Chelonian Conservation and Biology, 2008, 7(2): 188–194
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Growth, Population Structure, and Reproduction of Western Pond Turtles (*Actinemys marmorata*) on the Central Coast of California

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ABSTRACT. – We studied the population structure and growth of western pond turtles (*Actinemys marmorata*) at Vandenberg Air Force Base along the coast of central California in April 1995 and June 1996. We captured 179 individuals (115 males, 27 females) from 7 ponds during 26 days of trapping. Many turtles were adult-sized, but based on scute annuli, 74% were < 10 years of age, including many 2- to 3-year-olds. This population structure likely was due to a relatively fast growth rate, especially compared with closely related aquatic turtles in eastern North America. Mean clutch size was 5.2, but 66.7% of females were gravid, and 1 female produced 2 clutches. These reproductive data are similar to those reported for other populations in the southern portion of the species' range. Females reached reproductive maturity as early as 4 years of age. The relatively mild temperatures of California's Mediterranean climate, especially when compared to the seasonal extremes in more continental and northern regions of North America, may explain the different growth rates and population characteristics of freshwater turtles from these 2 regions of North America.

KEY WORDS. – Reptilia; Testudinidae; Emydidae; *Actinemys marmorata*; turtle; reproduction; population structure; clutch size; growth; California; USA

The western pond turtle (*Actinemys marmorata*) in the Pacific region of North America ranges from Washington State south into Baja California in Mexico (Storer 1930; Bury 1970; Bury and Germano 2008). It inhabits most aquatic systems, primarily west of the Cascade–Sierra Nevada–Peninsula Mountains. It is the only native aquatic turtle in California and southern Oregon, and only the western painted turtle (*Chrysemys picta bellii*) co-occurs with it in northern Oregon and Washington (Brown et al. 1995). Although occurring over a fairly wide region, little published information is available about its ecology and life history, such as population structure, reproduction, individual growth, and age at maturity. Only 2 studies (Reese and Welsh 1998; Germano and Bury 2001) have reported population structures of *A. marmorata*; 1 study included growth data for a few juvenile turtles (Storer 1930), and no data have been published on age at maturity. Concern has been raised about the possible extirpation of this species over much of its range (US Fish and Wildlife Service, 1992; Jennings and Hayes 1994), and as such, empirical data are needed on population dynamics and status.

The western pond turtle has a large range, and how it responds to varied ecological conditions can give insight into the plasticity of life histories of turtles in general. In the southern part of its range, *A. marmorata* inhabits a Mediterranean climate with mild wet winters (November–March) and long, hot, and dry summers and autumns (Rathbun et al. 2002). The northern part of its range has cold winters and rainfall is much higher and spread throughout the year. The climate in the southern part of the range also differs markedly from the continental climate in northeastern North America, which has much colder winters, warm summers, and much wetter conditions throughout the year. The mild climate in southeastern North America differs from a Mediterranean regime in its year-round abundant rainfall with no extended dry seasons. Aquatic turtles with extensive north–south ranges in continental eastern North America show significant variation in life-history traits (Wilbur and Morin 1988; Iverson et al. 1993; Litzgus and Mosseau 2006) that appear to be related, at least partially, to latitudinal climatic differences. The similar climatic variation within the range of *A. marmorata* may similarly affect its life history.

Our objective was to determine the population structure, growth, and reproductive capacity of *A. marmorata* on the central coast of California in order to compare these traits with populations of this species from other regions. Secondly, we wanted to compare our results with those of freshwater turtles from other regions of North America that also display a wide latitudinal distribution.

METHODS

Vandenberg Air Force Base encompasses 39,000 ha along the central coast of California near Lompoc in Santa Barbara County. Public access and use is restricted, thus creating relatively undisturbed habitats for wildlife, including turtles. The area has a mild but highly seasonal Mediterranean climate with a yearly mean temperature of 14.6°C, monthly maximum mean temperatures of 22.7°C in July and 24.0°C in October, and a minimum mean in December of 4.1°C (World Climate 2007). The 24-hour monthly mean temperatures vary by 11.5°C in December and 17.9°C in September. Most rainfall (86%) occurs from November through March and averages 369 mm per year (World Climate 2007). The vegetation on the base is generally made up of coastal sage scrub with riparian vegetation dominated by willows and alders along stream courses and around most ponds.

We captured turtles 5–20 April 1995 and 3–6 and 24–26 June 1996. Although we searched and trapped in several seasonal streams and in 10 permanent ponds in 1995, we caught turtles only in 7 ponds: 2 were < 1 ha with emergent vegetation, another was < 1 ha that was formerly a gravel borrow pit and surrounded by trees, Punchbowl Pond was 10.3 ha and lacked significant riparian vegetation, and a series of 3 ponds in Pine Canyon (approximately 1.0, 2.3, and 3.8 ha). All these ponds were within 1 km^2 (measured from aerial photographs viewed on GoogleEarth). Punchbowl and Pine Canyon ponds had emergent vegetation along their edges. Because of the large number of turtles caught in 1995, we retrapped at the gravel pit, Punchbowl Pond, and Pine Canyon ponds in 1996.

In 1995, we captured turtles in commercial nylon net and hoop funnel-traps with a single entrance, but in 1996 we used homemade wire-mesh traps with double funnels (Iverson 1979). We baited traps with canned sardines and left traps open at a site for 2–3 days. Traps were checked once a day and any turtles captured were removed and their weight, carapace length (CL), plastron length (PL), sex, age, and general condition determined. We estimated each individual's age by counting scute annuli from the carapace and plastron (Bury and Germano 1998; Germano and Bury 1998). Some turtles could only be classified as older than 15 years because scute rings were worn and edges of scutes were beveled; these animals were large and no longer depositing discernable rings (Germano and Bury 1998). 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). We individually marked turtles by notching marginal scutes (Cagle 1939; Bury 1972) before releasing them within a day of capture. In 1996, we took female turtles to a veterinary hospital in Lompoc for radiography to determine if they were gravid and how many eggs were present.

We made comparisons of the mass of males to females using CL as the covariate. We used the log transformation of body mass because this homogenized the residual variances and increased the explained percentage of variation. Slopes of lines between sexes were compared using analysis of covariance ($\alpha = 0.05$) on all females to males and after removing females carrying eggs from the analysis. We used analysis of variance ($\alpha = 0.05$) to test for differences in mean CL between sexes and the Wilcoxon rank sum test ($\alpha = 0.05$) to test for differences in upper decile CL between sexes.

Growth curves were constructed by fitting age and CL data to the Richards growth model (Richards 1959). Richards' model was superior to the best-fitting 3-parameter model (e.g., Logistic, Gompertz, or von Bertalanffy models). The 3-parameter models have fixed growth forms and are special cases of the flexible 4-parameter Richards model, which has a variable point of inflection specified by the shape parameter of the growth curve (*M*; Richards 1959; Causton 1969). The Richards growth model estimates 3 parameters using CL and age data: *M*, the shape of the growth curve; K, the growth constant; and *I*, the point at which curve inflection begins. The model uses the general formula

$$\mathrm{CL} = \text{asymptotic size}\left(1 + (\mathrm{M} - 1)\mathrm{e}^{(-\mathrm{K}^{*}(\mathrm{Age}-\mathrm{I})}\right)^{(1/1-\mathrm{M})}$$

to solve for CL at various ages. When *M* is -1, the Richards model is equivalent to the monomolecular model; an *M* value of -0.3 corresponds to the von Bertalanffy model; *M* approaching 0 approximates the Gompertz model; and an *M* value of 1 represents the logistic model. When M is > 1, the inflection point comes after reaching 50% of the asymptote. The model is undefined when *M* is 0 or < -1. The Richards model produces less-biased estimates of the growth function if the shape of the growth curve differs from that of a fixed-curve model (Leberg et al. 1989).

Following recommendations of Bradley et al. (1984), we used mean upper decile sizes of adults as asymptotic sizes because of the high values predicted from growth data with large confidence intervals. We also included sizes of juvenile turtles in male and female growth analyses because juvenile chelonians must grow rapidly to reach sizes that minimize predation risk (Wilbur and Morin 1988), such that male and female juveniles are expected to have similar growth rates prior to maturity (Gibbons and Greene 1990). Further, we used size of hatchlings (25–29 mm CL; Feldman 1982; Lovich and Meyer 2002) to anchor growth curves. Comparisons of growth rates between sexes were also made using mean and upper decile CL of adults and calculated CL (CCL) by 2-year intervals from ages 0 (hatchlings) to 10 years. We judged CCL to be significantly different between sexes if the mean of one sex did not intersect the 95% confidence interval of the other.

RESULTS

We caught 179 *A. marmorata* and 2 *Trachemys scripta elegans* (red-eared slider, an introduced species) during 26 days of trapping over 2 years. The overall sex ratio of 4.26 males to 1.00 females was significantly

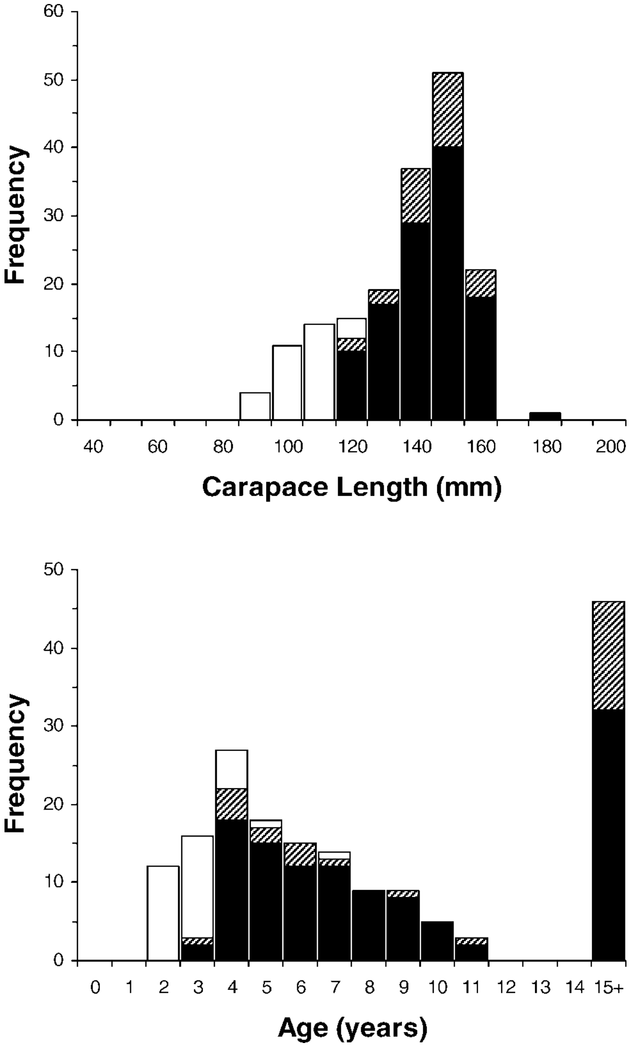

Figure 1. Frequency distribution of carapace lengths and ages of western pond turtles ($n = 179$) captured at Vandenberg Air Force Base, Santa Barbara County, California 1995–1996. Black bars represent males; striped bars, females; and open bars, turtles for which gender could not be determined.

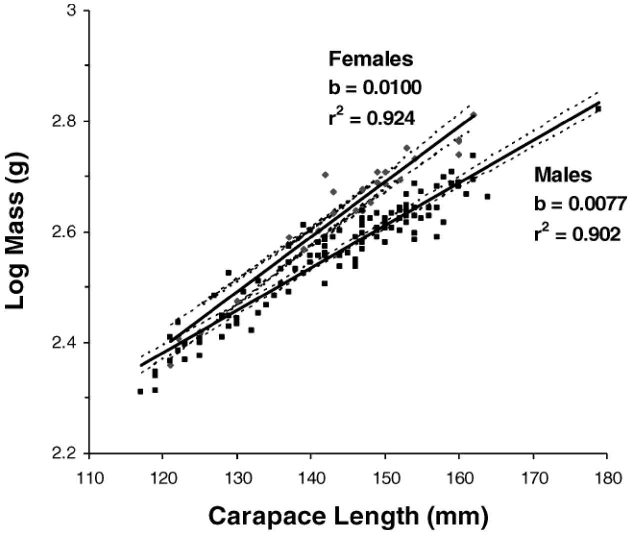

Figure 2. Relationship between log mass (g) and carapace length (mm) of adult male and female western pond turtles at Vandenberg Air Force Base, Santa Barbara County, California. Dashed lines are the 95% confidence intervals.

skewed ($\chi^2 = 53.3$, $p < 0.001$). Of the 179 turtles, 150 (83.8%) were adults (> 120 mm CL) and 29 (16.2%) were juveniles (Fig. 1). No turtles < 90 mm CL were caught. We estimated the age for 133 (74%) of the 179 turtles, and 73 of these (40.8%) were ≤ 5 years, including 12 estimated as 2 years old and 16 as 3 years old (Fig. 1).

Females were significantly heavier than males (Fig. 2) when females with eggs were excluded from the comparison ($F_{1,127} = 10.00$, $p = 0.002$). In June 1996, 12 of 18 females (66.7%) were gravid with a mean of 5.2 eggs (SE = 0.36; range, 3–7). One female (143 mm CL, 15+ years) was caught twice and had 7 eggs on 6 June and 5 eggs that were not well shelled (faint on radiograph) on 26 June. The smallest female with eggs ($n = 3$) was 139 mm CL and 5 years old, and the youngest female with eggs ($n = 7$) was 4 years old and 141 mm CL. Eleven of the females that we radiographed were estimated to be > 15 years, and 8 of these carried eggs (72.7%); 7 females were 4–7 years old, and 4 of these were gravid (57.1%).

The mean CL of females was not significantly different than that of males (Table 1; $F_{1,140} = 0.31$, $p = 0.579$). The largest females (upper decile size) averaged 160.7 mm CL ($n = 3$), which was not significantly different than the 162.1-mm CL average ($n = 11$) of the upper decile size of males (Table 1; $W = 24$, $p = 0.876$). Males, however, grew faster than females in their first 10 years of life (Fig. 3). Based on estimated CL from the growth model, males were significantly larger than females by age 6 (Table 2). On average, males reached 120 mm CL in 3.6 years versus 4.1 years for females, and males reached 150 mm CL in 8.3 years compared to 11.1 years for females.

DISCUSSION

Although adult-sized turtles greatly outnumbered smaller *A. marmorata* at Vandenberg Air Force, over 40% of the turtles we caught were 5 years or younger, with many 2- and 3-year-old turtles in the population. No hatchling turtles were caught. Storer (1930) noted that young *A. marmorata* were not common in collections, and few small turtles have been found at several sites sampled in the Central Valley of California (Germano and Bury

Table 1. Mean, sample size (n), and standard error (SE) of mass and carapace length (CL), and upper 10% CL of adult western pond turtles *(Actinemys marmorata)* captured at Vandenberg Air Force Base, Santa Barbara County, California, 1995–1996.

	Mass (g)			Carapace length (mm)			
	n	Mean	SE	*n*	Mean	SE	Upper 10%
Males	115	373.1	7.50	115	143.2	1.15	162.1
Females	27	448.7	20.0	27	144.8	2.09	160.7
Combined	142	387.5	7.59	142	143.6	1.00	161.9

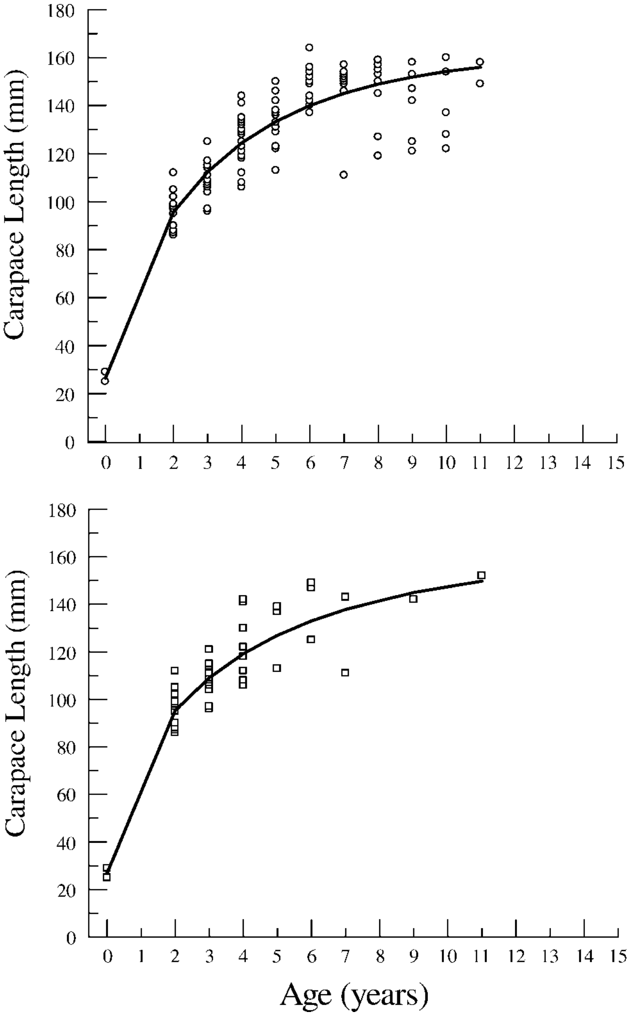

Figure 3. Growth curve of male (top) and female (bottom) western pond turtles at Vandenberg Air Force Base, California, based on carapace lengths using the Richards growth model (see Methods).

Table 2. Calculated carapace lengths (95% confidence interval) in millimeters of male and female *Actinemys marmorata* from Vandenberg Air Force Base, Santa Barbara County, California 1995–1996.[a]

	Calculated carapace lengths (mm)[b]	
Age (years)	Male	Female
0 (hatchling)	26.4	27.0
	(24.2–28.6)	(21.1–33.0)
2	95.7	95.3
	(93.5–97.9)	(89.4–101.2)
4	124.4	119.2
	(122.2–126.7)	(113.3–125.2)
6	140.0*	133.0*
	(137.8–142.2)	(127.1–139.0)
8	148.9*	141.8*
	(146.7–151.2)	(137.9–147.4)
10	154.2*	147.6*
	(152.0–156.4)	(141.5–153.3)

[a] Significant differences between the sexes are indicated by asterisks.

[b] Calculated carapace lengths at various ages were determined from growth equations for each sex (Fig. 3).

2001, Lechner 2004; Lubcke 2004). The lack of smaller turtles, particularly hatchlings, is typical of the population assessments of other turtle species, even those that have stable populations. For example, Agassiz (1857) found that first-year *Glyptemys* (*Clemmys*) *insculpta* could not be found even when > 100 turtles were caught in an afternoon by a large number of searchers. Small *Malaclemys terrapin* were not seen except in the stomach contents of crows (*Corvus brachyrynchos*; Coker 1906). Even for relatively stable populations that had been studied for many years with many hundreds of turtles caught, Frazer et al. (1990) had trouble estimating survivorship of *Trachemys scripta* aged 1–4 years because young were rarely seen. Similarly, few juvenile *Emydoidea blandingii* were caught at the George Reserve in Michigan (Congdon et al. 1993). The lack of captures of these smaller sizes is likely because of the secretive nature of very small turtles (Congdon et al. 1993). Because we caught relatively large numbers of turtles aged 2–5 years, we reason that hatchling and 1-year-old turtles are probably present but are not caught by the methods we used. These smallest turtles are the most vulnerable to predation, and they likely survive by staying in dense shoreline vegetation and not moving out into open water, where traps are typically set.

We found males to be over 4 times more abundant than females. We do not know if this skewed sex ratio is truly representative or if males were more likely to be caught in the traps we used. Uneven sex ratios are not uncommon in studies of turtles (Gibbons 1970; Bury 1979); for example, male-biased sex ratios were found for all 6 species of aquatic turtles caught in baited traps in Ellenton Bay in South Carolina (Gibbons 1990). However, sex ratios were either even or female-biased for these species based on captures using drift fences on land. These differences likely were based on the trapping method because females were intercepted when they ventured out of water to nest; whereas, males had a greater tendency to remain in the water and consequently encountered traps more often (Gibbons 1990). Differential mortality of females on roads has also been suggested as biasing sex ratios (Gibbs and Steen 2005); although, road mortality was not noted during our trapping. Equal sex ratios of *A. marmorata* have been found at 2 sites along the Mojave River near Barstow, California (Lovich and Meyer 2002); at the Chino Hills and the west fork of the San Gabriel River in southern California (Goodman 1997a); and at a section of Big Chico Creek at Chico, California (Lubcke 2004). Sex ratios of *A. marmorata* were either even or slightly female-biased at 4 sites in the San Joaquin Valley (Germano and Bury 2001) and ranged from 0.70:1.0 at a foothill section of Big Chico Creek to 2.3:1.0 at a site along the Sacramento River (Lubcke and Wilson 2007). At all these sites, turtles were caught using traps or by a combination of hand capture and trapping. Using hand capturing exclusively, Bury (1972) found males outnumbered females 1.17 to 1.00 over 4 years in a northern California stream. Despite the apparent skewed sex ratio that we found, there was a high proportion of young turtles in the Vandenberg population, indicating that reproduction had not been compromised.

Although our sample size was small, the mean clutch size was similar to that found for other populations of *A. marmorata*. Scott et al. (2008) found a mean clutch size of 5.7 ± 1.20 SE; (range, 3–8; $n = 97$ clutches) at coastal streams in central California, and Lovich and Meyer (2002) found a mean of 4.6 ± 0.90 SE eggs (range, 4–6; $n = 12$) from 2 close sites along the Mojave River. In southern California, Goodman (1997a) found a mean clutch size of 5.7 ± 0.42 SE (range, 2–8; $n = 16$) from the Chino Hills and a mean of 5.7 ± 0.25 SE eggs (range, 4–8; $n = 15$) from the west fork of the San Gabriel River, and Pires (2001) found a mean clutch size of 4.5 ± 0.25 SE (range, 2–8; $n = 31$) from the Santa Rosa Plateau. In contrast, Feldman (1982) found a mean clutch size of 7.3 ± 1.18 SE (range, 4–9; $n = 4$) from southern Oregon. More data are needed from northern populations to determine if clutch size varies with latitude.

We found 1 female at Vandenberg that produced 2 clutches in 1996. Double clutching also has been found for *A. marmorata* from coastal streams in central California (Scott et al. 2008), the Chino Hills (Goodman 1997b), the Santa Rosa Plateau (Pires 2001), and sites along the Mojave River (Lovich and Meyer 2002). In general, producing multiple clutches in 1 season may not be unusual for turtles. The production of 2 clutches has been found in *T. scripta elegans* from South Carolina (Frazer et al. 1990), and half of the females of *Clemmys guttata*, also from South Carolina, produced 2–3 clutches in a season (Litzgus and Mousseau 2003). Even in the harsh desert conditions of the Mojave Desert, female desert tortoises (*Gopherus agassizii*) may produce 2 and sometimes 3 clutches per year (Turner et al. 1986). The production of multiple clutches in a season is an important feature of a population's life history strategy, which may vary with latitude and environmental features.

The smallest gravid female we found at Vandenberg was 139 mm CL. The smallest female *A. marmorata* with eggs at coastal streams in central California was 140 mm CL (Scott et al. 2008); along the Mojave River, 133 mm (Lovich and Meyer 2002); at Chino Hills, 135 mm (Goodman 1997a); on the San Gabriel River, 137 mm (Goodman 1997a); and at Santa Rosa Plateau, 121 mm (Pires 2001). The small size of gravid females at Santa Rosa Plateau (10 of 24 females with eggs were $<$ 130 mm CL; Pires 2001) could be due to the overall small size of females at this site. The upper decile CL ($n = 3$) of females at the Santa Rosa Plateau was only 146.7 mm, whereas the upper decile CL at Vandenberg was 160.7 mm.

Growth and maturation of freshwater turtles is influenced by ambient air and water temperatures (Williamson et al. 1989; Brown et al. 1994), often in conjunction with basking behaviors. Microhabitat basking sites used by *A. marmorata* to regulate its metabolism are dynamic in space and time and include aerial basking, which is easily recognized, as well as more cryptic behaviors such as burying themselves in warm sand (Rathbun et al. 2002) and lying in algal mats that are warmer than ambient air and water (R. Bury, D. Germano, and G. Rathbun, *pers. obs.*). The Mediterranean climate as well as use of warm microhabitats may explain the rapid growth of turtles at our study site. Female turtles at Vandenberg reached 50% of their asymptotic CL in 1.2 years and 90% of that size in 8.9 years; whereas, males reached 50% in 1.4 years and 90% in 7.2 years. There are no published studies of growth for *A. marmorata* to compare with our data, but we can compare our data to growth rates of related species. In contrast to turtles at our site, female *Glyptemys insculpta* from Pennsylvania and Virginia (which are about the same size as A. *marmorata* as adults) reached 50% of their asymptotic CL in about 5 years and 90% size in about 17 years, and males reached 50% CL in about 7 years and 90% in about 27 years (from Lovich et al. 1990: fig. 1). Female *Emydoidea blandingii* from western Nebraska reached 50% CL in 3.7 years and 90% CL in 13.3 years and males reached 50% CL in 4.6 years and 90% CL in 14.2 years (Germano et al. 2000), and female *E. blandingii* from Michigan took about 6 years to reach 50% CL and 15.5 years to reach 90% CL, whereas males took about 5.5 years and 16 years to reach 50% and 90% CL, respectively (from Fig. 1 of Congdon and van Loben Sels 1991).

In conclusion, turtles at our study site grew quickly, matured at a young age, and included many young individuals despite an apparently male-biased sex ratio. We suspect that the overall mild temperatures characteristic of the Mediterranean climate at our study site, in concert with basking in microhabitats, was an important factor influencing the population structure and life history of *A. marmorata*. The unique Mediterranean climate regime at out study site also explains why growth rates in *A. marmorata* were greater than similarly sized turtles occurring in eastern and central North America that have continental weather patterns.

Acknowledgments

We especially thank Norman Scott, Jr., for supporting this study through a contract with Vandenberg Air Force Base. We thank Rochelle Germano and Susan Christopher for their help in 1996. Turtles were radiographed at the West Valley Veterinary Clinic in Lompoc, California. We thank R. Bruce Bury for providing helpful comments on an earlier version of this paper. Work was carried out with a California Scientific Collecting Permit.

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Received: 4 June 2007
Revised and Accepted: 4 April 2008