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Population Structure and Growth of the Turtle *Actinemys marmorata* from the Klamath–Siskiyou Ecoregion: Age, Not Size, Matters

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Determining the demographic structure of turtles is important to understanding their population status and conservation needs. Concern has been raised for the long-term persistence of the Western Pond Turtle (*Actinemys marmorata*) based on demographic analyses using size while ignoring age. Here, we compare the size versus age structures, and examine growth curves, for turtle populations from four sites in the Klamath–Siskiyou ecoregion of northern California and southern Oregon. We show that age structure does not correspond to size structure for two populations. Also, the most abundant of these populations had relatively few small turtles, which suggests inability of previous researchers to locate small turtles. Growth rates and adult size differed among populations, with turtles from two sites in the Coast Range significantly smaller and slower growing than turtles from either a reservoir on the eastern lower slopes of the Coast Range or the Klamath Basin east of the Cascade Mountains. Neither air temperature nor elevation explained the differences in size and growth rates. We hypothesize that larger body size and faster growth rates for some populations of *A. marmorata* may be due to high local productivity. We show that use of size alone gave an erroneous interpretation of population structure. Finding a few small-sized turtles in populations may not represent a lack of recruitment but, instead, a need to determine the proportion of young turtles based on their actual ages.

RATES of growth and adult body sizes of animals are important life history traits because they influence reproductive success (Stearns, 1992). For freshwater turtles, key attributes include clutch size, egg size, and age at maturity (Congdon and van Loben Sels, 1991; Iverson and Smith, 1993; Rowe, 1997). One of the most important demographic attributes of turtles is the age structure profile, which in many turtle populations consists of numerous adults and few young (Dunham and Gibbons, 1990; Gibbs and Amato, 2000).

Determining the age structure of a population is an important step in understanding its ecology because fecundity and survivorship vary by age in many species (Ricklefs, 1990; Charlesworth, 1994). Defining age structure can help determine temporal and spatial variation in population dynamics, including past changes in fecundity (Ricklefs, 1990). Although age structures investigated over short intervals can miss year to year changes, this is less likely to be the case with long-lived species.

The Western Pond Turtle (*Actinemys marmorata*) is a long-lived species where some adults may reach an age of >40 years in the wild (Bury and Germano, 2008). The pond turtle occurs along the Pacific coast of North America (Storer, 1930; Bury, 1970) with many populations found in areas densely populated by humans. Concerns for the survival of populations of this turtle have grown to the point that *A. marmorata* has some level of protection in all the states in which it occurs. Much of the concern for their continued existence is the result of the loss and modification of natural aquatic habitat. Areas particularly affected by habitat loss are southern California, from Baja to Santa Barbara County (Brattstrom, 1988), and the Central Valley of California (Jennings and Hayes, 1994), where previously abundant wetland habitats largely have been converted to agricultural and urban uses (U.S. Fish and Wildlife Service, 1998). Despite this loss of habitat, populations of *A. marmorata* still occur in many streams, ponds, rivers, marshes, and man-made aquatic habitats throughout their range (Bury and Germano, 2008). *Actinemys marmorata* was petitioned for listing range-wide (U.S. Fish and Wildlife Service, 1992) based on the premise that even robust populations were in jeopardy. This supposition was made because the size structure of most populations was adult-size biased and the presence of few juvenile-sized turtles was taken as an indication of a lack of recruitment. However, this petition was rejected (U.S. Fish and Wildlife Service, 1993). Still, efforts to assess trends in populations of *A. marmorata* require accurate recording and interpretations of population structure. Ultimately, we can gain insights into how long-lived species respond to differing environmental conditions by assessing age structures at many sites.

Our objective was to determine population structures and growth patterns of *A. marmorata* from four different sites in northern California and nearby Oregon to compare age distributions, sex ratios, and relative growth rates among sites. We also explored temperature and altitude-related reasons for differences seen in growth rates and demonstrate the need to assess ages of turtles in ways other than using size alone as a criterion.

MATERIALS AND METHODS

Study areas.—We sampled turtles at four sites in northern California and southernmost Oregon (Fig. 1). The data from several closely grouped sites in the ''Klamath Basin'' were combined for analysis: a shallow ditch next to Hwy. 97 south of Klamath Falls (city), Oregon; the Miller Island Wildlife Management Area, and Klamath River below JC Boyle Dam, Oregon; and the Lower Klamath Lake National Wildlife Refuge, California. These sites were between 1150 and 1250 m in altitude, and all occur on the eastern flanks of the Oregon Cascades or in the Klamath Lake Basin, which is an expansive area of marshes, shallow lakes, reservoirs, irrigation canals, and dikes in a high desert ecosystem (hereafter Klamath Basin sites). The other sites are in the Coast Range of northern California, which has a Mediterranean climate (mild wet winters and hot dry summers). We sampled turtles in several arms of Whiskeytown Reservoir

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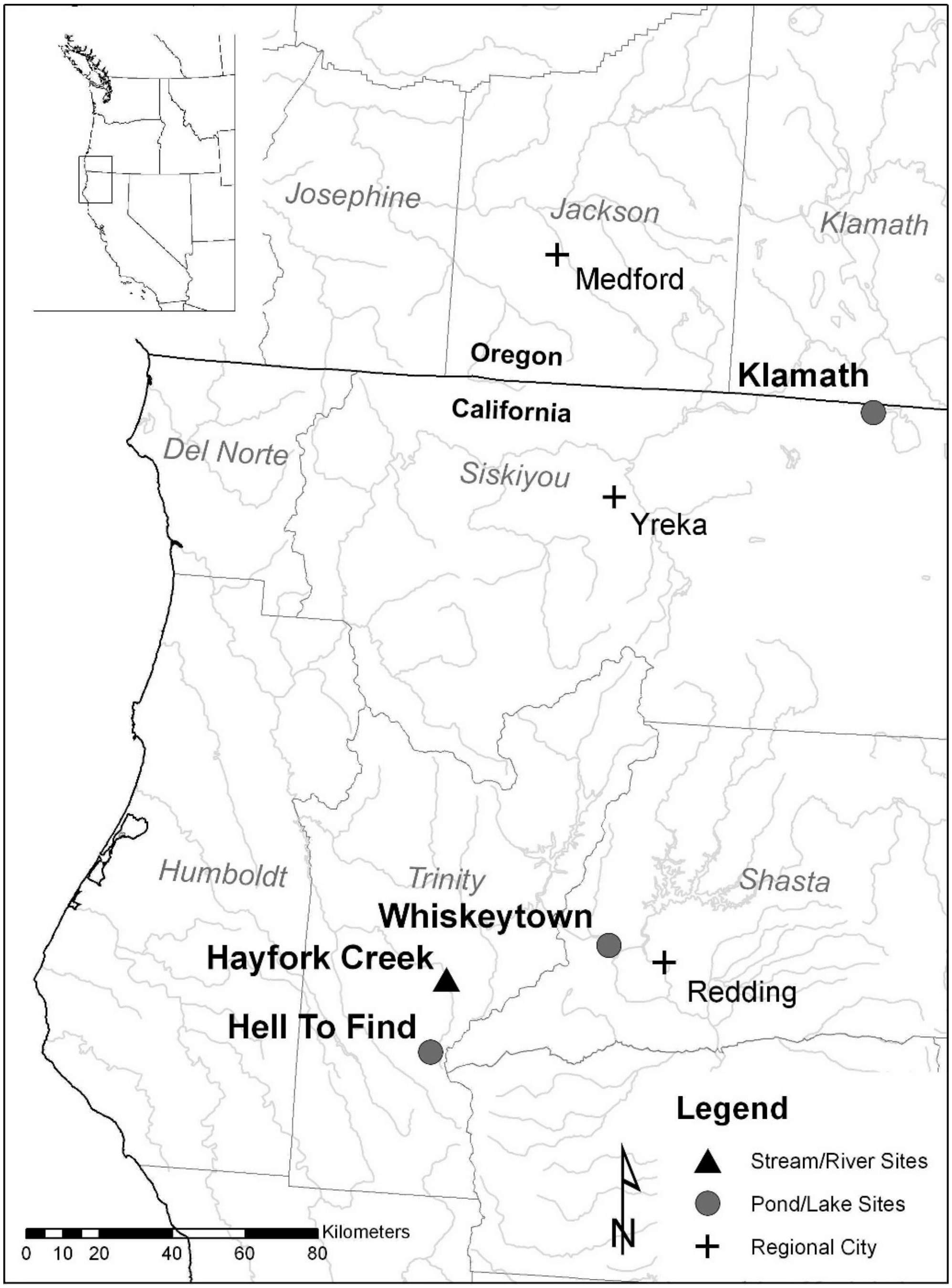

Fig. 1. Location of study sites for *Actinemys marmorata* in the Coast Range of northern California and in the Klamath Basin along the California–Oregon border.

(elev. 370 m at spillway) inside Whiskeytown National Recreation Area (NRA), Shasta Co., California. We captured turtles at Hayfork Creek (elev. 790–810 m), which is a rocky, clear-flowing stream measuring 3–6 m wide with long slow riffles punctuated at intervals with pools 1–4 m deep. Finally, we sampled turtles at Hell-to-Find Lake (elev. 1460 m), a small pond (approx. 0.2 ha) that is in the upper basin of Hayfork Creek.

Mean monthly maximum air temperatures vary slightly across the four sites with consistently highest values recorded at Whiskeytown NRA and consistently lowest maxima at Klamath (Fig. 2). Mean monthly minimum air temperatures are virtually the same for Klamath, Hayfork, and Hell-to-Find Lake but are appreciably greater throughout the year at Whiskeytown NRA (Fig. 2). In addition, no mean monthly temperatures ever are below freezing at Whiskeytown NRA, but are at or below freezing from October to April at the other three sites.

Field methods.—We captured turtles at Hell-to-Find Lake in 1996–1998, at Hayfork Creek 1995–1998, at Whiskeytown NRA in 2004, and in the Klamath basin in 1994, 2001, and 2007. Depending on the site, we used two methods to capture turtles. At Hell-to-Find Lake, Whiskeytown NRA, and in the Klamath Basin, we captured turtles in commercial nylon net traps and homemade wire-mesh traps (Iverson, 1979), both with double funnels. We baited traps with canned sardines, with traps open at sites for two days. We

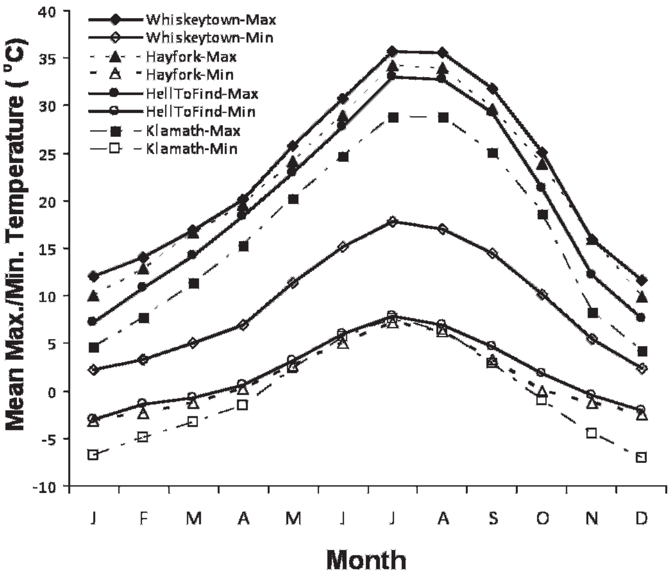

Fig. 2. Comparison of mean monthly air temperatures for four sites in northern California and southernmost Oregon where *Actinemys marmorata* were captured. Upper: maximum daily values summed by month; Lower: minimum daily values summed by month. (Data taken from http://www.wrcc.dri.edu/summary/Climsmnca.html.)

Table 1. Mean and Upper Decile Carapace Lengths (CL; SE = standard error, n = Sample Size) of Adult *Actinemys marmorata* Obtained at Four Sites in Northern California and Southernmost Oregon. Significant differences ($P < 0.05$) among sites are designated by a lack of a common letter and between males (M) and females (F) by asterisks.

	Mean			Upper decile		
Site	CL	SE	n	CL	SE	n
Hell-to-Find Lake						
All	143.1a	1.94	48	166.4a	1.89	5
M	144.3	3.02	24	169.0	1.25	3
F	142.0	2.41	24	159.3	2.76	3
Hayfork Creek						
All	141.1b	1.10	101	158.4b	0.99	10
M	142.6	1.70	40	158.5	1.03	4
F	140.2	1.42	61	158.2	1.57	6
Whiskeytown						
All	149.4c	1.99	59	170.3a	1.69	6
M	152.7	2.83	32	173.0	2.05	3
F	145.5	2.51	27	164.3	0.98	3
Klamath Basin						
All	169.7d	2.26	50	195.0c	2.77	5
M	175.5*	2.92	22	202.0	1.41	2
F	165.3*	3.05	28	187.7	0.72	3

checked traps at least daily (often in the morning and rebaited the same day in the evening), and we removed captured turtles for processing. At the Klamath Basin sites and at Hayfork Creek, we hand-captured some or all of the turtles, respectively. In total, we caught turtles for 87 trap days at Hell-to-Find Lake, 114 trap days at Whiskeytown NRA, and 98 trap days at the Klamath sites, and we spent 18 person days (=approx. eight person hours searching each) hand-capturing turtles at Hayfork Creek and three person days in the Klamath River. We used two methods to maximize captures of turtles in different habitats (flowing versus still waters). Although there is the possibility of bias in captures because of this, we found that hand-capturing at Hayfork Creek and trapping at Hell-to-Find Lake, sites that are part of the same aquatic system and are geographically close, gave the same size structure of populations (see Results). We take this as an indication that the different techniques did not significantly bias capture results.

For each captured turtle, we recorded mass, carapace length (CL), sex, and age. We determined an individual's age using scute annuli from the carapace and plastron. Although there is some controversy about using scute rings to determine ages of turtles (Wilson et al., 2003), the technique is reliable when one ring on individual scutes forms annually and upper limits are established. Only one complete ring forms in a year in *A. marmorata* based on recaptures of individuals 1–3 years later (Bury and Germano, 1998), but false rings occasionally occur and must be discounted (for criteria see Germano and Bury, 1998). We have found that scute annuli match the age of *A. marmorata* individuals up to about 15–16 yr (Bury and Germano, 1998). Scute annuli do not form much past sexual maturity in all species we have reviewed or studied (Germano and Bury, 1998), and some biologists have incorrectly tried to determine ages of turtles beyond this limit (Wilson et al., 2003). Some *A. marmorata*, therefore, could only be classified as older than 16 yr because scute rings were worn and edges of scutes were beveled; these animals were no longer depositing discernible rings (Germano and Bury, 1998). Even though the technique cannot be used to determine the age of old adult turtles, it still allows comparisons of age structure of a large segment of individuals among populations and for determining growth rates.

We defined the difference between adults and juveniles as 120 mm CL, the size at which most males developed secondary sexual characteristics such as indented plastron and longer tails of males compared to females (Bury and Germano, 2008). We individually marked turtles by notching marginal scutes with a file (Cagle, 1939; Bury and Germano, 1998). Most turtles were released within an hour at their capture site.

Statistical analysis.—We used ANOVA to test for differences in mean CL of adults among sites and between sexes, and if differences were found among sites, we used the Student-Newman-Keuls (SNK) multiple range test to determine where differences occurred. To minimize the effect of age structure on size estimates (Case, 1976), we also determined the upper decile CL of adult turtles. We tested for differences in upper decile CL between sexes using the Mann-Whitney test and among sites using the Kruskal-Wallis test followed by Mann-Whitney tests comparing ranks between each pair of sites if there were overall differences. Because significant differences in size was only found for mean CL at Klamath ($F_{1,49} = 5.39$, $P = 0.025$; Table 1), we considered that there was no consistent sexual size dimorphism, and we made comparisons among sites using all adults. We tested for differences from a 1:1 sex ratio at each site using Chi-square analysis with Yates correction for continuity. We also compared both the size (CL) and age structure of each population to one another using the Kolmogorov-Smirnov test.

Growth curves were constructed 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: M, the shape of the growth curve; K, the

Table 2. Percentage of Juveniles (<120 mm Carapace Length [CL]) and Adults (≥120 mm CL) and Percentage by Age Groups of *Actinemys marmorata* Caught at Four Sites in Northern California and Southernmost Oregon.

		Size		Age			
Site	*n*	Juveniles	Adults	0–4 yr	5–8 yr	9–12 yr	≥13 yr
Hell-To-Find Lake	94	33.0	67.0	13.8	17.0	23.4	45.8
Hayfork Creek	174	44.8	55.2	17.8	23.6	19.5	39.1
Whiskeytown	113	18.8	81.2	7.1	34.5	13.3	46.0
Klamath Basin	52	3.8	96.2	3.8	21.6	33.3	41.2

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. 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 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), defined as

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

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 non-linear fit than either K or M, and it produces values on an easily interpreted scale (Bradley et al., 1984), in our case, years. We also compared growth rates among sites using calculated carapace lengths (CCL) derived from the growth equations using three-year intervals from ages 3 to 12 years. We used ANOVA and SNK on mean and 95% confidence interval values of CCL at sites at each year interval to test for differences of growth rates among sites.

As a first approximation of determinants of growth of *A. marmorata*, we compared G to elevation and air temperature using Pearson product-moment correlation. We used weather data from stations closest to our capture sites: Tule Lake in the Klamath basin (1971–2000), Whiskeytown (1960–2009), Hayfork (1914–2006), and Forest Glen (1930–1985) for Hell-to-Find Lake (http://www.wrcc.dri.edu/summary/Climsmnca.html). We compared the monthly mean temperatures for the active season of *A. marmorata* (May–September) among sites using a two-way ANOVA with site and maximum/minimum temperatures as an interactive term. We limited comparisons to data for the active season because we believe this best represents when any temperature differences would affect turtle growth. We only used temperature measures in the correlation analysis if they differed significantly among sites.

RESULTS

We collected data on 434 *A. marmorata*: 94 at Hell-to-Find Lake, 174 at Hayfork Creek, 113 at Whiskeytown NRA, and 52 in the Klamath Basin. The mean CL of adult turtles among sites was significantly different ($F_{3,310} = 54.63$, $P < 0.001$), with all sites differing significantly from one another (q = 24.31–31.87; all $P < 0.05$; Table 1). The mean upper decile CL of turtles differed significantly (H = 19.66, df = 3, $P < 0.05$; Table 1). The mean upper decile CL of adults at Klamath was significantly larger than all other sites (U = 25.0–50.0, P = 0.004–0.001 for all comparisons), and mean upper decile CL of adults at Hayfork Creek was significantly smaller than all other sites (U = 43.5–58.0, P = 0.019–<0.001). The mean upper decile CL of adults at Hell-to-Find Lake and Whiskeytown NRA were intermediate in size (Table 1) and were not significantly different (U = 24.0, $P = 0.126$).

The ratio of males to females at Hell-to-Find Lake (35:32 or 1.09), Whiskeytown NRA (51:47 or 1.09), and Klamath Basin (22:28 or 0.79) did not differ significantly from 1:1 (X^2 = 0.06–0.50, P = 0.480–0.807), but the ratio at Hayfork Creek (40:62 or 0.65) was significantly female biased ($X^2 = 4.32$, $P = 0.038$). At Hayfork Creek, almost 45% of turtles were juvenile size (<120 mm CL), whereas only 3.8% of turtles caught in the Klamath Basin and 18.8% of turtles at Whiskeytown NRA were juvenile size (Table 2). The size structure among all populations was significantly different (D = 0.317–0.773, all $P < 0.001$), except between Hell-to-Find Lake and Hayfork Creek ($D = 0.139$, $P = 0.176$; Fig. 3).

The percentage of young turtles (0–4 yrs) was highest at Hayfork Creek (17.8%) and lowest at the Klamath Basin (3.8%), but the percentages of old turtles (13+ yrs) were about the same among sites, with the highest percentage (45.8%) for turtles from Hell-to-Find Lake (Table 2; Fig. 3). The age structures differed significantly between Hayfork and Klamath ($D = 0.236$, $P = 0.021$) and Whiskeytown and Klamath ($D = 0.266$, $P = 0.011$), but did not differ significantly among other pairwise comparisons (D = 0.120–0.202, P = 0.095–0.428). When comparing only younger turtles (<13 yr), there was no significant difference between age structures of Hayfork and Klamath ($D = 0.230$, $P = 0.123$).

Growth of turtles differed among sites (Table 3), with Klamath Basin turtles growing the fastest and Hayfork Creek turtles the slowest (Fig. 4). Turtles in the Klamath Basin grew significantly faster than turtles from any other population, and were 177 mm CL by age 12 (Table 3). Turtles from Whiskeytown NRA grew significantly faster than turtles from Hell-to-Find Lake and Hayfork Creek at all ages, and grew to 151 mm CL by age 12 (Table 3). There was no significance in growth rates between turtles from Hell-to-Find Lake and Hayfork Creek (Table 3).

Model fit of size to age using the Richards growth model was high, with R^2 ranging from 0.761 to 0.938 (Table 4). Using the growth model for each population, on average, turtles reached 120 mm CL in 8.7 yrs at Hayfork Creek,

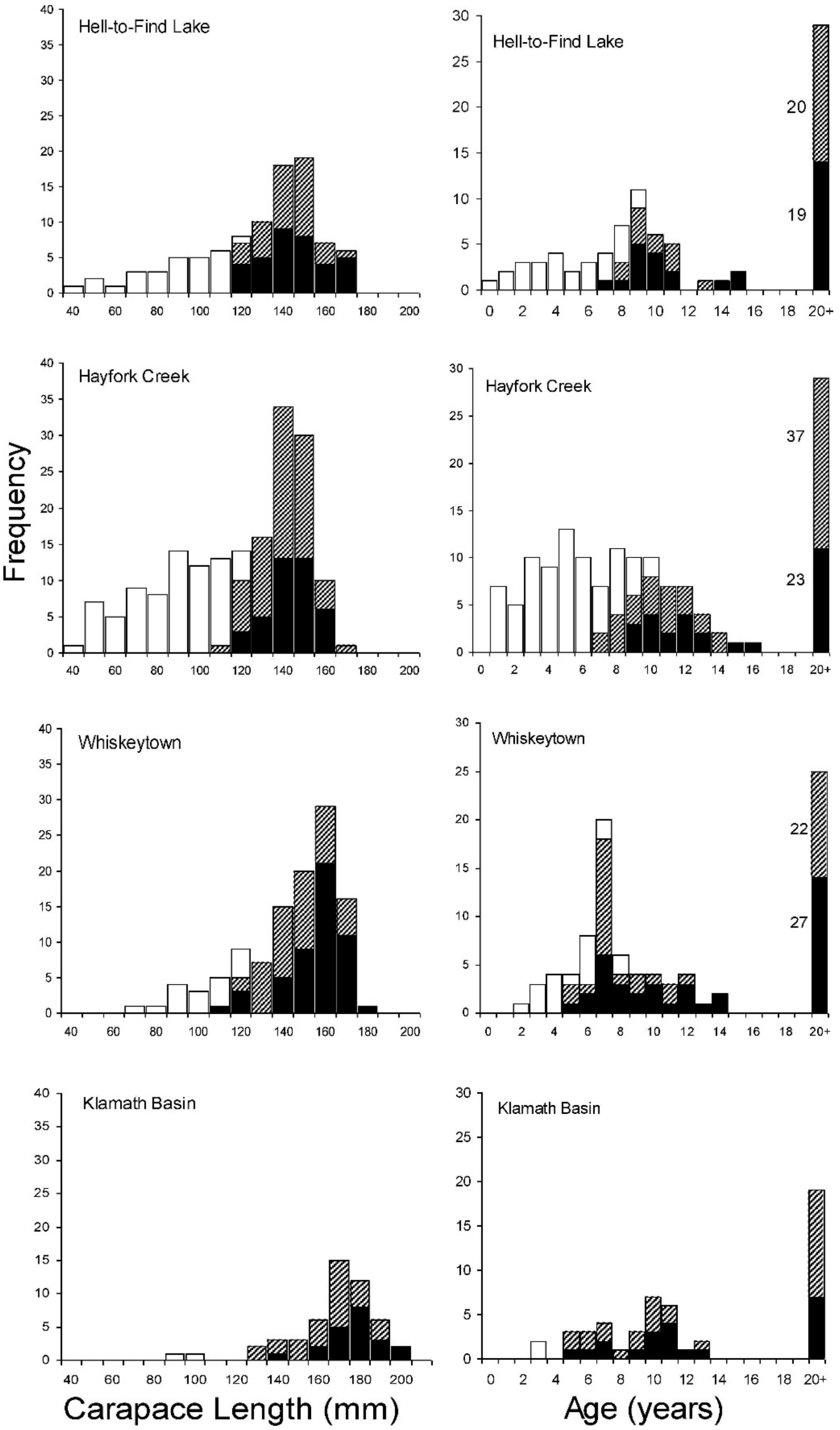

Fig. 3. Frequency distribution of carapace lengths (left) and ages (right) of *Actinemys marmorata* captured at four sites in northern California and southernmost Oregon. Black bars are males, striped bars are females, and open bars are turtles for which sex could not be determined. The number of old turtles (20+ yr) for Hell-to-Find Lake, Hayfork Creek, and Whiskeytown NRA were truncated to improve visibility of other ages; their numbers are shown to the side of the bars.

Table 3. Estimated Mean Carapace Lengths (95% Confidence Intervals) of *Actinemys marmorata* Based on Richards (1959) Growth Curves for Ages 3, 6, 9, and 12 Years from Four Sites in Northern California and Southernmost Oregon. Carapace lengths by age that are significantly different among sites are denoted by a lack of common letters.

	Age (years)			
Site	3	6	9	12
Hell-to-Find Lake	75.5a (71.1–79.8)	105.2a (100.8–109.5)	124.7a (120.3–129.1)	137.9a (133.7–142.1)
Hayfork Creek	69.1a (66.8–71.5)	99.7a (97.3–102.0)	122.0a (119.6–124.4)	136.6a (134.2–139.0)
Whiskeytown	86.4b (78.9–93.9)	119.3b (111.8–126.8)	138.9b (131.5–146.4)	150.9b (143.4–158.4)
Klamath Basin	112.0c (105.4–118.6)	146.6c (140.0–153.2)	165.7c (159.0–172.3)	176.9c (170.3–183.6)
	F = 34.39	42.49	37.96	33.93
	P = <0.001	<0.001	<0.001	<0.001

8.2 yrs at Hell-to-Find Lake, 6.1 yrs at Whiskeytown NRA, and only 3.5 yrs in the Klamath Basin. The duration of primary growth (G) at Hell-to-Find Lake (16.8 yrs) was ca. 45% longer than the duration at Klamath (11.6 yrs) and ca. 27% longer than turtles at Whiskeytown (13.2 yrs; Table 4).

The comparison of site and maximum/minimum temperatures resulted in a significant interaction ($F_{3,39} = 3.38$, $P = 0.030$). Although mean maximum temperatures were not significantly different, Whiskeytown had significantly higher mean minimum temperatures (15.0°C) than the other sites (q = 2.99–4.05, all $P < 0.05$; Fig. 5). Primary growth (G) of turtles was related to elevation for three of the sites (slower as elevation increased), but there was not a significant correlation (r = 0.298, $P = 0.702$) because Klamath sites are at a relatively high elevation yet turtles grew the fastest (Fig. 6). Primary growth of turtles also was not correlated to mean minimum air temperatures (r = −0.298, $P = 0.702$; Fig. 6).

DISCUSSION

Growth differed among three of four populations of *A. marmorata* we sampled, and size structure failed to match the age structure in half the populations (i.e., some large-sized turtles were young). At Hayfork Creek, the two measures of population structure were similar: 44.8% were juvenile size (<120 mm CL) and 43.1% of turtles were ≤8 yrs of age. The two population structures were more dissimilar at Hell-to-Find Lake, where we found 33.0% juvenile size but 40.4% were ≤8 yrs of age. Size distributions indicate virtually no reproduction had occurred recently at Whiskeytown NRA (approx. 19% juveniles) and the Klamath Basin sites (approx. 4%). Yet 41.6% of turtles at Whiskeytown NRA were ≤8 yrs of age and at Klamath Basin, 25.4% were ≤8 yrs and fully 45.1% were ≤10 yrs of age based on annuli counts. Many turtles of adult size were young individuals in those populations where individuals had high growth rates.

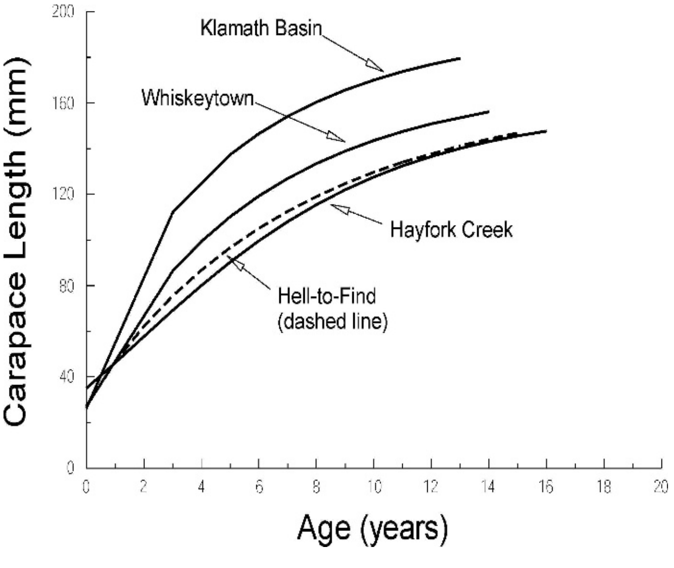

Fig. 4. Growth curves (carapace lengths on ages) of *Actinemys marmorata* captured at four sites in northern California and southernmost Oregon, using the Richards (1959) growth model.

The differences in size and age structures appear to reflect much faster growth rates at both Whiskeytown NRA and Klamath Basin than at Hell-to-Find Lake or Hayfork Creek. Klamath Basin turtles grew approximately 2.5 times as fast as Hayfork Creek turtles up to 120 mm CL. Size of adults varied significantly between all populations, with Klamath Basin turtles the largest and Hayfork Creek the smallest. The upper decile CL of Klamath Basin turtles were significantly larger than any of the other populations, and turtles at Whiskeytown NRA were greater than that for Hayfork Creek. Upper decile CL at Hell-to-Find Lake was not different from Hayfork Creek or Whiskeytown NRA. This pattern is similar to the growth rates where the largest turtles occurred where growth was fastest. In the adjacent Sacramento Valley, Lubcke and Wilson (2007) reported small adults at Big Chico Creek (mean CL = 150.2 ± 0.67 mm), a clear, cool stream in the foothills, but larger adults (mean CL = 176.0 ± 2.06 mm) in sloughs and oxbows off the Sacramento River, and larger yet (mean CL = 185.1 ± 1.41 mm) in canals on the valley floor. In both cases, the size of adult turtles appeared to differ with habitat types, with the smallest adult turtles found in cool, flowing streams.

We found equal sex ratios at three of our sites, which is consistent with sex ratios found in many other aquatic turtles (Gibbons, 1990), and at other sites for *A. marmorata* (Goodman, 1997; Germano and Bury, 2001; Lovich and Meyer, 2002). Although Hayfork Creek had significantly more females in the sample (n = 102 turtles), an earlier larger sample (n = 456) showed an even sex ratio (Bury, 1979). There may be more females present today than in the previous study at Hayfork Creek. However, we have studied this site for over 30 years without noting any changes in habitat conditions or other variables to explain an uneven sex ratio today. Further, larger sample sizes (>300 individuals) may be needed to accurately quantify the sex ratio in turtle populations (Bury, 1979).

Temperature has profound influences on turtle growth (Dunham and Gibbons, 1990), but we found the fastest

Table 4. Growth Parameters of Richards (1959) Growth Curves for *Actinemys marmorata* from Four Sites in Northern California and Southernmost Oregon. 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 time (G, in years) required to grow from 10 to 90% of asymptotic CL.

Site	R^2	M	K	I	G
Hell-to-Find Lake	0.938	−0.185	0.124	−2.39	16.8
Hayfork Creek	0.937	0.892	0.187	1.76	15.8
Whiskeytown	0.761	−0.184	0.158	−1.83	13.2
Klamath Basin	0.856	−0.688	0.154	−3.61	11.6

growing turtles in the Klamath Basin, which had the coolest mean maximum and minimum air temperatures during the growing season than the other sites. Whiskeytown NRA is on the edge of the Sacramento Valley, where days are hot and, due to its relatively low elevations, temperatures remain warm into the evening and at night. Whiskeytown NRA had significantly higher mean minimum temperatures during the growing season, but only produced the second fastest growth in turtles. Elevation differences among sites also did not correlate with growth rates because the Klamath Basin was the second highest elevation site yet had the fastest turtle growth.

There are other differences in the sites. Although in an area with relatively high air temperatures, the reservoir at Whiskeytown NRA has clear, cool waters fed directly by steep, mountain streams as well as diverted water (through underground tunnels) from Trinity Lake, which receives water from high elevation peaks with deep snow pack in winter (e.g., the Trinity Alps Wilderness Area). Hayfork Creek is also clear water, draining mountains (including the Yolla Bolly Wilderness Area), while Hell-to-Find Lake is slightly turbid waters and formed by rain and snow runoff. The Klamath Basin is in the high desert typical of the Great Basin (Loy et al., 2001), and one of the few desert areas that have *A. marmorata*. Although air temperatures are relatively cool compared to the other sites, nutrients and productivity are naturally high in the Klamath Basin due to volcanic soils as well as major agriculture use with intensive application of chemical fertilizers, which are known to run-off into waterways. Klamath Basin waters are eutrophic to hypereutrophic with resultant massive algal blooms and insect swarms (Bortleson and Fretwell, 1993; Boyer and Grue, 1995; National Research Council, 2003). Although we did not measure productivity differences among sites, we hypothesize that the higher productivity and food of Klamath waters enhance the growth rates of turtles, despite (1) its high elevation (ca. 1200 m), (2) a relatively short period for seasonal activity by turtles, and (3) summers with hot days but cool nights. Further research is needed to tease out the contributing factors to this distinct growth pattern of fast growth of turtles in an area expected to lack it based solely on temperature profiles.

There is an important conservation concern about how surveys are conducted for this species and how population structure is interpreted. Earlier studies have relied on sizes of turtles to indicate population structure and status (Reese and Welsh, 1998; Lovich and Meyer, 2002; Spinks et al., 2003; Lubcke and Wilson, 2007). Many populations consist

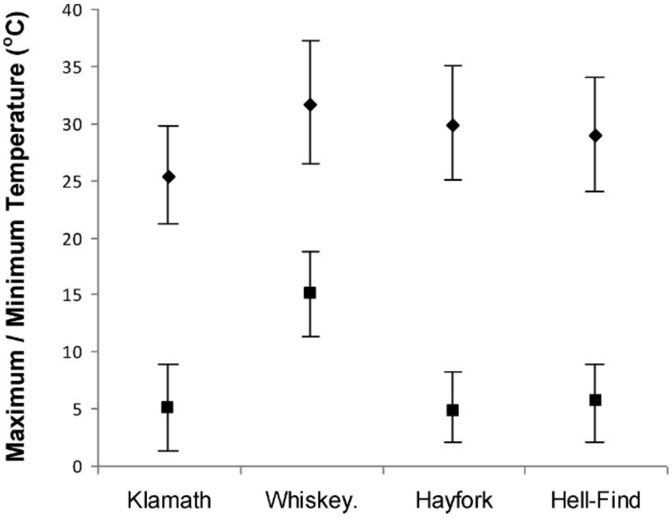

Fig. 5. Mean (±95% confidence intervals) maximum and minimum air temperatures for the active season (May–September) of *Actinemys marmorata* at four sites where turtles were captured.

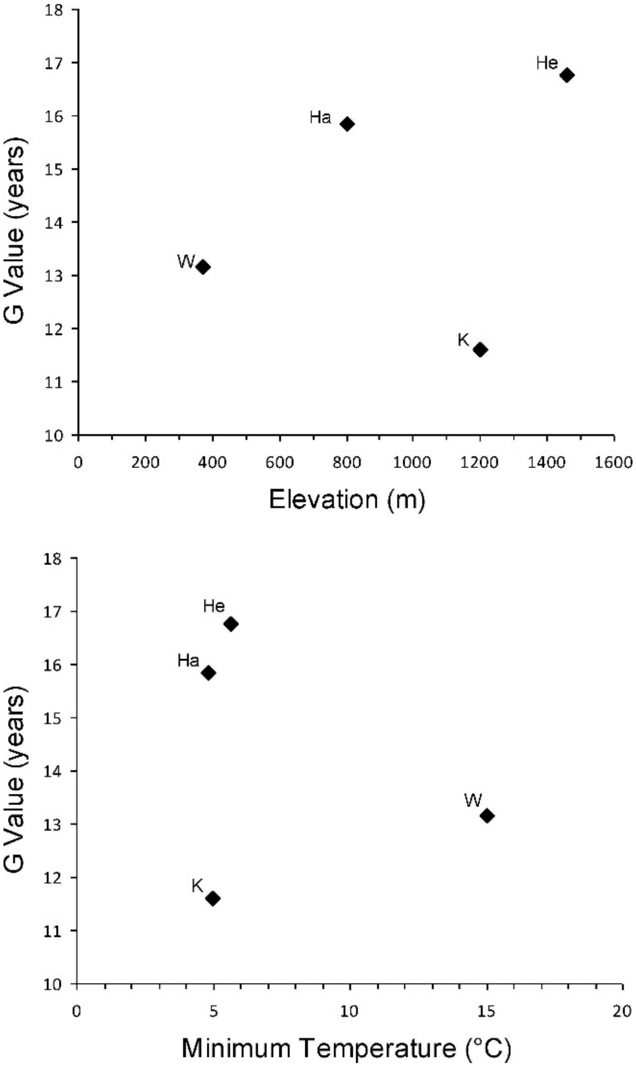

Fig. 6. Relationship between primary growth (G, in years) of *Actinemys marmorata* and elevation (top) and mean minimum temperatures (bottom) for three sites in northern California (W = Whiskeytown, Ha = Hayfork, He = Hell-to-Find) and one in southernmost Oregon (K = Klamath).

of mostly large turtles, a structure that often is interpreted to indicate little to no reproduction. If this were true, then even many extant populations could be headed for extinction. This was argued during proposed listing of the species (U.S. Fish and Wildlife Service, 1992).

In populations of *A. marmorata* that we have studied across the range of the species (Germano and Bury, 2001, 2009; Germano and Rathbun, 2008; Germano, 2010), including sites studied here, many young turtles have been found, even though size structures indicated little recent reproduction. Age determination is accurate in *A. marmorata* (Germano and Bury, 1998) and properly represents its population structure, particularly to reveal the true proportion of young in turtle populations. Thus, we suggest that age based on scute ring counts be included along with size data. Size alone should not be used as an indication of population trends or for conservation assessments of turtle populations.

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