JOURNAL
OF
HERPETOLOGY

Variation in Body Size, Growth, and Population Structure of *Actinemys marmorata* from Lentic and Lotic Habitats in Southern Oregon

DAVID J. GERMANO[1,2] AND R. BRUCE BURY[3]

[1]Department of Biology, California State University, Bakersfield, California 93311-1022 USA;
E-mail: dgermano@csub.edu
[3]U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, 3200 SW Jefferson Way,
Corvallis, Oregon 97331 USA; E-mail: buryb@usgs.gov

Journal of Herpetology, Vol. 43, No. 3, pp. 510–520, 2009

Variation in Body Size, Growth, and Population Structure of *Actinemys marmorata* from Lentic and Lotic Habitats in Southern Oregon

DAVID J. GERMANO[1,2] AND R. BRUCE BURY[3]

[1]*Department of Biology, California State University, Bakersfield, California 93311-1022 USA;*
E-mail: dgermano@csub.edu
[3]*U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, 3200 SW Jefferson Way,*
Corvallis, Oregon 97331 USA; E-mail: buryb@usgs.gov

ABSTRACT.—**Turtle body size and growth rates are affected by several environmental factors, including thermal regimes. Small lentic habitats in northern latitudes often are thermally stratified in summer and, overall, provide a warmer environment than lotic habitats, which usually lack stratification because of flowing current. Several studies indicate that the amount of food consumption and rate of growth of turtles are higher, and body size larger, in warmer environments than cooler habitats. However, few sites have been examined. To better test these patterns, we compared the growth, body size, and population structure of the Western Pond Turtle (*Actinemys marmorata*) from six small lentic and four lotic habitats in southern Oregon. We found that adult size and growth rates were the same for the four lotic habitats and variable but not consistently greater at lentic sites. There were a high proportion of large turtles at all lotic sites but a variable proportion of sizes among lentic sites. Age structures did not match size structures for most populations because we found many young turtles in these populations but few small-sized turtles. Thus, we caution against reliance on size alone as a measure of population structure or trends in turtle populations. Further, our study suggests that sampling at a relatively large number of sites (e.g., ≥3 of each habitat type) improves inference of results.**

Studying the life history of species across habitats and geographic areas can inform biologists how species respond to environmental variability. For instance, some life-history traits of freshwater turtles vary across geographic distance (Wilbur and Morin, 1988). At the same time, however, local variation in some traits may be significant (Gibbons, 1967; Lindeman, 1996; Rowe, 1997) and must be identified before broad geographic patterns can be discerned (Wilbur and Morin, 1988). Individual growth rate and adult body sizes of animals are important life-history traits because they often influence survivorship and reproductive success (Schaffer, 1974; Stearns, 1992; Charlesworth, 1994). For freshwater turtles, growth and body size affect age at maturity, clutch size, and egg size (e.g., Dunham and Gibbons, 1990; Congdon and van Loben Sels, 1991; Iverson and Smith, 1993).

Age structure is an important demographic parameter that may vary among populations as a result of interpopulation variation in individual growth rates. Most turtle populations have a size structure composed of many large turtles and relatively few small turtles (Bury 1979; Dunham and Gibbons, 1990; Gibbs and Amato, 2000). Besides the lack of young turtles in recapture data (Dunham and Gibbons, 1990), size structure may not accurately represent ages of turtles at a site because relatively rapid growth of individuals may result in adult-sized turtles that are fairly young when compared to similar-aged individuals in populations with relatively slow individual growth rates. Determining ages of turtles would be a more accurate depiction of population structure and may be important to understanding the turtle's ecology because fecundity and survivorship vary by age in many species (Ricklefs, 1990; Charlesworth, 1994). Defining age structure can help determine temporal variation in population dynamics, such as changes in fecundity in the past (Ricklefs, 1990). Although an age structure developed over a short interval could miss changes that occur year to year, this is less likely to be a problem with long-lived species, such as freshwater turtles.

Growth and body size of freshwater turtles can be affected by environmental parameters of aquatic habitats (Gibbons, 1970; Andrews, 1982). Because turtles are ectotherms, cooler habitats reduce rates of food consumption and growth of individuals compared to warmer environments (Williamson et al., 1989; Dunham and Gibbons, 1990; Avery et al., 1993). Several emydid turtles thermoregulate, at least during part of the year (Boyer, 1965; Grayson and

---

[2] Corresponding Author.

Dorcas, 2004; Edwards and Blouin-Demers, 2007) by aerial or aquatic basking (Spotila et al., 1990; Sajwaj and Lang, 2000; Edwards and Blouin-Demers, 2007). Freshwater turtles living in small lentic habitats could experience warmer water temperatures and faster growth rates than turtles that live in lotic sites. Ponds and marshes can develop a thermocline when days are calm (Mazumder and Taylor, 1994; Xenopoulos and Schindler, 2001), and the relatively warm water in the summer should increase growth rates of turtles beyond that of lotic habitats (Gibbons 1970; Christy et al., 1974; Parmenter, 1980). The flow of water in lotic habitats constantly mixes the water column and continuous groundwater inputs keeps water cool. Also, lentic habitats generally are more productive than lotic sites (Ricklefs and Miller, 2000) and have a higher diversity of macroinvertebrates and aquatic plants (Williams et al., 2003), which could also increase growth rates of turtles in ponds.

The Western Pond Turtle (*Actinemys marmorata*) occurs in a variety of habitats throughout its range, including streams, rivers, ponds, lakes, marshes, and artificial aquatic habitats along the Pacific coast of North America (Storer, 1930; Bury, 1970). The ecology of *A. marmorata* has been studied mostly in California (Reese and Welsh, 1998; Goodman and Stewart, 2000; Lovich and Meyer, 2002; Lubcke and Wilson, 2007; Germano and Rathbun, 2008) and age-size relationships in only four populations (Germano and Bury, 2001). In areas where populations of *A. marmorata* occur in both lentic and lotic habitats, we expect that thermal differences in these habitats should lead to faster rates of growth and larger body size of turtles in ponds and other lentic habitats.

Our objective was to determine whether habitat influences growth and body size among local populations of *A. marmorata* in lentic and lotic habitats of southern Oregon. Because of potential primary productivity and thermal advantages of living in lentic habitats when compared to lotic habitats, we predicted that individual growth rates would be relatively high, and body size relatively large, in turtles that live in lentic habitats. However, because of potential confounding effects of density and productivity among localities, we expected individual growth rates and body size to be highly variable among localities. To determine whether any variation in size structure among populations was caused by variations in individual growth rates among populations, we also compared age structures among populations. Growth curves were compared among populations to determine whether any growth rate variation occurred during the juvenile phase, the adult phase, or both.

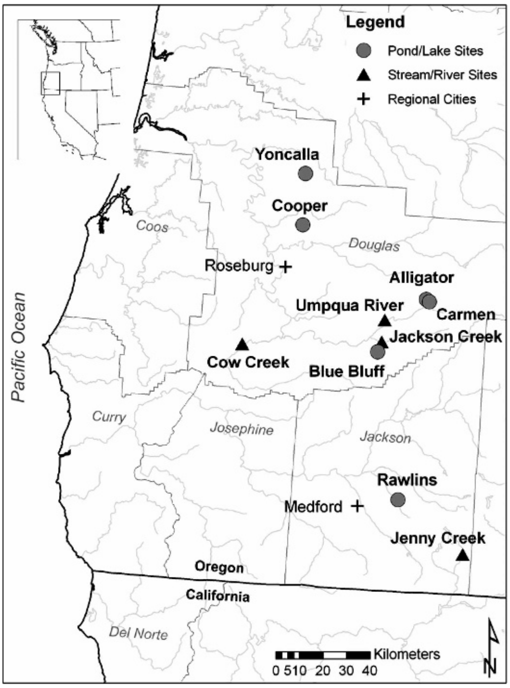

FIG. 1. Study Sites for *Actinemys marmorata* in southern Oregon.

MATERIALS AND METHODS

Study Sites.—We attempted to balance the number of sites by lentic (ponds and reservoirs) and lotic (streams and rivers) waters. We captured turtles from 1993–2007 at five ponds, one small reservoir, three streams, and one river in three river basins of southern Oregon (Fig. 1). Sites varied in size and elevation (Table 1) but represented the variability of topography and habitats of the mountainous terrain in the region.

Capture and Measurement of Turtles.—At the lentic sites, we captured turtles for two days in collapsible nylon net traps with single or double funnels. At the lotic sites, we captured most turtles by hand (diving into waters), but a few were taken in traps. We suspect that young and small turtles were underestimated by our capture methods, but we believe that our bias was consistent across sites.

For each captured turtle, we recorded sex, age, and standard body size measurements such as maximum carapace length (CL). We determined an individual's age using scute annuli from the carapace and plastron. We have found that scute annuli match the age of *A. marmorata* individuals up to about 15–16 yr (Bury and Germano, 1998). Some turtles could only be classified as being older than 20 yr because

TABLE 1. Attributes of sites and years of study where *Actinemys marmorata* were captured in ponds, reservoirs, streams, and rivers of southern Oregon.

Site	Elevation (m)	Approximate size (ha) or dimensions	Type of aquatic habitat	Years
Ponds and Reservoirs				
Yoncalla	120	2 ha	Adjacent unused logging ponds	1993–94
Cooper	244	ca. 150 m × 2.5 km	Artificial reservoir	1994
Alligator	895	1 ha	Impoundment of wetland	1995, 1997
Carmine	730	2 ha	Impoundment of wetland	1997–98, 2007
Blue Bluff	730	0.5 ha	Former gravel borrow pit	1994, 1996, 2007
Rawlins	724	0.5 ha	Impoundment of depression	1995–97
Streams and Rivers				
Cow Creek	305	2–3 m wide	Creek	1996
Jackson Creek	430	2 m wide	Creek	1994, 1996–97
S. Umpqua River	425	15 m wide	Small river	1997–98
Jenny Creek	1,115	2–3 m wide	Creek	1994–96

scute annuli were worn and edges of scutes were beveled; these animals were large and no longer depositing discernable annuli (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 turtles at the site of capture within 24 h.

Statistical Analysis.—We used ANOVA to test for differences in mean CL of adults among sites and between sexes with a site × sex term. To minimize the effect of age structure on size estimates (Case, 1976), we determined both the upper decile CL to compare the largest turtles among sizes and the largest three male and female CLs. We tested for differences in upper CL among sites using the Kruskal-Wallis test and tested upper trio differences between sexes at a site using Mann-Whitney tests. We also compared both the size (CL) and age structures of each population to one another using the Kolmogorov-Smirnov test.

The Richards' growth model (Richards, 1959) was used to construct individual curves where three parameters were estimated using CL and age: M, the shape of the growth curve; K, the growth constant; and I, the point at which curve inflection begins. Following Bradley et al. (1984), we used mean upper decile (or quartile) sizes of adults as asymptotic sizes because of the high values predicted from growth data with large confidence intervals. Further, we set hatchling size to be 25 and 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 among habitats and sites using the statistic, G, which represents the time required to grow from 10–90% of asymptotic size and is an indicator of the duration of primary growth (Bradley et al., 1984). It is defined as

$$G = \ln\left[\left(1 - 0.10^{1-M}\right) / \left(1 - 0.90^{1-M}\right)\right] / K.$$

The raw parameters K and M are closely linked in determining growth curves, and neither is useful for comparing growth between populations (Bradley et al., 1984). 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 on an easily interpreted scale (Bradley et al., 1984), in our case, years. We compared values of G between lentic and lotic habitats using ANOVA. We also grouped sites by similarity of growth curves and compared G-values among these sites using ANOVA. As a final measure of growth, we derived calculated carapace lengths (CCL) from the growth equations using 3-yr intervals from ages 3–12 yr. We compared CCL of habitats and combined sites among years using ANOVA with a habitat or site × year term. We considered all statistical tests significant at or below alpha = 0.05.

RESULTS

We captured 494 *A. marmorata* at 10 sites in southern Oregon. Most (N = 335; 67.8%) were adults and varied in number from 21–54 at each site (Table 1). We caught only *A. marmorata* at these sites. The mean CL of adults differed

TABLE 2. Minimum (Min.), maximum (Max.), mean, and upper decile carapace lengths (CL in mm; SE = standard error, N = sample size) of all adult *Actinemys marmorata*, and Min., Max., mean, and upper trio CL of males (M) and females (F) caught in two habitat types of southern Oregon. Significant differences ($P < 0.05$) among sites within habitat type are designated by a lack of a common letter and between sexes with an asterisk.

Site	Min.	Max.	Mean	SE	N	Upper decile	Upper trio	SE	N
Ponds and Reservoirs									
Yoncalla									
All	126	193	162.8^{a}	2.60	47	185.8^{a}		2.96	5
M	146	193	171.1*	2.51	24		189.0	4.00	3
F	126	182	154.2*	4.01	23		180.0	1.00	3
Cooper									
All	121	189	165.8^{a}	3.37	21	186.5^{a}		2.50	2
M	121	189	165.3	4.81	15		185.3	1.86	3
F	160	174	170.1	3.60	7		170.7	2.03	3
Alligator									
All	121	163	$143.6^{b,c}$	1.89	25	157.3^{b}		2.96	3
M	140	163	146.7	1.84	13		156.3	3.33	3
F	121	156	140.2	3.65	12		153.0	1.53	3
Carmine									
All	120	180	$154.2^{a,b}$	3.06	27	176.0^{a}		2.08	3
M	132	180	159.1	3.27	17		176.0	2.08	3
F	120	168	145.9	5.61	10		165.7	1.45	3
Blue Bluff									
All	119	183	$155.4^{a,b}$	3.34	25	181.7^{a}		0.67	3
M	124	183	161.2	4.56	13		181.7	0.67	3
F	119	174	149.1	4.60	12		168.3	3.48	3
Rawlins									
All	116	153	133.8^{c}	1.67	37	149.5^{b}		1.32	4
M	116	159	131.7	2.39	17		145.3	1.53	3
F	119	153	135.7	2.41	20		150.3	1.45	3
Streams and Rivers									
Cow Creek									
All	120	176	151.7^{b}	2.20	54	173.0^{a}		0.87	6
M	120	176	151.3	2.91	35		173.7	1.20	3
F	127	175	152.4	3.43	19		172.3	1.33	3
Jackson Creek									
All	119	195	$155.0^{a,b}$	2.42	39	179.3^{a}		5.25	4
M	119	195	156.8	4.51	15		179.0	8.19	3
F	120	174	153.9	2.88	24		173.7	0.33	3
South Umpqua									
All	118	195	$151.4^{a,b}$	3.63	25	181.0^{a}		7.21	3
M	129	195	157.5	5.48	11		175.3	9.84	3
F	118	177	146.6	4.80	14		171.7	2.91	3
Jenny Creek									
All	117	186	$155.0^{a,b}$	2.81	40	180.3^{a}		1.93	4
M	117	186	157.9	3.77	25		181.0	2.52	3
F	119	175	150.3	4.12	15		168.0	3.61	3

significantly among sites ($F_{9,320} = 11.00$, $P < 0.001$) and sex ($F_{1,320} = 12.29$, $P = 0.001$), but the site × sex term was not significant ($F_{9,320} = 1.85$, $P = 0.058$). There were no consistent differences in mean CL between turtles from lentic and lotic habitats (Table 2). The largest mean CL values were in populations from Yoncolla and Cooper, both lentic sites, but these were significantly larger only from turtles at Alligator and Rawlins, also lentic sites, and from turtles at Cow Creek, a lotic site (Table 2). Mean CL of turtles at Rawlins was significantly smaller than turtles from all other sites but Alligator (Table 2). There also was an overall significant difference in upper decile CL ($H_9 = 26.85$, $P = 0.0001$), and turtles from Alligator and Rawlins were significantly smaller than turtles from all other sites. Also, mean male CL significantly differed between females only at Yoncolla, and there were no significant differences in CL between sexes using the upper trio means (Table 2).

The total number of turtles captured at each site ranged from 24–83 (Table 3). The percent-

TABLE 3. Percentage of juvenile (<120 mm carapace length [CL]) and adult (≥120 mm CL) and percentage of young (0–4 yr) and old (15+ yr) *Actinemys marmorata* caught in two habitat types in southern Oregon.

Site	*N*	Juveniles	Adults	Young	Old
Ponds and Reservoirs					
Yoncalla	60	18.3	81.7	3.3	36.7
Cooper	24	12.5	87.5	12.5	66.7
Alligator	32	21.9	78.1	3.1	71.9
Carmine	50	46.0	54.0	36.0	12.0
Blue Bluff	39	35.9	64.1	30.8	20.5
Rawlins	83	57.8	42.2	20.5	19.3
Streams and Rivers					
Cow Creek	65	16.9	83.1	4.6	43.1
Jackson Creek	56	30.4	69.6	8.9	58.9
South Umpqua	32	25.0	75.0	9.4	46.9
Jenny Creek	53	28.3	71.7	3.8	73.6

age of juvenile turtles (<120 mm CL) in a population was 12.5–57.8% in lentic habitats and 16.9–30.4% in lotic habitats (Table 3). Size structures among lotic populations were not significantly different (D = 0.098–0.155, P = 0.435–0.985). However, the size distribution of turtles at Rawlins differed significantly from all other sites (D = 0.328–0.750, P < 0.001–0.002), lentic and lotic. The size structure of turtles at Cooper differed from all sites (D = 0.365–0.750, P < 0.001–0.002) except for that of Yoncolla (D = 0.217, P = 0.354), and Yoncolla differed from all sites (D = 0.281–0.581, P < 0.001–0.018) but that at the Cooper and Jenny Creek (D = 0.243, P = 0.061). Similarly, the size structure of turtles at Alligator differed from all sites (D = 0.327–0.480, P < 0.001–0.035) but that at Carmine (D = 0.269, P = 0.099) and South Umpqua (D = 0.313, P = 0.069). There was a high proportion of turtles <100 mm CL at Rawlins compared to

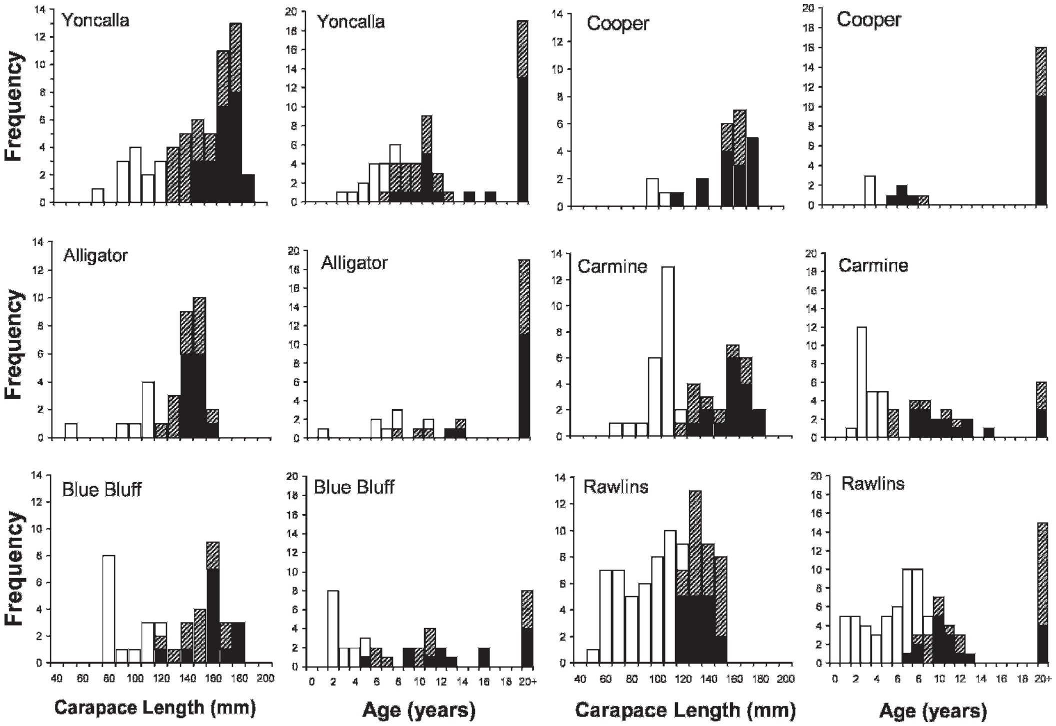

FIG. 2. Frequency distribution of carapace lengths and ages of *Actinemys marmorata* captured at ponds and a reservoir of southern Oregon. Black bars are males, hatched bars are females, and open bars are turtles for which gender could not be determined.

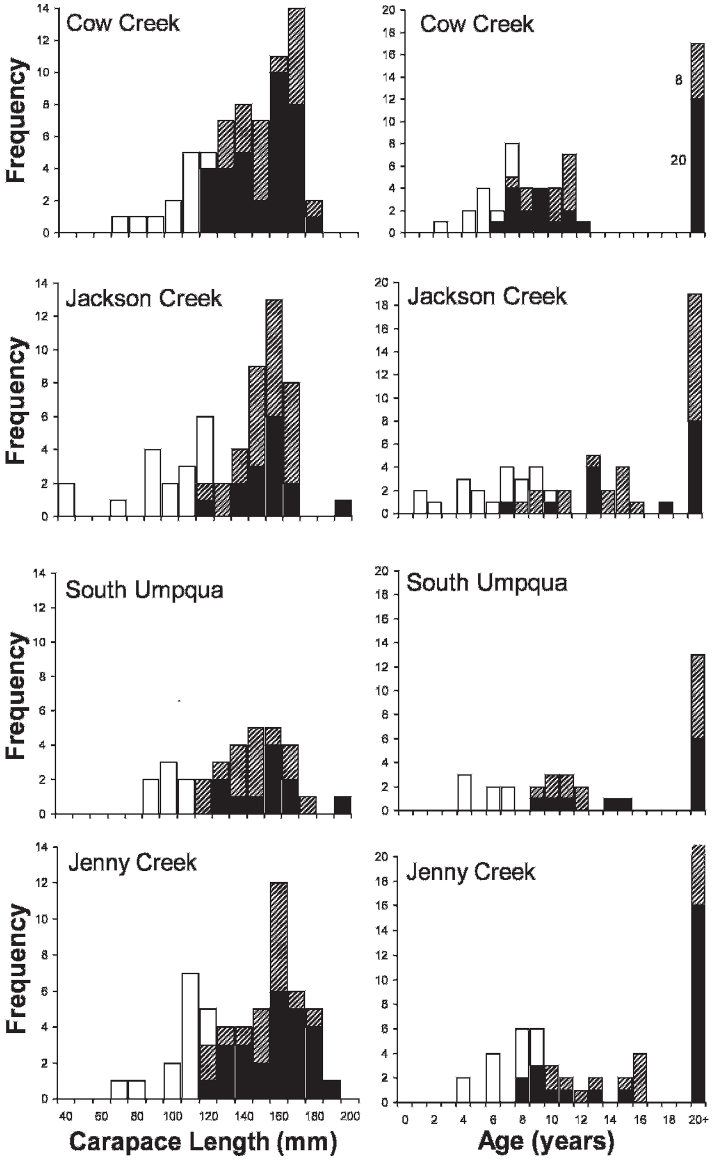

FIG. 3. Frequency distribution of carapace lengths (left) and age (right) of *Actinemys marmorata* captured at streams and a river of southern Oregon. Black bars are males, hatched bars are females, and open bars are turtles for which gender could not be determined.

the other populations, and almost all turtles at Alligator were between 100 and 160 mm CL (Fig. 2). All stream and river populations had size distributions that were skewed to larger body sizes (Fig. 3).

The percentage of young (0–4 yr) turtles at lentic sites varied from 3.1–36.0%, and the percentage of old (≥15 yr) turtles varied from 12.0–71.9% (Table 3). At lotic sites, the percentages of young turtles were much more similar varying from 3.8–9.4%, and the percentage of old turtles was 43.1–73.6% (Table 3). Like the size structures, the age structures among lotic sites also did not differ significantly (D = 0.103–0.148, P = 0.508–0.976). However, differences among lentic sites for age structure were not the same as differences for size structures. Unlike the size structure at Rawlins that differed significantly from all other lentic populations, age structure was not significantly different from that at Carmine (D = 0.195, P = 0.165) and Blue Bluff (D = 0.159, P = 0.480). Alligator

TABLE 4. Growth parameters of Richards growth curves (Fig. 4) for *Actinemys marmorata* from southern Oregon sites. Parameters describing model fit and growth curves are coefficient of determination (R^2), shape of curve (M), growth constant (K), inflection point of curve (I), and the summary growth statistic, G (years).

Site	R^2	M	K	I	G
Yoncalla	0.772	0.989	0.219	2.90	14.03
Cooper	0.980	1.13	0.307	2.51	10.52
Alligator	0.942	1.22	0.219	2.89	15.24
Carmine	0.911	−0.217	0.191	−1.67	10.76
Blue Bluff	0.966	−0.491	0.147	−3.15	12.90
Rawlins	0.910	1.57	0.224	2.83	16.88
Cow Creek	0.918	0.756	0.215	1.65	13.16
Jackson Creek	0.934	0.066	0.127	−0.937	17.67
South Umpqua	0.949	0.139	0.140	−0.591	16.41
Jenny Creek	0.937	0.423	0.138	0.999	18.28

differed from all lentic sites and all but one lotic site in size structure but did not have a significantly different age structure from that of Cooper ($D = 0.125$, $P = 0.974$) or any of the lotic sites ($D = 0.198–0.257$, $P = 0.100–0.383$). Likewise, the size structure of Cooper differed significantly from all sites but from that at Yoncalla, but the age structures were significantly different between these two sites ($D = 0.350$, $P = 0.022$). Further, the age structure at Cooper was not significantly different from those of Alligator, Cow Creek ($D = 0.236$, $P = 0.247$), South Umpqua ($D = 0.260$, $P = 0.266$), and Jenny Creek ($D = 0.270$, $P = 0.149$). There was a high proportion of young turtles at Carmine, Blue Bluff, and Rawlins (Fig. 2).

The growth model fit the data well for all populations with an R^2-value ≥ 0.910 for all curves except that from Yoncalla (Table 4). There was no difference in the mean growth rate (based on G) of turtles from lentic (13.4 yr) and lotic (16.4 years) habitats ($F_{1,9} = 3.654$, $P = 0.092$). Individual growth rates of turtles differed among sites, but several sites showed similar growth patterns: turtles from Carmine and Blue Bluff grew the fastest early but slowed markedly later in life; turtles from Alligator and Rawlins grew slowly throughout; turtles from Yoncalla, Cow Creek, and Cooper grew slowly earlier in life but maintained a high rate of growth until reaching adult size; and turtles from Jackson Creek, South Umpqua, and Jenny Creek grew at a slow rate throughout but higher than Alligator and Rawlins (Fig. 4). Mean growth rates differed significantly among sites that were combined by similar patterns of growth ($F_{3,9} = 9.299$, $P = 0.011$). Based on the summary growth statistic G, turtles from Jackson/South Umpqua/Jenny ($X = 17.45$ yr) grew more slowly than turtles from Carmine/Blue Bluff ($X = 11.83$ yr; SNK $q = 6.13$, $P < 0.05$) and Yoncalla/Cow Creek/Cooper ($X = 12.57$ yr; SNK $q = 5.95$, $P < 0.05$) but not from turtles at Rawlins/Alligator ($X = 16.06$ yr; SNK $q = 1.52$, $P > 0.05$). Growth rates did not differ significantly among the remaining combined sites (SNK $q = 0.81–4.21$, $P > 0.05$).

The mean CCL of *A. marmorata* was not significantly different between lentic and lotic habitats ($F_{1,38} = 2.68$, $P = 0.112$) or for the habitat × year interaction term ($F_{3,38} = 0.12$, $P = 0.949$) but was significantly different across years ($F_{3,38} = 59.38$, $P < 0.001$). The mean CCL among combined sites was significantly different ($F_{3,38} = 54.98$, $P < 0.001$) as it was among years ($F_{3,38} = 345.0$, $P < 0.001$), but the site × year interaction term was not significant ($F_{9,38} = 2.13$, $P = 0.069$). By age 3, turtles at Carmine and Blue Bluff were the largest, reaching an average size of 95.4–97.0 mm CCL, whereas the smallest turtles were at Alligator, Rawlins, and Jenny Creek (Table 5). By age 6, however, turtles from Cooper had reached the same size as turtles from Carmine and Blue Bluff (Table 5). By age 9, turtles at Cooper were the largest at almost 160 mm CCL, those at Carmine and Blue Bluff were smaller at 146–149 mm CCL, and turtles at Yoncalla and Cow Creek averaged 140.5 mm to almost 143 mm CCL (Table 5). Finally, by age 12, turtles at Yoncalla, Carmine, Blue Bluff, and Cow Creek had reached approximately the same large size; turtles from Jackson Creek, South Umpqua, and Jenny Creek were an intermediate size; and the smallest turtles were from Alligator and Rawlins (Table 5). Based on upper CL (Table 2), all turtles eventually reached 170–185 mm CL at the end of growth, except for turtles from Rawlins and Alligator, which only reached 150–155 mm CL.

DISCUSSION

Based on presumed thermal differences in aquatic habitat types of southern Oregon, we

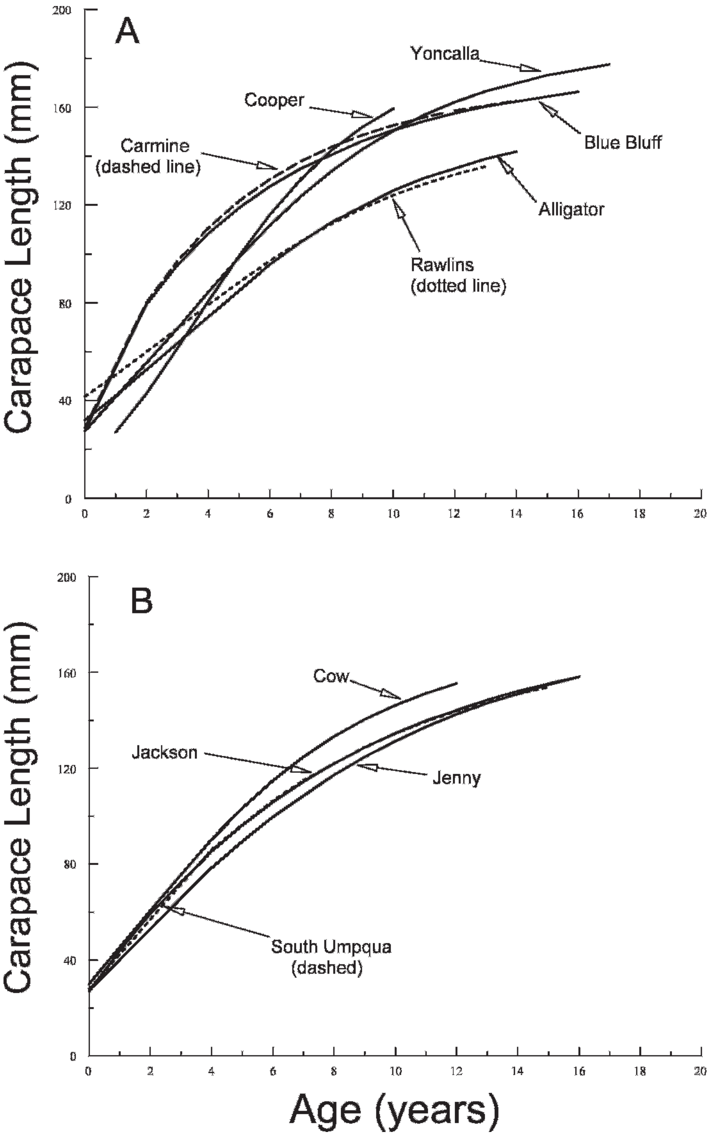

FIG. 4. Growth curve of *Actinemys marmorata* captured at (A) ponds and reservoirs or (B) streams and rivers in southern Oregon based on carapace lengths using the Richards growth model (see Materials and Methods).

predicted that *A. marmorata* from lentic habitats would grow faster and obtain larger body sizes than turtles from lotic sites. However, we found that the smallest and slowest-growing turtles were from two of the six pond sites. Although *A. marmorata* from lotic sites grew at the same rate and obtained similar body sizes, individual growth rates and body sizes of turtles from lentic sites were highly variable, and we did not find consistent differences based on habitat type. Turtles from three ponds and one stream site grew the fastest. Turtles from all but two ponds attained about the same adult size. In southern Oregon, growth and body size of *A. marmorata* does not seem to be primarily affected by habitat type. A number of studies have shown that growth and body size of freshwater turtles can vary among different aquatic sites within a small geographic area (Gibbons, 1970; Lindeman, 1996; Rowe, 1997; Lubcke and Wilson, 2007). Factors known or presumed to affect growth and body size of turtles are thermal regimes (Gibbons 1970; Christy et al., 1974; Parmenter, 1980) or food abundance (Parmenter, 1980; Dunham and Gibbons, 1990; Avery et al., 1993; Lindeman,

TABLE 5. Estimated mean calculated carapace lengths based on Richards growth curves (Fig. 4) for ages 3, 6, 9, and 12 yr of *Actinemys marmorata* from southern Oregon sites.

	Age (yr)			
Site	3	6	9	12
Yoncalla	69.4	111.7	142.8	162.1
Cooper	80.6	130.4	159.4	—
Alligator	63.9	95.7	119.9	135.3
Carmine	97.0	130.5	148.6	158.6
Blue Bluff	95.4	127.5	146.2	157.5
Rawlins	69.5	97.1	118.5	132.5
Cow Creek	76.0	114.9	140.5	155.5
Jackson Creek	73.1	105.9	128.7	144.5
South Umpqua	73.7	106.5	128.9	143.9
Jenny Creek	66.4	99.7	124.7	142.6

1996) and dietary shifts from carnivory to herbivory (Gibbons, 1967).

We did not measure food abundance at our sites, but lentic habitats generally are more productive than lotic sites (Ricklefs and Miller, 2000) and have a higher diversity of macroinvertebrates and aquatic plants (Williams et al., 2003), especially compared to the clear-water streams and river that we sampled. *Actinemys marmorata* is a dietary generalist feeding on a variety of aquatic invertebrates and small vertebrates, such as anuran tadpoles as well as algae and emergent vegetation (Evenden, 1948; Holland, 1985a,b; Bury, 1986). It remains unclear as to why, when productivity was presumably relatively high in lentic habitats, turtles in lentic habitats sometimes grew more slowly than did turtles in lotic habitats.

Differences in population structure among sites in our study were not attributable to habitat. Population structure is important to determine because it can show temporal variation in population size and age structure over time (Ricklefs, 1990). If only adult-sized turtles are found at a site, this could mean that reproduction is unsuccessful and that the site may be a sink for turtles that move in from surrounding sites. However, because growth rates can vary among sites, even within a small geographic area (Gibbons, 1967; Lindeman, 1996; Rowe, 1997), it is important to determine ages of as many individuals as possible. Variation in size and age structure often was not congruent at the sites we studied. Several populations with seemingly adult-biased size structure had a number of rapidly growing juveniles, a pattern that also occurs in some California populations of *A. marmorata* (Germano and Bury, 2001; Germano and Rathbun, 2008). To our knowledge, there are no other published studies on variation of age and size structure among freshwater turtle populations.

The variation in our results suggests a need to sample a relatively large number of sites to improve inference of results. We suggest sampling turtles at many sites rather than focusing efforts at one or few sites to reveal differences in growth rates and body sizes at landscape scales. Understanding the causes of differences in population structure and body size among populations of freshwater turtles would also benefit from measurements of thermal profiles of environments and how they vary temporally, as well as studies of the thermal ecology of turtles, productivity studies, and dietary studies. Information from this research may help determine the major factors influencing turtle growth and demographics.

Acknowledgments.—We thank L. Gangle, D. and R. Germano, G. Bury, C. Henson, C. Thomas, and C. Barclay for assistance capturing turtles. T. Farrell and S. Wray, Oregon Department of Fish and Wildlife (ODFW), provided logistic support and field assistance. Portions of the fieldwork were supported by the Bureau of Land Management—Roseburg District, U.S. Fish and Wildlife Service (Oregon Field Office), and the U.S. Geological Survey. We thank J. Rowe for offer extensive suggestions that improved the manuscript. Field methods were approved by the Animal Care Committee through Oregon State University, and research was conducted with a scientific take permit from Oregon Department of Fish and Wildlife.

LITERATURE CITED

ANDREWS, R. M. 1982. Patterns of growth in reptiles. *In* C. Gans and F. H. Pough (eds.), Physiology D, Physiological Ecology, pp. 273–320. Academic Press, London.

AVERY, H. W., J. R. SPOTILA, J. D. CONGDON, R. U. FISCHER JR., E. A. STANDORA, AND S. B. AVERY. 1993. Roles of diet protein and temperature in the growth and nutritional energetics of juvenile slider turtles, *Trachemys scripta*. Physiological Zoology 66:902–925.

Boyer, D. R. 1965. Ecology of the basking habit in turtles. Ecology 46:99–118.

Bradley, D. W., R. E. Landry, and C. T. Collins. 1984. The use of jackknife confidence intervals with the Richards curve for describing avian growth patterns. Bulletin of the Southern California Academy of Sciences 83:133–147.

Bury, R. B. 1970. *Clemmys marmorata* (Baird and Girard), Western Pond Turtle. Catalogue of American Amphibians and Reptiles 100:1–3.

———. 1972. Habitats and Home Range of the Pacific Pond Turtle, *Clemmys marmorata*, in a Stream Community. Unpubl. Ph.D. diss., University of California, Berkeley.

———. 1979. Population ecology of freshwater turtles. *In* M. Harless and H. Morlock (eds.), Turtles: Perspectives and Research, pp. 571–602. John Wiley and Sons, New York.

———. 1986. Feeding ecology of the turtle *Clemmys marmorata*. Journal of Herpetology 20:515–521.

Bury, R. B., and D. J. Germano. 1998. Annual deposition of scute rings in the western pond turtle, *Clemmys marmorata*. Chelonian Conservation and Biology 3:108–109.

———. 2008. *Actinemys marmorata* (Baird and Girard 1852)—Western Pond Turtle, Pacific Pond Turtle. *In* A. G. J. Rhodin, P. C. H. Pritchard, P. P. van Dijk, R. A. Samure, K. A. Buhlmann, and J. B. Iverson (eds.), Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group, pp. 1.1–1.9. Chelonian Monograph No. 5. Chelonian Research Foundation, Lunenburg, MA.

Cagle, F. R. 1939. A system for marking turtles for future identification. Copeia 1939:170–173.

Case, T. J. 1976. Body size differences between populations of the chuckwalla, *Sauromalus obesus*. Ecology 57:313–323.

Charlesworth, B. 1994. Evolution in Age-Structured Populations. Cambridge University Press, Cambridge.

Christy, E. J., J. O. Farlow, J. E. Bourque, and J. W. Gibbons. 1974. Enhanced growth and increased body size of turtles living in thermal and post-thermal aquatic systems. *In* J. W. Gibbons and R. R. Scharitz (eds.), Thermal Ecology, pp. 277–284, Technical Information Center, Office of Information Services, U.S. Atomic Energy Commission, Oak Ridge, TN.

Congdon, J. D., and R. C. van Loben Sels. 1991. Growth and body size in Blanding's Turtles (*Emydoidea blandingi*): relationships to reproduction. Canadian Journal of Zoology 69:239–245.

Dunham, A. E., and J. W. Gibbons. 1990. Growth of the slider turtle. *In* J. W. Gibbons (ed.), Life History and Ecology of the Slider Turtle, pp. 135–145. Smithsonian Institution Press, Washington, DC.

Edwards, A. L., and G. Blouin-Demers. 2007. Thermoregulation as a function of thermal quality in a northern population of Painted Turtles, *Chrysemys picta*. Canadian Journal of Zoology 85:526–535.

Evenden, F. G. 1948. Distribution of turtles of western Oregon. Herpetologica 4:201–204.

Feldman, M. 1982. Notes on reproduction in *Clemmys marmorata*. Herpetological Review 13:10–11.

Germano, D. J., and R. B. Bury. 1998. Age determination in turtles: evidence of annual deposition of scute rings. Chelonian Conservation and Biology 3:123–132.

———. 2001. Western Pond Turtles (*Clemmys marmorata*) in the Central Valley of California: status and population structure. Transactions of the Western Section of the Wildlife Society 37:22–36.

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

Gibbons, J. W. 1967. Variation in growth rates in three populations of the Painted Turtle, *Chrysemys picta*. Herpetologica 23:296–303.

———. 1970. Reproductive dynamics of a turtle (*Pseudemys scripta*) population in a reservoir receiving heated effluent from a nuclear reactor. Canadian Journal of Zoology 48:881–885.

Gibbs, J. P., and G. D. Amato. 2000. Genetics and demography in turtle conservation. *In* M. W. Klemens (ed.), Turtle Conservation, pp. 207–217. Smithsonian Institution Press, Washington, DC.

Goodman, R. H., Jr., and G. R. Stewart. 2000. Aquatic home ranges of female Western Pond Turtles, *Clemmys marmorata*, at two sites in Southern California. Chelonian Conservation and Biology 3:743–745.

Grayson, K. L., and M. E. Dorcas. 2004. Seasonal temperature variation in the Painted Turtle (*Chrysemys picta*). Herpetologica 60:325–336.

Holland, D. C. 1985a. An Ecological and Quantitative Study of the Western Pond Turtle (*Clemmys marmorata*) in San Luis Obispo County, California. Unpubl. master's thesis, California State University, Fresno.

———. 1985b. Western Pond Turtle (*Clemmys marmorata*): feeding. Herpetological Review 16:112–113.

Iverson, J. B., and G. R. Smith. 1993. Reproductive ecology of the Painted Turtle (*Chrysemys picta*) in the Nebraska sandhills and across its range. Copeia 1993:1–21.

Lindeman, P. V. 1996. Comparative life history of Painted Turtles (*Chrysemys picta*) in two habitats in the inland Pacific Northwest. Copeia 1996:114–130.

Lovich, J., and K. Meyer. 2002. The Western Pond Turtle (*Clemmys marmorata*) in the Mojave River, California, U.S.A.: highly adapted survivor or tenuous relict? Journal of Zoology, London 256:537–545.

Lubcke, G. M., and D. Wilson. 2007. Variation in shell morphology of the Western Pond Turtle (*Actinemys marmorata* Baird and Girard) from three aquatic habitats in Northern California. Journal of Herpetology 41:107–114.

Mazumder, A., and W. D. Taylor. 1994. Thermal structures of lakes varying in size and water clarity. Limnology and Oceanography 39:968–976.

Parmenter, R. P. 1980. Effects of food availability and water temperature on the feeding ecology of pond sliders (*Chrysemys s. scripta*). Copeia 1980:503–514.

REESE, D. A., AND H. H. WELSH JR. 1998. Comparative demography of *Clemmys marmorata* populations in the Trinity River of California in the context of dam-induced alterations. Journal of Herpetology 32:505–515.

RICHARDS, F. J. 1959. A flexible growth function for empirical use. Journal of Experimental Botany 10:290–300.

RICKLEFS, R. E. 1990. Ecology. W. H. Freeman and Company, New York.

RICKLEFS, R. E., AND G. L. MILLER. 2000. Ecology. 4th ed. W. H. Freeman and Company, New York.

ROWE, J. W. 1997. Growth rate, body size, sexual dimorphism and morphometric variation in four populations of Painted Turtles (*Chrysemys picta bellii*) from Nebraska. American Midland Naturalist 138:174–188.

SAJWAJ, T. D., AND J. W. LANG. 2000. Thermal ecology of Blanding's Turtles in central Minnesota. Chelonian Conservation and Biology 3:626–636.

SCHAFFER, W. M. 1974. Selection for optimal life histories: the effects of age structure. Ecology 55:291–303.

SPOTILLA, J. R., R. E. FOLEY, AND E. A. STANDORA. 1990. Thermoregulation in climate space of the Slider Turtle. *In* J. W. Gibbons (ed.), Life History and Ecology of the Slider Turtle, pp. 288–298. Smithsonian Institution Press, Washington, DC.

STEARNS, S. C. 1992. The Evolution of Life Histories. Oxford University Press, Oxford.

STORER, T. I. 1930. Notes on the range and life-history of the Pacific fresh-water turtle, *Clemmys marmorata*. University of California Publications in Zoology 32:429–441.

WILBUR, H. M., AND P. J. MORIN. 1988. Life history evolution in turtles. *In* C. Gans and R. B. Huey (eds.), Ecology B, Defense and Life History, pp. 387–439. Alan R. Liss, Inc., New York.

WILLIAMS, P., M. WHITFIELD, J. BIGGS, S. BRAY, G. FOX, P. NICOLET, AND D. SEAR. 2003. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in southern England. Biological Conservation 115:329–341.

WILLIAMSON, L. U., J. R. SPOTILA, AND E. A. STANDORA. 1989. Growth, selected temperature and CTM of young snapping turtles, *Chelydra serpentina*. Journal of Thermal Biology 14:33–39.

XENOPOULOS, M. A., AND D. W. SCHINDLER. 2001. The environmental control of near-surface thermoclines in boreal lakes. Ecosystems 4:699–707.

Accepted: 9 December 2008.