did not want to continually disturb them, especially at their terrestrial refuges. But in several cases we found alert turtles in direct sunlight with their head and legs extended and eyes open, as if basking. When we recaptured turtles to replace their transmitters, however, we sometimes excavated them from beneath 5 to 10 cm of leaf litter and duff. Some of these buried animals seemed to be dormant, with their eyes sealed shut with dried fluid. Whether buried or not, turtles at refuges were situated so that they could be exposed to direct sunlight during part of the day, although we did not collect data on basking frequency. In dense riparian vegetation and thick coastal sage scrub, refuges were located at the ecotone between dense woody vegetation and more open habitats. These edges were often well defined by edaphic factors, vehicle or foot paths, or fenced grassland pastures used for livestock grazing (Fig. 1).

Nesting Sites—In 1992 and 1993, between 4 May and 30 June, we radiotracked 10 gravid females during 15 terrestrial excursions to lay eggs. Also, tourists showed us a nest where they accidentally discovered a female laying eggs, and we found nests with fresh egg fragments that had been recently eaten, probably by a raccoon or striped skunk (*Mephitis mephitis*). However, because of the wariness of nesting females, we do not have complete records for all these animals; some are missing starting or finishing times to their excursions, and we never discovered the exact nesting sites for others (Table 1).

TABLE 1—Summary of nesting data for radio-tagged Pacific pond turtles during 1992 and 1993 in central coastal California.

ID	Creek[1]	Nest[2]	Start date of nesting excursion	Finish date of nesting excursion	Start time	Finish time	Maximum distance (m) from water	Elevation above creek bed (m)	Slope[3] (degrees)
15913	SS	E	28 May 92	31 May 92	—	—	75.0	12.5	20
85715	PC	P	—	8 Jun 92	—	—	27.5	1.3	0
95161	SS	A	5 Jun 92	5 Jun 92	1700	2000	16.0	3.5	30
95161	SS	A	6 Jun 92	6 Jun 92	0955	1135	15.0	3.0	0
95161	SS	A	8 Jun 92	8 Jun 92	0745	0953	18.0	4.4	30
21B38	SS	A	11 Jun 92	11 Jun 92	1735	—	35.0	3.0	0
21B38	SS	N	14 Jun 92	14 Jun 92	1630	1915	9.5	1.5	0
22857	SS	E	12 Jun 92	13 Jun 92	1415	—	35.0	3.0	0
2441D	PC	A	24 Jun 93	24 Jun 93	1700	1830	35.0	17.5	10
57D59	SS	N	13 Jun 92	13 Jun 92	1615	1917	15.0	1.0	10
62E4C	PC	N	30 Jun 93	1 Jul 93	—	—	80.0	0.5	0
85715	PC	A	28 Apr 92	28 Apr 92	1740	—	35.0	1.3	0
93D20	SS	E	4 May 92	8 May 92	—	—	170.0	11.0	10
93D20	SS	N	13 Jun 92	13 Jun 92	1615	1720	17.0	3.5	30
93D20	SS	A	7 Jun 93	7 Jun 93	—	—	33.0	1.0	0
—	AL	P	—	10 Aug 92	—	—	6.0	3.0	30
—	SS	N	– Jun 92	– Jun 92	—	—	30.0	5.2	10

[1] SS = San Simeon Creek, PC = Pico Creek, AL = Arroyo Laguna.

[2] E = nest location estimated ± 10 m, N = nest located, A = aborted nest, P = predated nest with egg shells.

[3] To nearest 10° from horizontal, which = 0°.

Of the 10 females that we radiotracked (those with identification numbers in Table 1), 7 successfully laid eggs on their first nesting trip, but 2 each abandoned at least 1 site before nesting, and 1 left at least 3 sites on 3 different days before successfully laying. Three of the 10 radio-tagged females (# 15913, # 22857, and # 93D20 in Table 1) spent 1 to 3 days traveling in upland areas, and we did not locate their exact nesting sites, but we know from palpation that they successfully oviposited. These 3 females moved a maximum of 35, 75, and 171 m perpendicular from water during their excursions (mean = 93.7 m). Five of the 10 radio-tagged females completed their land forays in less than 24 h and successfully nested. The average perpendicular distance from water for these females was 29.8 m (*SD* = ±28.8, range = 9.5 to 80.0 m).

In 10 cases, we had accurate times when females left the water to nest: 2 were in the morning, 1 was in the early afternoon, and 7 were in the evening (Table 1). We know that some of the animals that we radiotracked evaded us by nesting after dark (e.g., # 95161 in Table 1). In 7 of the 15 nesting excursions we obtained duration of turtles on land; 3 lasted about 1.5 h, 1 was about 2 hours long, and 3 were each about 3 h long. Four of these 7 excursions included successful nesting, and these lasted 1 to 3 h (Table 1).

Based on the 12 successful or abandoned nest sites by 8 different females that we radiotracked (nest cases N and A in Table 1), the average perpendicular distance from the nearest water was 28.2 m (*SD* = ±18.9, range = 9.5 to 80 m), the average elevation from nearest water was 3.8 m (*SD* = ±4.6, range = 0.5 to 17.5 m), and the average slope (measured to the nearest 10 degrees) was 10.0 degrees (*SD* = ±12.8, range = 0 to 30 degrees).

There was no evidence of strong nest-site fidelity. One female (# 95161 in Table 1) attempted to nest 3 times; after her first attempt she moved 50 m across the creek the next day, and then 2 days later returned to a site within about 3 m of her first excavation. Another female (# 21B38) moved about 200 m downstream between her first attempt and her successful nest 3 days later. A third female (# 93D20) successfully nested twice in 1 season, about 36 days and 500 m apart, and then the following year she nested about 50 m from her last site from the previous year.

Although it was not clear why some sites were abandoned, 1 female aborted her excavation because a rock prevented her from digging deep enough to complete a nest hole. We suspect that we inadvertently disturbed 1 or 2 females while they excavated their nests, causing them to abandon their partially dug holes.

All the successful and attempted nest sites were located on compact and hard soils in habitats that provided little vegetative cover and allowed long exposures to direct sunlight. These habitats included coastal sage scrub, exotic annual grasslands, and weed patches on disturbed soils (Fig. 1).

Resting Sites—During spring and summer months, when turtles were not at their land refuges, both sexes occasionally left the water. These locations were usually on dry sandbars and sandbanks near water, and typically were exposed to sunlight with some protective plant cover (Fig. 1). The sand at these sites was often warm to the touch, presumably due to heating from solar radiation. The turtles at these terrestrial basking sites were typically inactive, and did not take flight when disturbed, as did turtles basking on floating logs, emergent vegetation over water, or banks next to water. In 1992, we radiolocated 9 individuals (6 females and 3 males) at 28 different terrestrial basking sites. The average distance from water was 4.5 m (*SD* = ±3.0, range = 0.5 to 12.0 m), and the average elevation above water was 1.5 m (*SD* = ±0.7, range = 0.5 to 4.5 m). Because of the relatively long interval between radiolocations, we could not determine precisely how long turtles occupied these sites, but we estimate from 1 to 5 days.

Disturbances—While females were on land searching for oviposition sites, or even in the process of excavating a nest, they were exceptionally wary. The slightest unusual visual disturbance or sound by people in the general area usually caused them to cease their activity and return to water. While the turtles were at terrestrial refuges or terrestrial basking sites, they were not easily disturbed, and they were not noticeably vigilant.

We recaptured for radio replacement 17 of our turtles (27 total captures) while they were at land refuges. After re-tagging the turtles, they were usually released on the same day, and always by the next day. In 14 cases, our records are not clear whether the turtles were released at their land capture site or in the nearest water. Sometimes we released turtles in water with the hope that terrestrial predators would not find them after we disturbed their habitat on land.

In 13 of the 27 captures, our release data are unequivocal. Four were released into the nearest creek water, and all were next radiolocated back on land. Two of these 4 returned to within centimeters of their capture sites, one moved to a site about 90 m from its capture location, and the last was tracked to a new refuge about 150 m from its original location. The average change in location for these 4 turtles was 60.0 m, *SD* = ±73.5. Seven of the 13 turtles were released at their land capture sites after re-tagging, and by their next radiolocation they had moved an average of 57.0 m (*SD* = ±85.4 m, range = 2 to 248 m). One of the 13 turtles did not move from its release site, and another moved to the nearest water.

Discussion—The importance of Mediterranean climates on the abiotic features of streams, and in turn, the influence of these traits on aquatic animals, especially macroinvertebrates, has been the focus of numerous studies over the last 2 decades (reviewed by Gasith and Resh, 1999). However, effects of this highly seasonal and distinctive regime on lotic aquatic vertebrates, especially amphibians and reptiles, has not been well documented. This is not surprising, because the diversity of vertebrates that occupy aquatic habitats in this relatively adverse climate is low. Indeed, *Clemmys* is the only native turtle found in the Mediterranean climate of North American, and unfortunately there are few comparative data available on turtles that occupy the other regions of the world with this type of climate.

Some aquatic turtles in eastern North America spend long periods of time on land, but apparently this activity is related to foraging, or physiological states of dormancy—either aestivation or brumation (e.g., Gibbons, 1970; Bennett, 1972; Litzgus et al., 1999). We have used refuging to describe the extensive land excursions by our turtles because *C. marmorata* apparently does not forage while on land, and not all of our turtles routinely aestivated or brumated. We believe that our radio-tagged animals took refuge on land to avoid the back-to-back combination of late summer drought and winter flooding. However, our turtles exhibited flexibility in this behavior, as shown by the refuging habits of the turtles in the creeks compared to those in Pico Pond. Similar behavioral plasticity in land-use has been found throughout the distribution of *C. marmorata*, from Oregon (Holland, 1994; Holte, 1998) through northern and central California (Reese and Welsh, 1997; Davis, 1998) to southern California (Goodman, 1997; Lovich and Meyer, in press).

The best comparative data on terrestrial habitat use are from the Trinity River in northern California (Reese and Welsh, 1997). Compared to our turtles, these animals left the water earlier (September compared to October) and over a more concentrated period of time, and they returned to the river over a later and wider period of time (February through June compared to November through March). Reese and Welsh (1997) suggest that the timing of this overwintering by turtles in the Trinity River is related to avoiding high flows. We believe the difference in refuging patterns between these 2 populations is related to the frequent subzero winter temperatures in the Trinity River, and the more stable aquatic habitat of the Trinity River. For example, spring snow melt, a very large drainage basin, and regulated water flows from an upriver dam resulted in perennial flow in the river compared to our highly seasonal coastal streams.

The Trinity River turtles refuged an average of 203 m from water (Reese and Welsh, 1997), which was about 4 times greater than the ca. 50 m average distance for our coastal animals. We suspect that this relates to climatic, geographical, and habitat differences at the 2 study sites. Turtles travel inland to find suitable refuges (or nesting or basking) sites, which probably includes a complicated interaction of factors such as elevation, slope, moisture, solar exposure, and vegetative cover. This complexity, coupled with their behavioral flexibility, highlights the problem that resource managers face when they try to develop standardized distances from water for protecting upland turtle habitats. We believe that each site must be assessed individually, rather than trying to apply a standard formula to all aquatic systems.

Because our turtles used terrestrial refuges on average for nearly 4 months a year, and we observed them basking at these locations, we suspect that they changed sites to remain in suitable thermal locations, as the trajectory of the sun changed through time. It is not clear whether turtles in the Trinity River area basked while at refuge sites (Reese and Welsh, 1997, 1998), but their use of multiple locations suggests that they did.

Our observations have not changed the overall description of the nesting habits of this turtle (see Rathbun et al., 1992). However, our larger sample sizes show that there is considerable variation in diel timing and site selection of nesting. Our radio-tagged turtles also demonstrated that multiple clutches per year, and nestling overwintering, are common in central coastal California (G. Rathbun, pers. obser.).

The use and importance of basking sites in the Pacific pond turtles have been discussed by Bury and Wolfheim (1973), Holland and Goodman (1996), and Reese and Welsh (1998). Similar to these studies, we often observed our turtles basking in full sun on banks, floating logs, and low vegetation overhanging water. However, the Mediterranean climate and coastal location of our study site resulted in cool and windy springs, and cool and foggy summers (Dallman, 1998), with daytime air temperatures rarely exceeding 20°C. This climate limited the opportunities for basking, compared to inland areas where the daytime air temperatures often exceed 25°C for much of the summer. We speculate that the short-term use of sandy land sites that were several meters from water was related to the thermal requirements of the turtles, especially gravid females. These sites probably provided wind-sheltered locations that were warmer than sites next to or over water. These inland locations did not provide escape into water, and the turtles did not try to flee when disturbed. Rather, they remained motionless after withdrawing their head and legs. Reese and Welsh (1998) observed similar terrestrial basking behavior near the Trinity River, but only by gravid females.

Recent phylogenetic studies (Bickham et al., 1999) suggest that *C. marmorata* is probably not closely related to the 3 species of *Clemmys* from eastern North America. Also, the habitats of these eastern *Clemmys*, and the continental weather patterns of eastern North America (long periods of subfreezing temperatures during the winter, followed by hot and humid summers) are very different than the habitats and climate found in California. An ecological equivalent is the European pond turtle, *Emys orbicularis*, which not only lives in a Mediterranean climate in southern Europe (Dallman, 1998), but also is phylogenetically close to *C. marmorata* (Bickham et al., 1999). Unfortunately, most studies have focused on the basking and mating behaviors of *Emys* in aquatic habitats (e.g., Capula et al., 1994; Di Trani and Zuffi, 1997; Rovero et al., 1999), and relatively little is known about its use of terrestrial habitats. However, there is some indication that it may use land sites in the Mediterranean region in similar ways to what we found for the Pacific pond turtle (Naulleau, 1992).

In conclusion, on the coast of central California the Pacific pond turtle occurs in a Mediterranean climate with a highly seasonal climatic regime. The behavioral flexibility of *C. marmorata* in its use of terrestrial habitats in space and time has allowed it to occupy relatively small, ephemeral creeks in this region.

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