

GROWTH AND REPRODUCTION OF NORTHWESTERN POND TURTLES IN THE MID-WILLAMETTE VALLEY, OREGON

Authors: Germano, David J, Bury, R Bruce, and Bury, Gwendolynn W

Source: *Northwestern Naturalist*, 103(2) : 110-117

Published By: Society for Northwestern Vertebrate Biology

URL: <https://doi.org/10.1898/NWN20-21>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

GROWTH AND REPRODUCTION OF NORTHWESTERN POND TURTLES IN THE MID-WILLAMETTE VALLEY, OREGON

DAVID J GERMANO

*Department of Biology, California State University, Bakersfield, CA 93311 USA (emeritus);
dgermano@csub.edu*

R BRUCE BURY

Herpetological Conservation and Biology, 1410 NW 12th Street, Corvallis, OR 97330 USA

GWENDOLYNN W BURY

Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331 USA

ABSTRACT—The Northwestern Pond Turtle (*Actinemys marmorata*) ranges from Washington to the southern end of the Central Valley of California. Because of the extensive latitudinal range of the species, it is expected that several life-history traits will vary across the range. Most data on population structure and growth of *A. marmorata* have been gathered from southern Oregon and California, and reproductive data are sparse north of the southern end of the range. These data are important to a critical understanding of the species' biology and especially for making conservation judgments for a species some consider in need of protection. Thus, we collected key life-history information at the Luckiamute State Natural Area in the mid-Willamette Valley, Oregon. We found that the population structure, adult size, and growth were similar to southern Oregon sites. Clutch size from radiographs was 6.0 ± 1.18 SE (range = 5–8), smaller than sites at the southern end of the range. The slow growth rate of Luckiamute turtles may be explained by cooler temperature in the Willamette Valley compared to more southerly sites. Still, Luckiamute adults reach a slightly larger size than most turtles in more southerly sites. It just requires many more years to reach sexual maturity and achieve larger sizes in northern areas.

Key words: *Actinemys marmorata*, carapace lengths, clutch size, growth rates, Luckiamute State Natural Area, Northwestern Pond Turtles, Oregon, weight, Willamette Valley

The Northwestern Pond Turtle (*Actinemys marmorata*) ranges from Puget Sound, Washington, south to the San Francisco Bay Area and the southern end of the Central Valley of California (Bury and Germano 2008; Barela and Olson 2014). The range of the closely related Southwestern Pond Turtle (*Actinemys pallida*) extends south to Baja California Norte (Spinks and Shaffer 2005). Both species mostly occur in Mediterranean ecosystems (Moyle 1995; Bury and Pearl 1998) such as grassland, oak woodland, and open pine stands with moderately rainy winters and hot, dry summers. In the northern portion of its range, *A. marmorata* primarily occurs east of the Coast Range and Olympic Mountains in pockets that have oak woodland and open areas (such as the Willamette Valley, Oregon). These patches of suitable

habitat for *A. marmorata* are surrounded by dense coniferous forests typical of the Pacific Northwest. The species was earlier reported to occur in southwestern British Columbia (for example, Carl 1944; Seeliger 1945), but these populations may be introduced (Cook and others 2005) or, if native, they are now extirpated (Matsuda and others 2006). These turtles are found in a wide variety of waters, but prefer ponds, lakes, marshes, and slow parts of rivers and streams (Bury and others 2012).

Actinemys marmorata requires warmth for development of eggs, growth of juveniles, and physiological functions of all stages. In this study, we present new data collected at Luckiamute State Natural Area in the Willamette Valley of Oregon and compare these data to range-wide published data on growth rates,

clutch sizes, and adult body size. To better understand life-history features, we examine general weather patterns across the Pacific Northwest and the southern portion of the species range.

Although *A. marmorata* was first described from the Puget Sound in western Washington (Baird and Girard 1852), there are few published papers on the species in the northern portion of its range (Willamette Valley of Oregon northward) but these include a wide array of topics: general habits (Evensen 1948), genetics (Gray 1995; Spinks and Shaffer 2005), movements of hatchlings out of nests (Rosenberg and Swift 2013), and fossil record (Fisher 2018). In contrast, there are more studies of its life history and population ecology in southern Oregon (Germano and Bury 2009; Horn and Gervais 2018), adjacent Klamath-Siskiyou ecoregion (Reese and Welsh 1998; Bury and others 2010; Ashton and others 2015), and California (Storer 1930; Germano and Bury 2001; Lubcke and Wilson 2007; Bury and others 2012; Germano 2016, 2020, 2021).

Several life-history variables are important to understand the biology of turtles (Stearns 1992; Heppell 1998; Congdon and others 2018). To better define the ecology of *A. marmorata* in its northern region of occurrence, we determined its reproductive output (clutch size), body size and age structure, growth rates, and thermal envelope in the Willamette Valley of Oregon. Further, these life-history traits are essential to assess its status and develop measures for effective conservation actions. Today, the turtle is a Priority at Risk species in Oregon (ODFW 2006, 2015) and currently is under federal review as a Threatened species (USFWS 2015).

METHODS

We studied *A. marmorata* at the Luckiamute State Natural Area (LSNA) in the mid-Willamette Valley, Oregon (44°43' N, 123°09' W; 55 m elevation). LSNA abuts the Willamette River to the east and the town of Albany is about 9.5 km SSE of the site. Salem, Oregon, is 25 km NNE of the study area. We sampled turtles in 2 ponds that are about 500 m apart. In late spring, the west pond was approximately 2 ha in area and the eastern one was about 0.5 ha in size. Dense woodland partially surrounds both ponds, with cleared open ground for crops to the north. This

research site was previously a working farm with fields and some fruit trees, but currently serves to protect wildlife with some areas used for agriculture.

We captured *A. marmorata* using commercial nylon-net traps with double funnels (model FTC-FTD; Memphis Net & Twine Company, Inc., Tennessee). We baited traps with canned sardines for 5 trapping sessions lasting 1–3 d (18–20 June, 27–29 June, and 10–11 July 2012; 5–7 August 2013; and 29 July 2018). We checked traps once daily, usually starting at 0900. In 2012, we took turtles back to a laboratory in Corvallis, Oregon, to measure turtles and x-ray females for reproductive status, and we released turtles within 24 h. During the 2013 and 2018 trapping sessions, we measured turtles at their capture sites followed by immediate release.

For each captured turtle, we recorded carapace length (CL) to 1 mm, weight to 1 g, sex, and age (counting annuli following Germano and Bury 1998). Discernible scute rings become difficult to detect at 15–17 y for *A. marmorata* in the northern part of their range (Bury and Germano 1998). We classified some turtles when first captured as older than 15 y when rings were still fairly distinct but the edges of scutes along the midline of the plastron were beveled and >20 y when plastron rings were well worn, and the midline beveled. We defined turtles as adults if they were ≥ 120 mm CL and we individually marked turtles by notching marginal scutes with a file (Cagle 1939; Bury and Germano 1998). To determine if females were gravid and the number of eggs present, we radiographed female turtles (only 2012 turtles) using a portable X-ray machine.

We derived climate information from NOAA (2021) to compare thermal conditions of our site to other parts of the northern range of *A. marmorata*. Because aquatic turtle growth is affected by temperature (Koper and Brooks 2000; Germano 2010), we only compared lowlands and valleys in the range of the species. We used warm temperatures (# hours > 18°C tallied over a year) as a measure of thermal conditions for similar elevational habitats.

Statistical Analyses

We tested for differences from a 1:1 sex ratio using Chi-square analyses with Yates correction for continuity. Because CL data was not normal-

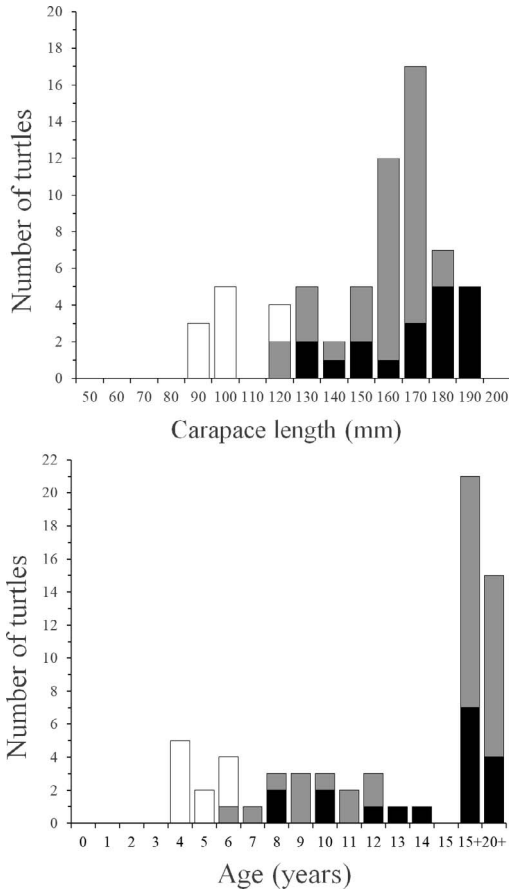


FIGURE 1. Distributions of carapace lengths (mm) and ages (years) of Northwestern Pond Turtles (*Actinemys marmorata*) from 2012–2018 from Luckiamute State Recreation Area in the Willamette Valley, Oregon. Black bars are males, grey bars are females, and open bars are juveniles.

ly distributed even after transformation, we compared the mean CL between the sexes using a Mann-Whitney U test. To minimize the effect of age structure on size estimates (Case 1976), we also determined the upper decile CL of females ($n=4$) and upper quartile CL of male turtles ($n=5$). Despite small sample sizes, these data were normally distributed and homoscedastic, and we compared mean upper sizes between sexes using ANOVA. We compared mean weights between sexes with ANCOVA with CL as the covariate, excluding weights of females that were gravid. For all tests, $\alpha=0.05$.

To determine growth rates of turtles, we fitted age and CL data to the Richards growth model

(Richards 1959). This growth model estimates 3 parameters using CL and age data in the general formula to solve for CL at various ages:

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

where M is the shape of the growth curve, K is the growth constant, and I is the point at which curve inflection begins. We did not use ages of turtles that we judged to be >15 y. For those turtles for which we could estimate age, we used continuous estimates (Lindeman 1997) based on a yearly activity period from 1 May to 30 September that could support growth. As an example, we would list a turtle caught with 2 scute rings on 20 June as 1.33 y old (1 full year of growth and an additional 0.33 of a year of growth when caught). Precision of the estimate of growth period is not critical but estimating age to a decimal fraction of a year improves fit of the curve (Lindeman 1997). We used mean upper sizes as the asymptotic CL in the model for each sex. To anchor growth curves, we used the lower and upper sizes of hatchlings from Fern Ridge Reservoir, near Eugene, Oregon (CL range = 26.4–32.3 mm, $n=28$; Holte 1998). Both this site and our study area are in the Willamette Valley 68 km apart (by air).

We compared rates of growth among habitats and sites using the G statistic, which represents the time required to grow 10–90% of asymptotic size and is an indicator of the duration of primary growth (Bradley and others 1984). It is defined as:

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

The raw parameters K and M are closely linked in determining growth curves and neither is useful for comparing growth between populations (Bradley and others 1984). The best overall measure of growth 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 and others 1984); in our case, years.

RESULTS

During our 5 trapping visits, we caught 65 *A. marmorata*: 10 juveniles, 19 males, and 36 females (Fig. 1). We did not catch any other turtle species. Males ranged in size from 126–193 mm CL and females from 120–184 mm CL (Table 1).

TABLE 1. Mean (range), sample size (n), and standard error (SE) of carapace length (CL) and weight and mean upper decile CL (UDCL) and weight (UDW) of adult Northwestern Pond Turtles (*Actinemys marmorata*) captured 2012–2018 at Luckiamute Landing State Natural Area in the Willamette Valley, Oregon. Weights of females excludes those that were gravid. The asterisk (*) is for upper quartile parameters.

	CL (mm)			UDCL	Weight (g)			UDW
	n	Mean (range)	SE		n	Mean (range)	SE	
Males	19	170.1 (126–193)	4.86	190.4*	19	715.1 (271–1010)	55.9	965.2*
Females	36	158.2 (120–184)	2.57	177.3	28	605.9 (259–850)	34.8	802.7*
Total Adults	55	162.3 (120–193)	2.47	182.5	47	650.1 (259–1010)	31.3	876.5

We could determine the age of 43.1% (ages 4–14 y; $n = 65$) of the turtles (Fig. 1); but, 55.4% ($n = 36$) were older turtles for which we could not determine their age (Fig. 1). The adult sex ratio (19M:36F) was significantly different than 1:1 ($\chi^2 = 4.655$, $df = 1$, $P = 0.031$). The mean CL of males was significantly larger than females ($U = 865.5$, $P = 0.012$), as was mean upper CLs ($F_{1,7} = 22.06$, $P = 0.002$). We found significant regressions of

weight to CL for both males ($F_{1,17} = 473.5$, $P < 0.001$) and females ($F_{1,26} = 264.4$, $P < 0.001$). Non-gravid females had a smaller mean weight than males for the population (Table 1) but, once size adjusted, mean weights were significantly greater for females than males at all CLs (slopes, $F_{1,43} = 0.489$, $P = 0.488$; elevations, $F_{1,43} = 185.8$, $P < 0.001$).

The mean clutch size of 11 gravid females was 6.0 ± 1.18 SE (range = 5–8). In June 2012, 42.3% (11 of 26) of females were gravid, but by 10–11 July, none of the 7 females we x-rayed had eggs. The smallest female with eggs was 154 mm CL and was 15+ y old, and the youngest female with eggs was 11.3 y old and had a CL of 167 mm.

The growth curve of female *A. marmorata* was lower than that of males, but because the growth curve of females was within the 95% confidence interval of males, growth is not significantly different between the sexes (Fig. 2). Using the growth equation of all adults, turtles reached 120 mm CL (small adult) by 5.9 y and 150 mm CL by 9.5 y (Fig. 2). The time to grow from 10%–90% of asymptotic size was 13.2 y (Table 2).

Thermal conditions varied widely in the northern range of *A. marmorata*. The average yearly total of warm temperatures was only 97 h at Olympia, Washington, as a northern coastal area (275 km N of Luckiamute) as compared to 360 h at Salem, Oregon (near Luckiamute) in the Willamette Valley, Oregon. There were 932 h at Medford (250 km S of Luckiamute) in southern Oregon near the California border and 1605 h at Whiskeytown National Recreation Area (435 km south), near Redding, in the upper Central Valley of California.

DISCUSSION

Here we report the 1st ecological research on multiple life-history features for a population of *A. marmorata* in the northern portion of its range.

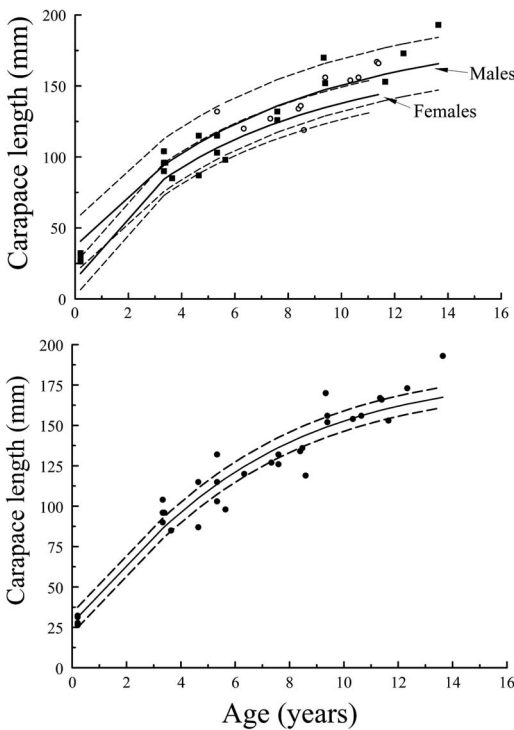


FIGURE 2. Top: Growth curves of female (open symbols) and male (squares) Northwestern Pond Turtles (*Actinemys marmorata*) from 2012–2018 from Luckiamute State Natural Area in the Willamette Valley, Oregon. The Coefficient of Determination (r^2) for the curve for females is 0.893 and for males 0.922. Bottom: Growth curve for all adults ($r^2 = 0.930$).

TABLE 2. Growth parameters from Richards growth curves and the upper decile carapace length (UDCL) for Northwestern Pond Turtles (*Actinemys marmorata*) from the Luckiamute Landing State Natural Area in the Willamette Valley, Oregon, another pond site in Oregon, and 2 still-water sites in California. Sites are listed north to south. Parameters describing model fit and growth curves are shape of curve (M), growth constant (K), inflection point of curve (I), and time required to grow from 10–90% of asymptotic size (G) in years.

Site	M	K	I	G (y)	UDCL (mm)	Reference
OREGON						
Luckiamute	0.4309	0.1921	0.7599	13.2	182.5	This study
Yoncalla	0.9885	0.2191	2.905	14.0	185.8	Germano and Bury 2009
CALIFORNIA						
Whiskeytown	–0.1839	0.1578	–1.832	13.2	170.3	Bury and others 2010
Fresno Wastewater Treatment Plant	0.0468	0.5582	–0.2355	4.00	185.9	Germano 2010

Actinemys marmorata occurs across a long latitudinal range from Washington to the southern end of the Central Valley in California and from sea level to 1524 m (5000 ft). In eastern North America, aquatic turtles with extensive north-south ranges show significant variation in some life-history traits (Wilbur and Morin 1988; Iverson and others 1993; Litzgus and Mosseau 2006) that appear to be related, at least partially, to latitudinal climatic differences. Because of marked climatic variation across the range of *A. marmorata*, the life history of this species should be similarly affected. A large difference in elevation could also affect life-history traits of *A. marmorata* similarly to changes in latitude because of changes in climate.

Female turtles at northern latitudes usually produce a larger clutch size than in southern latitudes (Wilbur and Morin 1988; Iverson and others 1993; Litzgus and Mosseau 2006), but this is not the case for *A. marmorata*, at least based on the limited comparisons we currently have. We found an average clutch size of 6.0 for 11 females. In the San Joaquin Valley at the southern part of the range, mean clutch sizes ($n \geq 5$ clutches) for 4 sites at about the same elevation as Luckiamute vary from 7.3 to 8.5 (Germano 2010, 2016, 2020, 2021). Although only based on 3 clutches for each site, we found the mean number of eggs in a clutch at 2 northern California sites to be 5.3 at Whiskeytown and 10.0 in the Klamath basin (unpubl. data). Although these data do not support females producing larger clutches in the northern part of the range than in the south, clutch sizes at many more sites in northern California and Oregon are needed to determine if clutch size is affected by latitude and climate in *A. marmorata*.

Size (carapace morphometrics) of turtles may also be larger at northern latitudes than southern latitudes because of a need for greater food-storage capacity during a shorter growing season (Reznick and others 1990; Henen 1997) or for greater fecundity to compensate for lower juvenile survival (Galbraith and Brooks 1987) than in the south. Male *A. marmorata* (mean = 170.1 mm CL) were significantly longer than females (mean = 158.2 mm CL) at LSNA with overall adult mean CL of 162.3 mm. A better comparison of size, however, is the mean upper decile (or quartile) CL, which was 182.5 mm. Mean upper decile size of *A. marmorata* at Yoncalla, a similar-elevation site in southern Oregon, was 185.8 mm (Germano and Bury 2009), 170.3 at Whiskeytown in northern California (Bury and others 2010), and 177.5 and 181.7 at settling ponds of wastewater treatment plants (Germano 2010) and 172.1 at Goose Lake (Germano 2016) in the southern end of the range. The slightly larger sizes of turtles at LSNA and Yoncalla were achieved with a much slower growth rate (Fig. 3) than the southern sites. It took over 13 y to grow from 10–90% of their size at LSNA, whereas it took only 4.00 y to grow the same duration at the most southern site (Table 2).

Growth is most likely affected to the greatest extent by temperatures and length of growing season. In general, temperatures increase greatly from north to south. The Luckiamute study area is near Salem in the Willamette Valley and has moderate temperatures. There are some hot summer days, but they are usually of short duration owing to Pacific winds. This difference in temperature is even more pronounced across the range of *A. marmorata*. Compared to Luckiamute, warm temperatures ($>18^{\circ}\text{C}$) are three

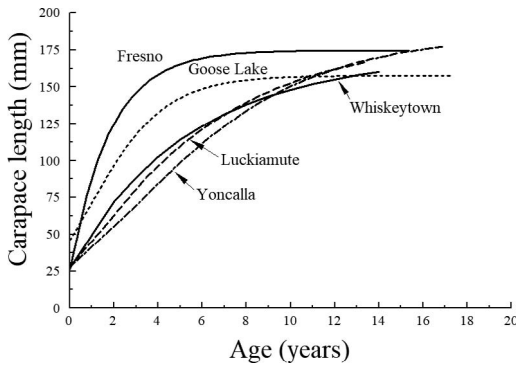


FIGURE 3. Growth comparisons of Northwestern Pond Turtles (*Actinemys marmorata*) from still-water sites in the San Joaquin Valley of California (Fresno: top solid line; Goose Lake: small dashed line), northern California (Whiskeytown: middle solid line), southern Oregon (Yoncalla: long, short dashed line), and northern Oregon (Luckiamute: dashed line).

times more frequent at Medford in southern Oregon and 4.5 times more frequent at Redding in northern California. Cooler climatic conditions appear to explain the much slower growth rate of turtles at Luckiamute versus those in more southerly sites. Still, adult turtles reach a slightly larger size as adults at Luckiamute than do turtles in more southern sites. Apparently, it requires many more years to achieve these sizes.

Actinemys marmorata is currently under review by the US Fish and Wildlife Service for possible listing as a Threatened species. Although the best biological information is needed for this assessment, much of the variability in the biology in *A. marmorata* is not known, particularly in the northern portion of its range. More focused studies on its growth, population sizes and structure, and reproduction are needed, especially in Oregon, to credibly determine its status.

ACKNOWLEDGMENTS

This work was conducted under scientific permits #093-12, 082-13, and 019-18 of the Oregon Department of Fish and Wildlife. We thank Jason Bracken, Christy Baggett, Mark Leppin, and others for field assistance.

LITERATURE CITED

ASHTON DT, BETTASO JB, WELSH HH JR. 2015. Changes across a decade in size, growth, and body condition of Western Pond Turtle (*Actinemys marmorata*) populations on free-flowing and regulated forks

of the Trinity River in northwest California. *Copeia* 103:621–633.

- BAIRD SF, GIRARD S. 1852. Descriptions of new species of reptiles collected by the U.S. Exploring Expedition under the command of Capt. Charles Wilkes, U.S.N. *Proceedings of the Academy of Natural Science of Philadelphia* 6:174–177.
- BARELA KL, OLSON DH. 2014. Mapping the Western Pond Turtle (*Actinemys marmorata*) and Painted Turtle (*Chrysemys picta*) in western North America. *Northwestern Naturalist* 95:1–12.
- BRADLEY DW, LANDRY RE, COLLINS CT. 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 RB, GERMANO DJ. 1998. Annual deposition of scute rings in the Western Pond Turtle, *Clemmys marmorata*. *Chelonian Conservation and Biology* 3:108–109.
- BURY RB, GERMANO DJ. 2008. *Actinemys marmorata* (Baird and Girard, 1852) - Western Pond Turtle, Pacific Pond Turtle. In: Rhodin AGJ, Pritchard PCH, van Dijk PP, Saumure RA, Buhlmann KA, Iverson JB, editors. *Conservation biology of freshwater turtles and tortoises: A compilation project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group*. Chelonian Research Monographs No.5. p 001.1-001.9. <http://doi:10.3854/crm.5.001.marmorata.v1.2008>.
- BURY RB, PEARL CA. 1999. Klamath-Siskiyou herpetofauna: Biogeographic patterns and conservation strategies. *Natural Areas Journal* 19:341–350.
- BURY RB, GERMANO DJ, BURY GW. 2010. Population structure and growth of the turtle *Actinemys marmorata* from the Klamath-Siskiyou ecoregion: Age, not size, matters. *Copeia* 2010:443–451.
- BURY RB, WELSH HH JR, GERMANO DJ, ASHTON D, editors. 2012. *Western Pond Turtle: Biology, sampling techniques, inventory and monitoring, conservation and management*. *Northwest Fauna* 7. 128 p.
- CAGLE FR. 1939. A system for marking turtles for future identification. *Copeia* 1939:170–173.
- CARL GC. 1944. *The reptiles of British Columbia*. 2nd edition. Victoria, BC: British Columbia Provincial Museum Handbook 3. 65 p.
- CASE TJ. 1976. Body size differences between populations of the Chuckwalla, *Sauromalus obesus*. *Ecology* 57:313–323.
- CONGDON JD, NAGLE RD, KINNEY OM. 2018. Front-loading life histories: The enduring influence of juvenile growth on age, size, and reproduction of primiparous female freshwater turtles. *Evolutionary Ecology Research* 19:353–364.
- COOK FR, CAMPBELL RW, RYDER GR. 2005. Pacific Pond Turtle (*Actinemys marmorata*) in British Columbia. *Wildlife Afield* 2:58–63.
- EVENDEN FG. 1948. Distribution of the turtles of western Oregon. *Herpetologica* 4:201–204.

- FISHER JL. 2018. Archaeology and biogeography of the Western Pond Turtle (*Actinemys marmorata*) in the Puget Sound Region. *Ethnobiology Letters* 9:180–188.
- GALBRAITH DA, BROOKS RJ. 1987. Survivorship of adult females in a northern population of Common Snapping Turtles (*Chelydra serpentina*). *Canadian Journal of Zoology* 65:1581–1586.
- GERMANO DJ. 2010. Ecology of the Western Pond Turtle (*Actinemys marmorata*) at sewage-treatment facilities in the San Joaquin Valley, California. *Southwestern Naturalist* 55:89–97.
- GERMANO DJ. 2016. The ecology of a robust population of *Actinemys marmorata* in the San Joaquin Desert of California. *Copeia* 104:663–676.
- GERMANO DJ. 2020. Ecology of Northwestern Pond Turtles in a Sierran foothill population, California. *California Fish and Wildlife Journal* 106:260–267.
- GERMANO DJ. 2021. Decadal change in a population of Western Pond Turtles at an isolated agricultural site in the San Joaquin Valley, California, USA. *Pacific Conservation and Biology* 27:236–243.
- GERMANO DJ, BURY RB. 1998. Age determination in turtles: Evidence of annual deposition of scute rings. *Chelonian Conservation and Biology* 3:123–132.
- GERMANO DJ, BURY RB. 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 DJ, BURY RB. 2009. Variation in body size, growth, and population structure of *Actinemys marmorata* from lentic and lotic habitats in southern Oregon. *Journal of Herpetology* 43:510–520.
- GRAY EM. 1995. DNA fingerprinting reveals a lack of genetic variation in northern populations of the Western Pond Turtle (*Clemmys marmorata*). *Conservation Biology* 9:1244–1254.
- HENEN BT. 1997. Seasonal and annual energy budgets of female Desert Tortoise (*Gopherus agassizii*). *Ecology* 78:283–296.
- HEPPELL SS. 1998. Application of life-history theory and population model analysis to turtle conservation. *Copeia* 1998:367–375.
- HOLTE DL. 1998. Nest site characteristics of the Western Pond Turtle, *Clemmys marmorata*, at Fern Ridge Reservoir, in west central Oregon [thesis]. Corvallis, OR: Oregon State University. 106 p.
- HORN RB, GERVAIS JA. 2018. Landscape influence on the local distribution of Western Pond Turtles. *Ecosphere* 9(7) e02346 <https://doi.org/10.1002/ecs2.2346>.
- IVERSON JB, BALGOOYEN CP, BURD KK, LYDDAN KK. 1993. Latitudinal variation in egg and clutch size in turtles. *Canadian Journal of Zoology* 71:2448–2461.
- KOPER N, BROOKS RJ. 2000. Environmental constraints on growth of Painted Turtles (*Chrysemys picta*) in northern climates. *Herpetologica* 56:421–432.
- LINDEMAN PV. 1997. Contribution toward improvement of model fit in nonlinear regression modelling of turtle growth. *Herpetologica* 53:179–191.
- LITZGUS JD, MOUSSEAU TA. 2006. Geographic variation in reproduction in a freshwater turtle (*Clemmys guttata*). *Herpetologica* 62:132–140.
- LUBCKE GM, WILSON DS. 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.
- MATSUDA BM, GREEN DM, GREGORY PT. 2006. Amphibians and reptiles of British Columbia. Victoria, BC: Royal BC Museum. 266 p.
- MOYLE PB. 1995. Conservation of native freshwater fishes in the Mediterranean-type climate of California, USA: A review. *Biological Conservation* 72:271–279.
- [NOAA] NATIONAL OCEAN AND ATMOSPHERIC ADMINISTRATION. 2021. National Weather Service. Available online at: https://wrcc.dri.edu/Climate/west_lcd.php or https://www.weather.gov/key/climate_heat_cool.
- [ODFW] OREGON DEPARTMENT OF FISH AND WILDLIFE. 2006. The Oregon Conservation Strategy. 375 p plus appendix. Available at: <https://www.oregonconservationstrategy.org>.
- [ODFW] OREGON DEPARTMENT OF FISH AND WILDLIFE. 2015. Guidance for conserving Oregon's native turtles including Best Management Practices. Oregon Department of Fish and Wildlife. 99 p. Available at: https://www.dfw.state.or.us/wildlife/living_with/docs/ODFW_Turtle_BMPs_March_2015.pdf.
- REESE DA, WELSH HH JR. 1998. Habitat use by Western Pond Turtles in the Trinity River, California. *Journal of Wildlife Management* 62:842–853.
- REZNICK DA, BRYGA H, ENDLER JA. 1990. Experimentally induced life-history evolution in natural population. *Nature* 346:357–359.
- RICHARDS FJ. 1959. A flexible growth function for empirical use. *Journal of Experimental Botany* 10:290–300.
- ROSENBERG DK, SWIFT R. 2013. Post-emergence behavior of hatchling Western Pond Turtles (*Actinemys marmorata*) in western Oregon. *American Midland Naturalist* 169:111–121.
- SEELIGER LM. 1945. Variation in the Pacific Mud Turtle. *Copeia* 1945:150–159.
- SPIKINS PQ, SHAFFER HB. 2005. Range-wide molecular analysis of the Western Pond Turtle (*Emys marmorata*): Cryptic variation, isolation by distance, and their conservation implications. *Molecular Ecology* 14:2047–2064.

- STEARNS SC. 1992. The evolution of life histories. Oxford, England: Oxford University Press. 249 p.
- STORER TI. 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.
- [USFWS] US FISH AND WILDLIFE SERVICE. 2015. Endangered and threatened wildlife and plants; 90-day findings on 10 petitions. Federal Register 80 FR 19259:19259–19263.
- WILBUR HM, MORIN PJ. 1988. Life history evolution in turtles. In: Gans C, Huey RB, editors. Biology of the Reptilia. Volume 16. Ecology B. Defense and life history. New York, NY: Alan R Liss, Inc. p 387–439.

Submitted 10 July 2021, accepted 9 November 2021.

Corresponding Editor: Jay Bowerman.