Herpetological Conservation and Biology 3(2):143-148
Submitted: 16 October 2007; Accepted: 16 July 2008.

REPRODUCTION OF PACIFIC POND TURTLES (*ACTINEMYS MARMORATA*) IN COASTAL STREAMS OF CENTRAL CALIFORNIA

NORMAN J. SCOTT[1,2], GALEN B. RATHBUN[1,3], THOMAS G. MURPHEY[1,4], MARGARET B. HARKER[1,5]

[1]U.S. Geological Survey, Western Ecological Research Center, Piedras Blancas Field Station, Post Office Box 70, San Simeon, California 93452, USA
[2]Corresponding Author/Present Address: Research Associate, Smithsonian Institution, c/o P.O. Box 307, Creston, California 93432, USA, e-mail: amphibscott@gmail.com
[3]Present Address: California Academy of Sciences (San Francisco), c/o P.O. Box 202, Cambria, California 93428-0202, USA, e-mail: grathbun@calacademy.org
[4]Present Address: U.S. Forest Service, 1616 Carlotti Drive, Santa Maria, California 93454, USA, e-mail: tmurphey@fs.fed.us
[5]Present Address: 1130 E Clarke 150-#243, Santa Maria, California 93455, USA, e-mail: margyeharker@aol.com

***Abstract.*—We studied the reproduction of Pacific Pond Turtles, *Actinemys marmorata*, in four coastal creeks in central California. Ovigerous females had carapace lengths (CL) between 140 mm and 164 mm ($\bar{x}$ = 152 mm). Oviposition occurred from late April to mid-July. The number of eggs in 97 clutches varied between three and eight ($\bar{x}$ = 5.7), and 39 females laid 0-2 ($\bar{x}$ = 1.3) clutches/yr. The average size of the first clutch was larger than the second, but the number of clutches laid one year did not affect the number laid the next year. Mean annual egg production per female was 7.2 eggs. The female pond turtles reported here have the largest minimum size at maturity (140 mm) of any population studied to date. The breeding season is similar to that in lowland southern California and about a month earlier than at higher elevations and latitudes. Clutch size is not correlated with CL at the local level, but it is in the overall range. Clutch size may be under tighter genetic control than clutch frequency, and the latter may be the mechanism by which females adjust to varying environmental conditions such as nutrient levels or temperature.**

Key Words.—Actinemys marmorata; California; Emydidae; Pacific Pond Turtles; reproduction; turtles

INTRODUCTION

Limited information exists on the reproduction of Pacific Pond Turtles (*Actinemys marmorata*) compared to that available for many other North American freshwater turtles. Van Denburgh (1922) reported on *A. marmorata* nesting habits and egg sizes. Rathbun et al. (1992) examined the nesting habitats of four female turtles in our study area. One previous study (Holland, D. C. 1994. The Western pond turtle: Habitat and history. Unpublished Final Report. Portland, OR: U.S. Department of Energy, Bonneville Power administration. http://www.efw.bpa.gov/Environment/EW/EWP/DOCS/REPORTS/WILDLIFE/W62137-1.pdf) commented on minimum size at maturity in individuals from southern California and Oregon, and Goodman (1997a, b) has data from two southern California sites. However, the average and variation in this parameter are unknown for any population. Reports on the sizes of about 190 clutches from throughout the range exist. Over large geographic areas, the number of eggs correlates with female carapace length (Holland 1994 *ibid*). There are reports of the clutch frequency for two southern California populations (Goodman 1997a; Lovich and Meyer 2002).

Previous studies on *A. marmorata* in coastal central California took place on the same populations that we studied. They include: (1) Holland (1985) who reported on the natural history and morphometrics of the Pico Creek population; (2) Rathbun et al. (1992) who examined nesting in the Arroyo Laguna system; and (3) Rathbun et al. (2002) who reported movement patterns and nesting behaviors of the populations reported herein. The objective of our paper is to summarize the reproductive traits of these populations.

MATERIALS AND METHODS

***Study Sites and Populations.*—**We studied turtles in the coastal portions of Oak Knoll Creek/Arroyo Laguna, Little Pico Creek, Pico Creek, and San Simeon Creek, which are within 17 km NW of Cambria, San Luis Obispo County, California, USA. All of the creeks include small lagoon systems at their mouths. Only San Simeon Creek flowed all year; the others dried in late summer, and all had torrential flows following winter storms. A small man-made pond was in the Pico Creek flood plain, upstream from the lagoon and about 50 m from the creek. Another man-made pond, used to store treated sewage, was in the uplands near San Simeon Creek. In addition, the lagoon at San Simeon Creek includes a small tributary that formed a permanent slough.

Turtles in the Pico Creek/Pond system move among the pond, an intermittent creek, and a tidal lagoon, but spend most of their time in the pond (Rathbun et al. 2002). Turtles in San Simeon Creek drainage use a permanent stream, a lagoon, and a slough, and they occasionally use the sewage infiltration ponds. Turtles in Arroyo Laguna and Little Pico occur in the only waters available to them, the stream and lagoon.

Field Methods.—We hand-captured or trapped, and palpated for eggs, 152 female *A. marmorata* with carapace lengths (CL) > 100 mm from 1992-1998. Radio transmitters (Custom design, ATS, Isanti, Minnesota, USA) were attached to 39 with CL > 139 mm with epoxy to the anterior carapaces (Rathbun et al. 2002). We measured CL to the nearest millimeter with calipers in a straight-line between the most anterior and posterior points of the carapace.

We caught and palpated radio-tagged turtles at intervals of approximately two weeks during the 2½ breeding seasons. If we detected eggs, we X-rayed the turtles. This provided additional clutch data on turtles that we captured but did not radiotag. Repeated X-rays are not thought to be injurious to female turtles or their eggs (Hinton et al. 1997).

We determined individual clutch intervals within a breeding season by counting the number of days between the final date that we felt the first and second clutches. This estimate either overestimated or underestimated the actual interval, but without an obvious bias in either direction.

We estimated the end of the nesting season as the last date we detected a clutch in a female. The actual laying date for that clutch was 1-13 days later.

Statistical Analyses.—We analyzed data using SPSS (1997. SPSS for Windows. Release 8.0.0, Chicago, Illinois) with an alpha level of $\alpha < 0.05$ for all tests. We tested for normality on all distributions using the Kolmogorov-Smirnov test with the Lillefors modification. We tested the relationship between carapace length, clutch size, and frequency using linear regression for normally distributed data, and Spearman's rho (r_s) for non-normal data.

We compared normal clutch data among streams by one-way ANOVA and a Bonferroni post hoc multiple comparisons test. For non-normal parameters, we made comparisons with the Kruskal-Wallis test followed by pair-wise Mann-Whitney U tests with a Bonferroni corrected alpha level. For females with multiple clutches, we used mean values in the calculation of most statistics; for the relationship between CL and clutch size, we used the maximum clutch size. Data are presented as means and standard deviation (SD). We based data on clutch frequency for those records spanning an entire nesting season.

RESULTS

Size at Maturity.—Of the 152 females with CL > 100 mm, the 43 females with detectable eggs ranged between 140 and 164 mm (mean = 151.6 mm, S = 5.7; Table 1, Fig. 1); and did not vary significantly among the drainages (F = 0.78, df = 3.42, P = 0.51). One radiotagged female did not lay eggs in two consecutive years, during which time her carapace grew from 149 mm to 151 mm. We considered her to be an anomaly, so we excluded her data from the productivity calculations.

Nesting Season.—The nesting season extended from late April through mid July, during which time females deposited zero, one, or two clutches (Fig. 2). The earliest laying date was between 22 and 30 April. We recorded shelled eggs from the first clutch as late as 15 July, although they deposited most before the end of June. They laid the earliest second clutch before 6 June, and we found the latest on 1 July.

Clutch Size.—The mean clutch size from 43 turtles was 5.7 (SD = 1.2, range = 3-8). Female CL was not significantly related to maximum clutch size (F = 1.62, df = 20,42, P = 0.44). Average clutch size varied significantly among drainages (F = 4.51, df = 3,39, P = 0.008, Fig. 3). Mean clutch size from Pico Creek females (mean = 4.7, SD = 1.0, n = 9) was significantly smaller than that from Little Pico (mean = 6.4, SD = 0.7, n = 7, Mean Difference = 1.74, P = 0.02) and San Simeon (mean = 6.2, SD = 1.2, n = 13, Mean Difference = 1.51, P = 0.02) creeks, but not from Arroyo Laguna (mean = 5.6, SD = 1.2, n = 14; Mean Difference = 0.94, P = 0.30). Arroyo Laguna, Little Pico, and San Simeon did not differ among themselves (all Mean Differences < 0.80, P > 0.73). Clutch size did not vary significantly among years (F = 0.24, df = 6,62, P = 0.96).

Clutch Frequency.—In some turtles, we did not palpate a single clutch for as long as 33 days, but the usual duration was 2-3 weeks. The estimated range of intervals between the laying of two clutches in the same season was 27-43 days. We tracked 39 turtles through 66 individual turtle nesting seasons, during which time they laid an average of 1.3 (SD = 0.7) clutches/yr (Table 1). Individual turtles laid no eggs in 10 seasons, a single clutch in 27 seasons, and double clutches in 29 seasons. Clutch frequency did not vary significantly with turtle size (N = 39, P = 0.99).

Twenty-five females laid two clutches in a single year; their average first clutch (mean = 6.0, SD = 0.9) contained significantly more eggs than their second clutch (mean = 5.3, SD = 1.3; t = 2.25, df = 25,24, P = 0.03). The number of clutches laid in one year seemed to have no effect on the number of clutches produced the next year. In 25 pair-wise comparisons between years, turtles laid more clutches the second year on eight occasions, on nine they laid fewer, and on eight they laid the same number of clutches. The number of clutches per year varied significantly among streams ($\chi^2 = 8.55$, $P < 0.04$). Females in Arroyo Laguna laid clutches significantly more often than those in San Simeon Creek ($U_{10,13} = 20.00$, $P = 0.004$).

Reproductive Output.—Mean annual egg production of 39 radiotagged females was 7.2 (SD = 3.9) eggs. It did not vary significantly with CL ($F = 1.18$, df = 1.37, $P = 0.28$) or among streams ($F = 1.43$, df = 3,35, $P = 0.25$). During 66 seasons, the total reproductive output of 39 females was > 478 eggs in 85 clutches (the size of one clutch was unknown).

TABLE 1. Carapace lengths and clutch sizes of 48 *Actinemys marmorata* from San Luis Obispo County, California, USA, 1992-1998. Annual clutch frequency is given for 39 radio-tagged turtles. Unless noted by an asterisk, egg numbers are the entire egg output of that turtle during the year (6-5 indicates 6 eggs in the first clutch and 5 in the second). A question mark (?) means that the clutch size is unknown. # = turtle ID number; CL = Carapace length

			Yearly Clutch Sizes						
Locality	**#**	**CL**	1992	1993	1994	1995	1996	1997	1998
Arroyo Laguna	00617	140			6-5				
	06171	148		6	7-5				
	53548	146					6*		
	8426F	148					8*		
	90E69	161		8	6-7				
	9340E	154					6*		
	94541	151			5-5		4*		
	A635F	156					4*		
	B0842	152			7-3				
	B4D2B	147			6-4				
	D096F	145			6-5		6*		
	D133E	143			0				
	D214E	164			6-7				
	D2F72	144			4-3				
	4F712	149					6*		
Little Pico	10E5C	145			0				
	23251	156			7-6		8		
	86708	150			7				
	92431	154			5				
	B4203	143		6-7	0	7	6		
	B4505	149		6-6	0				
	E653C	149			7-7				
	F3233	150			6-7				
Pico Creek/Pond	23207	156			4-5				
	2441D	154		3					
	62E4C	159		4					
	85715	153	4	5	0	3	5-4		
	92275	141					5-3		
	95B19	154		6					
	97427	152			5			6-4	
	B3B06	150			5-6				
	F665B	148					6*		
San Simeon Creek	02763	158			0				
	0315F	148						8	7
	15913	151	5*						
	21B38	163	7	7	8-5	7	7-4	6*	
	22857	153	8*						
	57D59	152	6-4	6	5				
	86430	152						0	7
	91708	153		7-4	6				
	92226	147						7	8
	92765	149						0	
	93D20	160							
	95161	154	7*						
	COA6B	163					6*	7-7	6-7
	C6513	155		7-5	5				
	C6F4B	143						?-5	3
	D2E4F	149	0						

* Incomplete clutch record. Turtles may have laid additional clutches. We excluded this record from clutch frequency calculations.

DISCUSSION

Size at Maturity.—The size of the smallest reproductive female turtles in a population varies considerably under different ecological regimes (Gibbons et al. 1981). Holland (1994) studied *Actinemys* throughout its range. He reported a southern California reproductive female with a CL of 111 mm, but 120 mm was the minimum reproductive size in most areas he studied. The smallest female with eggs found north of the Rogue River in Oregon had a CL of 131 mm. We palpated 25 females with CL between 119 and 140 mm during the breeding season (April-June) and only one (140 mm CL) was gravid. At other southern California sites, researchers found smaller gravid females with CL ranging from 129-139 mm (Goodman 1997b; Lovich and Meyer 2001).

Clutch Phenology, Size, and Frequency.—The May-July nesting season at our study site in coastal central California was about the same as that reported for a low elevation site in southern California (Goodman 1997a). These seasons were about a month earlier than the June-August period for a higher elevation southern California site (Goodman 1997b) and for Oregon (Holland 1994 *ibid*).

Holland (1994) gives an extreme range of 1-13 eggs in 168 clutches from throughout the range. Mean clutch sizes from

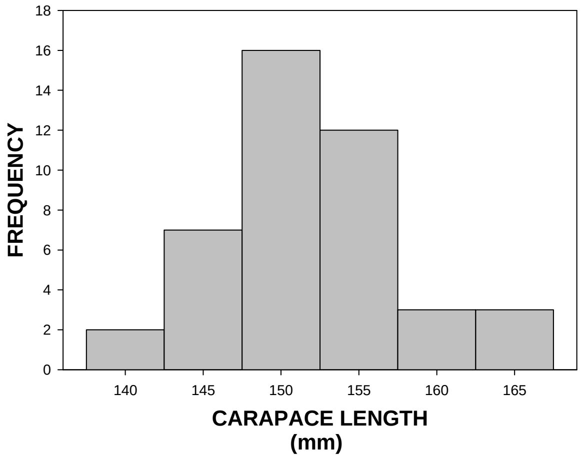


FIGURE 1. Distribution of carapace lengths of 43 gravid female *Actinemys marmorata* at first capture, 1992-1998, San Luis Obispo County, California, USA.

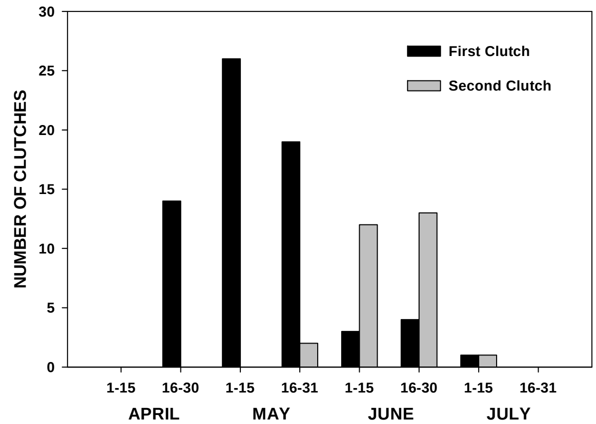


FIGURE 2. Last dates that 95 clutches could be felt within female *Actinemys marmorata*, 1992-1998, San Luis Obispo County, California, USA. Actual nesting dates would be 1-13 days later.

four coastal central California samples (mean = 5.6, n = 116; Congdon and Gibbons 1985; Rathbun et al. 1992; this study) are considerably smaller than those from interior California (mean = 8.0, n = 5, Storer 1930), and Oregon (mean = 7.3, n = 4, Feldman 1982; mean ≅ 7, n unknown, Holland 1994 *ibid*), but they are similar to those from two southern California sites (lowland mean = 5.7, SD = 1.7, n = 16; upland mean = 5.7, SD = 1.0, n = 15, Goodman 1997b). Lovich and Meyer (2002) recorded 12 relatively small clutches from the Mojave Desert of California (mean = 4.6, range 4-6).

Holland (1994) found a strong positive correlation (r = 0.69, n = 168) between carapace length and clutch size over the entire range of *A. marmorata*. However, this correlation did not hold in our study or at Goodman's (1997b) lowland site. There was a significant CL/clutch size correlation at Goodman's upland site and in the Mojave Desert turtles studied by Lovich and Meyer (2002).

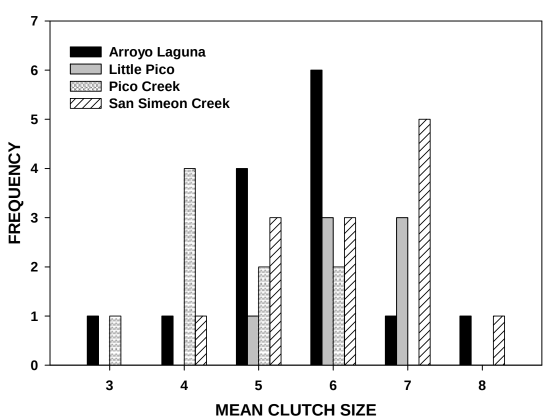


FIGURE 3. Distribution of egg clutch sizes among streams for 43 female *Actinemys marmorata*, 1992-1998, San Luis Obispo County, California, USA. Mean clutch sizes rounded to the nearest whole integer are used for multiple clutches from the same female.

Clutch frequency is a critical parameter for the development of realistic life tables. Unfortunately, it is time-consuming to determine accurately. Analyses of clutch size alone are interesting from a theoretical aspect (Iverson et al. 1993), but they are misleading for population analyses without knowing clutch frequency.

At Goodman's (1997a) southern California lowland site, 42% of 15 females observed during three seasons laid eggs in any given year; in our study, this figure was 85%. Goodman's gravid female laid two clutches in 10% of the seasons versus our figure of 44%. Overall, Goodman's turtles averaged 0.52 clutches/yr contrasted with 1.31 in our study. However, a few of Goodman's turtles may not have reached reproductive size or age. Goodman (1997a) used 110 mm as his criterion for minimum CL at first reproduction, a size that is considerably below our minimum of 140 mm. On the other hand, three of our turtles that failed to lay (CLs of 143, 145, and 149 mm) also may have been immature (Table 1). Goodman's (1997b) clutch frequency data for his upland site may be incomplete, and some turtles may have nested without his knowledge (Goodman, pers. comm.).

Holland (1994) stated that, although some turtles in central and southern California may lay eggs every year or even double-clutch, the "majority of females....examined or dissected during the approximate period when the species is known to be carrying eggs were not gravid". Thus, he concluded from this that either the majority of Pacific Pond Turtles oviposit every other year (or even triennially), or many females are reproductively senescent. On the central California coast, the first scenario is not true and the second is unlikely.

Holland (1994) may have overestimated the duration that females retain palpable eggs. We examined turtles several times each during years in which they laid eggs. Taking the observations from 15 April through 30 June, we recorded these turtles as lacking eggs (by palpation) 140 times out of 283 observations. We generally palpated a turtle five or six times during a season, and even turtles that laid two clutches would lack noticeable eggs on two or three of these occasions. Similarly, Turner et al. (1986) found that eggs of any single clutch in the Desert Tortoise (*Gopherus agassizii*) were only visible on X-rays for about 22 d.

One aspect of *A. marmorata* nesting that has not been suitably explored or discussed is the possibility that gravid females split clutches of eggs between two or more nests over several days. Split clutches within a single day have been documented for *Pseudemys floridana* from eastern North America (Ernst et al. 1994). Unfortunately, we did not design our study to detect clutch-splitting. Our data, and those of Lovich and Meyer (2002), suggest that it may occur. For example, in the two cases where we successfully monitored turtle nests, the number of overwintering nestlings that emerged or that we excavated was less than the number of shelled eggs that the females carried before nesting, as determined by X-ray. In addition, because we determined successful nesting by palpating females after nesting, and palpation only provides information on the presence or absence of eggs, not numbers, we may have missed cases of split clutches. The possibility of split clutches in *A. marmorata* definitely warrants closer examination.

We assume that clutch parameters are affected by multiple intrinsic (e.g., genetic, physiological) and extrinsic (e.g., temperature, nutrient) factors. The discrepancy in clutch frequency between the central coast and southern California turtles indicates that clutch frequency might be the most important way that turtles adjust to differing nutritional or thermal environments.

Acknowledgments.—We thank David Germano for several editing and review iterations, and especially for providing the impetus to resurrect the manuscript from limbo. The knowledge of Dan Holland was very helpful, especially at the beginning of our study. Nancy Siepel and Denise Woodard participated in the early stages of radiotracking. Glen Sproule, John Truax, Camille Hirst, and Ennis Olgorsolka graciously X-rayed gravid turtles for us. The California Department of Parks and Recreation partially funded the first years of this study through Woody Elliott. The California Department of Transportation, through Gary Ruggerone and Greg Smith, contributed funds from 1992 to 1999. Elliott and Smith issued permits to work in San Simeon State Park, and John Brode and Betsy Bolster issued our permit from the California Department of Fish and Game (SC-002460). The study benefited from discussions with Holland and Robert Goodman, who also provided unpublished data. The manuscript was improved by comments from Bruce Bury, Jeff Lovich, and anonymous reviewers. Susan Wright efficiently handled the administrative tasks.

LITERATURE CITED

Congdon, J.D., and J.W. Gibbons. 1985. Egg components and reproductive characteristics of turtles: Relationships to body size. Herpetologica 41:194-205.

Ernst, C.H., J.E. Lovich, and R.W. Barbour. 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington, D.C., USA.

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

Gibbons, J.W., R.D. Semlitsch, J.L. Greene, and J.P. Shubauer. 1981. Variation in age and size at maturity of the slider turtle (*Pseudemys scripta*). American Naturalist 117:841-845.

Goodman, R.H., Jr. 1997a. Occurrence of double clutching in the Southwestern Pond Turtle, *Clemmys marmorata pallida*, in the Los Angeles Basin. Chelonian Conservation and Biology 2:419-420.

Goodman, R.H. 1997b. The biology of the Western Pond Turtle (*Clemmys marmorata pallida*) in the Chino Hills State Park and the West Fork of the San Gabriel River. M.S. Thesis, California State Polytechnic University, Pomona, California, USA. 81 p.

Hinton, T.G., P.D. Fledderman, J.E. Lovich, J.D. Congdon, and J.W. Gibbons. 1997. Radiographic determination of fecundity: Is the technique safe for developing turtle embryos? Chelonian Conservation and Biology 2:409-414.

Holland, D.C. 1985. An ecological and quantitative study of the Western Pond Turtle (*Clemmys marmorata*) in San Luis Obispo County, California. M.A. Thesis, California State University, Fresno, California, USA. 181 p.

Iverson, J.B., C.P. Balgooyen, K.K. Byrd, and K.K. Lyddan. 1993. Latitudinal variation in egg and clutch size in turtles. Canadian Journal of Zoology 71:2448-2461.

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

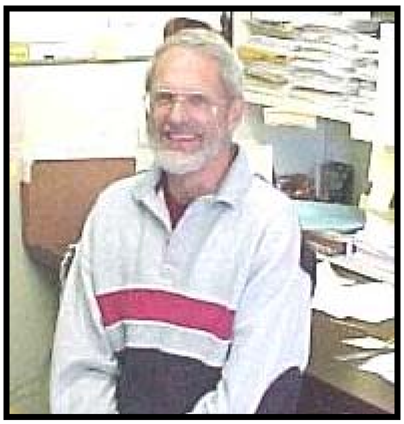
Rathbun, G.B., N. Siepel, and D. Holland. 1992. Nesting behavior and movements of Western Pond Turtles, *Clemmys marmorata*. Southwestern Naturalist 37:319-324.

Rathbun, G.B., N.J. Scott, Jr., and T.G. Murphey. 2002. Terrestrial habitat use by Pacific Pond turtles in a Mediterranean climate. Southwestern Naturalist 47:225-235.

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.

Turner, F.B., P. Hayden, B.L. Burge, and J.B. Roberson. 1986. Egg production by the Desert Tortoise (*Gopherus agassizii*) in California. Herpetologica 42:93-104.

Van Denburgh, J. 1922. The reptiles of western North America. An account of the species known to inhabit California and Oregon, Washington, Idaho, Utah, Nevada, Arizona, British Columbia, Sonora and Lower California. Volume II. Snakes and turtles. Occasional Papers, California Academy of Sciences 10:615-1028.



NORMAN J. SCOTT, JR., received his B.S. and M.Sc. at Humboldt State University, Claifornia, and PhD. from the University of Southern California. He served as a Director, 1982-84, and President, 1987, of the Society for the Study of Amphibians and Reptiles. He held positions at the Universidad de Costa Rica, the University of Connecticut, and the University of New Mexico, and the U.S. Fish and Wildlife Service. He retired in 2001 to Creston, California, from the U.S. Geological Survey. His academic interests are in the biology, ecology, taxonomy, biogeography, and evolution of reptiles and amphibians. He has authored or coauthored >70 papers, mostly on tropical reptiles and amphibians, but also monkey populations, duck taxonomy, and bird faunas

GALEN B. RATHBUN received his undergraduate degree from Humboldt State University, California, and his Ph.D. in Zoology from the University of Nairobi in Kenya. Then, he completed a postdoctoral fellowship at the Smithsonian Institution's National Zoological Park. His research interests include the behavioral ecology of vertebrates and conservation biology of declining species. Although much of his career has been spent studying Florida manatees and California sea otters, his current research involves understanding the basic life history of California red-legged frogs and Western pond turtles, and the impacts of cattle grazing on a community of small mammals in the San Joaquin Valley, California. He also continues research on the evolution of monogamy in some small mammals (especially elephant-shrews or sengis) in Namibia. Based on his long-standing interests in African small mammals, Galen is the founding Chair of the IUCN-SSC Afrotheria Specialist Group. Currenty, he is a Scientist Emeritus with the U.S. Geological Survey as well as a Research Associate and Fellow of the California Academy of Sciences.