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Abstract: Western Pond Turtles (*Actinemys [Emys] marmorata*) occur in habitats ranging from large rivers and reservoirs to small streams and ponds, as well as from sea level to about 2000-m elevation. This range of environments can affect population parameters such as body size, growth rates, survivorship, and reproductive output. We marked 321 individuals in 287 trap-days in 2007 and 2010 at a high-elevation pond on the southern flank of the Tehachapi Mountains in Southern California, USA. The population was female-biased (92 F:78 M in 2007, 113 F:60 M in 2010), and estimated to contain 412 individuals. Growth rates were relatively high compared with other populations of *A. marmorata*. Monthly survivorship was 0.989–1.000 for adults and juveniles and λ values denoted a stable population. Clutch size averaged 6.3 eggs, and we found 22 instances of intra-annual double-clutching, and possibly a third clutch for one female. Population traits of turtles at this high-elevation pond differed little from turtles at lower elevation sites at the same latitude. Despite conservation threats to this species, this population is indicative that *A. marmorata* can survive well in small habitats, many of which are human-created, and this has increased the amount of habitat for the species as other natural areas have been eliminated.

Key words: Ecology; Emydidae; Pond habitat; Reptilia; Western Pond Turtles

STUDYING the life history of species across habitats and geographic areas can be useful to determine how species respond to environmental variability. Growth rate, size, reproductive output, and survival in lizards are affected by elevation (Ballinger 1979; Smith et al. 1994; Ramírez-Bautista et al. 2011). Although not as well-studied, elevation is also known to affect body size in some turtle species (Christiansen and Moll 1973; Iverson and Smith 1993; Iverson et al. 1997). Changes in body size can result from differential growth rates (Shine and Iverson 1995), with maturation occurring sooner in turtles with high growth rates (Lindeman 1996; Bury et al. 2010; Germano 2010). The rates of growth and adult body sizes of animals are important life-history traits because they often influence reproductive success (Stearns 1992), particularly clutch size, egg size, and age at maturity (e.g., Congdon and van Loben Sels 1991; Iverson et al. 1997; Rowe 1997).

Western Pond Turtles (*Actinemys [Emys] marmorata*) are long-lived, with some adults exceeding 50 yr of age in the wild (Bury et al. 2012). The species occurs along the Pacific coast of North America (Storer 1930; Bury and Germano 2008) from sea level to ~2000-m elevation. A recent genetic analysis indicates that the species might consist of two sister taxa (Spinks et al. 2014). Differences in ecology and morphology occur between the two clades, but these differences are also consistent with clinal variation along the long north-to-south range of the species. Despite anthropogenic alteration of habitat, populations of *A. marmorata* still occur in many natural and man-made aquatic habitats throughout the core portion of their range (Bury and Germano 2008). Several aspects of the population and reproductive ecology for populations representing different parts of this range are well-studied (Goodman 1997a,b; Pires 2001; Lovich and Meyer 2002; Germano and Rathbun 2008; Scott et al. 2008; Germano and Bury 2009; Bury et al. 2010; Germano 2010).

Comparisons of population parameters of *A. marmorata* from sites at varying elevations might reveal if this species is affected by changing environmental conditions or if population parameters are generally fixed at a given latitude. Our objective was to determine the population structure, growth, reproduction, and survivorship of *A. marmorata* at a relatively high-elevation pond in southern California, USA. We compared several of these parameters to what has been found for *A. marmorata* inhabiting ponds of similar structure at various elevations across its range.

MATERIALS AND METHODS

Study Area

We sampled turtles at a high-elevation pond (1063 m) on the southwestern flank of the Tehachapi Mountains near the town of Gorman, Los Angeles County, California. Using a 2010 aerial photograph from Google Earth (available at <http://earth.google.com>), we estimate that the area of the pond was about 1.3 ha when full. According to a nearby resident, this spring-fed pond dries fully every year. In each of the 2 yr we sampled turtles, the pond decreased in area by ~33% from April through August. The pond is at the base of a hillside and a two-lane paved road is directly adjacent to the southern edge of the pond (34°46'57.80"N, 118°48'22.04"W, datum = WGS84). There were occasional portions of the littoral zone with emergent rushes (*Juncus* sp.), and much of the western and northern edges of the pond was overhung by willows (*Salix* sp.).

Field Methods

We captured turtles in 2007 and 2010 using both nylon net traps with double funnels (model FT-FA; Nylon Net Co., Memphis, Tennessee) and wire-mesh traps with double funnels (see Iverson 1979). We baited traps with canned sardines and traps were open either for 3 or 4 d. We checked traps daily, usually starting at 0700 h; we transported trapped subjects to Bakersfield for processing and released them the next morning back at their capture site. We trapped the site

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during five sampling periods in 2007 (1–4 May, 29 May–1 June, 26–29 June, 17–20 July, and 7–9 August) and five periods in 2010 (4–7 May, 1–4 June, 29 June–2 July, 29–31 July, and 17–19 August). In 2007, we used 7–9 traps per session to capture turtles (total trap-days = 157) and we set 6–9 traps per session in 2010 (total trap-days = 130).

For each captured turtle, we recorded mass (± 1 g), carapace length (CL; ± 1 mm), sex, and age following Germano (2010). We determined age using scute annuli from the carapace and plastron (Bury and Germano 1998; Germano and Bury 1998). Turtles at this site grow fairly rapidly and discernible scute rings become hard to detect at 10–12 yr. Because of scute ring wear, we classified some turtles when first captured as older than 15 yr because scute rings were worn and edges of scutes were beveled. If the shell was not well-worn, however, we classified a turtle as older than 10 yr. In 2010, we were able to determine exact ages of some turtles >10 yr because we had estimated ages based on annuli in 2007.

For most turtles, we defined the difference between adults and juveniles as 120-mm CL, the size at which most males developed secondary sexual characteristics in their shells and tails (Bury and Germano 2008; Bury et al. 2012). We ascertained some smaller turtles to be males (109–120-mm CL), however, because these individuals showed unmistakable secondary characteristics of the sex. We individually marked turtles by notching marginal scutes with a file (Cagle 1939; Bury and Germano 1998).

We radiographed females in Bakersfield using a portable X-ray machine to determine whether they were gravid and how many eggs were present. Within each sampling period, we radiographed all females even if they previously had been captured in a previous period. We used the number and development of eggs (faint shell versus distinct shell) as an indication of multiple clutches in a season for females that were caught multiple times within a year. We determined the percentage of females gravid by season (May–August), by size, and by age. Because we only found one female of <135 -mm CL with eggs, we used females that were >134 -mm CL to determine seasonal gravidity. In the analysis of size and age, we used the smallest size of a female if she was caught multiple times for females ≥ 10 and ≥ 15 yr in age. For those females for which we could determine age, we used data in the analysis from multiple captures as age and size increased. We deleted from analyses of gravidity any captures of females without eggs made in early May or late July or August for seasonal counts of gravidity because the percentage of females gravid was low in these sampling periods.

Size and Growth Analysis

Neither CL nor mass data were normally distributed, even after various transformations. Therefore, we used Kruskal–Wallis tests to compare CL and mass between the sexes, with sex and year forming four groups. If we detected differences among groups, we used pairwise Mann–Whitney comparisons ($\alpha = 0.01$). To minimize the effect of age structure on size estimates (Case 1976), we also determined the upper decile CL (UDCL) and upper decile mass (UDM) of adult turtles, and we tested for differences between years and sexes in the manner described above. We tested for departures from a 1:1

sex ratio by year, and across all years, using chi-square analyses with Yates correction for continuity. We also compared both the size (CL) and age structure of turtles within each year using Kolmogorov–Smirnov tests.

We used Kolmogorov–Smirnov tests to compare the population structure of turtles at our study site to selected ponds throughout the range of the species: (1) Vandenberg Air Force Base (VAFB), San Luis Obispo Co., California, ~ 150 km distant, with multiple ponds ranging from 2 to 10 ha in size and 44 to 130 m in elevation (Germano and Rathbun 2008); (2) Yoncalla, Douglas Co., Oregon, USA, ~ 1000 km distant, with one pond 2 ha in size and 120 m in elevation (Germano and Bury 2009); (3) Rawlins, Oregon, ~ 880 km distant, with one pond 0.5 ha in size and 724 m in elevation (Germano and Bury 2009); and, (4) Hell-To-Find Lake, Trinity Co., California, ~ 730 km distant, with one pond 0.2 ha in size and 1460 m in elevation (Bury et al. 2010). For all tests $\alpha = 0.05$, except as noted.

We constructed growth curves by fitting age and CL data to the Richards' growth model (Richards 1959). The Richards' growth model estimates three parameters using CL and age data in the general formula to predict CL at various ages:

$$CL = \text{asymptotic size} (1 + (M - 1)e^{(-K \times (\text{Age} - I))})^{1/(1-M)} \quad [1]$$

where M is the shape of the growth curve, e is the inverse of the natural logarithm, K is the growth constant, and I is the point at which curve inflection begins.

We used continuous age estimates (Lindeman 1997) based on a yearly period of 1 May to 30 September that could support growth. Following Bradley et al. (1984), we used means of adult UDCL as asymptotic sizes because of the high values predicted from growth data with large confidence intervals. Further, we set hatchling size to be 25–29-mm CL based on field data of recent hatchlings (Storer 1930; Feldman 1982; Lovich and Meyer 2002) to anchor growth curves. We made comparisons of growth rates between sexes using the statistic G , which represents the time required to grow from 10% to 90% of asymptotic size and is an indicator of the duration of primary growth (Bradley et al. 1984):

$$G = \ln((1 - 0.10^{1-M}) / (1 - 0.90^{1-M})) / K \quad [2]$$

The best overall growth measure is G because it is less affected by instability of the nonlinear fit than either K or M , and it produces values (in our case, years) on an easily interpreted scale (Bradley et al. 1984). We also made comparisons of growth rates between sexes using calculated carapace lengths (CCL) derived from the growth equations using 2-yr intervals from ages 2 to 12 yr. We judged CCL to be significantly different between the sexes if the mean of one sex did not intersect the 95% prediction interval of the other.

We compared growth of turtles at Gorman pond to other ponds in the range for which growth curve data were available (the same ponds for which we compared population structure). In some instances this required reanalyzing growth data to include decimal fractions of years rather than whole years. We compared the growth parameters and asymptotic CLs for adults irrespective of sex.

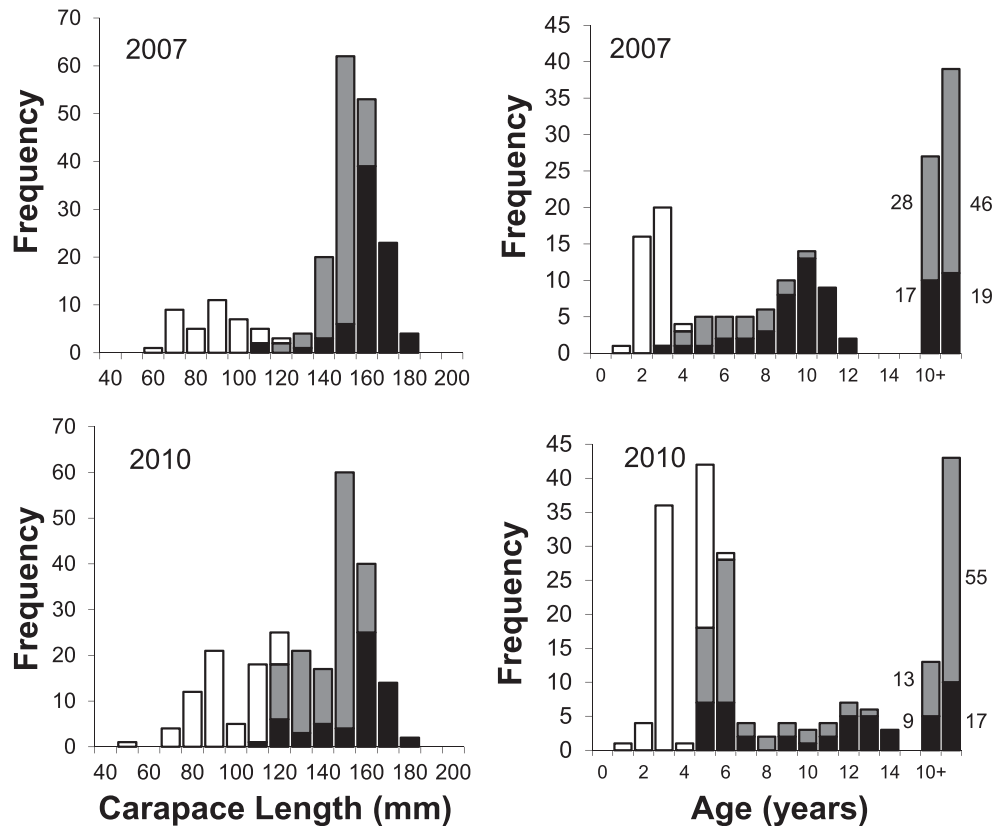


FIG. 1.—Frequency distribution of carapace lengths (left) and ages (right) in 2007 (top) and 2010 (bottom) of *Actinemys marmorata* captured at a pond near Gorman, California, USA. Black bars are males, gray bars are females, and open bars are turtles for which sex could not be determined. The number of old turtles (≥ 10 and ≥ 15 yr) were truncated to improve visibility of other ages; their numbers are shown to the side of the bars.

Survival and Population Size Analysis

We calculated recapture and demographic vital rates in Program MARK using encounter histories derived from our record of individual encounters (White and Burnham 1999). Time intervals between sampling sessions were entered into MARK models to reflect variation in time intervals within and between years. We calculated population size (N), apparent survival (Φ), and recapture rates (p) using open population Cormack–Jolly–Seber (CJS) and POPAN models in Program MARK (Lebreton et al. 1992; White and Burnham 1999). We generated CJS model sets based on sex (male, female, juvenile) to test whether Φ or p was best estimated independent of sex or time, by sex or time, or by a sex–time interaction. Model selection was based on Akaike Information Criterion (AIC_c) values, with lower values denoting greater parsimony (Burnham and Anderson 2002).

Traditionally, encounter rates are used to calculate the probability that an individual will leave a population. If the encounter rates are reversed, then the probability of an individual entering the population can be estimated (Pradel 1996); as such, λ = rate of individuals entering a population or cohort. Using Pradel models, λ estimates the realized growth rates of the age class from which the encounter rates were generated, but is not necessarily equivalent to the growth rate of the population. Still, it provides an important metric of the life-history characteristics of a population. Pradel’s λ was estimated by Program MARK in conjunction with the CJS-model described above.

RESULTS

We trapped 207 Pond Turtles (78 males, 92 females, 37 juveniles) at the Gorman pond in 2007, and 240 Pond

TABLE 1.—Sample size (n), mean (± 1 SE), and range of carapace length (CL) and mass, and upper 10% CL (UDCL) and mass (UDM) of adult Western Pond Turtles (*Actinemys marmorata*) captured at a pond near Gorman, California, USA, in 2007 and 2010. Mass of females excludes those that were gravid at time of capture.

	CL (mm)			UDCL	Mass (g)			
	n	Mean \pm SE	Range		n	Mean \pm SE	Range	UDM
2007								
Males	78	160.1 \pm 1.30	109–179	174.4	78	626.3 \pm 12.3	194–828	777.1
Females	92	147.9 \pm 0.82	120–164	159.8	65	562.7 \pm 10.1	284–695	671.1
2010								
Males	60	154.3 \pm 2.18	113–177	173.6	60	571.2 \pm 20.7	217–826	775.8
Females	113	143.6 \pm 1.08	118–156	158.9	66	536.1 \pm 12.9	317–680	670.3

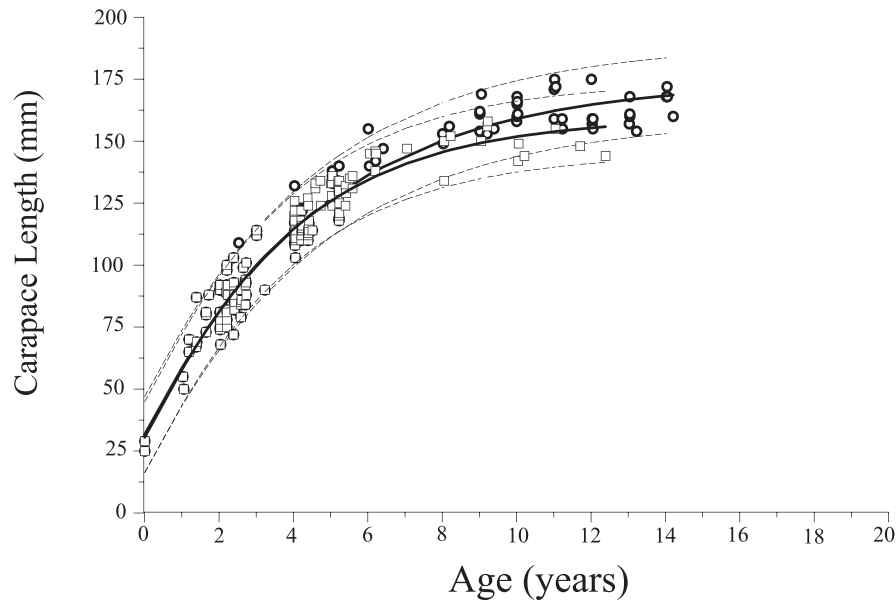


FIG. 2.—Growth curves (with 95% CIs) of male (circles) and female (squares) *Actinemys marmorata* captured at a pond near Gorman, California, USA, using the Richards' growth model.

Turtles (60 males, 113 females, 67 juveniles) in 2010 (Fig. 1). The total number of individuals we captured in the 2 yr was 321 turtles. The mean CLs of turtles differed by sex and year ($H = 110.86$, $df = 3$, $P < 0.001$), with males larger than females within and between years ($W = 5163.5$ – 10983.0 , $P < 0.001$), but interannual differences for each sex were absent (female $W = 10447.5$, $P = 0.02$; male $W = 5741.5$, $P = 0.17$; Table 1). Similarly, the mean UDCL of turtles differed ($H = 25.63$, $df = 3$, $P < 0.0001$), with males larger than females within and between years ($W = 45.0$ – 124.0 , $P = 0.001$ to <0.001), but interannual differences for each sex were absent (female $W = 105.0$, $P = 0.45$; male $W = 70.5$, $P = 0.49$; Table 1). Mean mass differed as a function of sex and year ($H = 30.90$, $df = 3$, $P < 0.001$), but this pattern was driven by the males being larger than females (for both years, $W = 3561.0$ – 6918.0 , $P < 0.001$). All other comparisons of mass were similar (Table 1). Upper decile mass differed among groups ($H = 30.90$, $df = 3$, $P < 0.001$) and males in both years had larger mean UDM than females ($W = 28.0$ – 92.0 , $P < 0.003$); but interannual differences for each sex were absent (female $W = 51.0$, $P = 0.90$; male $W = 61.0$, $P = 0.95$; Table 1).

The ratio of males to females in 2007 (78:92 or 0.85) did not differ from 1:1 ($\chi^2 = 0.99$, $P = 0.32$), but the ratios in 2010 (60:113 or 0.53) and overall (97:144 or 0.67) were

TABLE 2.—Calculated carapace lengths (CL in mm; 95% CI) of male and female Western Pond Turtles (*Actinemys marmorata*) from a pond near Gorman, California, USA, in 2007 and 2010. Calculated CLs at various ages were determined from growth equations for each sex (Fig. 2).

Age (yr)	Calculated CL (mm)	
	Males	Females
2	81.3 (66.0–96.6)	81.5 (67.2–95.8)
4	114.8 (99.5–130.1)	114.7 (100.4–129.1)
6	136.3 (121.0–151.6)	134.5 (120.2–148.8)
8	150.2 (135.0–165.5)	145.6 (131.3–159.9)
10	159.1 (143.8–174.4)	151.8 (137.5–166.1)
12	164.8 (149.5–180.0)	155.3 (141.1–169.6)

female-biased ($\chi^2 = 8.78$ – 15.63 , $P \leq 0.003$). In 2007, 17.9% of turtles were juveniles (<120 -mm CL), whereas 27.9% of turtles caught in 2010 were juveniles (Fig. 1). However, the size structures between years did not differ ($D = 0.36$, $P = 0.27$). The percentage of young turtles (0–5 yr) was 22.2% in 2007 and 35.0% in 2010 (Fig. 1). We were able to estimate age of 46.9% of turtles in 2007 and 60.0% of turtles in 2010. The age structures did not differ between years ($D = 0.42$, $P = 0.19$). The overall size structure of captured turtles at Gorman pond did not differ from that at VAFB ($D = 0.29$, $P = 0.39$), but was different from that at Hell-To-Find ($D = 0.47$, $P = 0.03$), Rawlins ($D = 0.53$, $P = 0.01$), and Yoncalla ($D = 0.53$, $P = 0.01$) ponds. In contrast, the overall age structure of turtles at Gorman pond did not differ from that at any other site ($D = 0.18$ – 0.41 , $P \geq 0.08$).

Growth of females was not different from males during the first few years, but began to separate from males by age 6

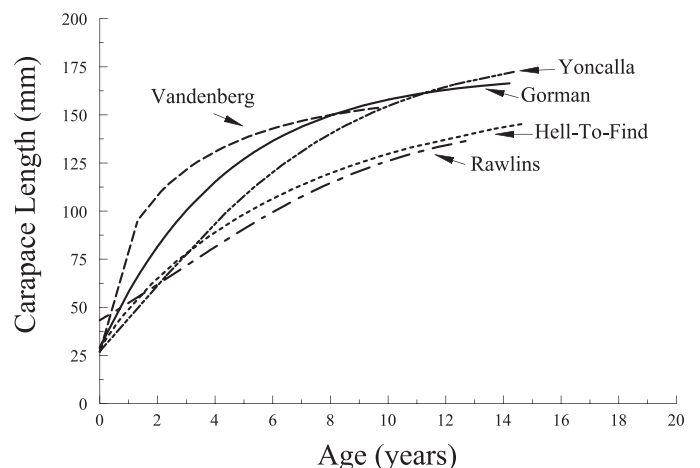


FIG. 3.—Growth curves of *Actinemys marmorata* at Gorman pond compared with turtles from ponds at Vandenberg Air Force Base nearby in central California, USA; Hell-To-Find pond in northern California; and Rawlins and Yoncalla ponds in southern Oregon, USA.

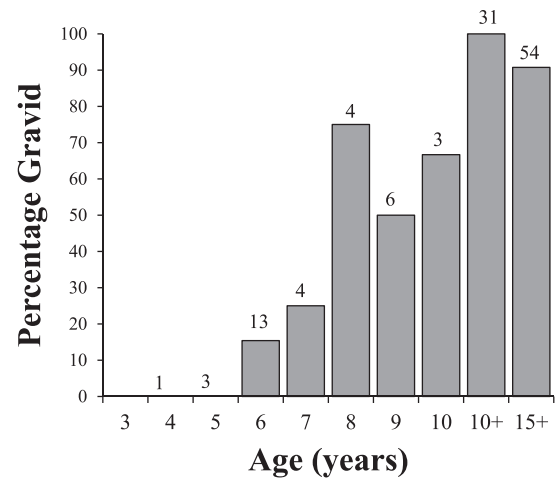
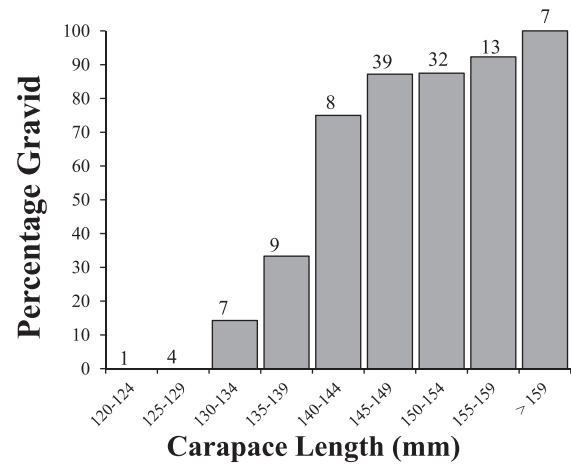
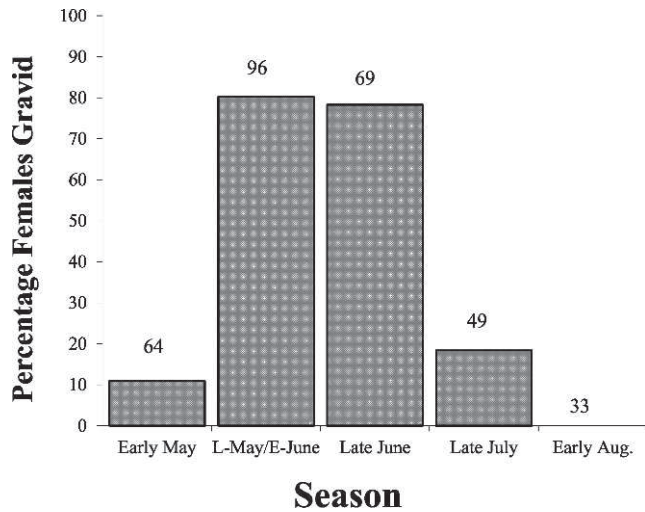


FIG. 4.—The percentage of gravid *Actinemys marmorata* females over the season of activity at a pond near Gorman, California, USA. The data are pooled for 2 yr (2007 and 2010). The numbers above the bars are the number of females radiographed during the period shown.

(Fig. 2). The growth model fit the data well, with r^2 values equaling 0.95 and 0.93 for males and females, respectively. Model parameters for males were $M = 0.1276$, $K = 0.2308$, $I = -0.5162$, and for females were $M = 0.3098$, $K = 0.3003$, $I = -0.0475$. These gave the growth parameter (G) of 9.92 yr for males and 8.10 yr for females, although calculated CLs for males and females were not significantly different through age 12 (Table 2). We also determined the mean age at 120-mm CL, the size that male *A. marmorata* can generally be distinguished from females. On average, males reached 120-mm CL in 4.43 yr and females in 4.45 yr.

The overall growth of *A. marmorata* captured at the Gorman pond was faster than at other ponds except for turtles at VAFB, a site of low-elevation ponds at about the same latitude (Fig. 3). By age 11, turtles at Yoncalla ponds in Oregon matched the growth rate of turtles at the Gorman pond; however, turtles at Gorman exceeded the growth rate of turtles at either Hell-To-Find Lake or Rawlins pond (Fig. 3). These growth differences are reflected in primary growth, G , which took the least amount of time (6.74 yr) at Vandenberg Air Force Base (Table 3). Compared with turtles from VAFB ponds, those from the Gorman pond took almost 2.6 yr longer for primary growth, and primary growth at the three higher latitude sites took 13.2–17.1 yr (Table 3). Turtles from the Gorman pond were larger (based on upper-decile CL) than turtles at VAFB, Hell-To-Find,

FIG. 5.—The percentage of gravid *Actinemys marmorata* females based on size (top) and age (bottom) at a pond near Gorman, California, USA. The data are pooled for 2 yr (2007 and 2010). The numbers above the bars are the number of females radiographed at that size or age.

and Rawlins, but were smaller than turtles from the Yoncalla ponds in Oregon (Table 3).

The pattern of female gravidity was similar across years. Only a few females were gravid in early May (10.9%), many were gravid by late May (80.2%) through late June (78.3%), and no females with eggs were found in either year in August (Fig. 4). Mean (± 1 SE) clutch size was 6.3 ± 0.13 , with the preponderance of clutches having 5–8 eggs ($n = 142$, range 1–11). We found 22 second clutches and one female in 2010 might have produced a third clutch (6 May, 6 eggs; 3 June, 7 eggs; and 1 July, 10 eggs). The smallest female with eggs was

TABLE 3.—Elevation, growth parameters from Richards' growth curves, and the upper decile carapace length (UDCL) for Western Pond Turtles (*Actinemys marmorata*) from five ponds in California and Oregon, USA. Sites are arranged from south to north by latitude. Parameters describing model fit and growth curves are shape of curve (M), growth constant (K), inflection point of curve (I), and time required to grow from 10% to 90% of asymptotic size (G , in yr).

Site	Elevation (m)	M	K	I	G (yr)	UDCL (mm)
Central California						
Gorman	1063	0.0799	0.2415	-0.5625	9.33	171.2
Vandenberg	44–130	-1.5790	0.2135	-4.4840	6.74	161.9
Northern California						
Hell-To-Find	1460	-0.3629	0.1150	-3.5280	17.10	166.4
Southern Oregon						
Rawlins	724	1.6630	0.2350	2.8020	16.60	150.0
Yoncalla	120	0.6080	0.2030	1.4850	13.20	185.8

TABLE 4.—Apparent survivorship (Φ), recapture rate (p), population size (N), and lambda (λ) for different life-history stages of Western Pond Turtles (*Actinemys marmorata*) captured at a pond near Gorman, California, USA, in 2007 and 2010. 95% CIs are indicated in parentheses.

	Φ	p	N	λ
Male	0.989 (0.982–0.994)	0.309 (0.268–0.354)	118 (109–133)	0.99 (0.98–1.00)
Female	0.994 (0.987–0.997)	0.279 (0.243–0.319)	169 (157–185)	1.00 (0.99–1.00)
Juvenile	1.000 (0.999–1.000)	0.161 (0.128–0.200)	125 (115–139)	1.02 (1.01–1.02)

134-mm CL, but high levels (>70%) of gravidity occurred only when female CL exceeded 140 mm (Fig. 5). The youngest female with eggs ($n = 2$) was 5.21 yr old, although females were more likely to be gravid when >8 yr old (Fig. 5). All females categorized in the ≥ 10 -yr group were gravid, as were 90.7% of females in the ≥ 15 -yr group. Clutch size did not vary as a function of female body size ($F_{1,86} = 3.47$, $P = 0.07$).

Apparent monthly survival was high for all classes, and was 0.989 for males, 0.994 for females, and 1.00 for juveniles; λ values denoted a stable population (Table 4). Recapture rates were low, with juveniles having lower rates than either adult males or females (Table 4). The population size estimate for this pond was 412 turtles pooled across all life-history stages, with fewer males than juveniles or females (Table 4). The best model to explain encounter histories was $\Phi(\text{time})p(\text{sex} \times \text{time})$, where Φ varied between samples and p varied across sex and time independent of each other (Table 5). Capture rates were lower during the late-summer sampling periods (Table 6), which would account for this variation in Φ and p .

DISCUSSION

The population of *A. marmorata* at this small, high-elevation pond is illustrative of many populations of this species that have been documented throughout its range. At these sites, the turtles generally occur in large numbers, reproduce well, and have high survivorship. The population structure is similar to other ponds in the range of *A. marmorata*. The size structure at the Gorman pond is dominated by adult-sized turtles (>120-mm CL), and there is a large number of relatively young turtles, both similar to what has been reported from other sites (Germano and Rathbun 2008; Germano and Bury 2009; Bury et al. 2010; Germano 2010). Neither the size structure nor age structure of turtles at the Gorman pond differed from that of turtles at a low-elevation, coastal site (VAFB) having a similar latitude to Gorman. For these population traits, differences in elevation do not appear to affect *A. marmorata*.

Based on our comparisons of sites across the range of the species, an interaction of elevation and latitude appears to influence the growth of *A. marmorata*. Turtles at the Gorman pond did not grow as fast as those at VAFB, but grew much faster than turtles at the high-elevation Hell-To-Find Lake in northern California. A difference between these sites is that the Gorman pond is within a treeless area, except for willows directly encircling part of the pond; whereas, Hell-To-Find Lake is surrounded by conifers and is on a forested mountainside. Turtles at the pond at Yoncalla, the highest latitude site in our comparison, grew much more slowly than turtles at Gorman until age 11 yr, when growth exceeded that of turtles at Gorman. The pond at Yoncalla is a low-elevation pond that is only partially surrounded by trees.

The large number of turtles at the Gorman pond is, at least in part, attributable to a relatively high rate of reproduction. The average clutch size of 6.3 eggs is higher than that seen for other populations of *A. marmorata* in the southern end of their distribution (values ranging from 4.5–5.7; Goodman 1997a; Pires 2001; Scott et al. 2008). The female in 2010 that may have produced three clutches had six eggs in early May that showed faintly on the x-ray image and then seven well-shelled eggs 27 d later. It is possible that the clutch in June was the final stage of the clutch seen in May. Double clutching by *A. marmorata* has been described from other southern sites (Goodman 1997b; Pires 2001; Lovich and Meyer 2002; Germano and Rathbun 2008; Scott et al. 2008). In spite of being found at a high elevation, female turtles at the Gorman pond appear to mature and become reproductive at 8 yr, at which time they have completed most of their body growth (even though they can be distinguished from males based on secondary sexual characteristics at a little over 4 yr).

Our estimates of monthly survivorship are also comparatively high and might overestimate this parameter. Adult monthly survivorships of 0.989–0.994 would produce a yearly survivorship of 87.6–93.0% if carried over 12 mo, or 93.6–96.5% over the ~6 mo that these turtles are likely active in the water (the pond dries each year). These results do fit the Type III survivorship model typical of many turtle species

TABLE 5.—Parameters for a Cormack–Jolly–Seber model that analyzed the effects of sex (male, female, juvenile) and time on apparent survivorship (Φ) and recapture rates (p) of Western Pond Turtles (*Actinemys marmorata*) captured at a pond near Gorman, California, USA, in 2007 and 2010.

Model	AIC _c	Δ AIC _c	AIC _c weights	# Parameters	QDeviance
$\Phi(\text{time})p(\text{sex} \times \text{time})$	1943.82	0.00	0.86	35	705.368
$\Phi(\text{time})p(\text{time})$	1948.19	4.37	0.09	17	748.535
$\Phi(\text{sex} \times \text{time})p(\text{time})$	1950.40	6.58	0.03	35	711.956
$\Phi(\text{time})p(\text{sex})$	1958.97	15.15	0.00	12	769.751
$\Phi(\text{sex} \times \text{time})p(\text{sex} \times \text{time})$	1962.40	18.58	0.00	50	690.033
$\Phi(\text{sex} \times \text{time})p(\text{sex})$	1972.87	29.05	0.00	30	745.401
$\Phi(\text{sex})p(\text{sex} \times \text{time})$	1976.85	33.03	0.00	30	749.384
$\Phi(\text{sex})p(\text{time})$	1981.04	37.22	0.00	12	791.813
$\Phi(\text{sex})p(\text{sex})$	2068.42	124.60	0.00	6	891.520

TABLE 6.—Total captures of individual Western Pond Turtles (*Actinemys marmorata*) and captures per trap night (CPTN; including recaptures) by session at a pond near Gorman, California, USA, in 2007 and 2010. Abbreviations before months are E = early, M = mid, L = late (see Methods for exact dates).

	2007					2010				
	E May	L May	L June	M July	E Aug	E May	E June	L June	L July	M Aug
Male	60	36	28	18	14	37	41	15	8	14
Female	31	47	30	31	19	37	53	47	22	17
Juvenile	4	12	10	7	13	24	37	25	18	12
CPTN	3.44	3.14	2.08	2.22	2.52	2.72	5.06	4.71	2.70	2.61

(Iverson 1991a). Persistence of turtles in small, ephemeral habitats appears to be dependent on annual frequency of nesting and variation in juvenile survivorship (Iverson 1991b; Riedle et al. 2012). Survivor values (λ) for this population indicate stable adult age classes and a slightly increasing juvenile class.

Is the population of turtles at the Gorman pond typical for *A. marmorata* in the range of the species? Certainly, the density of turtles at this site (322 turtles/ha) is among the highest recorded (other estimates of high density range from 228 to 325 turtles/ha; Bury et al. 2012; Pilliod et al. 2013). Most populations do not support such high numbers (Bury et al. 2012). Other parameters (e.g., population structure, reproductive output, growth rate) are similar to populations of *A. marmorata* in other parts of their range, indicating that the population of turtles at the Gorman pond might not be anomalous.

The recently proposed elevation of two subspecies of *A. marmorata* to species status (Spinks et al. 2014) would place turtles from the Gorman site in the southern species, *A. (Emys) pallida*. The recent interest in conserving the entire species complex has included a petition to the U.S. Fish and Wildlife Service to list the species (Center for Biological Diversity 2015). Whether or not the taxonomic revision is validated, *A. marmorata* (sensu lato) has lost much habitat in southern California, the Central Valley, and in the Bay area of San Francisco and Oakland (Brattstrom 1988; Bury and Germano 2008). In contrast, the landscape in the foothills and mountains has gained hundreds of sites suitable for the species because of the construction of artificial ponds, especially for watering livestock. Many of these new habitats support large numbers of turtles that appear to be fairly stable (Germano and Bury 2009; Bury et al. 2010). Similarly, the coastal region of central California has many new habitats (DJG, personal observation) that might partially offset habitat losses further south in the species' distribution. A range-wide assessment of the status of the putative two species is needed to determine what level of protection is needed for either species before conservation measures are enacted.

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