CONSERVATION BIOLOGY OF FRESHWATER TURTLES AND TORTOISES

A Compilation Project of the IUCN SSC Tortoise and Freshwater Turtle Specialist Group

Edited by

Anders G.J. Rhodin, John B. Iverson, Peter Paul van Dijk,
Craig B. Stanford, Eric V. Goode, Kurt A. Buhlmann, and Russell A. Mittermeier

Actinemys marmorata (Baird and Girard 1852) –
Northwestern Pond Turtle

R. Bruce Bury, David J. Germano, and Don T. Ashton

Chelonian Research Monographs
Number 5 (Installment 20) 2026: Account 135

Published by
Chelonian Research Foundation and Turtle Conservancy

in association with
IUCN SSC Tortoise and Freshwater Turtle Specialist Group, Re:wild,
Turtle Conservation Fund, and International Union for Conservation of Nature / Species Survival Commission

Chelonian Research Monographs
Contributions in Turtle and Tortoise Research

CHELONIAN RESEARCH MONOGRAPHS (CRM) (ISSN 1088-7105) is an international peer-reviewed scientific publication series for monograph-length manuscripts, collected proceedings of symposia, edited compilations, and other longer research documents focused on turtles and tortoises. The series accepts contributions dealing with any aspects of chelonian research, with a preference for conservation or biology of freshwater and terrestrial turtles and tortoises. Bibliographic and other reference materials are also of potential interest. Submit manuscripts directly to Anders Rhodin at the e-mail address above. The series is published on an occasional basis, from 1996–2016 by Chelonian Research Foundation, and from 2017 and on by Chelonian Research Foundation and Turtle Conservancy.

Published CRM Issues

CRM 1. The Galápagos Tortoises: Nomenclatural and Survival Status. 1996. By Peter C.H. Pritchard. 85 pp. Open-access pdf available here.

CRM 2. Asian Turtle Trade: Proceedings of a Workshop on Conservation and Trade of Freshwater Turtles and Tortoises in Asia. 2000. Edited by Peter Paul van Dijk, Bryan L. Stuart, and Anders G.J. Rhodin. 164 pp. Open-access pdf available here.

CRM 3. Biology and Conservation of Florida Turtles. 2006. Edited by Peter A. Meylan. 376 pp. Open-access pdf available here.

CRM 4. Defining Turtle Diversity: Proceedings of a Workshop on Genetics, Ethics, and Taxonomy of Freshwater Turtles and Tortoises. 2007. Edited by H. Bradley Shaffer, Nancy N. FitzSimmons, Arthur Georges, and Anders G.J. Rhodin. 200 pp. Open-access pdf available here.

CRM 5 (Installments 1–20, 135 species accounts to date). Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN SSC Tortoise and Freshwater Turtle Specialist Group. 2008–2026. Edited variously by Anders G.J. Rhodin, John B. Iverson, Peter Paul van Dijk, Kurt A. Buhlmann, Peter C.H. Pritchard, Craig B. Stanford, Eric V. Goode, Raymond A. Saumure, and Russell A. Mittermeier. 1,506 pp. to date. All accounts available as open-access pdf downloads: follow links here.

CRM 6. Turtles on the Brink in Madagascar: Proceedings of Two Workshops on the Status, Conservation, and Biology of Malagasy Tortoises and Freshwater Turtles. 2013. Edited by Christina M. Castellano, Anders G.J. Rhodin, Michael Ogle, Russell A. Mittermeier, Herilala Randriamahazo, Rick Hudson, and Richard E. Lewis. 184 pp. Open-access pdf available here.

CRM 5 (Installment 8). Turtles and Tortoises of the World During the Rise and Global Spread of Humanity: First Checklist and Review of Extinct Pleistocene and Holocene Chelonians. 2015. TEWG [Turtle Extinctions Working Group: Anders G.J. Rhodin, Scott Thomson, Georgios L. Georgalis, Hans-Volker Karl, Igor G. Danilov, Akio Takahashi, Marcelo S. de la Fuente, Jason R. Bourque, Massimo Delfino, Roger Bour, John B. Iverson, H. Bradley Shaffer, and Peter Paul van Dijk]. 66 pp. Open-access pdf available here.

CRM 7. Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status (8th Ed.). 2017. TTWG [Turtle Taxonomy Working Group: Anders G.J. Rhodin, John B. Iverson, Roger Bour, Uwe Fritz, Arthur Georges, H. Bradley Shaffer, and Peter Paul van Dijk]. 292 pp. Open-access pdf available here.

CRM 8. Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status (9th Ed.). 2021. TTWG [Turtle Taxonomy Working Group: Anders G.J. Rhodin, John B. Iverson, Roger Bour, Uwe Fritz, Arthur Georges, H. Bradley Shaffer, and Peter Paul van Dijk]. 472 pp. Open-access pdf available here.

CRM 9. Range-Wide Demographic Collapse and Extinction Dynamics of the Endemic Burmese Roofed Turtle, *Batagur trivittata*, in Myanmar. 2024. Steven G. Platt, Win Ko Ko, Kalyar Platt, Tint Lwin, Swann Htet Naing Aung, Khin Myo Myo, Me Me Soe, Myo Min Win, Kyaw Thu Zaw Wint, Htun Thu, Shine Hsu Hsu Naing, Brian D. Horne, and Thomas R. Rainwater. 26 pp. Open-access pdf available here.

CRM 10. Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status (10th Ed.). 2025. TTWG [Turtle Taxonomy Working Group: Anders G.J. Rhodin, John B. Iverson, Uwe Fritz, Natalia Gallego-García, Arthur Georges, H. Bradley Shaffer, and Peter Paul van Dijk]. 575 pp. Open-access pdf available here.

Other Chelonian Research Foundation & Turtle Conservancy Publications

Turtles in Trouble: The World's Most Endangered Tortoises and Freshwater Turtles – 2025. TCC [Turtle Conservation Coalition: Craig B. Stanford, Anders G.J. Rhodin, Peter Paul van Dijk, Torsten Blanck, Eric V. Goode, Rick Hudson, Andrew D. Walde, Jordan Gray, Russell A. Mittermeier, and Vivian P. Páez. (Eds.)]. 2025. 77 pp. Open-access pdf available here.

Tortoises in the Mist: Turtle Poetry for Conservationists. Anders G.J. Rhodin and Eric V. Goode (Eds.)]. 2021. 106 pp. Open-access pdf available here.

CHELONIAN RESEARCH MONOGRAPHS (CRM) issues are variously available for purchase from Chelonian Research Foundation and Turtle Conservancy. Contact either Turtle Conservancy (www.turtleconservancy.org) or Chelonian Research Foundation (www.chelonian.org/crm; 564 Chittenden Dr., Arlington, VT 05250 USA; 978-807-2902; RhodinCRF@aol.com) for prices, titles, and to place orders for available print copies. Chelonian Research Foundation (founded in 1992) and Turtle Conservancy (founded in 2005 as Chelonian Conservation Center, renamed in 2010) are nonprofit tax-exempt organizations under section 501(c)(3) of the Internal Revenue Code.

Conservation Biology of Freshwater Turtles and Tortoises:
A Compilation Project of the IUCN SSC Tortoise and Freshwater Turtle Specialist Group
Rhodin, Iverson, van Dijk, Stanford, Goode, Buhlmann, and Mittermeier (Eds.)
Chelonian Research Monographs (ISSN 1088-7105) No. 5 (Installment 20), doi:10.3854/crm.5.135.marmorata.v2.2026

Actinemys marmorata (Baird and Girard 1852) – Northwestern Pond Turtle

R. Bruce Bury[1], David J. Germano[2], and Don T. Ashton[3]

[1]*1410 NW 12th Street, Corvallis, Oregon, 97331 USA [clemmys@gmail.com];*
[2]*Department of Biology, California State University at Bakersfield, Bakersfield, California, 93311 USA (retired) [dgermano@csub.edu];*
[3]*Applied River Sciences, 980 7th Street, Arcata, California, 95521 USA [don@riversciences.com]*

Summary. – The Northwestern Pond Turtle, *Actinemys marmorata* (family Emydidae), currently ranges from northern Washington State through western Oregon and south to central California, USA. It may have formerly ranged from southwestern British Columbia, Canada, but is now likely extirpated or was possibly introduced there. It was recently split from the Southwestern Pond Turtle (*A. pallida*) that has its range in central coastal California south to Baja California, Mexico. Adult *A. marmorata* are medium-sized freshwater turtles with a usual straightline (maximum) carapace length (SCL) of 150–180 mm, although some males exceed 220 mm SCL. They are primarily aquatic during their activity period that spans from spring through early fall. They prefer quiet waters, including marshes, ephemeral wetlands, ponds, streams, and rivers as well as artificial water bodies such as canals, cattle ponds, and reservoirs. Some populations persist in intermittent waters present for only 4–6 mo each year. Overwintering habits vary, with most turtles residing in flowing waters moving to upland sites, while others may remain in still waters year-round. They are generalist omnivores, although juveniles primarily feed on invertebrates while adults may include aquatic plants in the diet. Males begin to display secondary sexual characteristics (SSC) by 120 mm SCL while females mature around 140 mm SCL. Individuals tend to grow more slowly in the northern portions of their range where ambient temperatures are lower and the growing season is shorter. In Oregon and northern California, males attain SSC at 6–10 yrs old and females begin to reproduce by about 10 yrs of age. In southern populations, males may attain SSC at 2–4 yrs and females as early as 4 yrs of age. Sex ratios typically are close to 1:1. Most populations have 30–60% of turtles <12 yrs old. Annual survivorship of adults is > 0.7 but this needs better documentation. Survivorship of eggs and hatchlings is low. Mean clutch size is usually from 4.5 to 8.5 eggs (range 2–13), depending on geographic location and environmental conditions. Eggs are typically 32–42 mm long and 18–25 mm wide. Most nesting occurs in late May to mid-July. Double clutching is known in some populations but appears to be ≤5%. The species exhibits temperature-dependent sex determination, with warmer temperatures (≥29°C) producing a higher proportion of females. Current evidence suggests that hatchlings tend to remain in the nest chamber through the winter and emerge in early spring. Populations appear to be declining in the northern portions of its range, near urban centers, and at some remote locations. Robust populations remain in the core of its range in southern Oregon and northern California as well as in some rural and agricultural areas in the southern range. The primary threats are habitat loss, alteration, and fragmentation of both aquatic and terrestrial habitats. Introduced species also pose threats through predation, competition, and disease transmission. Historically, *A. marmorata* was collected for the food and pet trades; these practices have been outlawed, although the level of continued illegal collection is not known. Greater effort is needed to protect and manage aquatic habitats as well as nesting and overwintering sites in adjacent uplands.

Distribution. – USA. Pacific coast states from northwestern Washington, western Oregon, northern, central, and southern Central Valley of California, with a few isolated populations in western Nevada. Possibly native (or introduced) in extreme southwestern British Columbia, Canada, but now apparently extirpated.

Synonymy. – *Emys marmorata* Baird and Girard 1852, *Clemmys marmorata, Geoclemmys marmorata, Chelopus marmoratus, Melanemys marmorata, Clemmys marmorata marmorata, Actinemys marmorata, Actinemys marmorata marmorata, Emys marmorata marmorata, Emys nigra* Hallowell 1854, *Clemmys wosnessenskyi* Strauch 1862, *Geoclemmys wosnessenskyi.*

Subspecies. – None currently recognized (formerly two recognized: *Actinemys marmorata marmorata* and *Actinemys marmorata pallida*).

Status. – IUCN 2026 Red List (in press): Vulnerable (VU A2bcde+4bce, E), assessed 2024; IUCN 2025 Red List: Vulnerable (VU A1cd [ver. 2.3]), assessed 1996; CITES: Not Listed; California: Species of Special Concern; Oregon: Sensitive Critical; Washington: Endangered; US ESA: Proposed Threatened.

Taxonomy. — The taxonomic affinities and inferred phylogenetic relationships of the Northwestern Pond Turtle (*Actinemys marmorata*) have shifted repeatedly since the species was first described (see Bury 1970; Bury et al. 2012a; TTWG 2021, 2025). The first specimens were collected in 1841 in the vicinity of Puget Sound in western Washington and described by Baird and Girard (1852) as *Emys marmorata*, referring to the marmorated (marbled, veined, or streaked) pattern of the carapace and skin. Turtles collected from Poso Creek in Kern County in the Central Valley of California were later described as *Emys nigra* by Hallowell (1854), based on the dark coloration of specimens collected, but this taxon has not been recognized recently, and is synonymized under *A. marmorata*. Agassiz (1857) examined these specimens along with turtles from the San Francisco Bay Area and placed them in the genus *Actinemys*, referring to their range as extending from Puget Sound, Washington, to Monterey, California. Strauch (1862) described *Clemmys wosnessenskyi* from Sacramento (also a synonym of *A. marmorata*) and reclassified the genus to *Clemmys*, which became the most widely accepted taxonomic affinity for over a hundred years (Bury and Ernst 1977; Bettelheim et al. 2005; Ernst and Lovich 2009). Morphological and genetic evidence suggested that this turtle does not belong in the genus *Clemmys* (Bickham et al. 1996; Feldman and Parham 2001; Holman and Fritz 2001; Fritz et al. 2011). Feldman and Parham (2002) and Parham and Feldman (2002) proposed placement in the genus *Emys*, along with the Blanding's Turtle (*Emys* [= *Emydoidea*] *blandingii*), the European Pond Turtle (*Emys orbicularis*), and the Sicilian Pond Turtle (*Emys trinacris*). This view was adopted by some others (Spinks et al. 2003; Spinks and Shaffer 2005, 2009; Spinks et al. 2010, 2014). However, Holman and Fritz (2001) and Stephens and Wiens (2003) suggested that these turtles are not closely related to any extant species and should be placed in their own genus, *Actinemys*. Seidel and Ernst (2016) recognized *Actinemys* and reported that the genus is most closely related to *Emydoidea blandingii* and the two *Emys* species in Europe. The genus *Actinemys* is recognized by the Turtle Taxonomy Working Group (TTWG 2021, 2025) and it is recommended in publications of standardized names for North American herpetofauna (Collins and Taggart 2002; Iverson et al. 2017; Taggart and Carr 2025) and globally (Fritz and Havas 2007). Thus, we follow the genus name *Actinemys*, except when referring to historical uses of the genus name *Clemmys*.

Several common names have been used historically, but Western Pond Turtle or Pacific Pond Turtle were most

Figure 1. Adult female *Actinemys marmorata* basking on an emergent boulder in the Rogue River, Josephine County, Oregon. Photo by Don T. Ashton.

Figure 2. Many adult male *Actinemys marmorata* in the San Joaquin Valley of California develop distinct yellow coloring on all or parts of the marginal and costal scutes. Fresno County, California. Photo by David J. Germano.

widely used and referred to the single *sensu lato* species spanning from Puget Sound to Baja California, Mexico (Bury and Germano 2008; Bury et al. 2012a). The genus *Actinemys* is sister to the clade including *Terrapene, Emys*, and *Emydoidea* (Thomson et al. 2021).

In 1945, a subspecies of *Clemmys marmorata* was described (Seeliger 1945): the Southwestern Pond Turtle, *Clemmys marmorata pallida,* with a broad range of intergradation with the Northwestern Pond Turtle, *C. m. marmorata*, in central California from the American River south through the San Joaquin Valley (Stebbins 2003). The name *marmorata* comes from the Latin *marmor* (= marble), representing the marbled pattern of the carapace and skin, and *pallida* is from the Latin *pallidus* (= pale), in reference to the light background color of the sides and ventral surface of the neck (Bury 1970).

Holland (1992) hypothesized three groups in the Western Pond Turtle (then *C. marmorata*) based on morphology: 1) the Columbia River group along the Oregon-Washington border; 2) the northern group occurring from Washington to central California; and 3) the southern group along the central coast of California south to Baja California. However, there were no published descriptions of these proposed taxa. Using DNA fingerprinting, Gray (1995) reported low levels of genetic variation within and among several populations throughout the range, although significant differences were present between northern and southern populations, supporting the subspecies division. Spinks and Shaffer (2005) reported genetic differences indicating four clades in two groups: 1a) from the Transverse Ranges of southern California south into Baja California; 1b) Ventura and Santa Barbara counties

Figure 3. Young subadult *Actinemys marmorata* with clearly visible growth rings on the plastron, apparently approaching the end of its third growth season. Klamath Lake region, Oregon. Photo by R. Bruce Bury.

Figure 4. *Actinemys marmorata* hatchling in early May after recently emerging from overwintering in the nest chamber; no growth annuli have been produced and the umbilical patch is visible between the abdominal scutes. Trinity County, California. Photo by James B. Bettaso.

Figure 5. Distinguishing adult male and female *Actinemys marmorata*. (**Top left**) The snout of males is more angular and throat is often pale compared to (**top right**) the blunt snout and mottled throat of females. (**Bottom left**) In adult males, the cloaca is positioned beyond the margin of the carapace and the tail base is thicker, (**bottom right**) whereas the cloaca of females is positioned even with or inside the posterior edge of the carapace and the tail is narrower. Tuolumne River, Tuolumne County, California. Photos by Don T. Ashton.

in central coastal California; 2a) the San Joaquin Valley and adjacent foothills; and 2b) all the remaining populations to the north. These data suggested considerable genetic fragmentation within the species (*sensu lato*), especially in the southern half of its range. Spinks et al. (2010, 2014) used a suite of genetic markers to suggest a split that elevates the two subspecies to species level: the Northwestern Pond Turtle (*A. marmorata*), corresponding to clades 2a and 2b described by Spinks and Shaffer (2005), and the Southwestern Pond Turtle (*A. pallida*) corresponding to clades 1a and 1b in Spinks and Shaffer (2005). A subsequent population genetics study added clarification of the range boundaries between the two species, confirming broad zones of sympatry with known or suspected admixture (Shaffer and Scott 2022). Future taxonomic studies will be aided by a reference genome for *A. marmorata* completed as part of the California Conservation Genomics Project (Todd et al. 2022).

Description. — *Actinemys marmorata* is a moderate-sized semi-aquatic freshwater turtle (Figs. 1–3). Adults usually reach a straightline carapace length (SCL) of 150–180 mm (Bury 1995a; Germano and Bury 2009; Ashton et al. 2015; Germano 2016). Maximum SCL is commonly measured, although some researchers measure midline SCL because this measurement is less prone to chipping or wear. The difference between maximum and midline SCL for adult turtles range from 2–5 mm (a 1–3% difference for adult turtles), although not all publications state whether maximum or midline SCL is reported. Lubcke and Wilson (2007) reported maximum SCL approaching 200 mm for large females with some males exceeding 220 mm SCL, including a male with a maximum SCL of 241 mm (Fidenci 2005; Lubcke and Wilson 2006, 2007). Adults usually weigh 400–900 g with some individuals exceeding 1,000 g (Lubcke and Wilson 2007; Germano 2010, 2021; Germano et al. 2022). Hatchlings emerge from

Figure 6. *Actinemys marmorata* (**top**) tends to have triangular inguinal scutes (green asterisk) compared to smaller or absent inguinals (white asterisk) in *A. pallida* (**below**), although there is considerable variability in this trait. Photos by Don T. Ashton.

the nest at 20–30 mm SCL and 5–7 g (Storer 1930; Feldman 1982; Hill 2006).

Carapace color is usually dark brown or dull yellow-olive, with or without darker streaks or vermiculations (Fig. 1). Many adult males in the Central Valley of California develop distinct yellow coloring on all or part of the marginal and costal scutes of the carapace (see Fig. 2). The plastron is cream or light-yellow, sometimes with dark areas on parts of the scutes (Fig. 3). The skin is brown or yellow-brown, often with small dark dots and vermiculations. Hatchlings usually have subtle yellow striping on the limbs and sometimes the neck, but these disappear in their first year (Fig. 4). The carapace is low and broad and lacks a keel or serrations and is generally widest posterior to the middle (across the 8th marginals). Vertebral scutes are broader than long, and the first vertebral touches four marginals and the nuchal (Carr 1952; Ernst et al. 1994; Ernst and Lovich 2009). Turtles in flowing waters may be more elongate than those living in standing waters (Lubcke and Wilson 2007; Angielczyk et al. 2011). The hind foot is webbed to the base of the claws (Ernst and Lovich 2009).

The sexes can be visually differentiated when secondary sexually dimorphic characteristics develop in males. Male *A. marmorata* can usually be distinguished from females by the time they reach a size of 120 mm SCL, when individuals are assumed to be adults, although actual size and age at maturity varies depending on environmental conditions (Bury et al. 2012b; Snover et al. 2015). A suite of characteristics are often used to determine sex (Fig. 5). In adult males, when the tail is extended, the cloaca is posterior to the edge of the carapace and the tail base is thicker compared to females with the cloaca at, or anterior, to the carapace margin and a narrower tail base. Adult males tend to have a concave plastron in the femoral region, while the plastron of adult females tends to be flat or slightly convex. The head of adult males is more robust, and the snout more angular than seen in females. Adult males usually have a light-colored throat while females have a brown or yellow-brown throat with moderate to extensive flecking, retaining the pattern and coloration of juveniles.

Average SCL of males is larger than females in most populations, and males can reach a larger maximum size (Lubcke and Wilson 2007; Germano and Bury 2009; Germano 2010; Ashton et al. 2015; Germano 2016). The carapace of adult females tends to be more domed (greater height) than in males and juveniles.

Hatchlings and young juvenile turtles lack visible external sexually dimorphic characteristics, but sex can be determined without sacrifice of neonates by laparoscopic examination of gonads and accessory ducts (Geist et al. 2015; Terry 2018) or by immunoassay of blood samples to detect specific proteins involved in sex differentiation (Tezak et al. 2020).

Distinguishing from Co-occuring Species. — It can be challenging to reliably distinguish *A. marmorata* from its congener *A. pallida* based on morphology. In general, *A. marmorata* tends to have larger triangular inguinal scutes (Fig. 6) compared to smaller or no inguinals in *A. pallida*, although there is much variability in this trait, especially along contact zones between the two species where admixture occurs (Seeliger 1945; Buskirk 1990, 2002). Often, the throat of male *A. marmorata* is lighter-colored and contrasts with the darker sides of the head and neck, whereas male *A. pallida* has a more uniform coloration of the throat and neck, often with dark vermiculations (Germano et al. 2026), similar to the pattern of females and juveniles (Seeliger 1945; Buskirk 2002).

All of these morphological and color distinctions can be subtle and unreliable for confirming species identification, particularly in populations along the boundaries between the two described species of *Actinemys*. Also, the contact zones often include individuals with genetic admixture adding to the challenge of distinguishing these congeners (Spinks et al. 2014; Shaffer and Scott 2022). Machine learning methods trained on plastron images were effective at classifying different emydid species and distinguishing between two species of *Trachemys*, but performed poorly at distinguishing the two species of *Actinemys*, although including additional characters may improve model performance (Burroughs et al. 2024).

Actinemys marmorata is differentiated from the native Western Painted Turtle (*Chrysemys picta bellii*), which co-occurs in northern Oregon and western Washington, by the reddish plastron, olive-green or blackish-green carapace, and bright red and yellow stripes on the neck and legs of *C. p. bellii* (Bury 1995b). The Red-eared Slider (*Trachemys scripta elegans*) is an invasive turtle across the range of *A. marmorata*. These invasive turtles are readily distinguished by the serrated posterior margin of the carapace, while *A. marmorata* lacks serrations, although there may be mild scalloping of the posterior marginals (Bury 1995c). Most *T. s. elegans* have yellow stripes on the neck, face, and limbs, as well as a red patch behind the eye (Bury 1995c). These markings often fade in older adults and are indistinct in melanistic individuals; thus, when viewed from a distance, some *T. s. elegans* may resemble adult *A. marmorata*. Even when markings are not distinct, the species can be distinguished by slight differences in the shape of the snout and eyes of adults and the serrated posterior edge of the carapace on *T. s. elegans*.

The Snapping Turtle (*Chelydra serpentina*) has been introduced to many sites in California and has been found in Oregon and Washington (Hays et al. 1999; ODFW 2015; Bury and Matsuda 2022). *Chelydra serpentina* is distinguished by its robust head, thick forelimbs, large keeled tail, serrated posterior edge of the carapace, and reduced plastron, and adults obtain a much larger size than *Actinemys* spp. (Bury 1995d). The Spiny Softshell (*Apalone spinifera*) is a highly aquatic turtle distinguished by its long pointy snout, soft leathery shell, reduced plastron, and dorso-ventrally

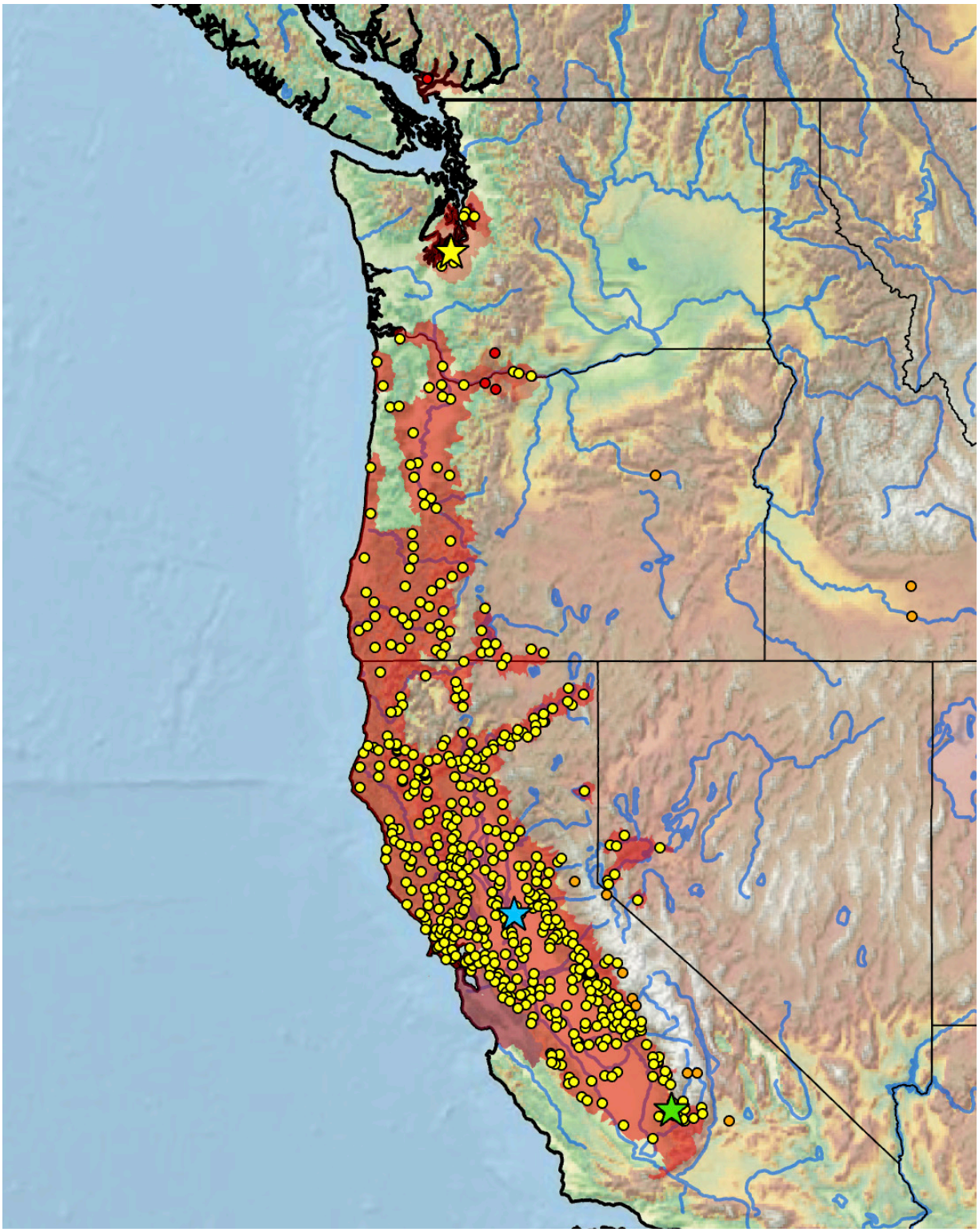

Figure 7. Estimated historical indigenous distribution of *Actinemys marmorata* in Washington, Oregon, and California, USA, and British Columbia, Canada. The native range is predominantly west of the Sierra Nevada and Cascade mountainous crests. A few populations are found east of the mountains, including western Nevada. Yellow dots = museum and current and historical occurrence records of presumed native populations based on literature and online records (TTWG 2025); orange dots = probable non-native introductions, translocations, or erroneous records; red dots = apparently extirpated populations; stars = type localities (yellow = *Emys marmorata*; green = *Emys nigra*; blue = *Clemmys wosnessenskyi*). Colored shading = estimated historical indigenous range (dark red = extant; light red = apparently extirpated; purple = approximate area of partial hybridization with *A. pallida*). Distribution is based on fine-scaled GIS-defined level 12 HUCs (hydrologic unit compartments) constructed around verified localities and then adding HUCs that connect known point localities in the same watershed or physiographic region, and similar habitats and elevations as verified HUCs, and further adjusted based on data from the literature and the authors. Map by Chelonian Research Foundation.

flattened shape. It has been introduced to the west coast of North America at several locations in the Central Valley of California where it occurs in agricultural canals and south of San Francisco Bay (Bury and Luckenbach 1976; Jennings 1983), and there are reported observations from sites in Oregon and Washington (Bury and Matsuda 2022). Over a dozen other non-native turtle species, likely released pets, may be encountered in the range of *A. marmorata*, adding complication to field identification (see Bury and Luckenbach 1976; Jennings 1987; Bury and Matsuda 2022).

Distribution. — *Actinemys marmorata* is native to the Pacific Coast states of the United States, primarily west of the Cascade and Sierra Nevada crests with a few localities east of the mountains (Fig. 7). Populations occur or previously occurred from extreme southwestern coastal British Columbia, Canada (although either extirpated or introduced there), and the Puget Sound region of Washington and from western Oregon to south of San Francisco Bay and the northern (Sacramento) and southern (San Joaquin) portions of the Central Valley of California, and inland to the western slopes of the Cascade Mountains in Washington, Oregon, and northern California, primarily west of the Sierra Nevada in northern to central California (Bury 1970; Nussbaum et al. 1983; Hays et al. 1999; Bury and Germano 2008; Barela and Olson 2014; Fisher 2018; USFWS 2023a).

In the Klamath Basin of northern California and southern Oregon, some robust populations are found east of the Cascade Mountains. A small population also occurs in Bend, Oregon, east of the Cascade Mountains, but this may represent an introduction (S. Wray, pers. comm.). East of the Sierra Nevada in western Nevada, disjunct populations in the Truckee, Carson, and Humboldt rivers (LaRivers 1942; Banta 1963; Bury 2017) appear to be genetically related to northern clade populations (Spinks and Shaffer 2005), although their origin is uncertain. They may have been originally moved there by Native Americans or settlers (Cary 1889; Bettelheim 2020). However, they may be native, as other populations occur nearby in northeast California in high desert habitat (Bury 2017).

There are other outlying locality reports that may represent introduced individuals or are misidentified specimens or displaced individuals: one male collected along Canyon Creek, Grant County, Oregon (Black and Storm 1970); and one juvenile taken in 1894 from along the Snake River, Jerome County, Idaho (Slater 1962). Two turtles collected in coastal British Columbia, Canada (Gregory and Campbell 1984; Matsuda et al. 2006), and other observations in southwestern British Columbia may be the result of introductions (Cook et al. 2005), although they may also have been native, but now extirpated.

Along the contact zone with *A. pallida*, particularly from the San Francisco Bay Area south to Monterey Bay, and along the Transverse Ranges at the southern end of the Central Valley of California there are broad areas with admixture individuals (Shaffer and Scott 2022; USFWS 2023a). *Chrysemys picta bellii* co-occurs with *A. marmorata* in western Washington south to the middle of the Willamette Valley, Oregon, and appears to be more abundant than *A. marmorata* in the Portland area and along the Columbia River in northern Oregon (Gordon 1939; Evenden 1948; Gervais et al. 2009; Holley 2021; Guderyahn 2025).

Habitat and Ecology. — *Actinemys marmorata* requires a combination of aquatic and terrestrial habitats to complete life-history functions. Foraging, courtship, and mating occurs in the water, nesting occurs on land, and overwintering may occur on land or underwater. Due to its use of aquatic and terrestrial habitats along with its central trophic position, the species provides important ecosystem services to habitats it occupies through energy flow, nutrient cycling, and bioturbation (Ernst and Lovich 2009; Lovich et al. 2018). The species occupies a variety of permanent and intermittent aquatic habitats, including rivers, streams, lakes, natural ponds, vernal pools, coastal marshes, estuaries, and human-constructed environments such as irrigation canals, reservoirs, and ponds associated with agriculture, livestock (cattle ponds), logging operations, and waste-water treatment, and it is capable of tolerating brackish waters (Germano and Bury 2001, 2009; Buskirk 2002; Germano 2010; Bury et al. 2012b; Agha et al. 2020; Tu and Trulio 2022; Figs. 7, 8).

Prior to 1800, extensive wetlands extended across much of the lowland range of *A. marmorata*. The Central Valley of California had lakes, meandering rivers, and marshes covering at least 787,000 ha (Harding 1960; USFWS 2015). Large marshes in the Willamette Valley and Klamath Basin of Oregon have historical accounts describing abundant populations of *A. marmorata*. Northeastern California had extensive wetlands, including Eagle Lake on the Modoc Plateau. West of the Sierra Nevada, rivers, ponds, and lakes, including Clear Lake in northern California, supported abundant populations and some remain as a stronghold for the species. The once extensive wetlands and back-dune ponds in coastal sand-dune complexes have been reduced by development. For the most part, only remnants of former wetland habitats remain, and arid lands, common to western North America, separate many of the remaining turtle populations (e.g., Germano et al. 2011).

This turtle is most often found where aquatic habitats have abundant basking sites, underwater refugia, and standing or slow-moving waters (Bury et al. 2012b). Aquatic habitats with access to emergent basking structures are most likely to support populations (Fidenci 2000), although if emergent basking sites are absent, turtles will bask on the shore or vegetation mats. In larger lakes and reservoirs, these turtles tend to use near-shore habitats rather than deeper open waters. In rivers, the species is most abundant in slower waters (e.g., side pools) that are deep and have basking sites (Reese and Welsh 1998a). Along a

Figure 8. *Actinemys marmorata* uses a wide variety of aquatic habitats, including: (**top left**) larger bodies of water, such as lakes and reservoirs, Klamath County Oregon; (**top right**) larger rivers, often with rocky substrates, Josephine County, Oregon; (**bottom left**) in shallow pools of creeks and rivers, Trinity County, California; and (**bottom right**) floodplain ponds and marshes, Stanislaus County, California. Photos by Don T. Ashton.

western Oregon river, turtles were clumped at only a few sites (Bury et al. 2012b; Horn and Gervais 2018). Turtles in streams often reside in pools where there is deeper water for escape from terrestrial predators and a lack of swift currents. Turtles aggregate in these microhabitats at densities often several times greater than in swifter-moving sections of flowing waters (Bury 1972a). Along a northern California stream, there was a high correlation between turtle abundance and the number of basking sites such as logs or boulders (Bury 1972a).

In marshes and wetlands, emergent basking sites may include mats of vegetation or mud banks. Along the coast, *Actinemys* species have been observed in tidal marshes, brackish sloughs, and estuaries (Stebbins 1954; Neill 1958; Agha et al. 2018a,b, 2019). In tidally influenced coastal areas, *A. marmorata* appears to modify its behavior to temporarily tolerate salinity of 15 parts per thousand, which exceeds the tolerance of a conspecific population of turtles residing in nearby freshwater habitats, although extended exposure times (>2 weeks) resulted in weight loss (Agha et al. 2019).

Individuals may spend a considerable portion of each year on land. Based on radio-tracking studies, some turtles remain out of water for more than half a year (Reese 1996; Reese and Welsh 1997; Zaragoza et al. 2015; Purcell et al. 2017). Because much of the range of *A. marmorata* is in a Mediterranean climate (mild, wet winters; dry, hot summers), many natural watercourses and ponds are intermittent or exhibit greatly reduced waters in summer. When ponds and streams become dry, turtles may aestivate in upland areas (Bondi and Marks 2013; Purcell et al. 2017). Similar behavior has been documented for the congener to the south, *A. pallida* (Rathbun et al. 2002; Pilliod et al. 2013; Germano et al. 2026).

The species is adapted to cope with natural drought cycles (Germano, in press), although prolonged drought can result in high mortality (Leidy et al. 2016; Purcell et al. 2017). Synergistic effects of prolonged drought and wildfire indirectly resulted in mass mortality in a population of the congener, *A. pallida* (Lovich et al. 2017). Physiological studies are needed to confirm if there is a slowing of metabolism during aestivation periods, as there is with overwintering dormancy (Ultsch 2006). Adult turtles can also travel considerable distances across terrestrial habitats, in excess of 1 km, to reach disconnected aquatic habitats (Reese 1996; Purcell et al. 2017).

Figure 9. *Actinemys marmorata* occurs in a wide variety of altered aquatic habitats, including: (**top left**) a modified canal between a railroad levy and highway, Klamath County, Oregon; (**top right**) a large wetland managed for water storage, Goose Lake, Kern County, California; (**bottom left**) a stock pond for cattle in the Sierra Nevada foothills, Madera County, California; and (**bottom right**) a wastewater treatment facility, Fresno County, California. Photos by David J. Germano, except bottom left by Don T. Ashton.

Predators. — A diverse array of native animals is known to prey upon *A. marmorata*, and there are many suspected predators that lack documented observations. Eggs, hatchlings, and smaller turtles are most susceptible to predation, but adults are also taken. Mammalian predators known to consume eggs or turtles include the Northern Raccoon (*Procyon lotor*), Gray Fox (*Urocyon cineroargenteus*), Coyote (*Canis latrans*), Black Bear (*Ursus americanus*), Western Spotted Skunk (*Spilogale gracilis*), Striped Skunk (*Mephitis mephitis*), and North American River Otter (*Lontra canadensis*) (Bury 1972a; Manning 1990; Studebaker 2008; Rose et al. 2023). Even when nests are protected by exclosure cages, eggs and neonates in the nest chamber may fall prey to subterranean predators such as rodents (Alvarez 2021), insects, and possibly snakes. The Virginia Opossum (*Didelphis virginianus*) is a suspected predator of *A. marmorata* nests; this non-native predator was introduced to the western states a century ago and is now widespread, especially across human-occupied landscapes (urban, suburban, and rural), and is considered naturalized in the West. Native California Red-legged Frogs (*Rana draytonii*) are capable of eating hatchling and small *A. marmorata,* as they ingest large prey such as mice, voles, and small garter snakes (Dodd 2013); however, there are no reported observations or evidence of this to date in diet studies (e.g., Hayes and Tennant 1985; Bishop et al. 2014).

Several native avian predators eat young *Actinemys*, including observations of a Great Blue Heron (*Ardea herodias*) eating small turtles (Niemela and Bury 2012) and a Great Heron (*Ardea alba*) consuming a hatchling (Germano and Buchroeder 2018). Other suspected avian predators include Osprey (*Pandion haliaetus*), Common Raven (*Corvus corax*), and American Crow (*Corvus brachyrhynchos*). Corvids are known to opportunistically feed on hatchling turtles and eggs (Moldowan 2023), but direct observations of corvids feeding on *A. marmorata* are lacking.

Various invertebrates including crayfish (Order Decapoda), and giant water bugs (Order Hemiptera, family Belostomatidae) are known to prey upon hatchlings of other freshwater turtle species (Bradsell et al. 2002; Ohba 2011), but predation on *A. marmorata* hatchlings by these invertebrates has not been reported. Ants, beetles, and other insects have been found consuming hatchlings in the nest chamber, but it is unclear whether the insects

were scavenging on dead hatchlings or were the cause of death (U.S. Army Corps of Engineers, unpubl. data).

Introduced aquatic predators may pose a threat in some locations. American Bullfrogs (*Lithobates catesbeianus*; formerly *Rana catesbeiana*) are predators on young turtles (Moyle 1973; Nussbaum et al. 1983; Nicholson et al. 2020), but their effect on populations is not well understood (Germano et al. 2026). Largemouth Bass (*Micropterus salmoides*) is implicated as a threat to recruitment of young *A. marmorata* (e.g., Manzo et al. 2021; USFWS 2023a,b) but there is no direct evidence of such predation (Rosenberg et al. 2009; Germano et al. 2026). Invasive predators are further discussed in the Threats to Survival section.

Diet. — The species feeds primarily in aquatic environments and is considered omnivorous, although animal material usually constitutes most of the diet (Ernst and Lovich 2009). Foods may include a wide variety of invertebrates, vertebrates, and plant materials. Its diet consists of the larvae of dragonflies, mayflies, stoneflies, caddisflies, midges, beetles, and other insects, annelids, mollusks, crayfish, and other aquatic invertebrates (Bury 1986; Karres 2016). Native fishes and amphibians (eggs, larvae, and adults) are also eaten, but these are seldom found in the diet (<10%; Bury 1986; Wilcox 2019). Vertebrates may be scavenged when dead or weakened (Evenden 1948; Bury 1986; Karres 2016; Peek et al. 2021). Further, turtles may eat small to large amounts of vegetation, including filamentous green algae, tule, cattail roots, alder catkins, and water lily pods (Evenden 1948; Bury 1986). Males appear capable of consuming slightly larger prey items than females, while females were more likely to consume plant materials than males (Bury 1986). Turtles can employ neustophagia (gape-and-suck feeding) to obtain small prey items in the water column (Bury 1986). In the wild, this mode of feeding has been observed in the congener, *A. pallida*, for consuming *Daphnia* species (Holland 1985a).

Behavior. — Although they may be conspicuous during atmospheric basking, individuals of *A. marmorata* are usually wary and most individuals rapidly depart from basking sites when they see or hear people. However, they can become habituated to repeated disturbances such as recreational rafts floating downriver or cars crossing over a bridge. Thus, habituated individuals may only flush when something unusual happens; a car stops or a raft turns to approach them. Emergent basking sites (logs, boulders, banks) can become crowded with turtles and, at these times, turtles may display aggressive interactions (pushing, open-mouth gestures, biting) among all size and sex classes (Bury and Wolfheim 1973). Similar behavior has been reported for the congener, *A. pallida* (Holland 1985b). When resting or hiding, turtles often seek underwater refuge beneath boulders, large woody debris, root masses, or undercut banks where they often wedge themselves into crevices or hide in the substrate. Turtles disturbed in shallow water often remain motionless, attempt to hide in floating vegetation or may dig into soft substrates (e.g., sand, organic debris). Turtles are usually observed during the day, but nocturnal basking, foraging, and nesting movements may occur during the summer (McKnight et al. 2023; S. Cross, pers. comm.; Ashton and Bury, pers. obs.).

Actinemys marmorata has a relatively small home range, although longer movements do occur on occasion. In a California stream during one summer, males had a home range that averaged 1 ha of water surface, while the home range size of females averaged only 0.3 ha and juveniles 0.4 ha (Bury 1972a, 1979). Movements up and down this stream (based on mark-recapture from one summer to the next) differed between sex and age class (mean values): males, 367 m; females 149 m; juveniles 145 m.

Adults occasionally move long distances within or among watercourses; a few turtles moved over 1 km in a three-year period, and one marked turtle moved more than 1.5 km in a two-week period (Bury 1972a). A mark-recapture study on two forks of a large river in northern California spanning two decades showed 80% of recaptures were within 0.5 km of a previous capture location, although 3% of recaptures were >2 km away (Ashton, unpubl. data). This pattern was replicated on both river forks and was based on 1,201 captures of 298 individual turtles. While males tended to have greater distance between recaptures (median recapture distance = 217 m) compared to females (92 m), females had the longest documented distance between captures, sometimes exceeding 5 km, and included long round-trip journeys (Ashton, unpubl. data).

Significant overland distances have also been reported for movements between water sources, for terrestrial overwintering, and nesting forays. In response to drought, a female moved 2.6 km overland to a new water source (Purcell et al. 2017). Overwintering locations >400 m from water have been documented (Reese and Welsh 1997). Female nesting distances of >400 m from water also have been reported (Storer 1930; Holland 1994), although most nests are found within about 50 m of the edge of the water (Bury et al. 2012b; Davidson and Alvarez 2020).

Growth and Maturity. — Like most temperate zone turtles, the age of young *A. marmorata* can be determined by counting annual growth rings, or annuli, on the plastral scutes (Bury and Germano 1998; Germano and Bury 1998) (see Fig. 3). Chelonians can exhibit indeterminate or determinate growth patterns (Congdon et al. 2012; Omeyer et al. 2018; Edmonds et al. 2021). *Actinemys marmorata* appears to follow a determinate growth pattern; as they approach their adult size, deposition of annuli is less discernible, and after maturity, growth slows considerably, essentially ceasing when an individual reaches its maximum potential size (Germano 2016, 2020, 2021; Germano et al. 2022). Therefore, mark-recapture is needed to determine the age of older individuals, as annuli

counts or body size no longer provide a reliable estimate of age. Rocky habitats can further reduce the utility of annuli counts for estimating the age of individual turtles, as annuli are worn smooth prematurely by the coarse substrates (Ashton et al. 2015).

Growth rates of *A. marmorata* individuals are highly variable across the range and among different habitat types. In general, individuals appear to grow more slowly in northern portions of their range than toward the south, but there are exceptions due to localized environmental differences. In Oregon and northern California, turtles deposit 15–16 annuli before growth rings no longer indicate age (Germano and Bury 2009; Bury et al. 2010; Germano et al. 2022). In the southern part of the range, 8–12 annuli are typically produced before primary growth (10–90% of growth) slows (Germano 2010, 2016, 2021; Germano et al. 2022). In two ponds in the Willamette Valley of Oregon, primary growth took 13 yrs (Germano et al. 2022). Primary growth took 10–17 yrs in reservoirs, 13–18 yrs in streams and rivers in southern Oregon (Germano and Bury 2009), and 13–17 yrs in northern California (Bury et al. 2010). In the San Joaquin Valley, California, primary growth at two semi-natural sites on the valley floor took 5–7 yrs (Germano 2016, 2021) and at a lower foothill reservoir 7 yrs (Germano et al. 2022), but at two sewage treatment facilities in the valley, primary growth only took 3–4 yrs (Germano 2010).

Using 120 mm and 150 mm SCL as bench-mark sizes for *A. marmorata*, turtles in the Willamette Valley, Oregon, reached these lengths at 6 and 9 yrs, respectively (Germano et al. 2022), and in southern Oregon ponds/reservoirs at 4–9 and 7–18 yrs, respectively, and streams/rivers at 6–8 and 11–14 yrs, respectively (Germano and Bury 2009). In northern California, turtles reached 120 mm SCL at 6–8 yrs and 150 mm SCL at 11–16 yrs, but in the Klamath Lake basin of southern Oregon, 120 mm SCL was reached in only 3 yrs and 150 mm SCL in 6 yrs (Bury et al. 2010). The Klamath Lake Basin is high desert habitat at about 1,200 m elevation, yet turtles grow relatively fast, likely because waters are eutrophic (Bury et al. 2010). In the San Joaquin Valley, 120 mm SCL is reached in 2–3 yrs and 150 mm SCL at 4–6 yrs at three semi-natural sites (Germano 2016, 2021), but at 2 yrs and 3–5 yrs, respectively, in eutrophic waters at two sewage treatment plants (Germano 2010). In northern California, Ashton et al. (2015) found that juvenile growth was significantly slower in colder waters downstream of a hypolimnetic release dam versus a warmer free-flowing fork of the same river, and the colder water resulted in smaller adult body sizes compared to turtles growing in the warmer water of the free-flowing river fork.

Male *A. marmorata* begin to display secondary sexual characteristics at 110–120 mm SCL, although the age at which males start producing sperm (becoming mature) has not been determined for any population. Using the size at which males can be visually distinguished from females confidently (120 mm SCL) as a surrogate for maturity, males generally reach this size in Oregon and northern California mountains when 7–11 yrs old (Germano, unpubl. data), but in southern sites, males reach 120 mm SCL between 2 and 3 yrs (Germano 2016, 2021; Germano et al. 2022). In the Klamath Basin of southern Oregon (in high desert), males reach 120 mm SCL at about 4 yrs (Germano, unpubl. data), similar to more southerly populations.

Maturity in females can be approximated by noting when females start producing eggs. In the Willamette Valley in northern Oregon, the smallest females with eggs were 154 mm SCL, based on x-ray radiography (Germano et al. 2022), while in the southern portions of the San Joaquin Valley in California, eggs were detected at 148 mm SCL at 5-Mile Slough near Fresno (Germano 2021), 144 mm SCL at sewage treatment ponds near Fresno (Germano 2010), 125 mm SCL at Goose Lake in Kern County (but the female was 20+ yrs old; Germano 2016), and 145 mm SCL at a Sierran foothills site (Germano 2020).

The youngest ages of confirmed adult females for these same sites were 11 yrs in Oregon (Germano et al. 2022) and 4–5 yrs for valley floor sites in the San Joaquin Valley (Germano 2010, 2016, 2021), but 10 yrs for the Sierran foothill site (Germano 2020). The sample size (n = 16) for this foothill site was the smallest of these southern populations. At the 5-Mile Slough site, 77.8% of females >145 mm SCL were gravid (Germano 2021), and at the Goose Lake site, 40.0–63.2% of females >135 mm SCL were gravid over 11 yrs of study (Germano 2016). In Trinity County, northern California, gravid females were at least 132 mm SCL and >9 yrs old (Ashton and J. Bettaso, unpubl. data).

Holland (1994) noted the smallest gravid female from northern California was 130 mm SCL and estimated it to be 10–12 yrs old, and from central Oregon, the smallest gravid female was 138 mm SCL and estimated to be 12–14 yrs old. Holland (1994) reported the smallest gravid female observed in Klickitat County, Washington, was 141 mm SCL and estimated as 12–17 yrs old. In summary, male sex becomes externally discernible at around 110–120 mm SCL and 4–6 yrs of age (actual maturity unknown), while females reach maturity around 130–145 mm SCL and 5–10 yrs of age, with considerable variation across the range and among individuals.

Longevity. — Long-term data indicate that *A. marmorata* can live for many decades (Bury et al. 2019, 2023; Kauffmann and Garwood 2022). In a mark-recapture study at one site in northern California, only about 5% of marked adults were recaptured after 30 yrs and only 2% beyond 40 yrs (Bury 1972a; Bury et al. 2019). However, this is an open population, and many individuals may have moved outside the study area, which reduces their chance of recapture. One female in this study was recaptured after 50 yrs (1968 to 2018) and she was 5 yrs old when initially marked; another

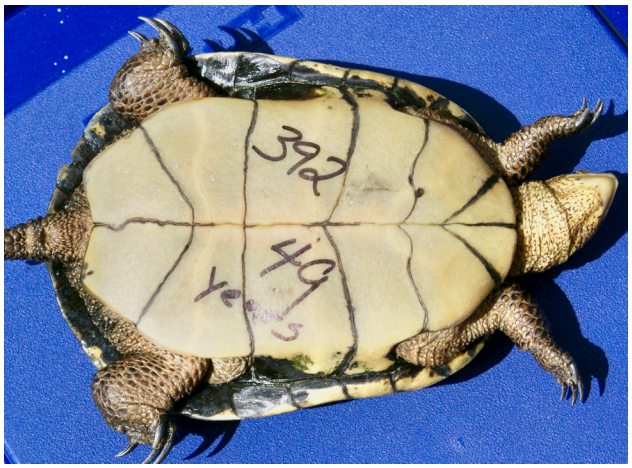

Figure 10. A wild female *Actinemys marmorata* known to be 49 yrs old based on mark-recapture data. Photo by David J. Germano.

recaptured female turtle was confirmed to be 49 yrs old (Fig. 10). A radiograph showed that the 55 yr-old female was carrying nine eggs. A few other individuals originally marked as adults of unknown age were recaptured 40 yrs later. Interestingly, the turtles known to be well beyond 40 yrs old appeared in good health with no outward signs of advanced age (Bury and Ashton, pers. obs.)

Reproductive Biology. — Courtship and mating in *A. marmorata* occur underwater from March to September (Buskirk 2002; Bury et al. 2012b). Observations of courtship behavior in the wild have been recorded in April, May, and September (Ashton 2007; Bettelheim 2009). Similar courtship behavior and timing have been described for the congener *A. pallida* (Holland 1988; Goodman 1997a). Mating can happen almost any time of the active season but oviposition is strongly seasonal. Ova must be fertilized prior to calcification of eggshells, which appears to occur over a period of several weeks or more prior to nesting (Ashton, unpubl. data). Postcopulatory sperm storage is common in reptiles (Gist and Jones 1987), including turtles in general (Congdon et al. 1987; Phillips et al. 2013, 2014) and emydid turtles specifically (Pearse et al. 2001) but has not been studied in *A. marmorata*.

Most nesting occurs from late-May to early July with the peak of nesting in early to mid-June (Germano et al. 2012; Riensche et al. 2019). At Goose Lake in the San Joaquin Valley of California, 33% of females were gravid in late April, and depending on the year, 57–77% of females were gravid from May to early July (Germano 2016). Reproduction at this site might last longer, but in all but one year, water in the basin dried in June or July as the water district pumped water into agricultural canals. Also, the percentage of gravid females might have been higher because capture relied on them entering baited traps (Germano 2016), which did not necessarily mean a female would be caught multiple times in any one year.

Nesting occurs on land, generally above the normal high-water level. Females tend to seek out open areas for

Figure 11. Eggs of *Actinemys marmorata* are elliptical-oval and symmetrical in shape (not tapered). Trinity County, California. Photo by James B. Bettaso.

nesting with few or no shrubs and trees nearby (Rathbun et al. 1992; Holland 1994; Bury et al. 2012b; Davidson and Alvarez 2020), but nesting has been observed in areas with understory and overstory vegetation in Lake County, California (Bettelheim et al. 2006). Females are noted for long overland treks to nest, moving as far as 400 m away from water and up to 90 m in elevation (Storer 1930); however, most nests are found within 50 m of water (Holland 1994; Bury et al. 2012b; Davidson and Alvarez 2020). In the San Francisco Bay Area, Riensche et al. (2019) found that females nested an average of 24 m from water on south-facing slopes, but did not find evidence of nest fidelity based on 15 females tracked with radio telemetry over 5 yrs. For 68 nests at their study site, Davidson and Alvarez (2020) reported average distance to water of 9.4 m on moderate slopes (9% average). Combining their nest data with values from the literature, they calculated a mean distance to water of 51 m for 505 nests (Davidson and Alvarez 2020). Some females display nest-area fidelity but studies documenting annual nest location for individual females is limited to a few years, with no long-term (>5 yrs) studies (Goodman 1997b; Holte 1998; K. Beal, unpubl. data).

Eggs of *A. marmorata* (Fig. 11) are elliptical-oval and symmetrical in shape (not tapered) and are 32–42 mm long and 18–25 mm in diameter (Holland 1994; Ernst and Lovich 2009; Bury et al. 2012b). Their mass ranges from 7–11 g and the eggshell has a rigid "bone-china" texture, similar to that of bird eggs (Holland 1994; Bury et al. 2012b). The eggshells are slightly hydrophilic and cannot withstand prolonged submersion if they are to remain viable (Feldman 1982; Holte 1998).

Eggs of the most common invasive turtles can be easily distinguished from eggs of *A. marmorata*. The eggs of *T. s. elegans* have an elliptical-oval shape similar to eggs of *A. marmorata*, but the shell has a softer semi-flexible parchment texture that yields to light pressure (Ernst et al. 1994; Ashton, pers. obs.). The eggs of *C. serpentina* are spherical with a flexible shell, resembling a soft ping-pong ball (Yntema 1970).

Clutch size in emydid turtles is positively correlated with body size (e.g., Congdon and Gibbons 1985; Cong-

don and van Loben Sels 1991) and this appears to be the case for *A. marmorata* (Holland 1994; Bury et al. 2012b). Mean clutch size may also vary depending on geographic location, environmental conditions, and availability of resources to females. Average clutch size in Washington was 6.5 eggs (range 5–10; *n* = 9) (Holland 1994), 6.0 eggs (5–8; *n* = 11) in northern Oregon (Germano et al. 2022), 7.0 eggs (2–12; *n* = 57) from a west-central Oregon site (Holte 1998), and 7.3 eggs (4–9; *n* = 4) in southern Oregon (Feldman 1982). Storer (1930) reported clutch sizes for two nests in northern California as seven eggs near Ukiah and nine eggs from Lower Klamath Lake, California. In the Klamath Basin in far southern Oregon, the mean was 10.0 eggs (7–13; *n* = 3); and from Whiskeytown National Recreation Area in northern California the mean was 5.3 eggs (5–6; *n* = 3) (Germano and Bury, unpubl. data). In the Central Valley of California, Storer (1930) found 11 eggs in a nest near Davis and eight eggs in a nest near Modesto. Average clutch sizes in San Joaquin Valley sites were 7.4 eggs (6–10; *n* = 6) (Germano 2021), 8.2–8.5 eggs (3–13; *n* = 58) from two sewage treatment plants (Germano 2010), 7.3 eggs (6–9; *n* = 6) at a Sierran foothill site (Germano 2020), and 7.0 eggs (4–11; *n* = 113) at Goose lake in the southernmost part of the range (Germano 2016). Overall, average recorded clutch size in *A. marmorata* is 7.3 eggs (2–13; *n* = 274) across its range.

The number of clutches a female produces per year is variable and, as for the number of eggs, may depend on body size, resource availability, and site conditions. A single clutch per year may occur, but when resources are scarce, females may skip nesting in some years (Holland 1994). More than one clutch within a year by a female may be rare in northern populations (F. Slavens, unpubl. data), but to the south, multiple females have been shown to produce two clutches in one season in the Central Valley of California (Germano 2010, 2016; Germano and Riedle 2015). Evidence of nesting in consecutive years, alternate years, and double-clutching is also reported for the congener, *A. pallida* (Goodman 1997a,b).

Incubation duration ranges from 73–132 days under artificial conditions (Lardie 1975; Feldman 1982). Christie and Geist (2017) report a similar incubation period (75–134 days) from mixed natural and laboratory settings. Incubation duration was influenced by nest temperature, with longer durations at lower temperatures (Geist et al. 2015; Christie and Geist 2017). Eggs hatch in late summer. Hatchlings tend to overwinter in the nest chamber and emerge the following spring, although fall or winter emergence may occur occasionally at some locations (Reese and Welsh 1997; Holte 1998; Rosenberg and Swift 2013). Similar variability in hatchling emergence is seen in the congener *A. pallida* (Rathbun et al. 2002) and other North American freshwater turtles (Ultsch 2006; Janzen et al. 2018). Timing of emergence from the nest needs further study, especially in the southern portion of its range. Rosenberg and Swift (2013) found that hatchlings may remain near the nest for up to two months after emergence, slowly moving from the nest to water with an average travel time to water of 49 days.

Temperature-Dependent Sex Determination. — Nest chamber temperature during egg development affects sex determination in many species of chelonians (Vogt and Bull 1982; Krueger and Janzen 2023). Studies of temperature-dependent sex determination (TDSD) have shown that *A. marmorata* eggs have a pivotal incubation temperature around 29°C with an equal number of male and female hatchlings produced. Eggs incubated at higher mean temperatures resulted in a higher proportion of female hatchlings. Constant incubation temperatures >30°C produced all females, while temperatures <27°C produced all males (Ewert et al. 1994; Geist et al. 2015; Christie and Geist 2017).

In the field, there are high levels of daily temperature fluctuation in natural nests with most varying >20°C in a consistent diurnal pattern, with extreme temperatures commonly below 20°C at night and often exceeding 40°C in the afternoon (Geist et al. 2015). In the wild, egg viability was reduced by 50% as maximum nest temperatures exceeded 40°C and by 90% above 45°C (Christie and Geist 2017). In captivity, eggs incubated at a constant 31°C showed reduced hatching success (Gordon 2009). Incubation temperature also appears to have a strong influence on hatchling metabolic rate and growth rate, but maternal mass also plays an important role (Dallara 2011; Gallanty 2021). Most studies on the effects of incubation temperature of *A. marmorata* eggs were conducted with eggs collected from, or nests monitored at, a single site in Lake County, northern California (Gordon 2009; Dallara 2011; Geist et al. 2015; Christie and Geist 2017; Gallanty 2021). An earlier study (Ewert et al. 1994) used eggs collected from northern California and southern Oregon, so it may be informative to repeat this type of study in other parts of the species' range. However, Ewert et al. (1994) suggested there may be little variability in pivotal incubation temperature within a species relative to differences observed between species.

Population Structure. — Populations seem to have a high proportion of adult turtles (>120 mm SCL; Germano and Bury 2001, 2009; Bury et al. 2010; Germano 2016). The percentage of juvenile turtles (<120 mm SCL) in ponds and reservoirs in southern Oregon ranged from a low of 12% to a high of 58%, and for streams and rivers from a low of 17% to a high of 30% (Germano and Bury 2009). At six lentic sites (including a reservoir) in Trinity County, northern California, Sloan (2012) found that 20% were <125 mm SCL.

The relative proportion of turtles >20 yrs old in most populations is much lower than expected based on body size (Germano and Bury 2001, 2009; Bury et al. 2010; Germano 2016). Age distributions at these same sites showed up to 88% of turtles in ponds and reservoirs could be assigned

an age, and as high as 36% of these turtles were ≤4 yrs old, and from streams and rivers up to 57% of turtles could be assigned an age and 9% of these were ≤4 yrs old (Germano and Bury 2009). From three sites in northern California, 19–45% of the turtles were juveniles; up to 61% of the turtles could be assigned an age and up to 18% were ≤4 yrs old (Bury et al. 2010). Of turtles captured along the Russian River (including a temporary reservoir) in Sonoma County, California, 27% were 0–5 yrs old, 31% were 6–11 yrs old, and 42% were >11 yrs old (Cook and Martini-Lamb 2004). At six lentic sites (including a reservoir) in Trinity County, northern California, Sloan (2012) found that 24% could be assigned an age <10 yrs old.

In the southern part of the range, high proportions of young turtles are present at many sites. At a site on the San Joaquin Valley floor surrounded by irrigated agriculture, 34% of turtles were juveniles in 1999 and 37% in 2009 (Germano 2021); 84% of captured turtles had visable annuli and could be assigned an age by annuli count and, of these turtles, 61% were ≤5 yrs old in 1999 and 98% could be assigned an age with 94% being ≤5 yrs old in 2009 (Germano 2021). Goose Lake at the southern end of the San Joaquin Valley was studied for 12 yrs with over 730 turtles marked, and 42% of first captures were juveniles. Ages could be assigned to 76% of these first captures and 56% were ≤5 yrs old (Germano 2016). Of these youngest turtles, 24% were 2 yr-old turtles, although only 20 hatchlings were caught in the 12 yrs of the study. In contrast, at two sewage treatment plants in the San Joaquin Valley, only 6–7% of turtles were classified as juveniles; 44–48% of turtles could be assigned an age by annuli count and of these, 25–31% were ≤4 yrs old (Germano 2010). Throughout the range of *A. marmorata*, we have caught few hatchlings and 1-yr-old turtles, even though high numbers of 2-yr-old and older turtles are captured. Thus, hatchlings and 1-yr-old turtles are under-represented by our methods (mostly trapping but also hand-capture).

Sex ratio tends to be close to 1M:1F in natural settings, although significant deviations have been reported. Many *A. marmorata* populations that we have studied away from urban centers consist of relatively equal numbers of males and females (Germano and Bury 2009; Ashton et al. 2015; Germano 2020, 2021), while some sites show skewed sex ratios. Germano (2016) reported a sex ratio of 2.3M:1.0F (n = 737). Bury et al. (2010) studied four separate areas in northern California and southern Oregon; three of these areas had sex ratios that were not significantly different from 1M:1F (combined n = 215), but one population was skewed towards females (0.6M:1.0F, n = 105).

Using a combination of museum specimens and contemporary data, Nicholson et al. (2020) suggested a sex ratio near 1M:1F in the early part of the 20th century with a shift towards male-biased populations in the past 20 yrs. In their analyses using data for *A. marmorata* and *A. pallida* combined, they found that proximity to roads and road density surrounding turtle-occupied waters was correlated with male-biased sex ratios, presumedly due to road mortality of females during nesting movements (Nicholson et al. 2020).

Generally, annual survival is relatively high for adults and larger juveniles (>80 mm SCL), but survival of eggs, hatchlings, and smaller juveniles can be quite low (Bury 1979; Holland 1994; Bury et al. 2012b; Pramuk et al. 2013; Gregory et al. 2024a). Adult annual survival of emydid turtles is often >80% and can exceed 90% (Iverson 1991; Litzgus 2006; Ruane et al. 2008). At a tidal marsh area at San Francisco Bay, California, annual survival of *A. marmorata* varied from 77% to 96% (Agha et al. 2020). Mean annual survival estimates at a site in the Central Valley of California was 81% for males, 73% for females, and 84% for juveniles >80 mm SCL (Germano 2016). This information points out the importance of long-term studies on *Actinemys* and other chelonian species. Management plans to maintain or recover populations should span decades to account for delayed population responses of these long-lived animals with slow population changes.

Thermoregulation. — As a heliothermic organism, *A. marmorata* uses a variety of thermoregulatory behaviors to harness radiant and convective heat energy from the sun. The activity cycle of *A. marmorata* is largely determined by temperature (Bury 1972a; Reese and Welsh 1998b; Ruso et al. 2017). Turtles are most active when water temperatures are above 15°C. During atmospheric basking, adult turtles elevate and maintain body temperatures near 32°C through a repertoire of thermoregulatory behaviors (Bury 1972a, 1979). They expose the shell to direct sun for heating, then may dunk the head, limbs, or entire body in water for cooling. Turtles often rotate the body axis, extend or retract the head and/or limbs, and change diurnal patterns of basking to optimize solar exposure. In northern California, most atmospheric basking occurs early in the day (0900–1100 hrs) when water temperatures are low (Bury 1972a). Amount of time spent basking out of water can vary widely, even in the same watershed (Ruso et al. 2017).

Actinemys marmorata also engages in aquatic basking by moving into warmer water within or on top of submerged vegetation, algal mats, or in shallow waters. The amount of time spent basking out of water declines as water temperature increases (Bury 1972a; Horn and Gervais 2018) and turtles may remain in the water during hot summers (Bury et al. 2012b), which can result in development of colonial protozoa or filamentous algae on the shell (Germano 2000; Bury et al. 2015). Individuals of the congener *A. pallida* are known to raise their body temperatures by seeking warm dry sand on a sandbar (Rathbun et al. 2002). Turtles may be active year-round in warmer areas, but at reduced levels in late fall and winter. Turtles have been observed emergent-basking on warm days in February and have even been seen and radio-tracked moving under the ice in central Oregon (Holland 1994). Six turtles were observed moving

beneath the ice of a frozen pond in northern California on a cold morning in January (Wilcox and Alvarez 2023).

Overwintering. — Although some animals may be active on a year-round basis, most individuals become inactive in September–November and re-emerge in March–April (Reese and Welsh 1997). This species displays what can be called a mixed-mode strategy of overwintering. In lentic habitats, turtles may overwinter on land, underwater, or in undercut areas along banks (Holland 1994; Reese 1996; Riensche et al. 2019). In the congener *A. pallida*, when ponds began to dry in the summer or fall, turtles tended to seek terrestrial habitat for overwintering (Pilliod et al. 2013), which has also been seen in a coastal stream (Rathbun et al. 2002).

When inhabiting lotic environments, *A. marmorata* tends to leave the watercourse in the fall and moves into upland habitats, presumedly to avoid risks of winter high-flow events (Reese and Welsh 1997). Turtles may aggregate in winter; 43 animals were found in an area of approximately 1 m^2 in a pond in western Oregon (Holland 1994). At terrestrial overwintering sites turtles burrow into leaf litter (usually under shrubs and trees), under woody debris, or in mammal burrows, up to 400–500 m from water and may emerge from these sites to bask on warm days, and also may move among several overwintering sites over the course of several months (Reese and Welsh 1997; Bondi 2009; Ashton, unpubl. data). Individuals may return to the same terrestrial overwintering sites in successive years (Reese 1996; Bondi and Marks 2013).

Population Status. — Considerable attention has been given to the status of populations across the range of *A. marmorata*, although a great deal of localized uncertainty remains and criteria for trends vary widely (USFWS 1993; Jennings and Hayes 1994; Hays et al. 1999; Thomson et al. 2016; Nicholson et al. 2020; Manzo et al. 2021; USFWS 2023a,b; Gregory et al. 2024a,b). Multiple species status reviews and conservation assessments have been conducted (Rosenberg et al. 2009; Hallock et al. 2017; Shaffer and Scott 2019). These authors all reached similar conclusions, reporting a general declining trend, with dramatic decreases near human population centers, while some robust populations remain in many localities away from urban centers.

Habitat alteration for human uses has dramatically reduced availability of suitable turtle habitat across large areas, leading to mild to severe population declines in large regions of the species' range, especially in lowlands. In contrast, some populations in foothills and mountainous parts of their range may have benefited where streams and rivers were augmented by stock ponds, log ponds, and other standing waters created by humans over the last century (Bury et al. 2012b). The species is depleted in urban areas and human-dominated landscapes (Fulton et al. 2022). Two regions in particular show especially marked declines in abundance and number of populations: the Central Valley of California and Washington State.

In the Central Valley of California, turtle populations have been reduced by several factors. Historical collection for food was substantial in the late 1800s and early 1900s (Bettelheim and Wong 2022). Then, much of the natural habitat for the species, especially in the southern portion (San Joaquin Valley), was converted for human use. Most of this habitat has been drained or channelized to support extensive agricultural production, urban and suburban development, and transportation corridors. Still, the species has not been extirpated from the San Joaquin Valley. Some water bodies in the Central Valley still support relatively large populations of turtles with population structures that indicate successful reproduction and long-term stability (Germano and Bury 2001; Germano 2010, 2016, 2021) and a massive system of agricultural irrigation canals serves to connect otherwise fragmented habitats (Fulton et al. 2022).

In Washington, this turtle had once been found at many sites around Puget Sound (Johnson 1995; Hays et al. 1999; Hallock et al. 2017), but there are no earlier estimates of density (e.g., based on mark/recapture studies). A few individuals found in outlying areas of Puget Sound in the 1990s may represent translocations (Hays et al. 1999). Today, most former populations in Washington appear to have been extirpated (Bury 1995a; Hays et al. 1999). Along the southern border of Washington, some populations remain near the Columbia River (Hallock et al. 2017). Six populations are known to remain in Washington (two south of Puget Sound and four along the Columbia River), and these have been augmented by head-starting. A major head-starting effort has released over 1,500 turtles in Washington and they appear to be surviving (Vander Haegen et al. 2009). Unfortunately, many of these head-started turtles now appear to have shell disease (Haman et al. 2019), which may be due to rapid growth of captive-reared juveniles and subsequent release of turtles with lower bone density. Although abundance appears to be increasing slowly, viability of these Washington populations is still dependent on active management (Hallock et al. 2017).

In its core area of southern Oregon and northern California, a few populations can reach high densities. Bury (1979) reported densities of approximately 420 turtles/ha in a stream population. Some small ponds or streams may have high densities of turtles (Holland 1994), but context is important, as high counts may reflect seasonal concentrations of turtles due to contraction of water bodies during late summer and early fall (Storer 1930; Bury 1972a; Bondi 2009; Bondi and Marks 2013). The largest populations of *A. marmorata* occur in areas with Mediterranean climate, where summers are hot and dry with much of the annual precipitation falling in winter. These conditions can result in scarce surface water during the primary activity period of the species, due to increased evaporation rates and lack of precipitation during a long, warm, dry season. In most areas, the species occurs in disjunct populations over large areas (e.g., aggregations of turtles along segments of riv-

ers and streams, often separated by segments with few or no turtles, or in isolated ponds and lakes separated by landscapes unsuitable to this semi-aquatic turtle).

Threats to Survival. — Throughout the range of *A. marmorata*, there are many factors with the potential to threaten the persistence of populations, that may ultimately result in local and regional declines or extirpations. Still, turtles have evolved strategies for populations to endure and persist over time while facing many natural threats, including predation, drought, floods, and wildfire, although these threats have been exacerbated by human activity over the past two centuries and as new human-caused threats have emerged. The level of threat by factor has changed over time; early on, commercial harvest and habitat conversion for agriculture and development had the largest effects on populations. Newer emerging threats include invasive species and climate change. Level of threat for any given factor is not uniform across the range, but for many factors the level of threat increases with proximity to urban centers.

Collection. — Historically, *A. marmorata* was collected for food or pets in significant numbers, but these practices have been greatly reduced in recent decades. In the 19th and early 20th centuries, *A. marmorata* was exploited for food (Storer 1930; Buskirk 1990; Bettelheim 2005; Bettelheim and Wong 2022). Harvest began as early as the 1860s (Lockington 1879) and collecting efforts in the 1880s included the use of a small schooner operated on Tulare Lake (now a groundwater recharge facility and croplands) in the San Joaquin Valley of California. In a review of historical commercial harvest records, Bettelheim and Wong (2022) report a single-year harvest for 1895 exceeding 42,000 kg (94,000 lbs), consisting of approximately 63,000 turtles, with many of these turtles destined for San Francisco markets (Smith 1895). Records of the U.S. Bureau of Fisheries indicate that the catch peaked at the end of the 1890s but commercial trade continued until at least the 1930s, exacerbating population declines caused by habitat loss and other factors. Commercial overharvest of this species closely follows the pattern noted for the California Red-legged Frog (*Rana draytonii*), which also was taken for food (Jennings and Hayes 1985).

Collection for the pet trade or opportunistic collection for personal pets may have had localized impacts, but there is little information on the extent of this threat. Collection for pets is now prohibited throughout the range of *A. marmorata* and it is presumed to have declined in recent decades; however, we found some online postings for "captive-bred Western Pond Turtles for sale" including small turtles, but their origin may be suspect. It is illegal to sell turtles <10 cm (4 in) in the United States (USFDA 1975; USCDC 2015; reviewed in Montague et al. 2022). Although there are no reliable estimates of the total take for pets, in the early 1960s one of us (RBB) was asked by a reptile dealer to help collect this species. When asked for a number to collect, the dealer replied that they had just exported 500 turtles to Europe and needed that many additional turtles to fill orders. Collection for scientific purposes is limited and regulated and mostly associated with collection of eggs for head-starting or authorized translocations (e.g., moving turtles out of an active construction zone).

Habitat Alteration. — Habitat conversion and altered hydrology are major threats to *A. marmorata* populations, historically and currently. Draining of wetlands for development and conversion for agriculture has greatly reduced or eliminated habitats used by turtles. Massive water development projects have changed the location, flow, and use of water across much of the range of this species, particularly in the Central Valley and adjacent foothills of California and the Willamette Valley of Oregon.

In California, extensive turtle habitat was lost with the draining of Tulare Lake, Buena Vista Lake, and Kern Lake in the southern San Joaquin Valley and the surrounding marshes and sloughs for conversion to agricultural uses (Harding 1960; Dahl and Allord 1996). Construction of dams that divert water to cities and agricultural fields alter hydrologic regimes, reducing floods and allowing for encroachment by riparian vegetation along rivers. This, in turn, promotes development of berms leading to down-cutting of the channel and faster flows, reducing availability of suitable turtle-rearing habitat (Reese and Welsh 1998a,b). Hypolimnetic releases from dams result in cooler summer water temperatures, which reduce turtle growth (Ashton et al. 2015; Snover et al. 2015). Reservoirs with large seasonal drawdowns inhibit growth of aquatic vegetation and associated invertebrate populations that are prey for turtles (Bury et al. 2012b; U.S. Army Corps of Engineers, unpubl. data). Responses of this turtle to changes in reservoir habitat during drawdown varies with size and depth of the water body, drawdown profile, cover, and other factors. Also, recreational activities often associated with reservoirs (e.g., fishing, boating, water-skiing, and swimming) cause disturbance to normal behavioral routines of the turtles and may increase stress and reduce fitness. Further, reservoirs may support proliferation of invasive species to the detriment of native turtles.

On the other hand, reservoirs can provide large areas of lentic habitats suitable for turtles, with the potential for greater carrying capacity than pre-dam fluvial environments. A population of *A. marmorata* in Whiskeytown National Recreation Area, a large reservoir in northern California, had many turtles and they had a balanced age distribution with some young turtles, indicating recent recruitment (Bury et al. 2010). This large reservoir usually has a stable water level in summer. Small impoundments with permanent or intermittent water are also inhabited by turtles, and population densities can be high, particularly if vegetation (e.g., trees, tules, cattails) and basking sites are allowed to become established along shorelines (Cook and

Martini-Lamb 2004; ODFW 2015). Elimination of water bodies reduces habitat availability for this species.

Roads. — Turtles are negatively impacted by roads in many regions (Steen et al. 2006; Brehme et al. 2018; Boyle et al. 2021). Female *A. marmorata* travel on land when moving to and from nesting areas, and females, males, and juveniles may all move between aquatic habitats or to terrestrial overwintering sites (Bury et al. 2012b). Roads can create dispersal barriers, fragment habitat, and increase the risk of exposure to contaminants (e.g., oil spills, road surface runoff), invasive species introductions, collection or poaching, and direct mortality through collision with vehicles, which may in turn lead to skewed sex ratios.

Based on correlations, Nicholson et al. (2020) showed increasing male-biased sex ratios as proximity to roads and density of roads increased, suggesting female-biased road mortality. The effect of the roads may depend on road configuration and orientation to occupied habitats. A population of *A. marmorata* at 5-Mile Slough in the San Joaquin Valley is directly adjacent to a two-lane state highway and supports a large turtle population with abundant young animals (Germano 2021). Another site adjacent to a two-lane paved road in the Tehachapi Mountains in southern California has a population of *Actinemys* with many young turtles and females significantly outnumbering males (Germano and Riedle 2015). Further evidence of the possible significant detriment of roads on nearby *Actinemys* populations is needed.

Contaminants. — As long-lived omnivores, turtles have high capacity for bioaccumulation of contaminants (Gibbons et al. 2000; Rowe 2008). Chemical contamination of waterways and water bodies can have direct and indirect effects on resident turtles. Accidental spills of contaminants are a persistent issue for waters in the mountainous west because roadways often occur along streams and rivers (Bury 1972a,b). A diesel spill into a northern California stream resulted in trophic collapse, with loss of many macroinvertebrates and fishes; while turtles were temporarily affected by the chemical contamination, many of the affected turtles were recaptured in subsequent years (Bury 1972b). Additionally, railways often follow along watercourses or near shores of waterbodies, posing risk of large spill events. In a train derailment in 1993 near Yoncalla, Oregon, the fuel tanks of three locomotives were punctured, releasing >6,000 gallons of diesel fuel that heavily impacted 10 km of Yoncalla and Elk creeks as well as contaminating soils adjacent to the creeks; negative impacts to turtles were reported (ODFW 1995; Bury pers. obs.). In 1991, near Dunsmuir, California, a train accident caused a chemical tank car to fall into the Sacramento River releasing 19,000 gallons of the herbicide metam-sodium, impacting aquatic life for over 35 km of river and extending into Lake Shasta (Glowaski 2003; Allen et al. 2005); however, they reported no data on direct impacts to turtles from this spill.

Non-point source exposure poses a risk for contaminant bioaccumulation for long-lived turtles with delayed maturation and low annual fecundity (Rowe 2008). While it may be difficult to pinpoint the source, pesticides leaching into waters from local applications, or from aerial pesticide drift, can enter the food chain and accumulate in the tissues of long-lived turtles (Rowe 2008). Pesticides have been found in the eggs and bodies of *A. marmorata* (Henny et al. 2003). Heavy metals, and especially mercury, have been detected in *A. marmorata* blood samples (Meyer et al. 2013, 2014, 2016). Polo-Cavia et al. (2010) found that turtles living in a water-pollution control plant in the Central Valley of California had impaired immune function, yet they had larger body size and higher body condition than turtles from natural habitats in nearby foothills, indicating that body condition is not a good predictor of immunocompetence. They concluded that studies on the effects of contaminants may need to look beyond basic biometric parameters to determine if there is a negative effect on individuals or populations.

In some rivers and reservoirs, toxic algal blooms in late summer into fall have increased due to human addition of nutrients and agricultural runoff into standing and flowing waters (e.g., Kudela et al. 2008; Glibert 2020) and may be exacerbated by burrowing activities of invasive crayfish (Yamamoto 2010) and perhaps the effects of climate change (Moore et al. 2008; Chapra et al. 2017; Gobler 2020). The effect of toxic algae on *A. marmorata* has not been examined; however, a study on the effect of harmful algal blooms on Painted Turtles (*Chrysemys picta*) showed no increased stress levels but did significantly lower anti-bacterial capacity following exposure to cyanotoxins (Refsnider et al. 2021). Thus, there may be indirect or delayed effects from chronic exposure to cyanotoxins which are not immediately apparent (e.g., Polo-Cavia et al. 2010).

Invasive Species. — Proliferation of invasive animal and plant species poses a variety of threats to ecosystems worldwide, including throughout the range of *A. marmorata*. By definition, invasive species have negative ecological or economic impacts in the new environment where they are not native (Meshaka et al. 2022), but the impacts may not be felt equally across ecosystem elements. The International Union for Conservation of Nature (IUCN) list of 100 of the Worst Invasive Alien Species (Lowe et al. 2000) includes species that co-occur with *A. marmorata*, such as the Red-eared Slider (*T. s. elegans*), American Bullfrog (*L. catesbeianus*), and Largemouth Bass (*M. salmoides*). For *A. marmorata*, invasive species may impart negative effects, but in other cases, the effects may be neutral, or even positive (e.g., as a food source). Negative impacts may be direct or indirect, and can arise through predation, competition, vectoring of parasites and pathogens, or alteration of habitats or food webs. Additional research is needed to assess the level of threat that various invasive species may pose for *A. marmorata*. Here we discuss some

of the invasive species with known or suspected effects on *A. marmorata*, or their habitats.

Non-native turtles may pose a threat to *A. marmorata*, especially near human population centers. The invasive turtle *T. s. elegans* now occurs in many locations throughout the lowland range of *A. marmorata* in California (Patterson 2006; Thomson et al. 2010; Hayes et al. 2018; Fulton et al. 2022) and the Pacific Northwest (Bury 1995c; ODFW 2015; Bury and Matsuda 2022), with population increases of this turtle found predominately near urban and suburban areas (Spinks et al. 2003; Bettelheim et al. 2006; Nicholson et al. 2020; Fulton et al. 2022).

Compared to *A. marmorata*, *T. s. elegans* has a larger clutch size (mean 10 eggs; range of 1–18 eggs) and greater propensity for multiple clutches in a nest season (1–5 clutches per season) resulting in higher annual fecundity (Iverson 2023). Eggs of *T. s. elegans* are often larger with mean length 35.8 mm (range 24.6–44.2), mean width 22.8 mm (range 17.0–27.3; Ernst and Lovich 2009) and their hatchlings and juveniles grow faster than *A. marmorata*. Adult *T. s. elegans* reach larger body size and compete with *A. marmorata* for resources including prey, basking sites, and nesting habitat. These introduced turtles can alter the basking behavior of *A. marmorata*, causing a shift in basking location and reduction in time spent basking (Lambert et al. 2013, 2019).

Mating interference may have bioenergetic impacts where invasive turtles are present. A mating attempt of a male *A. pallida* with a female *T. s. elegans* was observed in southern California (Leatherman and Jennings 2007). In an experimental setting, Cadi and Joly (2004) observed mating attempts by *T. s. elegans* with female *Emys orbicularis* in France. Currently, we do not know the level of mating interference by *T. s. elegans* with *A. marmorata* and it has not been documented in the literature.

Invasive populations of the Snapping Turtle (*C. serpentina*) occur in California (Bury and Luckenbach 1976) and Oregon (ODFW 2015; Bury and Matsuda 2022). Distribution of *C. serpentina* in Oregon is currently under investigation by the Oregon Department of Fish and Wildlife (ODFW 2015; S. Barnes, pers. comm.). Detrimental impacts of *C. serpentina* on *A. marmorata* populations are suspected but have not been studied. *Chelydra serpentina* is most commonly found in habitats near human population centers, but is increasingly being detected in more remote areas, such as the Wild and Scenic Section of the Rogue River in southwest Oregon (e.g., ODFW, unpubl. data). Invasive *T. s. elegans* and *C. serpentina* are known to transfer pathogens and parasites to other turtle species (Siddall and Desser 2001; Héritier et al. 2017) including to *A. marmorata* (Silbernagel et al. 2013; Lambert et al. 2021; Sim et al. 2021). Some of these pathogens and parasites are further discussed in the next subsection.

The American Bullfrog, *L. catesbeianus*, is a large ranid frog native to eastern North America and now has established populations in all states west of the Rocky Mountains (Dodd and Jennings 2021; Meshaka et al. 2022). It has been introduced to most countries on four continents (Adams and Pearl 2007). This ambush predator consumes a wide variety of invertebrate and vertebrate prey. Invasive populations of *L. catesbeianus* can impact native species through competition and predation (Moyle 1973; Bury and Whelan 1984; Wu et al. 2005). Negative impacts are reported from other locations (Hays et al. 1999; Woodruff et al. 2025) or inferred from correlations (Nicholson et al. 2020). Gut content analyses of *L. catesbeianus* have found hatchling turtles at multiple locations in Washington, Oregon, and California.

Correlative comparisons have suggested that *L. catesbeianus* can decrease the proportion of young turtles in a population (Nicholson et al. 2020). In southern Washington ponds, removal of *L. catesbeianus* led to increased numbers of hatchlings in the turtle population (F. Slavens, pers. comm.). The successful eradication of *L. catesbeianus* from several isolated ponds in the Sierra Nevada resulted in subsequent detection of hatchling turtles where they had not been seen in surveys for many years prior to eradication of *L. catesbeianus*, and some of the culled frogs contained hatchling *A. marmorata* in their gut contents (Kamoroff et al. 2020; Woodruff et al. 2025). The effect of *L. catesbeianus* on *A. marmorata* populations likely varies widely across the range and the magnitude of the effect may be influenced by many factors, including habitat type, climate regime, and food web dynamics.

The impacts of *L. catesbeianus* on populations of *Actinemys* are questioned by some authors (Hayes and Jennings 1986; Germano et al. 2012, 2026). First, these invasive frogs co-exist with *A. marmorata* at many lowland locations and the turtles are abundant (Germano and Bury, pers. obs.). There are juvenile turtles in the population so recruitment is happening. Perhaps the hatchlings and small turtles remain in vegetation or shallows until larger size, but we lack information on this critical part of their life history. Determining population-level effects of *L. catesbeianus* on *A. marmorata* populations would benefit from long-term and experimental studies.

Largemouth Bass, *M. salmoides*, is often implicated as a threat to recruitment of young *A. marmorata* (e.g., Manzo et al. 2021; USFWS 2023a,b); however, there is no direct evidence that *M. salmoides* eat young *A. marmorata* (Rosenberg et al. 2009). Controlled experiments with *T. s. elegans* hatchlings showed that *M. salmoides* would initially ingest hatchling *T. s. elegans* but then spit them out shortly after ingestion, presumably due to antipredator behaviors such as clawing or biting by the hatchling (Semlitsch and Gibbons 1989; Britson and Gutzke 1993; Britson 1998). Furthermore, after repeated attempts, the bass learned to avoid the hatchlings.

Other introduced sport fishes, such as Brown Bullhead (*Ameiurus nebulosus*), are also presumed predators of

hatchling turtles, but direct evidence of predation on *A. marmorata* is anecdotal. While direct evidence of predation by introduced sport fishes is limited, or lacking, their effect on food web dynamics is significant and is likely to reduce prey availability for hatchling, juvenile, and adult turtles (Moyle 1973; Hays et al. 1999; Adams and Pearl 2007).

Invasive crayfish species can disrupt aquatic food webs (Kats et al. 2013; Garcia et al. 2015) and degrade water quality (Anastácio and Marques 1997; Yamamoto 2010), but they may also provide an abundant food source for some native species, including *A. marmorata* (Karres 2016). The Red Swamp Crayfish (*Procambarus clarkii*) is expanding its distribution in the range of *A. marmorata* and is a known prey item of *A. marmorata* (Karres 2016), but it is unknown whether it preys on *A. marmorata* hatchlings (Larson and Olden 2011; Pearl et al. 2013). The Virile Crayfish (*Faxonius virillis*) is a recent invader in Oregon and is known to displace native crayfish, as well as the invasive *P. clarkii*, but effects on *A. marmorata* populations have not been documented.

Invasive vegetation is also a conservation concern (Ringold et al. 2008); while numerous plant species may pose some level of threat, we only list a few examples. Non-native grasses and other invasive vegetation displace native plant communities (Cushman and Gaffney 2010) and can reduce the quality of turtle nesting habitat (e.g., Quackgrass, *Elytigia repens*; Johnsongrass, *Sorghum halepense*), reduce connectivity between aquatic and terrestrial habitats (e.g., Reed Canary Grass, *Phalaris arundinacea*), reduce hydroperiod (e.g., tamarisk, *Tamarix* spp.), and alter food webs (Poff et al. 2011). Invasive plants can also increase the risk of fire in nesting habitats and riparian zones, including grasses (e.g., Giant Reed, *Arundo donax*; Cheatgrass, *Bromus tectorum*; Buffelgrass, *Cenchurs cillaris*), and trees including tamarisk species (Dwire and Kauffman 2003; Lambert et al. 2010). Singly or combined, these impacts can reduce primary productivity and reduce prey for native turtles. Removal of invasive vegetation has resulted in harm to individual turtles during mowing (Alvarez et al. 2017) and mechanical removal of invasive aquatic vegetation or dense algae (Alvarez et al. 2021). Effects of chemical control methods for invasive aquatic vegetation on turtles are unknown.

Pathogens, Parasites, Commensals, and Symbionts.— A diverse array of organisms has been reported to use *A. marmorata* as a host, although health impacts from some of these organisms have not been determined. A fungal-associated shell disease has received the most attention in recent years and detrimental impacts have been reported. In Washington, many *A. marmorata* (up to 60%) have been diagnosed with this shell disease, and almost all of these were head-started turtles (Haman et al. 2019). This 'shell-devouring' condition is hypothesized to be associated with the recently described fungal pathogen, *Emydomyces testavorans* (Woodburn et al. 2019; Hoyer et al. 2023; Mutlow et al. 2023; Brunner et al. 2024). This fungus has been isolated from *Actinemys* and other freshwater turtles and appears to be related to the fungus *Ophidiomyces ophiodiicola*, which causes Snake Fungal Disease (Woodburn et al. 2021). Several recent studies have examined the underlying infection (Wright et al. 2021; Flaminio et al. 2022; Cerreta et al. 2023; Green et al. 2025).

Infection by *E. testavorans* is referred to as NWPT Shell Disease (Haman et al. 2019) or Pond Turtle Shell Disease (Lambert et al. 2021), and superficially presents similarly to Septicemic Cutaneous Shell Disease, which is often found in captive freshwater turtles. Turtles with loss of keratin on the carapace and plastron were found in a spring-fed pond near Monterey, California (Lambert et al. 2021). At this site, *E. testavorans* was isolated from *T. s. elegans* but not from *A. marmorata* (Lambert et al. 2021); however, *A. marmorata* showed extensive loss of keratin and other anomalies consistent with Pond Turtle Shell Disease, while the invasive *T. s. elegans* only showed superficial signs of disease. The cause for these conflicting results remains uncertain, but the invasive turtles may have some resistance and yet play a role in spreading this fungal pathogen to native turtles (Lambert et al. 2021). The geographic extent of this emerging infectious keratinophilic fungus is unknown; thus, surveys with testing for surveillance of *E. testavorans* are needed.

In 1990, an apparent Upper Respiratory Tract Disease (URTD) occurred at a site in Klickitat County, Washington, resulting in the death of 35–40% of that population of *A. marmorata*. Although the causative agent was not identified, a virus or mycoplasma was suspected (Hays et al. 1999). In 1993, multiple *A. marmorata* carcasses (n = 42) exhibiting signs of URTD were recovered from a site in Tehama County, California; but again, the causal agent was not identified (Holland 1994). A female *A. marmorata* exhibiting signs of UTRD was collected in Eugene, Lane County, Oregon; the turtle died the next day, and necropsy concluded that UTRD was the cause of death. *Trachemys s. elegans* was present at the Klickitat County and Lane County sites and may have served to vector the disease (Holland 1994).

To assess the potential for pathogen introduction from *T. s. elegans* to *Actinemys* species, Silbernagel et al. (2013) sampled turtles from 10 pond sites in California, representing northern (n = 3), central (n = 3), and southern (n = 4) regions of the state. Each region included at least one pond with both species, and one pond where only *Actinemys* was present. Using a combination of methods, they tested for presence of *Ranavirus*, *Herpesvirus*, *Mycoplasma*, and *Salmonella*. All *T. s. elegans* (n = 33) and all *Actinemys* (n = 145) tested negative for *Ranavirus* and *Herpesvirus*. Both species of *Actinemys* as well as *T. s. elegans* tested positive for *Mycoplasma*, with prevalence lower to the north and highest to the south (Silbernagel et

Figure 12. Non-native leeches, *Placobdella parasitica,* using *Actinemys marmorata* as host in the Rogue River, Josphine County, Oregon. (**Top**) Leeches were sometimes seen on the shell, but (**bottom**) they were most often found hidden at the interface of the skin and shell. Photos by Don T. Ashton.

al. 2013). Enterobacteria were detected in cloacal swabs of both turtle taxa, but *Salmonella* was not detected in either (Silbernagel et al. 2013). Sim et al. (2021) found emydid herpesvirus in captive *A. marmorata* co-housed with *T. s. elegans*, suggesting the potential for transfer of these pathogens from invasive turtles. Research into healthy microbiome constituents and pathogenic mechanisms is ongoing (e.g., Green et al. 2025).

Internal and external parasites of *A. marmorata* have been reported, but prevalence and distribution are not well known. Internal parasites include a variety of helminths

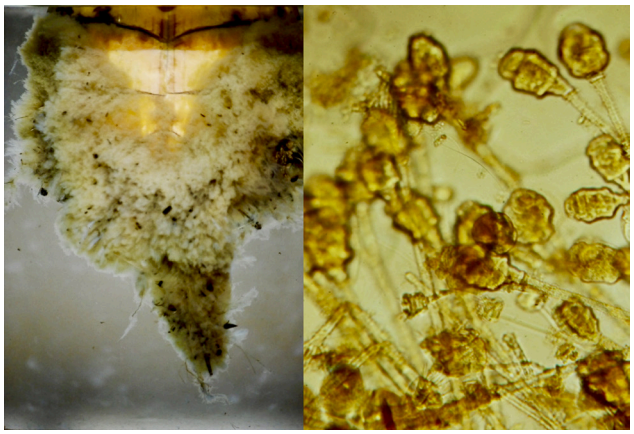

Figure 13. Heavy infestation of colonial protozoans, *Epistylis niagarae*, (**left**) on the posterior of *Actinemys marmorata*, and (**right**) close-up of the colonial protozoan. Goose Lake, Kern County, California. Photo by David J. Germano.

(e.g., trematodes and nematodes), sometimes with hundreds of specimens in a single turtle (Ingles 1930; Thatcher 1954). Leeches are common ectoparasites on freshwater turtles in central and eastern North America, but leeches that specialize on turtles are only rarely reported using *A. marmorata* as a host, and published literature often lacks confirmed taxonomic identification (Holland 1994; Bury et al. 2012b; Wilcox and Alvarez 2023). The North American Smooth Turtle Leech, *Placobdella parasitica*, native east of the Rocky Mountains, was collected from *T. s. elegans* in California (Moser et al. 2005) and has been identified using *A. marmorata* as a host in Oregon (Fig. 12; Reilly et al. 2023; Phillips et al. 2025). These blood-feeding parasites are known to transfer blood parasites between turtles (Siddall and Desser 2001; Héritier et al. 2017). Health impacts from these parasitic leeches and potential associated pathogens have not been determined for *A. marmorata*.

External commensals include colonial protozoans, such as *Epistylis niagarae*, that may attach to some turtles in warm waters (Fig. 13; Germano 2000). Filamentous algae can cover the shell partly to fully in some populations, especially those in warm ponds (Bury et al. 2015). A barnacle (*Amphibalanus subalbidushave*) was found attached to a female *A. marmorata* inhabiting brackish waters in a San Francisco Bay estuary, California (Agha et al. 2018b). The level of impact, if any, from commensal organisms attached to the shell has not been evaluated thoroughly for *A. marmorata*, although colonial protozoans did not seem to affect individuals at Goose Lake in California (Germano 2000).

Symbiotic bacterial communities are important components in the health and/or disease of freshwater turtles. External and internal bacterial communities have been described for *A. marmorata* from a variety of habitats in the San Francisco Bay Area, with *T. s. elegans* co-occurring at some sites (Lambert et al. 2021; White et al. 2023; Green et al. 2025). Disturbance to natural symbiotic communities can lower fitness of the host organism (Petersen and Round 2014; Green et al. 2025).

Climate Change. — Impacts of climate change on chelonian distribution, species richness, and extinctions have been predicted globally (Ihlow et al. 2012; Butler et al. 2016; Butler 2019; Berriozabal-Islas et al. 2020). An assessment of vulnerability to climate stressors in northern California rated *A. marmorata* as moderate-high based on sensitivity to climate stressors, projected future climate conditions and adaptive capacity of the species (Sims et al. 2019).

Population viability analyses have indicated that a drying climate in the range of *A. marmorata* could severely impact populations leading to localized extirpations and eventually extinction (Manzo et al. 2021; USFWS 2023a,b; Gregory et al. 2024a,b). Sea level rise is expected to increase seawater infiltration into estuaries, coastal marshes, and

river mouths, reducing habitat suitability for *A. marmorata* populations living along the coastline (Agha et al. 2018a, 2019).

Actinemys marmorata relies on aquatic habitats for vital life-history functions (e.g., feeding, mating) and spends most its activity period in water. Thus, earlier seasonal drying of small or ephemeral water bodies reduces time available for obtaining resources. Changes in precipitation patterns, including more rain instead of snow at higher elevations not only effects hydroperiod of streams and ponds, but may also increase frequency and magnitude of large flood events. Along rivers and streams in foothills, occasional high flow events can be beneficial to maintain nesting habitats and deep pools, but unusually large flood events can cause direct mortality of eggs and hatchlings in the nest chamber (Holte 1998) and injure overwintering adults (Cummings et al. 2022). Flood events may displace native turtles (Mitrus and Hejduk 2011; Jones and Sievert 2009) and facilitate dispersal of invasive species (Diez et al. 2012). Changes in precipitation patterns will undoubtedly result in increased pressure on water resources for human use, with potential for further impacts to turtle habitats in many regions (Scanlon et al. 2005; Kemp et al. 2015).

Although this species has evolved with periodic droughts, multi-year droughts can have significant impacts on populations. Prolonged drought in California from 2012–2016 resulted in high mortality in some *Actinemys* populations (Leidy et al. 2016; Purcell et al. 2017), but not others (Germano, in press). Reduced precipitation and hotter, drier summers is predicted to increase wildfire intensity and frequency. Wildfire can cause mortality in turtles estivating or overwintering in leaf litter in terrestrial habitats (Bury 2004), although direct evidence of mortality is limited and largely anecdotal. Further, prescribed burning to reduce wildfire risk often occurs at times outside of the natural fire season, when turtles may be overwintering on land. Potential effects of prescribed fire on *A. marmorata* has received little attention (Russell et al. 1999) but is of increasing importance as this proactive approach to reduce wildfire intensity is employed at larger scales to combat wildfire risks exacerbated by climate change. Wildfire also affects water quality and food web dynamics downstream, reducing prey availability for *A. marmorata*, an effect further exacerbated by drought (e.g., Lovich et al. 2017).

While *Actinemys* turtles have evolved strategies to cope with effects of wildfire and drought, the synergistic interaction of wildfire effects and prolonged drought may be beyond the natural capacity for these turtles to endure. Insights on the interactive effects of drought and wildfire on *Actinemys* species are provided by Lovich et al. (2017). After two years of severe drought and one year after a wildfire burned the surrounding landscape, Lovich et al. (2017) found that the water quality was poor, with high salinity, dissolved solids, turbidity, and alkaline conditions with low dissolved oxygen, likely due to inputs of ash, sediments, and nutrients following the fire. Turtles were covered in a mineral evaporite and exhibited signs of malnourishment and dehydration, and there was an apparent collapse of the aquatic food web. Two years after the fire and four years into the drought, resident turtles appeared to have been extirpated from the site; five discovered turtle carcasses examined in necropsy showed signs of starvation. Thirty-two turtles in poor condition were collected and sent to a rehabilitation facility where six of those died despite veterinary care and 26 turtles were later released but there was no follow-up monitoring. In some situations, however, multi-year droughts may not cause irreparable harm to populations of *Actinemys*. At a site in the Tehachapi Mountains (an intersection of the distributions of *A. marmorata* and *A. pallida*) in southern central California, the number of turtles was lower after the 2012–2016 drought, but females remained reproductive and new turtles were found, including young, and survivorship of remaining turtles was high (Germano, in press).

Actinemys marmorata exhibits temperature-dependent sex determination, with sex of embryos determined during the middle of incubation, with warmer nest temperatures producing a greater proportion of females (Christie and Geist 2017). Predicted increases in spring and summer temperatures due to changing climate could skew the sex ratio of emerging hatchlings. Over time, this may skew sex ratios sufficiently to cause population declines if females do not compensate by modifying the timing or location of nesting (Butler et al. 2016; Janzen et al. 2018; Butler 2019; Krueger and Janzen 2023; Roberts et al. 2023).

Human Recreation and Disturbance Impacts. — Human activities can have local effects on *A. marmorata* populations. Turtles are sometimes deliberately shot while basking or are inadvertently caught while fishing (Bury et al. 2012b). Disruption of basking and nesting behavior due to recreational activities may have energetic costs; population-level effects of this type of disturbance are uncertain.

In suburban and urban environments, where supplemental food from human habitations results in artificially high populations of native or invasive predators, this may result in increased nest predation (Prange et al. 2003; G. Rathbun, pers. comm.). This is also an issue in campgrounds and recreation areas where human activity is often accompanied by refuse and food, which can attract and subsidize native predators, potentially leading to an increased risk of nest predation by Raccoons, Gray Foxes, Western Spotted Skunks, and Striped Skunks, as well as suspected predators of eggs and hatchlings such as corvids and Opossums. The presence of humans also tends to drive away larger carnivores that would otherwise prey on medium-sized predators to keep their populations in check. Areas associated with recreation also have an increased probability of harboring non-native species, such as intentionally released sport fishes or unwanted pets, or inadvertently dispersed plants,

animals, and microorganisms. As discussed above, nonnative species can impact individual turtles and populations through predation, competition, habitat alteration, disease, and food web disruption. On the other hand, observation of native turtles in the wild by recreationists and the general public can instill a sense of appreciation and foster interest in conservation (Dupuis-Desormeaux et al. 2022).

Conservation Measures Taken. — *Actinemys marmorata* is protected by US state laws throughout its range. It is listed as State Endangered in Washington; Sensitive-Critical in Oregon, Species of Special Concern in California, and is considered a Priority Species in Nevada.

Actinemys marmorata has recently (2024) been assessed as Vulnerable (VU A2bcde+4bce, E) on the IUCN Red List of Threatened Species, but this has not yet been officially published (Bury et al., in press). It was previously assessed as Vulnerable in 1996 (TFTSG 1996), and also provisonally assessed as Vulnerable by the IUCN SSC Tortoise and Freshwater Turtle Specialist Group in 2011 (Rhodin et al. 2018).

Although habitat loss and alteration are the primary threats to conservation of this species, these state laws may not confer effective protection of turtle habitat. Indirectly, various land management provisions provide partial to full protection of habitat, including waters designated as Wild and Scenic Rivers, wilderness areas, and state and national parks.

The species still occurs in some state and federal parks at low elevations, including Humboldt Redwoods State Park (northern California) and Point Reyes National Seashore (north of San Francisco), and lower elevation protected areas offer sanctuary near urban centers. National Parks at higher elevations also provide habitat protection for *A. marmorata* populations, including Yosemite, Sequoia, and Kings Canyon National Parks. State Wildlife Management Areas, federal Waterfowl Production Areas, and National Wildlife Refuges provide some habitat protections to many wetlands and ponded areas along the Pacific slopes of western North America.

In Washington, all six known populations are on lands protected for turtle recovery, either through landowner agreements or on lands purchased by Washington Department of Fish and Wildlife and operated as wildlife areas (Hallock et al. 2017). However, throughout much of the species' range, particularly at lower elevations where turtles were historically most abundant, protected lands are fragmented by urbanization, agriculture, and transportation infrastructure.

U. S. Endangered Species Act (ESA). — Federal listing may afford habitat protections to support conservation or recovery of *Actinemys* populations. In the 1990s the species was petitioned for listing under the Endangered Species Act, but it was determined to not be warranted, with the Service stating that "the Western Pond Turtle does not meet either the definition of an endangered species or a threatened species at the present time" (USFWS 1993). More recently, a renewed petition to list was filed (CBD 2012) and the US Fish and Wildlife Service determined that a species status review was warranted (USFWS 2015). As a result of this review, USFWS has issued a Proposed Rule to list both species of Western Pond Turtle as Threatened under the Endangered Species Act (USFWS 2023a). This effort includes the Section 4(d) Rule, where the Service can specify exemptions for specific activities such as routine maintenance of waterways and ponds, habitat restoration, and invasive species management, to be specified in the Final Rule. Both *A. marmorata* and *A. pallida* remain under consideration for listing as Threatened under a special review for "Long-term Actions" (USFWS 2025).

If the proposed federal listing as Threatened under the Endangered Species Act is finalized, prior to initiation of projects that alter turtle habitat or that may affect the species, a Section 7 consultation (Federal agencies) must be conducted, or a Section 10 permit must be acquired if "take" of the species may occur without a Federal nexus (i.e., action, funding, or on Federal land). Implementation of Avoidance and Mitigation Measures will be required. Follow-up monitoring is strongly recommended.

Conservation Strategies and Plans. — Conservation strategies to guide protection and recovery of the species and preservation / restoration of habitats have been implemented in every state where *A. marmorata* occurs: the Comprehensive Wildlife Conservation Strategy, Wildlife Action Plan, and Department of Natural Resources Aquatic Habitat Conservation Plan in Washington; Conservation Strategy in Oregon; Wildlife Action Plan in California; and Wildlife Action Plan in Nevada. Within these four states, there are numerous county and private Habitat Conservation Plans. Best Management Practices and conservation planning documents specific to *A. marmorata* have been developed for Washington (Hays et al. 1999; Hallock et al. 2017), Oregon (Rosenberg et al. 2009; ODFW 2015), California (Yarnal 2019), across Department of Defense facilities (DoD 2020), and range-wide (Bury et al. 2012c; RCC 2020).

Habitat Restoration and Invasive Species Control. — Following the curtailment of commercial harvest and completion of most water control projects (dams, irrigation canals), habitat alteration remains the primary cause of contemporary turtle population declines, which is often coupled with increased pressure from invasive species. The conservation strategies and plans mentioned above include protection and/or restoration of physical habitat and invasive species components. Addition of basking platforms helps in counts of turtles during visual surveys (Alvarez 2006), since turtles preferentially select basking objects away from shore (Bury, pers. obs.). Habitat restoration projects often aim to control invasive plants in terrestrial and aquatic habitats to restore natural ecological communities. Cutting, mowing, digging, burning,

and chemical control are options used depending on the type and level of vegetative threat and potential impacts to other ecosystem components.

Management or eradication of American Bullfrogs has received considerable attention, with past and ongoing efforts in California (Kamoroff et al. 2020; Woodruff et al. 2025), Oregon (C. Yee, pers. comm.), and Washington (Hallock et al. 2017; F. and K. Slavens, pers. comm.). Preliminary data from projects indicate an increase in turtle recruitment following reduction or elimination of bullfrogs (Hallock et al. 2017; Woodruff et al. 2025). Bullfrog removal methods include gigging or shooting adults, dip-netting or trapping tadpoles, and dip-netting of egg masses; usually a combination of methods has been needed to reduce robust populations. Sustained effort may be needed to combat re-invasion, and removal may not be possible across a large landscape.

Feasibility of such efforts must be considered when allocating limited funding and staffing for turtle conservation. Also, bullfrogs have ecosystem effects far beyond potential impacts to turtle populations. Control or removal of introduced bass, catfish, and other sport fishes has received less attention, possibly due to the popularity of recreational sport fisheries. To date, there is little evidence documenting population-level impacts on *Actinemys* by these introduced fishes.

Nest Protection. — Nest predation can be high, with perceived losses of >90% of the annual cohort at some locations (Holland 1994). In these situations, protection of known nests with predator-exclusion cages, or protection of known nesting areas with fencing, have been employed as conservation measures at many locations (Holte 1998; Alvarez et al. 2014; ODFW 2015). These protective measures have been effective for improving hatching success, although results of these efforts are often contained in unpublished reports or unanalyzed data, and efforts such as these are only feasible at selected sites where resources are available to detect intact nests, apply exclosures, and monitor them to ensure release of emerging hatchlings.

Head-start Programs. — Head-starting is the practice of rearing vulnerable eggs and neonates in a protected setting to reduce predation risk (Burke 2015). Ongoing head-start programs for *A. marmorata* are collaborative efforts with agencies, universities, zoos, veterinarians, and local interest groups. Zoos involved in head-starting programs include Woodland Zoo in Washington, Oregon Zoo (in Portland, with releases in Washington), and San Francisco, Oakland, and San Diego Zoos in California (Geist et al. 2015; Terry 2018; AZA 2019; Yarnal 2019). Limited head-starting previously occurred in Oregon, but has been discontinued (ODFW 2015).

In an effort to address steep population declines in Washington state, a head-starting program was initiated in 1990 as a joint project with Washington Department of Fish and Wildlife, Woodland Park Zoo, Portland Zoo, the Center for Wildlife Conservation, and Bonneville Power Administration, with eggs collected from the wild. In 1991, captive breeding was added, starting with nine adult turtles from Washington and three from Oregon and was expanded in subsequent years to include additional turtles from other locations (Hays et al. 1999). Head-starting in Washington has often been coupled with long-term monitoring of released turtles (Vander Haegen et al. 2009). Head-start efforts in Washington have released over 1,500 turtles (Hallock et al. 2017), but many head-started turtles subsequently developed shell disease (Haman et al. 2019).

Knowledge and experience gained through these programs provide valuable contributions to science; however, head-starting to augment or reintroduce populations in the wild should only be considered as a last resort or as a stop-gap measure until causes of declines can be determined and corrected (Burke 2015). Careful, long-term monitoring, including health screenings, of donor and recipient populations are important elements of head-start programs (Keller et al. 2012; Buhlmann et al. 2015; Michell and Michell 2015). Head-starting should only be conducted by authorized facilities following strict protocols, including full documentation, health screening, DNA sequencing, and follow-up monitoring. We point out that there are potential adverse effects of head-starting (e.g., mixing of gene pools, introduction of disease) that need to be carefully considered before head-starting is conducted on other than an experimental basis (Pramuk et al. 2013; Bury 2015; Smith 2015; Lopez 2019; RCC 2020). The long-term survival prospects of the species must be considered because these actions, if applied incorrectly, may dilute efforts to effectively protect and manage wild populations and their habitat (Germano et al. 2012, 2026). Addressing the causes for population declines and applying management and restoration actions to allow for self-sustaining populations in the wild are preferred over head-starting.

Translocation and Reintroduction. —Translocation involves moving animals out of harm's way during construction or other disturbance activities, or the intentional movement across further distances for population augmentation. Reintroduction is an effort to establish populations in locations where they have been extirpated. Translocation and reintroduction have occurred in Washington (Vander Haegen et al. 2009; Hallock et al. 2017), Oregon (Holland 1994), and California (Terry 2018), either by moving adults or releasing head-started turtles. There have been attempts to translocate individuals away from construction projects in California and Oregon, but the results remain unpublished. It is imperative to rigorously monitor the results of these efforts to evaluate the potential effectiveness of this mitigation strategy. Some translocated turtles are known to return to their natal sites (Ernst and Lovich 2009; Otten et al. 2023; L. Hunt, unpubl. data), which subjects them to increased stress

Figure 14. Research is ongoing to aid the conservation of *Actinemys marmorata*. (**Left**) Hatchling with radio-telemetry transmitter to investigate habitat use, Trinity County, California; and (**right**) Adult female with radio-telemetry transmitter to study overwintering behavior, Klamath County, Oregon. Photos by Don T. Ashton.

and mortality risk. Further, translocation may mix stocks of genetically differentiated forms. Earlier attempts to translocate amphibians and reptiles were frequently ineffective as conservation strategies (Dodd and Seigel 1991). Translocation and reintroduction efforts with careful planning and implementation have increasingly been found to be successful (e.g., Cayot 2021; Rimple et al. 2024). Future translocations should be coupled with monitoring to evaluate their effectiveness.

Meetings and Working Groups. — Many meetings have been organized to discuss the status and conservation needs of *A. marmorata*. A Western Pond Turtle Group was established in 1991 to promote communication and coordinate research on the species. Interested parties included representatives from federal and state agencies, several universities, zoos, industry, and private citizens. Activities waned but were re-energized about 2010. These efforts have expanded to include three regional Western Pond Turtle Working Groups in Oregon and a new one in northern California to support active communication among various stakeholders in turtle conservation. Oregon's Turtle Working Group holds periodic local meetings and, in January 2026, hosted a range-wide conference that included participants from California and Washington to facilitate regional coordination.

A Western Pond Turtle range-wide conservation coalition developed a management strategy to foster a comprehensive and coordinated group of stakeholders across the range of both *Actinemys* species to manage, conserve, research, and support the species in perpetuity (RCC 2020). Sessions on the biology and status of *Actinemys* have occurred at over half a dozen annual meetings of The Wildlife Society, the Society for Northwestern Vertebrate Biology, and Partners in Amphibian and Reptile Conservation. Conferences sponsored by The Wildlife Society focused solely on Western Pond Turtles were held in 2005 and 2015 at Sonoma State University, Rohnert Park, as well as workshops in 2025 in Oakland and Humboldt County, California. Smaller, regional workshops on biology and field methods have been provided at multiple locations in Oregon and California in recent years.

Standardized Protocols. — A Western Pond Turtle "handbook" published by Northwest Fauna provides an overview of sampling considerations and field methods for all life stages (Bury et al. 2012c); an update of this turtle handbook is currently being prepared. Oregon has released guidelines on how to protect and improve habitat (ODFW 2015), as well as a visual encounter survey protocol (ODFW 2020). These results contributed to the Species Status Assessment prepared for evaluation under the ESA (USFWS 2023a,b). Local and project-specific sampling protocols are also found in various reports (e.g., Snover and Adams 2016). While there have been sustained efforts to promote use of standardized protocols there remains some variability among researchers across the extensive range of this species, so it is important to document and report the details of methods used to allow for comparisons between studies, regions, and over time.

Conservation Measures Proposed. — The proposed ESA listing (USFWS 2023a) supports the implementation of actions outlined in existing management strategies, and if the proposed ESA listing is finalized, additional actions will be required (see Endangered Species Act section above). The Western Pond Turtle Range-wide Management Strategy outlines nine categories of action intended to ensure long-term viability of wild populations (RCC 2020). Efforts focused on protection and recovery of turtles in their native habitats have the greatest conservation value. These include: 1) coordination of implementation strategies; 2) distribution and abundance surveys; 3) identification of management regions and priority conservation areas within each region; 4) investigation of genetic diversity; 5) investigation of threats in order to enhance recovery efforts; 6) amelioration of threats, particular in priority conservation areas; 7) minimizing direct and indirect adverse effects; 8) consideration of population augmentation; and 9) developing and implementing outreach and education programs (RCC 2020).

Translocation and reintroduction may be evaluated as ways to increase population redundancy after causes for localized declines have been identified and ameliorated (Hays et al. 1999; RCC 2020). Rehabilitation of degraded habitats is detailed elsewhere (Bury et al. 2012c; ODFW 2015). The Turtle Working Groups have committees devoted to developing a system for archival of data from prior, current and future studies, sharing of marking code series used, surveillance monitoring for disease, exploring research technology innovations, developing management plans, defining future research goals, and promoting education. To facilitate the inclusion of turtles in interdisciplinary resource management decisions with multiple stakeholders and diverse objectives, tools are being applied by cooperating partners to evaluate complex management decisions and to promote proactive management (e.g., Martin et al. 2009; Irwin et al. 2011; St. Clair and Burns 2013), including partnering on a structured decision-making model (US Army Corps of Engineers, US Geological Survey, Oregon State University) and a decision-support system (Bureau of Reclamation, Hoopa Valley and Yurok Tribes, Applied River Sciences).

Captive Husbandry. — It is illegal to keep *A. marmorata* in captivity in any state where it occurs without permits from state wildlife departments. Basic husbandry, nutrition, and medicine standards for aquatic turtles can be found in the veterinary literature (Johnson 2004; Rawski et al. 2018), but published sources specific to *A. marmorata* are limited (Pramuk et al. 2013; Geist et al. 2015). We include some general information here, but detailed husbandry techniques are not provided.

If housing captive turtles near their location of origin, outdoor enclosures protected from predators are preferred. For indoor environments, mimicking natural temperature ranges and diel patterns is preferred. Nutrition is an important consideration for general health, growth, and shell health (Hallock et al. 2017). A variety of live or natural foods can be supplemented with vitamins or commercially available turtle foods and other pet foods (Rawski et al. 2018). Prior to wild release of any captive turtles, a full health screening must be performed, including a thorough physical exam combined with blood, nasal, and fecal testing (Smith 2015), and DNA sequencing (Lopez 2019).

Current Research. — The number of field studies and published research on *A. marmorata* has grown rapidly in recent years, but some important information remains in unpublished reports and data sets that are not readily available to contribute to the knowledge of this species. An overview of future research needs was provided by Germano et al. (2012), including: estimates of occurrence and density, geographic variation (across latitudinal and elevational gradients); habitat use; life-history traits (e.g., fecundity, longevity); daily and seasonal activities; diet; conservation issues (e.g., role of head-starting); monitoring issues; effects of roads, disease, invasive species; habitat loss; contaminants; wildfire and prescribed burning; and climate change. These should be conducted using scientific methods and with the goal of publishing results. These are all active fields of current research but most projects are being done in a single area or are limited in geographic scope (Fig. 14). Since publication of the Northwest Fauna monograph (Bury et al. 2012a), there have been many scientific studies on the ecology and life history of *A. marmorata*, with increased interest in response to the proposed listing of the species as Threatened under the Endangered Species Act (USFWS 2023a). Studies on potential impacts of invasive species are receiving greater attention at many locations throughout its range.

The Western Pond Turtle Range-wide Conservation Coalition developed a management strategy with a set of long-term monitoring sites to determine trends over time (RCC 2020). Numerous groups of researchers have initiated long-term research and monitoring projects, including Washington (WDFW), Oregon (ODFW, Western Oregon University), and California (Green Diamond Resource Company, Sonoma State University, Sonoma Water District, California State University Bakersfield). Additional research results are expected to appear in peer-reviewed literature in the coming years.

Continued study is underway to better define the contact and admixture zones between the two species of *Actinemys* (H.B. Shaffer, pers. comm.) to be combined with results of the most recent genetic studies (Shaffer and Scott 2022; Todd et al. 2022). Research into microbiomes, disease, and effects of pathogens and parasites is ongoing and expanding (e.g., Reilly et al. 2023; Green et al. 2025). Current, ongoing, and proposed research along with increased regulatory oversight are expected to aid in the conservation and management of this species.

Acknowledgments. — We thank Anders Rhodin and John Iverson for their helpful comments, reviews, and editing of the manuscript. We also thank Jeff Alvarez, Susan Barnes, James Bettaso, Matthew Bettelheim, Ryan Bourque, Gwendolynn Bury, Farley Connelly, David Cook, Ninette Daniele, Nicholas Geist, Rob Grasso, Dan Holland, Jade Keehn, Brett Lovelace, Oliver Miano, Laura Patterson, Galen Rathbun, Devin Reese, Jason Reilly, Bradley Shaffer, Frank and Kate Slavens, Kathleen Smith, Alan Striegle, Samuel Sweet, Hartwell Welsh, Jr., Jeff Wilcox, and Simon Wray for conversations that aided in development of this species account and for their extensive efforts towards the conservations of this species. We thank James Bettaso for the use of his photographs. We also appreciate the assistance and information from the US Fish and Wildlife Service, including Brad Nissen, Andrew Dennhardt, and Chelsea Waddell, Bureau of Land Management, US Army Corps of Engineers, as well as state wildlife agencies in California, Oregon, and Washington. All interpretations remain our own.

Literature Cited

Adams, M.J. and Pearl, C.A. 2007. Problems and opportunities managing invasive bullfrogs: is there any hope? In: Gherardi, F. (Ed.). Biological Invaders in Inland Waters: Profiles, Distribution, and Threats. Invading Nature – Springer Series in Invasion Ecology 2. Dordrecht: Springer Netherlands, pp. 679–693.

Agassiz, L. 1857. Contributions to the Natural History of the United States of America. First Monograph. Volume I. Part I. Essay on Classification. Part II. North American Testudinata. Boston: Little, Brown and Co., 452 pp.

Agha, M., Ennen, J.R., Bower, D.S., Nowakowski, A.J., Sweat, S.C., and Todd, B.D. 2018a. Salinity tolerances and use of saline environments by freshwater turtles: implications of sea level rise. Biological Reviews 93:1634–1648.

Agha, M., Riley, M.K., Sanford, E., Carlton, J.T., Newman, W.A., and Todd, B.D. 2018b. A review of epizoic barnacles reported from freshwater turtles with a new record from California. Herpetological Review 49:25–28.

Agha, M., Yanagitsuru, Y.R., Fangue, N.A., Nowakowski, A.J., Kojima, L.V., Cech Jr., J.J., Riley, M.K., Freeman, J., Cocherell, D.E., and Todd, B.D. 2019. Physiological consequences of rising water salinity for a declining freshwater turtle. Conservation Physiology 7(1):coz054.

Agha, M., Yackulic, C.B., Riley, M.K., Peterson, B., and Todd, B.D. 2020. Brackish tidal marsh management and the ecology of a declining freshwater turtle. Environmental Management 66:644–653.

Allen, M., Gast, T., and Payne, T.R. 2005. Recovery of Fish Populations in the Upper Sacramento River Following the 1991 Cantara Spill. Final Report to California Department of Fish and Wildlife. Contract #CTC 96010.

Alvarez, J.A. 2006. Use of artificial basking substrate to detect and monitor Pacific Pond Turtles (*Emys marmorata*). Western North American Naturalist 66:129–131.

Alvarez, J.A. 2021. *Actinemys marmorata* (Northwestern Pond Turtle). Nesting after injury. Herpetological Review 52:124–125.

Alvarez, J.A., Davidson, K., and Foster, S.M. 2014. *Actinemys marmorata* (Western Pond Turtle). Nest predation association. Herpetological Review 45:307–308.

Alvarez, J.A., Kittleson, G.A., Davidson, K., and Asseo, L.M. 2017. Potential injury and mortality in *Actinemys* (*Emys*) *pallida* during restoration and maintenance activities. Western Wildlife 4:81–85.

Alvarez, J.A., Gaitan, R., Shea, M., and Foster, S.M. 2021. Unintended entrainment of Western Pond Turtle (*Actinemys marmorata*) during algae control on a newly restored wetland. Ecological Restoration 39(4):223–225.

Anastácio, P.M. and Marques, J.C. 1997. Crayfish, *Procambarus clarkii*, effects on initial stages of rice growth in the lower Mondego River valley (Portugal). Freshwater Crayfish 11:608–617.

Angielczyk, K.D., Feldman, C.R., and Miller, G.R. 2011. Adaptive evolution of plastron shape in emydine turtles. Evolution: International Journal of Organic Evolution 65:377–394.

Ashton, D.T. 2007. *Actinemys* (= *Clemmys*) *marmorata marmorata* (Northwestern Pond Turtle). Courtship behavior. Herpetological Review 38:327–328.

Ashton, D.T., Bettaso, J.B., and Welsh, H.H., 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(3):621–633.

AZA [American Zoo Association]. 2019. Western Pond Turtle SAFE Action Plan, 24 pp. https://assets.speakcdn.com/assets/2332/programplan_wpt_2019-2021.pdf.

Baird, S.F. and Girard, C. 1852. Descriptions of new species of reptiles collected by the U.S. Exploring Expedition under the command of Capt. Charles Wilkes, Proceedings National Academy Sciences, Philadelphia 6:174–177.

Banta, B.H. 1963. On the occurrence of *Clemmys marmorata* (Reptilia:Testudinata) in western Nevada. Wasmann Journal of Biology 21:75–77.

Barela, K.L and Olson, D.H. 2014. Mapping the Western Pond Turtle (*Actinemys marmorata*) and Painted Turtle (*Chrysemys picta*) in western North America. Northwestern Naturalist 95:1–12.

Berriozabal-Islas, C., Ramírez-Bautista, A., Torres-Ángeles, F., Mota Rodrigues, J.F., Macip-Ríos, R., and Octavio-Aguilar, P. 2020. Climate change effects on turtles of the genus *Kinosternon* (Testudines: Kinosternidae): an assessment of habitat suitability and climate niche conservation. Hydrobiologia 847:4091–4110.

Bettelheim, M.P. 2005. Marmorata: the famed mud turtle of the San Francisco market. California History 82:26–42.

Bettelheim, M.P. 2009. *Actinemys* (= *Clemmys*) *marmorata* (Western Pond Turtle). Courtship behavior. Herpetological Review 40:212–213.

Bettelheim, M.P. 2020. Tewaquaptewa, trailfinders, and turtles – the unexpected origins of Western Pond Turtle shells in the Hopi Snake Dance. Bibliotheca Herpetologica 14:51–60.

Bettelheim, M.P. and Wong, C. 2022. A review of the historical market effect of the West Coast commercial fishery on Western Pond Turtles. Western Wildlife 9:5–16.

Bettelheim, M.P., Terry, D.A., and Dunaeva, J. 2005. A selective translation of Alexander Strauch's "chelonological studies","global distribution", and ''comments" specific to the Western Pond Turtle (*Clemmys marmorata*), including a bibliography of his known herpetological works. Bibliotheca Herpetologica 5:10–27.

Bettelheim, M., Bury, R.B., Patterson, L., and Lubcke, G. 2006. *Trachemys scripta elegans* (Red-eared Slider). Reproduction in northern California. Herpetological Review 37:459–460.

Bickham, J.W., Lamb, T., Minx, P., and Patton, J.C. 1996. Molecular systematics of the genus *Clemmys* and the intergeneric relationships of emydid turtles. Herpetologica 52:89–97.

Bishop, M.R., Drewes, R.C., and Vredenburg, V.T. 2014. Food web linkages demonstrate importance of terrestrial prey for the threatened California Red-legged Frog. Journal of Herpetology 48:137–143.

Black, J.H. and Storm, R. 1970. Notes on the herpetology of Grant County, Oregon. Great Basin Naturalist 15:9–12.

Bondi, C.A. 2009. A comparison of Western Pond Turtle (*Actinemys marmorata*) movements in perennial and intermittent portions of a northwestern California river system. M.A. Thesis, Humboldt State University, California.

Bondi, C.A. and Marks, S.B. 2013. Differences in flow regime influence the seasonal migrations, body size, and body condition of Western Pond Turtles (*Actinemys marmorata*) that inhabit perennial and intermittent riverine sites in northern California. Copeia 2013:142–153.

Boyle, S.P., Keevil, M.G., Litzgus, J.D., Tyerman, D., and Lesbarrères, D. 2021. Road-effect mitigation promotes connectivity and reduces mortality at the population-level. Biological Conservation 261(109230):1–10. https://doi.org/10.1016/j.biocon.2021.109230.

Bradsell, P., Prince, J., Kuchling, G., and Knott, B. 2002.

Aggressive interactions between freshwater turtle, *Chelodina oblonga*, hatchlings and freshwater crayfish, *Cherax* spp.: implications for the conservation of the critically endangered Western Swamp Turtle, *Pseudemydura umbrina*. Wildlife Research 29:295–301.

Brehme, C.S., Hathaway, S.A., and Fisher, R.N. 2018. An objective road risk assessment method for multiple species: ranking 166 reptiles and amphibians in California. Landscape Ecology 33:911–935.

Britson, C.A. 1998. Predatory responses of Largemouth Bass (*Micropterus salmoides*) to conspicuous and cryptic hatchling turtles: a comparative experiment. Copeia 1998:383–390.

Britson, C.A. and Gutzke, W.H. 1993. Antipredator mechanisms of hatchling freshwater turtles. Copeia 1993:435–440.

Brunner, T.J., Wong, A.D., Adamovicz, L., Simmons, A., Ospina, E., and Keller, K.A. 2024. *Emydomyces testavorans* DNA is detected from shell swabs of companion chelonians. Journal of Exotic Pet Medicine 50:49–53.

Buhlmann, K.A., Koch, S.L., Butler, B.O., Tuberville, T.D., Palermo, V.J., Bastarache, B.A., and Cava, Z.A. 2015. Reintroduction and head-starting: tools for Blanding's Turtle (*Emydoidea blandingii*) conservation. Herpetological Conservation and Biology 10:436–454.

Burke, R.L. 2015. Head-starting turtles: learning from experience. Herpetological Conservation and Biology 10:299–308.

Burroughs, R.W., Parham, J.F., Stuart, B.L., Smits, P.D., and Angielczyk, K.D. 2024. Morphological species delimitation in the Western Pond Turtle (*Actinemys*): can machine learning methods aid in cryptic species identification? Integrative Organismal Biology 6:1–20.

Bury, R.B. 1970. *Clemmys marmorata*. Catalogue of American Amphibians and Reptiles 100:1–3.

Bury, R.B. 1972a. Habits and home range of the Pacific Pond Turtle, *Clemmys marmorata*, in a stream community. Ph.D. Dissertation, University of California, Berkeley, California.

Bury, R.B. 1972b. The effects of diesel fuel on stream fauna. California Department of Fish and Game Bulletin 58: 291–295.

Bury, R.B. 1979. Population ecology of freshwater turtles. In: Harless, M. and Morlock, H. (Eds.) Turtles: Perspectives and Research. New York, NY: John Wiley and Sons, pp. 571–602.

Bury, R.B. 1986. Feeding ecology of the turtle *Clemmys marmorata*. Journal of Herpetology 20:515–521.

Bury, R.B. 1995a. Western Pond Turtle: *Clemmys marmorata* (Baird and Girard). In: Storm, R.M. and Leonard, W.P. (Eds.). Reptiles of Washington and Oregon. Washington: Seattle Audubon Society, pp. 34–37.

Bury, R.B. 1995b. Painted Turtle: *Chrysemys picta* (Schneider). In: Storm, R.M. and Leonard, W.P. (Eds.). Reptiles of Washington and Oregon. Washington: Seattle Audubon Society, pp. 30–34.

Bury, R.B. 1995c. Slider: *Trachemys scripta* (Schoepff). In: Storm, R.M. and Leonard, W.P. (Eds.). Reptiles of Washington and Oregon. Washington: Seattle Audubon Society, pp. 38–39.

Bury, R.B. 1995d. Snapping Turtle: *Chelydra serpentina* (Linnaeus). In: Storm, R.M. and Leonard, W.P. (Eds.). Reptiles of Washington and Oregon. Washington: Seattle Audubon Society, pp. 28–29.

Bury, R.B. 2004. Wildfire, fuel reduction, and herpetofaunas across diverse landscape mosaics in northwestern forests. Conservation Biology 18:968–975.

Bury, R.B. 2008. Do urban areas favor invasive turtles in the Pacific Northwest? In: Brown, R. and Mitchell, J. (Eds.). Urban Herpetology. Salt Lake City, Utah: Herpetological Conservation Number 3, pp. 343–345.

Bury, R.B. 2015. Learning about head-starting turtles from a symposium. Herpetological Conservation and Biology 10:297–298.

Bury, R.B. 2017. Biogeography of Western Pond Turtles in the western Great Basin: dispersal across a Northwest Passage? Western Wildlife 4:72–80.

Bury, R.B. and Ernst, C.H. 1977. *Clemmys*. Catalogue of American Amphibians and Reptiles 203:1–2.

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

Bury, R.B. and Germano, D.J. 2008. *Actinemys marmorata* (Baird and Girard) – Western Pond Turtle, Pacific Pond Turtle. In: Rhodin, A.G.J., Pritchard, P.C.H., van Dijk, P.P., Saumure, R.A., Buhlmann, K.A., and Iverson, J.B. (Eds.). The Conservation Biology of Freshwater Turtles and Tortoises. Chelonian Research Monographs No. 5, pp. 001.1–9. doi:10.3854/crm.5.001. marmorata.v1.2008.

Bury, R.B. and Luckenbach, R.A. 1976. Introduced amphibians and reptiles in California. Biological Conservation 10:1–14.

Bury, R.B. and Matsuda, B.M. 2022. Introduced and extralimital species of freshwater turtles in the Pacific Northwest. In: Meshaka, W.E., Collins, S.L., Bury, R.B., and McCallum, M.L. (Eds.). 2022. Exotic Amphibians and Reptiles of the United States. Gainesville, FL: University of Florida Press, pp. 65–89.

Bury, R.B. and Whelan, J.A. 1984. Ecology and management of the bullfrog. U.S. Department of the Interior, Fish and Wildlife Service. Resource Publication 155, 23 pp.

Bury, R.B. and Wolfheim, J.H. 1973. Aggression in free-living pond turtles (*Clemmys marmorata*). BioScience 23:659–662.

Bury, R.B., Germano, D.J., and Bury, G.W. 2010. Population structure and growth of the turtle *Actinemys marmorata* from the Klamath–Siskiyou ecoregion: age, not size, matters. Copeia 2010:443–451.

Bury, R.B., Welsh, H.H., Jr., Germano, D.J., and Ashton, D.T. (Eds.). 2012a. Western Pond Turtle: Biology, Sampling Techniques, Inventory and Monitoring, Conservation and Management. Seattle, Washington: Northwest Fauna 7, 128 pp.

Bury, R.B., Ashton, D.T., Welsh, H.H., Jr., Reese, D.A., and Germano, D.J. 2012b. Synopsis of biology. In: Bury, R.B., H.H. Welsh, Jr., D.J. Germano, and D.T. Ashton (Eds.). Western Pond Turtle: Biology, Sampling Techniques, Inventory and Monitoring, Conservation, and Management. Northwest Fauna 7, pp. 9–19.

Bury, R.B., Ashton, D.T., Germano, D.J., Karraker, N.E., Reese, D.A., and Schlick, K.E. 2012c. Sampling of turtles: trapping and snorkeling. In: Bury, R.B., Welsh, H.H., Jr., Germano, D.J., and Ashton, D.T. (Eds.). Western Pond Turtle: Biology, Sampling Techniques, Inventory and Monitoring, Conservation, and Management. Northwest Fauna 7, pp. 37–50.

Bury, R.B., Wehr, J.D., Bury, G.W., Baggett, C., and Doten, K. 2015. High incidence of filamentous algae on Western Pond Turtles, *Actinemys marmorata*, in the Willamette Valley, Oregon. Northwestern Naturalist 96:150–153.

Bury, R.B., Bury, G.W., Ashton, D.T., Bettaso, J., and Germano, D.J. 2019. Longevity of the Western Pond Turtle (*Actinemys marmorata*) based on studies over 50 years (Abstract). Northwestern Naturalist 100:136–137.

Bury, G.W., Bury, R.B., Ashton, D.T., Bettaso, J., and Germano, D.J. 2023. Age in a population of Northwestern Pond Turtles (*Actinemys marmorata*): long-lived individuals and averages (Abstract). Northwestern Naturalist 102:153.

Bury, R.B., Germano, D.J., and Ashton, D.T. In press. *Actinemys marmorata*. IUCN Red List of Threatened Species.

Buskirk, J.R. 1990. An overview of the Western Pond Turtle,

Clemmys marmorata. In: Beaman, K., Caporaso, F., McKeown, S., and Graff, M. (Eds.). Proceeding, First International Symposium on Turtles and Tortoises: Conservation and Captive Husbandry, pp. 16–23.

Buskirk, J.R. 2002. The Western Pond Turtle, *Emys marmorata*. Radiata 11:3–30.

Butler, C.J. 2019. A review of the effects of climate change on chelonians. Diversity 11(138):1–22.

Butler, C.J., Stanila, B.D., Iverson, J.B., Stone, P.A., and Bryson, M. 2016. Projected changes in climatic suitability for *Kinosternon* turtles by 2050 and 2070. Ecology and Evolution 6:7690–7705.

Cadi, A. and Joly, P. 2004. Impact of the introduction of the Red-eared Slider (*Trachemys scripta elegans*) on survival rates of the European Pond Turtle (*Emys orbicularis*). Biodiversity & Conservation 13:2511–2518.

Carr, A. 1952. Handbook of Turtles: The Turtles of the United States, Canada, and Baja California. Ithaca, NY: Cornell University Press, 542 pp.

Cary, W.M. 1889. Biennial Report of the Fish Commissioner of the State of Nevada 1887-1888. Carson City, Nevada: pp. 3–7.

Cayot, L.J. 2021. Española Island: from near extinction to recovery. In: Gibbs, J.P., Cayot, L.J., and Aquilera, W.T. (Eds.) Galapagos Giant Tortoises. London: Academic Press, pp. 435–450.

CBD [Center for Biological Diversity]. 2012. Petition to list 53 amphibians and reptiles in the United States as threatened or endangered under the Endangered Species Act. 454 pp. https://www.biologicaldiversity.org/campaigns/amphibian_conservation/pdfs/Mega_herp_petition_7-9-2012.pdf.

Cerreta, A.J., Reinhart, J.M., Forsythe, L.R., O'Connor, M.R., Tang, K.N., Cox, S., and Keller, K.A. 2023. Bioencapsulation is a feasible method of terbinafine administration in *Emydomyces testavorans*-infected Western Pond Turtles (*Actinemys marmorata*). American Journal of Veterinary Research 84:1–8.

Chapra, S.C., Boehlert, B., Fant, C., Bierman Jr., V.J., Henderson, J., Mills, D., Mas, D.M., Rennels, L., Jantarasami, L., Martinich, J., and Strzepek, K.M. 2017. Climate change impacts on harmful algal blooms in US freshwaters: a screening-level assessment. Environmental Science & Technology 51(16):8933–8943.

Christie, N.E. and Geist, N.R. 2017. Temperature effects on development and phenotype in a free-living population of Western Pond Turtles (*Emys marmorata*). Physiological and Biochemical Zoology 90:47–53.

Collins, J.T. and Taggart, T.W. 2002. Standard Common and Current Scientific Names for North American Amphibians, Turtles, Reptiles & Crocodilians. Lawrence, KS: Center for North American Herpetology, 44 pp.

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

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

Congdon, J.D., Breitenbach, G.L., van Loben Sels, R.C., and Tinkle, D.W. 1987. Reproduction and nesting ecology of Snapping Turtles (*Chelydra serpentina*) in southeastern Michigan. Herpetologica 43:39–54.

Congdon, J.D., Gibbons, J.W., Brooks, R.J., Rollinson, N., and Tsaliagos, R.N. 2012. Indeterminate growth in long-lived freshwater turtles as a component of individual fitness. Evolutionary Ecology 27:445–459.

Cook, D.G. and Martini-Lamb, J. 2004. Distribution and habitat use of Pacific Pond Turtles in a summer impounded river. Transactions of the Western Section of the Wildlife Society 40:84–89.

Cook, F.R., Campbell, R.W., and Ryder, G.R. 2005. Pacific Pond Turtle (*Actinemys marmorata*) in British Columbia. Wildlife Afield 2:58–63.

Cummings, K.L., Lovich, J.E., Puffer, S.R., Greely, S., Otahal, C.D., and Gannon, J. 2022. Injuries and abnormalities of the Southwestern Pond Turtle (*Actinemys pallida*) in the Mojave River of California. Western North American Naturalist 82:719–733.

Cushman, J.H. and Gaffney, K.A. 2010. Community-level consequences of invasion: impacts of exotic clonal plants on riparian vegetation. Biological Invasions 12:2765–2776.

Dahl, T.E. and Allord, G.J. 1996. History of Wetlands in the Conterminous United States. National Water Summary, Technical Aspects of Wetlands, US Geological Survey, 8 pp.

Dallara, A.Z. 2011. The role of maternal effect, incubation temperature, and gender of juvenile growth of captive-raised Western Pond Turtle hatchlings (*Emys marmorata*). M.S. Thesis, Sonoma State University, Rohnert Park, California.

Davidson, K.A. and Alvarez, J.A. 2020. A review and synopsis of nest site selection and site characteristics of Western Pond Turtles. Western Wildlife 7:42–49.

Diez, J.M., D'Antonio, C.M., Dukes, J.S., Grosholz, E.D., Olden, J.D., Sorte, C.J., Blumenthal, D.M., Bradley, B.A., Early, R., Ibáñez, I., and Jones, S.J. 2012. Will extreme climatic events facilitate biological invasions? Frontiers in Ecology and the Environment 10:249–257.

DoD [Department of Defense]. 2020. Recommended Best Management Practices for the Western Pond Turtle on Department of Defense Installations. Department of Defense, Partners in Amphibian and Reptile Conservation, 16 pp. https://www.denix.osd.mil/dodparc/denix-files/sites/36/2021/01/Pond-Turtles-BMP_Final_508_v2.pdf.

Dodd, C.K., Jr. 2013. Frogs of the United States and Canada. Baltimore, MD: John Hopkins University Press, 982 pp.

Dodd, C.K., Jr. and Jennings, M.R. 2021. How to raise a bullfrog: the literature on frog farming in North America. Bibliotheca Herpetologica 15:77–100.

Dodd, C.K., Jr. and Seigel, R.A. 1991. Relocation, repatriation and translocation of amphibians and reptiles: are they conservation strategies that work? Herpetologica 47:336–350.

Dupuis-Desormeaux, M., Lovich, J.E., and Gibbons, J.W. 2022. Re-evaluating invasive species in degraded ecosystems: a case study of Red-eared Slider turtles as partial ecological analogs. Discover Sustainability 3:15.

Dwire, K.A. and Kauffman, J.B. 2003. Fire and riparian ecosystems in landscapes of the western USA. Forest Ecology and Management 178:61–74.

Edmonds, D., Dreslik, M.J., Lovich, J.E., Wilson, T.P., and Ernst, C.H. 2021. Growing as slow as a turtle: unexpected maturational differences in a small, long-lived species. PloS One 16(11):e0259978.

Ernst, C.H. and Lovich, J.E. 2009. Turtles of the United States and Canada. Baltimore, Maryland: John Hopkins University Press, 827 pp.

Ernst, C.H., Lovich, J.E., and Barbour, R.W. 1994. Turtles of the United States and Canada. Washington DC: Smithsonian Institution Press, 578 pp.

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

Ewert, M.E., Jackson, D.R., and Nelson, C.E. 1994. Patterns of temperature-dependent sex-determination in turtles. Journal of Experimental Zoology 270:3–15.

Feldman, C.R. and Parham, J.F. 2001. Molecular systematics of emydine turtles. Chelonian Conservation and Biology 4:224–228.

Feldman, C.R. and Parham, J.F. 2002. Molecular phylogenetics of emydine turtles: taxonomic revision and the evolution of shell kinesis. Molecular Phylogenetics and Evolution 22:388–398.

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

Fidenci, P. 2000. Relationships between cattle grazing and the Western Pond Turtle *Clemmys marmorata* populations in Point Reyes National Seashore. M.S. Thesis, University of San Francisco, California.

Fidenci, P. 2005. *Actinemys marmorata* (Western Pond Turtle). Size. Herpetological Review 36:440.

Fisher, J.L. 2018. Archaeology and biogeography of the Western Pond Turtle (*Actinemys marmorata*) in the Puget Sound Region. Ethnobiology Letters 9:180–188.

Flaminio, K.P., Cox, S., Haman, K., Allender, M., Groves, B., and Court, M. 2022. Pharmacokinetics of nebulized terbinafine in plasma and keratin of Northwestern Pond Turtles (*Actinemys marmorata*) associated with emydomycosis. Journal of Herpetological Medicine and Surgery 32:48–55.

Fritz, U. and Havas, P. 2007. Checklist of Chelonians of the World. Vertebrate Zoology 57:149–368.

Fritz, U., Schmidt, C., and Ernst, C.H. 2011. Competing generic concepts for Blanding's, Pacific and European Pond Turtles (*Emydoidea, Actinemys* and *Emys*)—which is best? Zootaxa 791:41–53.

Fulton, A.M., Rose, J.P. and Halstead, B.J. 2022. Rural turtles: estimating the occupancy of Northwestern Pond Turtles and non-native Red-eared Sliders in agricultural habitats in California's Sacramento Valley and Sacramento-San Joaquin River Delta. Northwestern Naturalist 103:97–109.

Gallanty, E.A. 2021. Incubation temperature and maternal identity affect standard metabolism in Western Pond Turtles (*Actinemys marmorata*). M.S. Thesis, Sonoma State University, Rohnert Park, California.

Garcia, C., Montgomery, E., Krug, J., and Dagit, R. 2015. Removal efforts and ecosystem effects of invasive Red Swamp Crayfish (*Procambarus clarkii*) in Topanga Creek, California. Bulletin of the Southern California Academy of Sciences 114:12–21.

Geist, N.R., Dallara, Z., and Gordon, R. 2015. The role of incubation temperature and clutch effects in development and phenotype of head-started Western Pond Turtles (*Emys marmorata*). Herpetological Conservation and Biology 10:489–503.

Germano, D.J. 2000. Occurrence of a colonial protozoan on the Western Pond Turtle, *Clemmys marmorata*. Herpetological Natural History 7:67–71.

Germano, D.J. 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, D.J. 2012. Counting annuli and age determination. In: Bury, R.B., Welsh, H.H., Jr., Germano, D.J., and Ashton, D.T. (Eds.).Western Pond Turtle: Biology, Sampling Techniques, Inventory and Monitoring, Conservation, and Management. Northwest Fauna 7, pp. 125–126.

Germano, D.J. 2016. The ecology of a robust population of *Actinemys marmorata* in the San Joaquin Desert of California. Copeia 104:663–676.

Germano, D.J. 2020. Ecology of Northwestern Pond Turtles in a Sierran foothill population, California. California Fish and Wildlife Journal 106:260–267.

Germano, D.J. 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, D.J. In press. Surviving drought: Western Pond Turtles (*Actinemys*) persist at a pond after historic period of low rainfall. Knowledge and Management of Aquatic Ecosystems.

Germano, D.J. and Buchroeder, B. 2018. Predation of a Western Pond Turtle (*Actinemys marmorata*) by a Great Egret (*Ardea alba*). Western Wildlife 5:13–15.

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

Germano, D.J. and Bury, R.B. 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 Bury, R.B. 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.

Germano, D.J. and Riedle, J.D. 2015. Population structure, growth, survivorship, and reproduction of *Actinemys marmorata* from a high elevation site in the Tehachapi Mountains, California. Herpetologica 71:102–109.

Germano, D. J., Rathbun, G.B., Saslaw, L.R., Cypher, B.L., Cypher, E.A., and Vredenburgh, L. 2011. The San Joaquin Desert of California: ecologically misunderstood and overlooked. Natural Areas Journal 31:138–147.

Germano, D.J., Bury, R.B., and Welsh, H.H., Jr. 2012. Future research and management actions. In: Bury, R.B., Welsh, H.H., Jr., Germano, D.J., and Ashton, D.T. (Eds.).Western Pond Turtle: Biology, Sampling Techniques, Inventory and Monitoring, Conservation, and Management. Northwest Fauna 7, pp. 81–92.

Germano, D.J., Bury, R.B., and Bury, G.W. 2022. Growth rates and reproduction of Northwestern Pond Turtles in the Willamette Valley, Oregon. Northwestern Naturalist 103:110–117.

Germano, D.J., Bury, R.B., and Valdez-Villavicencio, J.H. 2026. *Actinemys pallida* (Seeliger, 1945) – Southwestern Pond Turtle. In: Rhodin, A.G.J., Iverson, J.B, van Dijk,P.P., Stanford, C.B., Goode, E.V, Buhlmann, K.A., and Mittermeier, R.A. (Eds.). Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs 5(20):134.1–17. doi: 10.3854/crm.5.134.pallida.v1.2026.

Germano, D.J., Bury, R.B., and Valdez-Villavicencio, J.H. In press. *Actinemys pallida*. IUCN Red List of Threatened Species.

Gervais, J.A., Rosenberg, D.K., Barnes, S., Puchy, C., and Stewart, E. 2009. Conservation Assessment for Western Painted Turtles in Oregon. Corvallis, Oregon: Oregon Wildlife Institute. Unpublished report, 61 pp. https://www.oregonwildlife.org/publication/conservation-assessment-for-the-western-painted-turtle-chrysemys-picta-bellii-in-oregon.

Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S., and Winne, C.T. 2000. The global decline of reptiles, déjà vu amphibians. BioScience 50:653–666.

Gist, D.H. and Jones, J.M. 1987. Storage of sperm in the reptilian oviduct. Scanning Microscopy 1(4):1839–1849.

Glibert, P.M. 2020. Harmful algae at the complex nexus of eutrophication and climate change. Harmful Algae 91:101583.

Glowaski, S.C. 2003. A comparison of growth rates of wild Rainbow Trout (*Oncorhynchus omyiss*) in the Upper Sacramento River before and after the Cantata Spill of 1991. M.S. Thesis, Humboldt State University, Arcata, California.

Gobler, C.J., 2020. Climate change and harmful algal blooms:

insights and perspective. Harmful Algae 91:101731.

Goodman, R.H. 1997a. The biology of the Southwestern 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.

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

Gordon, K. 1939. The Amphibia and Reptilia of Oregon. Oregon State University, Studies Zoology 1:1–82.

Gordon, R.A. 2009. Effects of incubation temperature on the embryonic development and hatching success of the Western Pond Turtle (*Emys marmorata*). M.S. Thesis, Sonoma State University, Rohnert Park, California.

Gray, E.M. 1995. DNA fingerprinting reveals a lack of genetic variation in northern populations of the Western Pond Turtle (*Clemmys marmorata*). Conservation Biology 9:1244–1255.

Green, N., Norwood, A., Sidhe, C., Mutlow, A., Aymen, J., Stiles, R., Bushell, J., Lim, T., Culver, E., Reeder, N., and Timmer, M. 2025. Shell lesion prevalence and bacteriome associations in threatened Western Pond Turtles (*Actinemys marmorata* and *Actinemys pallida*) in California, USA. Journal of Wildlife Diseases 61:574–586.

Gregory, K.M., Darst, C., Lantz, S.M., Powelson, K., Ashton, D., Fisher, R., Halstead, B., Hubbs, B., Lovich, J., and McGowan, C.P. 2024a. Population viability analysis for two species of imperiled freshwater turtle. Chelonian Conservation and Biology 23:1–12.

Gregory, K.M., Darst, C., Lantz, S.M., Powelson, K., and McGowan, C.P. 2024b. Effects of drought, invasive species, and habitat loss on future extinction risk of two species of imperiled freshwater turtle. Climate Change Ecology 7:100078.

Gregory, P.T. and Campbell, R.W. 1984. The Reptiles of British Columbia. Handbook British Columbia Provincial Museum 44, 103 pp.

Guderyahn, L.B. 2025. Multi-scale ecology of native freshwater turtles in the Pacific Northwest Ph.D. Dissertation, Portland State University, Portland, Oregon.

Hallock, L.A., McMillan, A., and Wiles, G.J. 2017. Periodic status review for the Western Pond Turtle in Washington. Olympia, WA: Washington Department of Fish and Wildlife, 18 pp.

Hallowell, E. 1854. Descriptions of new reptiles from California. Proceedings National Academy of Sciences, Philadelphia 7:91–97.

Haman, K., Hallock, L., Schmidt, T., Holman, E., and Murphie, B. 2019. Shell disease in Northwestern Pond Turtles (*Actinemys marmorata*) in Washington State, USA. Herpetological Review 50:495–502.

Harding, S.T. 1960. Water in California. Palo Alto, CA: N-P Publications, 231 pp.

Hay, O.P. 1903. Two new species of fossil turtles from Oregon. University of California Publication, Bulletin of Department of Geological Sciences 3:237–241.

Hayes, F.E., Turner, D.G., and Weidemann, D.E. 2018. Relative abundance of invasive Red-eared Sliders (*Trachemys scripta elegans*) and native Western Pond Turtles (*Emys marmorata*) at Clear Lake, Lake County, California. Chelonian Conservation and Biology 17:309–313.

Hayes, M.P. and Jennings, M.R. 1986. Decline of ranid frog species in western North America: are bullfrogs (*Rana catesbeiana*) responsible? Journal of Herpetology 20:490–509.

Hayes, M.P. and Tennant, M.R. 1985. Diet and feeding behavior of the California Red-legged Rrog, *Rana aurora draytonii* (Ranidae). Southwestern Naturalist 30:601–605.

Hays, D.W., McAllister, K.R., Richardson, S.A., and Stinson, D.W. 1999. Washington State Recovery Plan for the Western Pond Turtle. Seattle, WA: Washington Department of Fish and Wildlife, 66 pp.

Henny, C.J., Beal, K.F., Bury, R.B., and Goggans, R. 2003. Organochlorine pesticides, PCBs, trace elements and metals in Western Pond Turtle eggs from Oregon. Northwest Science 77:46–53.

Héritier, L., Valdeón, A., Sadaouui, A., Gendre, T., Ficheux, S., Bouamer, S., Kechemir-Issad, N., Du Preez, L., Palacios, C., and Verneau, O. 2017. Introduction and invasion of the Red-eared Slider and its parasites in freshwater ecosystems of southern Europe: risk assessment for the European Pond Turtle in wild environments. Biodiversity Conservation 26:1817–1843.

Hill, P.M. 2006. *Actinemys marmorata* (Western Pond Turtle). Neonates. Herpetological Review 37:76–77.

Holland, D.C. 1985a. *Clemmys marmorata* (Western Pond Turtle). Feeding. Herpetological Review 16(4):112–113.

Holland, D.C. 1985b. 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.

Holland, D C. 1988. *Clemmys marmorata* (Western Pond Turtle). Behavior. Herpetological Review 19:87–88.

Holland, D.C. 1992. Level and pattern in morphological variation: a phylogeographic study of the Western Pond Turtle (*Clemmys marmorata*). Ph.D. Dissertation, University of Southwestern Louisiana, Lafayette, Louisiana.

Holland, D.C. 1994. The Western Pond Turtle: Habitat and History. Portland, OR: U.S. Department of Energy, Bonneville Power Administration, DOE/BP-62137-1, 293 pp. https://www.osti.gov/biblio/171287.

Holley, J.P. 2021. An examination of limiting factors of *Chrysemys picta bellii* (Western Painted Turtles) in the Lower Willamette River Basin, Oregon. M.E.M. Thesis, Portland State University, Portland, Oregon.

Holman, J.A. and Fritz, U. 2001. A new emydine species from the Middle Miocene (Barstovian) of Nebraska, USA, with a new generic arrangement for the species of *Clemmys* sensu McDowell (1964) (Reptilia: Testudines: Emydidae). Zoologische Abhandlungen Staatliches Museum für Tierkunde Dresden 51:331–354.

Holte, D.L. 1998. Nest site characteristics of the Western Pond Turtle, *Clemmys marmorata*, at Fern Ridge Reservoir, in west central Oregon. M.S. Thesis, Oregon State University, Corvallis, Oregon.

Horn, R.B. and Gervais, J.A. 2018. Landscape influence on the local distribution of Western Pond Turtles. Ecosphere 9:e02346.

Hoyer, L.L., Hogan, E.K., Adamovicz, L., Allender, M.C., Terio, K.A., and Hernandez, A.G. 2023. Genome sequence of *Emydomyces testavorans* type strain 16-2883 (ATCC TSD-145), an onygenalean fungus associated with freshwater aquatic turtle shell lesions. Microbiology Resource Announcements 12(9):e00222–23.

Ihlow, F., Dambach, J., Engler, J.O., Flecks, M., Hartmann, T., Nekum, S., Rajaei, H., and Rödder, D. 2012. On the brink of extinction? How climate change may affect global chelonian species richness and distribution. Global Change Biology 18:1520–1530.

Ingles, L.G. 1930. A new species of *Telorchis* from the intestine of *Clemmys marmorata*. Journal of Parasitology 17:101–103.

Irwin, B.J., Wilberg, M.J., Jones, M.L. and Bence, J.R. 2011. Applying structured decision making to recreational fisheries management. Fisheries 36:113–122.

Iverson, J.B. 1991. Patterns of survivorship in turtles (order Testudines). Canadian Journal of Zoology 69:385–391.

Iverson, J.B. 2023. Reproductive output in the Pond Slider, *Trachemys scripta*, in Arkansas, USA, with range-wide comparisons. Chelonian Conservation and Biology 22:197–205.

Iverson, J.B., Meylan, P.A., and Seidel, M.E. 2017. Testudines—Turtles. In: Crother, B.I. (Ed.) Scientific and Standard English Names of Amphibians and Reptiles of North America North of Mexico (8th Ed.). Society for the Study of Amphibians and Reptiles. Herpetological Circular 43, pp. 82–91.

Janzen, F.J., Hoekstra, L.A., Brooks, R.J., Carroll, D.M., Gibbons, J.W., Greene, J.L., Iverson, J.B., Litzgus, J.D., Michael, E.D., Parren, S.G., Roosenburg, W.M., Strain, G.F., Tucker, J.K., and Ultsch, G.R. 2018. Altered spring phenology of North American freshwater turtles and the importance of representative populations. Ecology and Evolution 8:5815–5827.

Jennings, M.R. 1983. An annotated check list of the amphibians and reptiles of California. California Fish and Game 69:151–171.

Jennings, M.R. 1987. Annotated checklist of the amphibians and reptiles of California (2nd Ed.). Southwestern Herpetological Society, Special Publication No. 3, 48 pp.

Jennings, M.R. and Hayes, M.P. 1985. Pre-1900 overharvest of the California Red-legged Frog (*Rana aurora draytonii*): the inducement for bullfrog (*Rana catesbeiana*) introduction. Herpetologica 41:94–103.

Jennings, M.R. and Hayes, M.P. 1994. Amphibian and reptile species of special concern in California. Rancho Cordova, CA: California Department of Fish and Game, Inland Fisheries Division, 255 pp.

Johnson, J.H. 2004. Husbandry and medicine of aquatic reptiles. Seminars in Avian and Exotic Pet Medicine 13:223–228.

Johnson, M.L. 1995. Reptiles of the State of Washington (first published 1954). In: McAllister, K. (Ed.). Distribution of Amphibians and Reptiles in Washington. Northwest Fauna 3, pp. 4–79.

Jones, M.T. and Sievert, P.R. 2009. Effects of stochastic flood disturbance on adult wood turtles, *Glyptemys insculpta*, in Massachusetts. Canadian Field-Naturalist 123:313–322.

Kamoroff, C., Daniele, N., Grasso, R.L., Rising, R., Espinoza, T., and Goldberg, C.S. 2020. Effective removal of the American Bullfrog (*Lithobates catesbeianus*) on a landscape level: long term monitoring and removal efforts in Yosemite Valley, Yosemite National Park. Biological Invasions 22:617–626.

Karres, N. 2016. Diet and foraging ecology of an assemblage of Western Pond Turtles (*Actinemys marmorata*) living in two Northern California urban streams. M.S. Thesis, Sonoma State University, Rohnert Park, California.

Kats, L.B., Bucciarelli, G., Vandergon, T.L., Honeycutt, R.L., Mattiasen, E., Sanders, A., Riley, S.P., Kerby, J.L., and Fisher, R.N. 2013. Effects of natural flooding and manual trapping on the facilitation of invasive crayfish-native amphibian coexistence in a semi-arid perennial stream. Journal of Arid Environments 98:109–112.

Kauffmann, M. and Garwood, J. 2022. The Klamath Mountains: A Natural History. Kneeland, CA: Backcountry Press, 496 pp.

Keller, K.A., Guzman, D.S.M., Paul-Murphy, J., Byrne, B.A., Owens, S.D., Kass, P.H., and Weber III, E.S. 2012. Hematologic and plasma biochemical values of free-ranging Western Pond Turtles (*Emys marmorata*) with comparison to a captive population. Journal of Herpetological Medicine and Surgery 22:99–106.

Kemp, K.B., Blades, J.J., Klos, P.Z., Hall, T.E., Force, J.E., Morgan, P., and Tinkham, W.T. 2015. Managing for climate change on federal lands of the western United States: perceived usefulness of climate science, effectiveness of adaptation strategies, and barriers to implementation. Ecology and Society 20(2):17.

Krueger, C.J. and Janzen, F.J. 2023. On the origin of patterns of temperature-dependent sex determination. Evolution 77:1091–1100.

Kudela, R.M., Lane, J.Q., and Cochlan, W.P. 2008. The potential role of anthropogenically derived nitrogen in the growth of harmful algae in California, USA. Harmful Algae 8:103–110.

Lambert, A.M., D'Antonio, C.M., and Dudley, T.L. 2010. Invasive species and fire in California ecosystems. Fremontia 38:29–36.

Lambert, M.R., Nielsen, S.N., Wright, A.N., Thomson, R.C., and Shaffer, H.B. 2013. Habitat features determine the basking distribution of introduced Red-eared Sliders and native Western Pond Turtles. Chelonian Conservation and Biology 12:192–199.

Lambert, M.R., McKenzie, J.M., Screen, R.M., Clause, A.G., Johnson, B.B., Mount, G.G, Shaffer, H.B., and Pauly, G.B. 2019. Experimental removal of introduced slider turtles offers new insight into competition with a native, threatened turtle. PeerJ 7:e7444.

Lambert, M.R., Hernández-Gómez, O., Krohn, A.R., Mutlow, A., Patterson, L., Rosenblum, E.B., Timmer, M., Willis, J., and Bushell, J. 2021. Turtle shell disease fungus (*Emydomyces testavorans*): first documented occurrence in California and prevalence in free-living turtles. Ichthyology & Herpetology 109:958–962.

Lardie, R.L. 1975. Notes on eggs and young of *Clemmys marmorata marmorata* (Baird and Girard). Occasional Papers, Museum of Natural History, University of Puget Sound 47:654.

LaRivers, I. 1942. Some new amphibian and reptile records from Nevada. Journal of Entomology and Zoology 34:53–68.

Larson, E.R. and Olden, J.D. 2011. The state of crayfish in the Pacific Northwest. Fisheries 36:60–73.

Leatherman, B.M. and Jennings, M.R. 2007. *Actinemys marmorata* (Pacific Pond Turtle) and *Trachemys script elegans* (Red-eared Slider). Reproductive behavior. Herpetological Review 38:327.

Leidy, R.A., Bogan, M.T., Neuhaus, L., Rosetti, L., and Carlson, S.M. 2016. Summer die-off of Western Pond Turtle (*Actinemys marmorata*) along an intermittent coast range stream in central California. Southwestern Naturalist 61:71–74.

Litzgus, J.D. 2006. Sex differences in longevity in the Spotted Turtle (*Clemmys guttata*). Copeia 2006:281–288.

Lockington, W.N. 1879. Notes on some Reptiles and Batrachia of the Pacific Coast. American Naturalist 7:780–783.

Lopez, R.L. 2019. Use of DNA sequencing to identify the origin of Northwestern and Southern Pond Turtles in captive breeding programs. M.S. Thesis, California State University, Fresno, California.

Lovich, J.E., Ennen, J.R., Agha, M., and Gibbons, J.W. 2018. Where have all the turtles gone, and why does it matter? BioScience 68:771–781.

Lovich, J.E., Quillman, M., Zitt, B., Schroeder, A., Green, D.E., Yackulic, C., Gibbons, P., and Goode, E. 2017. The effects of drought and fire in the extirpation of an abundant semi-aquatic turtle from a lacustrine environment in the southwestern USA. Knowledge & Management of Aquatic Ecosystems 418(18):1–11.

Lowe, S., Browne, M., Boudjelas, S., and De Poorter, M. 2000. 100 of the world's worst invasive alien species: a selection from the global invasive species database. Vol. 12. International Union for the Conservation of Nature, Species Survival Commission:

IUCN SSC Invasive Species Specialist Group, 12 pp.

Lubcke, G.M. and Wilson, D. 2006. *Actinemys marmorata* (Pacific Pond Turtle). Size. Herpetological Review 37:339.

Lubcke, G.M. and Wilson, D. 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.

Manning, T. 1990. Summer feeding habits of River Otter (*Lutra canadensis*) on the Mendocino National Forest, California. Northwestern Naturalist 71:38–42.

Manzo, S., Nicholson, E.G., Devereux, Z., Fisher, R.N., Brown, C.W., Scott, P.A., and Shaffer, H.B. 2021. Conservation of Northwestern and Southwestern Pond Turtles: threats, population size estimates, and population viability analysis. Journal of Fish and Wildlife Management 12:485–501.

Martin, J., Runge, M.C., Nichols, J.D., Lubow, B.C., and Kendall, W.L. 2009. Structured decision making as a conceptual framework to identify thresholds for conservation and management. Ecological Applications 19:1079–1090.

Matsuda, B.M., Green, D.M., and Gregory, P.T. 2006. Amphibians and Reptiles of British Columbia. Victoria, Canada: Royal British Columbia Museum Handbook, 266 pp.

McKnight, D.T., Ard, K., Auguste, R.J., Barhadiya, G., Benard, M.F., Boban, P., Dillon, M.L., Downs, C.T., DeGregorio, B.A., Glorioso, B.M., Goodman, R.M., Hird, C., Hollender, E.C., Kennedy, M., Kidman, R.A., Massey, A., McGovern, P., Mühlenhaupt, M., Ostovar, K., Podgorski, D., Price, C., Reinke, B.A., Streeting, L.M., Venezia, J., Young, J., and Nordberg, E.J. 2023. Nocturnal basking in freshwater turtles: a global assessment. Global Ecology and Conservation 43:e02444.

Meshaka, W.E., Jr., Collins, S.L., Bury, R.B., and McCallum, M.L. 2022. Exotic Amphibians and Reptiles of the United States. Gainesville, FL: University Press of Florida, 245 pp.

Meyer, E., Sparling, D., and Blumenshine, S. 2013. Regional inhibition of cholinesterase in free-ranging Western Pond Turtles (*Emys marmorata*) occupying California mountain streams. Environmental Toxicology and Chemistry 32:692–698.

Meyer, E., Eagles-Smith, C.A., Sparling, D., and Blumenshine, S. 2014. Mercury exposure associated with altered plasma thyroid hormones in the declining Western Pond Turtle (*Emys marmorata*) from California mountain streams. Environmental Science & Technology 48:2989–2996.

Meyer, E., Eskew, E.A., Chibwe, L., Schrlau, J., Simonich, S.L.M., and Todd, B.D. 2016. Organic contaminants in Western Pond Turtles in remote habitat in California. Chemosphere 154:326–334.

Michell, K. and Michell, R.G. 2015. Use of radio-telemetry and recapture to determine the success of head-started Wood Turtles (*Glyptemys insculpta*) in New York. Herpetological Conservation and Biology 10:525–534.

Mitrus, S. and Hejduk, L. 2011. Extreme flows and possible threats to small populations of the European Pond Turtle. In: Banasik, K., Oygarden, L., and Henjdek, L. (Eds). Prediction and Reduction of Diffuse Pollution, Solid Emission and Extreme Flows in Rural Areas – Case Study of Agricultural Catchment. Warszawa, Poland: Wydawnictwo, SGGW, pp. 129–137.

Moldowan, P.D. 2023. Hyperpredation of freshwater turtles and tortoises by subsidized Corvids. Herpetological Monographs 37:70–94.

Montague, L.E., Marcotrigiano, J.M., Keane, N.E., Marquardt, H.E., Sevin, J.A., and Karraker, N.E. 2022. Online sale of small turtles circumvents public health regulations in the United States. PLoS One 17(12):e0278443.

Moore, S.K., Trainer, V.L., Mantua, N.J., Parker, M.S., Laws, E.A., Backer, L.C., and Fleming, L.E. 2008. Impacts of climate variability and future climate change on harmful algal blooms and human health. Environmental Health 7(Suppl. 2):1–4.

Moser, W.E., Quelvog, B.D., and Hovingh, P. 2005. First report of an eastern United States species of blood-feeding leech, *Placobdella parasitica* (Euhirudinea, Glossiphoniidae) in California. Proceedings of the California Academy of Science 56:91–92.

Moyle, P.B. 1973. Effect of introduced bullfrogs, *Rana catesbeiana*, on the native frogs of the San Joaquin Valley, California. Copeia 1973:18–22.

Mutlow, A., Wenninger, M., and Sim, R.R. 2023. *Emydomyces testavorans* Fact Sheet. American Association of Zoo Veterinarians, Infectious Disease Manual, 4 pp.

Neill, W.T. 1958. The occurrence of amphibians and reptiles in saltwater areas, and a bibliography. Bulletin of Marine Science of the Gulf and Caribbean 8:1–97.

Nicholson, E.G., Manzo, S., Devereux, Z., Morgan, T.P., Fisher, R.N., Brown, C., Dagit, R., Scott, P.A., and Shaffer, H.B. 2020. Historical museum collections and contemporary population studies implicate roads and introduced predatory bullfrogs in the decline of Western Pond Turtles. PeerJ 8:e9248.

Niemela, S.A. and Bury, R.B. 2012. Hatchlings of the Western Pond Turtle (*Actinemys marmorata*) in diet of Great Blue Heron (*Ardea herodias*). Northwestern Naturalist 93:84–85.

Nussbaum, R.A., Brodie, E.D., Jr., and Storm, R.C. 1983. Amphibians and Reptiles of the Pacific Northwest. Moscow, Idaho: University Press of Idaho, 322 pp.

ODFW [Oregon Department of Fish and Wildlife]. 1995. Yoncalla Creek diesel spill: joint environmental assessment and restoration plan. ODFW and US Fish and Service report, 34 pp.

ODFW [Oregon Department of Fish and Wildlife]. 2015. Guidance for Conserving Oregon's Native Turtles including Best Management Practices. Oregon Dept. of Fish and Wildlife. 99 pp. https://www.dfw.state.or.us/wildlife/living_with/docs/ODFW_Turtle_BMPs_March_2015.pdf.

ODFW [Oregon Department of Fish and Wildlife]. 2020. Visual Encounter Survey Protocol for Western Pond Turtles. Prepared by Samara Group and Oregon Native Turtle Working Group for ODFW, 27 pp. https://www.dfw.state.or.us/conservationstrategy/docs/Appendix_N_VES_Protocol_April_2020.pdf.

Ohba, S.Y. 2011. Field observation of predation on a turtle by a giant water bug. Entomological Science 14:364–365.

Omeyer, L.C., Fuller, W.J., Godley, B.J., Snape, R.T., and Broderick, A.C. 2018. Determinate or indeterminate growth? Revisiting the growth strategy of sea turtles. Marine Ecology Progress Series 596:199–211.

Otten, J.G., Williams, L., and Refsnider, J.M. 2023. Assessing translocation success and long-distance homing in riverine turtles 10 years after a freshwater oil spill. Conservation Science and Practice 5(4):e12922.

Parham, J.F. and Feldman, C.R. 2002. Generic revision of emydine turtles. Turtle and Tortoise Newsletter 6:28–30.

Patterson, L.C. 2006. Life history and ecology of an introduced population of Red-eared Sliders (*Trachemys scripta elegans*) in the Central Valley of California with implications for the conservation of the Western Pond Turtle (*Emys marmorata*). M.S. Thesis, California State University, Sacramento, California.

Pearl, C.A., Adams, M.J., and McCreary, B. 2013. Habitat and co-occurrence of native and invasive crayfish in the Pacific Northwest, USA. Aquatic Invasions 8:171–184.

Pearse, D.E., Janzen, F.J., and Avise, J.C. 2001. Genetic markers

substantiate long-term storage and utilization of sperm by female Painted Turtles. Heredity 86:378–384.

Peek, R.A., Kupferberg, S.J., Catenazzi, A., Georgakakos, P., and Power, M.E. 2021. *Actinemys marmorata* (Northwestern Pond Turtle) feeding on *Dicamptodon tenebrosus* (Coastal Giant Salamander). Northwestern Naturalist 102:261–264.

Petersen, C. and Round, J.L. 2014. Defining dysbiosis and its influence on host immunity and disease. Cellular Microbiology 16:1024–1033.

Phillips, A.J., Reilly, J., Ashton, D., Richardson, D.J., Sei, M., and Moser, W.E. 2025. Introduced *Placobdella parasitica* in the lower Rogue River, Oregon: origin story. Aquatic Invasions 20:251–272.

Phillips, K.P., Jorgensen, T.H., Jolliffe, K.G., Jolliffe, S.M., Henwood, J., and Richardson, D.S. 2013. Reconstructing paternal genotypes to infer patterns of sperm storage and sexual selection in the Hawksbill Turtle. Molecular Ecology 22:2301–2312.

Phillips, K.P., Mortimer, J.A., Jolliffe, K.G., Jorgensen, T.H., and Richardson, D.S. 2014. Molecular techniques reveal cryptic life history and demographic processes of a critically endangered marine turtle. Journal of Experimental Marine Biology and Ecology 455:29–37.

Pilliod, D.S., Welty, J.L., and Stafford, R. 2013. Terrestrial movement patterns of Western Pond Turtles (*Actinemys marmorata*) in central California. Herpetological Conservation and Biology 8:207–221.

Poff, B., Koestner, K.A., Neary, D.G., and Henderson, V. 2011. Threats to riparian ecosystems in western North America: an analysis of existing literature. Journal of the American Water Resources Association 47:1241–1254.

Polo-Cavia, N., Engstrom, T., López, P., and Martín, J. 2010. Body condition does not predict immunocompetence of Western Pond Turtles in altered versus natural habitats. Animal Conservation 13:256–264.

Pramuk, J., Koontz, F., Tirhi, M., Zeigler, S., Schwartz, K., and Miller, P. (Eds.). 2013. The Western Pond Turtle in Washington: A Population and Habitat Viability Assessment. Apple Valley, Minnesota: IUCN/SSC Conservation Breeding Specialist Group, 82 pp.

Prange, S., Gehrt, S.D., and Wiggers, E.P. 2003. Demographic factors contributing to high raccoon densities in urban landscapes. Journal of Wildlife Management 67:324–333.

Purcell, K.L., McGregor, E.L., and Calderala, K. 2017. Effects of drought on Western Pond Turtle survival and movement patterns. Journal of Fish and Wildlife Management 8:15–27.

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

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

Rawski, M., Mans, C., Kierończyk, B., Świątkiewicz, S., Barc, A., and Józefiak, D. 2018. Freshwater turtle nutrition – a review of scientific and practical knowledge. Annals of Animal Science 18:17–37.

RCC [Range-wide Conservation Coalition]. 2020. Western Pond Turtle Range-wide Management Strategy. 24 pp. https://www.fws.gov/node/263209.

Reese, D.A. 1996. Comparative demography and habitat use of Western Pond Turtles in northern California: the effects of damming and related alterations. Ph.D. Dissertation, University of California, Berkeley, California.

Reese, D.A. and Welsh, H.H., Jr. 1997. Use of terrestrial habitat by Western Pond Turtles, *Clemmys marmorata*: implications for management. In: Van Abbema, J. (Ed.). Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles - An International Conference. New York Turtle and Tortoise Society, pp. 352–357.

Reese, D.A. and Welsh, H.H., Jr. 1998a. Habitat use by Western Pond Turtles in the Trinity River, California. Journal of Wildlife Management 62:842–853.

Reese, D.A. and Welsh, H.H., Jr. 1998b. 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.

Refsnider, J.M., Garcia, J.A., Holliker, B., Hulbert, A.C., Nunez, A., and Streby, H.M. 2021. Effects of harmful algal blooms on stress levels and immune functioning in wetland-associated songbirds and reptiles. Science of the Total Environment 788(147790):1–8.

Reilly, J.M., Ashton, D.T., Holley, J.P., McClarnon, M.C, Moser, W.M., and Phillips, A.J. 2023. Rogue turtles with exotic leeches: Northwestern Pond Turtle (*Actinemys marmorata*) as a host for the Common North American Turtle Leech (*Placobdella parasitica*). Herpetological Conservation and Biology 18:529–539.

Rhodin, A.G.J., Stanford, C.B., van Dijk, P.P., Eisemberg, C., Luiselli, L., Mittermeier, R.A., Hudson, R., Horne, B.D., Goode, E.V., Kuchling, G., Walde, A., Baard, E.H.W., Berry, K.H., Bertolero, A., Blanck, T.E.G., Bour, R., Buhlmann, K.A., Cayot, L.J., Collett, S., Currylow, A., Das, I., Diagne, T., Ennen, J.R., Forero-Medina, G., Frankel, M.G., Fritz, U., García, G., Gibbons, J.W., Gibbons, P.M., Gong, S., Guntoro, J., Hofmeyr, M.D., Iverson, J.B., Kiester, A.R., Lau, M., Lawson, D.P., Lovich, J.E., Moll, E.O., Páez, V.P., Palomo-Ramos, R., Platt, K., Platt, S.G., Pritchard, P.C.H., Quinn, H.R., Rahman, S.C., Randrianjafizanaka, S.T., Schaffer, J., Selman, W., Shaffer, H.B., Sharma, D.S.K., Shi, H., Singh, S., Spencer, R., Stannard, K., Sutcliffe, S., Thomson, S., and Vogt, R.C. 2018. Global conservation status of turtles and tortoises (Order Testudines). Chelonian Conservation and Biology 17(2):135–161.

Riensche, D.L., Riensche, S.K., and Riensche, R.E. 2019. Habitat use, movement patterns, and nest site selection by Western Pond Turtles (*Actinemys marmorata*) in a managed central California rangeland pond. Northwestern Naturalist 100:90–101.

Rimple, R.J., Kohl, M.T., Buhlmann, K.A., and Tuberville, T.D. 2024. Translocation of long-term captive Eastern Box Turtles and the efficacy of soft-release: implications for turtle confiscations. Northeastern Naturalist 31:37–54.

Ringold, P.L., Magee, T.K., and Peck, D.V. 2008. Twelve invasive plant taxa in US western riparian ecosystems. Journal of the North American Benthological Society 27:949–966.

Roberts, H.P., Willey, L.L., Jones, M.T., Akre, T.S., King, D.I., Kleopfer, J., Brown, D.J., Buchanan, S.W., Chandler, H.C., deMaynadier, P., Winters, M., Erb, L., Gipe, K.D., Johnson, G., Lauer, K., Liebgold, E.B., Mays, J.D., Meck, J.R., Megyesy, J., Mota, J.L., Nazdrowicz, N.H., Oxenrider, K.J., Parren, M., Ransom, T.S., Rohrbaugh, L., Smith, S., Yorks, D., and Zarate, B. 2023. Is the future female for turtles? Climate change and wetland configuration predict sex ratios of a freshwater species. Global Change Biology 29:2643–2654.

Rose, T., Vickers, W.E., Cardenas, S.A., and Black, J.M. 2023. North American River Otter diet includes invasive Sacramento Pikeminnow, and herpetofauna on South Fork Eel River, northern California. Northwestern Naturalist 104:229–241.

Rosenberg, D.K. and Swift, R. 2013. Post-emergence behavior of hatchling Western Pond Turtles (*Actinemys marmorata*) in western Oregon. American Midland Naturalist 169:111–121.

Rosenberg, D.K., Gervais, J., Vesely, D., Barnes, S., Holts, L., Horn, R., Swift, R., Todd, L., and Yee, C. 2009. Conservation Assessment for Western Pond Turtles in Oregon. Corvallis, OR: Oregon Wildlife Institute, Unpublished Report, 60 pp. http://oregonwildlife.org/documents/wpt_cons_ass.pdf.

Rowe, C.L. 2008. The calamity of so long life: life histories, contaminants, and potential emerging threats to long-lived vertebrates. BioScience 58:623–631.

Ruane, S., Dinkelacker, S.A., and Iverson, J.B. 2008. Demographic and reproductive traits of Blanding's Turtles, *Emydoidea blandingii*, at the western edge of the species' range. Copeia 2008:771–779.

Ruso, G.E., Meyer, E., and Das, A.J. 2017. Seasonal and diel environmental conditions predict Western Pond Turtle (*Emys marmorata*) behavior at a perennial and an ephemeral stream in Sequoia National Park, California. Chelonian Conservation and Biology 16:20–28.

Russell, K.R., Van Lear, D.H., and Guynn, D.C., Jr. 1999. Prescribed fire effects on herpetofauna: review and management implications. Wildlife Society Bulletin 1999:374–384.

Scanlon, B.R., Reedy, R.C., Stonestrom, D.A., Prudic, D.E., and Dennehy, L.F. 2005. Impact of land use and land cover change on groundwater recharge and quality in the southwestern US. Global Change Biology 11:1577–1593.

Seeliger, L.M. 1945. Variation in the Pacific Mud Turtle, *Clemmys marmorata*. Copeia 1945:150–159.

Seidel, M. and Ernst, C.H. 2016. A systematic review of the turtle family Emydidae. Vertebrate Zoology 67:1–122.

Semlitsch, R.D. and Gibbons, J.W. 1989. Lack of Largemouth Bass predation of hatchling turtles (*Trachemys scripta*). Copeia 1989:1030–1031.

Shaffer, H.B. and Scott, P.A. 2019. Assessment for the Western Pond Turtle. Final report to U. S. Fish and Wildlife Service, by University of California, Los Angeles, 116 pp. https://www.ioes.ucla.edu/wp-content/uploads/2021/04/UCLA-IoEs-Practicum-USFWS-Native-Turtle-Final-Report-2019v3.pdf.

Shaffer, H.B. and Scott, P.A. 2022. Summary of *Actinemys* population genetic results provided to the USFWS. Report, posted in the federal register with the proposed ESA listing. UCLA and Eckerd College, 22 pp. https://www.regulations.gov/document/FWS-R8-ES-2023-0092-16387.

Siddall, M.E. and Desser, S.S. 2001. Transmission of *Haemogregarina balli* from Painted Turtles to Snapping Turtles through the leech *Placobdella ornata*. Journal of Parasitology 87:1217–1218.

Silbernagel, C., Clifford, D.L., Bettaso, J., Worth, S., and Foley, J. 2013. Prevalence of selected pathogens in Western Pond Turtles and sympatric introduced Red-eared Sliders in California, USA. Diseases of Aquatic Organisms 107:37–47.

Sim, R.R., Ossiboff, R.J., Nelson, J., and Oddo, T. 2021. Emydid herpesvirus 1 infections in Western Pond Turtles (*Actinemys marmorata*) and a Red-eared Slider (*Trachemys scripta elegans*) with fatal and nonfatal outcomes. Journal of Zoo and Wildlife Medicine 52:1275–1279.

Sims, S.A., Hilberg, L.E., Reynier, W.A., and Kershner, J.M. 2019. Northwestern Pond Turtle (*Actinemys marmorata*): Northern California Climate Change Vulnerability Assessment Synthesis. Version 1.0. Bainbridge Island, WA: EcoAdapt, 31 pp. https://www.cakex.org/documents/northwestern-pond-turtle-climate-change-vulnerability-assessment-northern-california.

Slater, J.R. 1962. Variations and new range of *Clemmys marmorata*. Occasional Papers, Museum of Natural History, University of Puget Sound 20:204–205.

Sloan, L.M. 2012. Population structure, life history, and terrestrial movements of Western Pond Turtles (*Actinemys marmorata*) in lentic habitats along the Trinity River, California. M.S. Thesis, Humboldt State University, Arcata, California.

Smith, H.M. 1895. Notes on a reconnaissance of the fisheries of the Pacific coast of the United States in 1894. Bulletin U.S. Fisheries Commission 14:223–288.

Smith, P.C. 2015. First do no harm: recognizing and mitigating the risk of disease introduction associated with chelonian head-starting initiatives. Herpetological Conservation and Biology 10:550–558.

Snover, M.L and Adams, M.J. 2016. Herpetological Monitoring and Assessment on the Trinity River in Trinity County, California: Final Report. No. 2016-1089. United States Geological Survey in cooperation with the Trinity River Restoration Program, 121 pp. https://pubs.usgs.gov/of/2016/1089/ofr20161089.pdf.

Snover, M.L., Adams, M.J., Ashton, D.T., Bettaso, J.B. and Welsh, H.H., Jr. 2015. Evidence of counter-gradient growth in Western Pond Turtles (*Actinemys marmorata*) across thermal gradients. Freshwater Biology 60:1944–1963.

Spinks, P.Q. and Shaffer, H.B. 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.

Spinks, P.Q. and Shaffer, H.B. 2009. Conflicting mitochondrial and nuclear phylogenies for the widely disjunct *Emys* (Testudines: Emydidae) species complex, and what they tell us about biogeography and hybridization. Systematic Biology 58:1–20.

Spinks, P.Q., Pauly, G.B., Crayon, J.J., and Shaffer, H.B. 2003. Survival of the Western Pond Turtle (*Emys marmorata*) in an urban California environment. Biological Conservation 113:257–267.

Spinks, P.Q., Thomson, R.C., and Shaffer, H.B. 2010. Nuclear gene phylogeography reveals the historical legacy of an ancient inland sea on lineages of the Western Pond Turtle, *Emys marmorata* in California. Molecular Ecology 19:542–556.

Spinks, P.Q., Thomson, R.C., and Shaffer, H.B. 2014. The advantages of going large: genome-wide SNPs clarify the complex population history and systematics of the threatened Western Pond Turtle. Molecular Ecology 23:2228–2241.

St. Clair, T. and Burns, R. 2013. Decision support system literature review and potential implementation scenarios for the Trinity River Restoration Program. Report to the Trinity River Restoration Program by Atkins (consultants), 66 pp. https://www.trrp.net/library/document?id=2115.

Stebbins, R.C. 1954. Amphibians and Reptiles of Western North America. New York, NY: McGraw-Hill, 528 pp.

Stebbins, R.C. 2003. A Field Guide to Western Reptiles and Amphibians. Boston, MA: Houghton-Mifflin Co., 533 pp.

Steen, D.A., Aresco, M.J., Beilke, S.G., Compton, B.W., Condon, E.P., Dodd, C.K, Jr., Forrester, H., Gibbons, J.W., Greene, J.L., Johnson, G., and Langen, T.A. 2006. Relative vulnerability of female turtles to road mortality. Animal Conservation 9:269–273.

Stephens, P.R. and Wiens, J.J. 2003. Ecological diversification and phylogeny of emydid turtles. Biological Journal of the Linnean Society 79:577–610.

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.

Strauch, A. 1862. Chelonologische Studien. Memoires L'Acadamie Science St. Petersbourg (ser. 7) 5:1–196.

Studebaker, R.S. 2008. Natural history notes: *Actinemys marmorata* (Western Pond Turtle). Predation attempt. Herpetological Review 39:463–464.

Taggart, T.W. and Carr, J. 2025. Testudines – Turtles. In: Nicholson, K.E. (Ed.). Scientific and Standard English Names of Amphibians and Reptiles of North America North of Mexico, with Comments Regarding Confidence in Our Understanding. (9th Ed.). Society for the Study of Amphibians and Reptiles, pp. 55–63.

Terry, D. 2018. Comparison of growth rates of soft release and hard release in a founder population of Northwestern Pond Turtles (*Actinemys marmorata*). M.S. Thesis, Sonoma State University, Rohnert Park, California.

Tezak, B., Sifuentes-Romero, I., Milton, S., and Wyneken, J. 2020. Identifying sex of neonate turtles with temperature-dependent sex determination via small blood samples. Nature, Scientific Reports 10(1):5012.

TFTSG [Tortoise and Freshwater Turtle Specialist Group]. 1996. *Actinemys marmorata*. The IUCN Red List of Threatened Species 1996: e.T4969A11104202.

Thatcher, V.E. 1954. Helminth parasites of the Pacific Terrapin *Clemmys marmorata* (Baird and Girard). M.A. Thesis, Oregon State University, Corvallis, Oregon.

Thomason, C.A., Mullen, N., Belden, L.K., May, M., and Hawley, D.M. 2017. Resident microbiome disruption with antibiotics enhances virulence of a colonizing pathogen. Nature, Scientific Reports 7(16177):1–8.

Thomson, R.C., Spinks, P.Q., and Shaffer, H.B. 2010. Distribution and abundance of invasive Red-eared Sliders (*Trachemys scripta elegans*) in California's Sacramento River Basin and possible impacts on native Western Pond Turtles (*Emys marmorata*). Chelonian Conservation and Biology 9:297–302.

Thomson, R.C., Wright, A.N., and Shaffer, H.B. 2016. California Amphibian and Reptile Species of Special Concern. Oakland, CA: University of California Press, 390 pp.

Thomson, R.C., Spinks, P.Q., and Shaffer, H.B. 2021. A global phylogeny of turtles reveals a burst of climate-associated diversification on continental margins. Proceedings of the National Academy of Sciences 118:e2012215118.

Todd, B.D., Jenkinson, T.S., Escalona, M., Beraut, E., Nguyen, O., Sahasrabudhe, R., Scott, P.A., Toffelmier, E., Wang, I.J., and Shaffer, H.B. 2022. Reference genome of the Northwestern Pond Turtle, *Actinemys marmorata*. Journal of Heredity 113:624–631.

Tu, B. and Trulio, L. 2022. Livestock ponds as long-term habitat for Southwestern Pond Turtles (*Actinemys pallida*) in rangeland landscapes. Chelonian Conservation and Biology 21:277–282.

TTWG [Turtle Taxonomy Working Group: Rhodin, A.G.J., Iverson, J.B., Bour, R., Fritz, U., Georges, A., Shaffer, H.B., and van Dijk, P.P.]. 2021. Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status (9th Ed.). In: Rhodin, A.G.J., Iverson, J.B., van Dijk, P.P., Stanford, C.B., Goode, E.V., Buhlmann, K.A., and Mittermeier, R.A. (Eds.). Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs 8:1–472.

TTWG [Turtle Taxonomy Working Group: Rhodin, A.G.J., Iverson, J.B., Fritz, U., Gallego-García, N., Georges, A., Shaffer, H.B., and van Dijk, P.P.]. 2025. Turtles of the World: Annotated Checklist and Atlas of Taxonomy, Synonymy, Distribution, and Conservation Status (10th Ed.). In: Rhodin, A.G.J., Iverson, J.B., van Dijk, P.P., Stanford, C.B., Goode, E.V., Buhlmann, K.A., and Mittermeier, R.A. (Eds.). Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs 10:1–575.

Ultsch, G.R. 2006. The ecology of overwintering among turtles: where turtles overwinter and its consequences. Biological Reviews 81:339–367.

USCDC [United States Center for Disease Control]. 2015. Menu of state turtle-associated salmonellosis laws. Office for State, Tribal, Local, and Territorial Support, Centers for Disease Control and Prevention, 13 pp. https://www.cdc.gov/phlp/docs/turtle-menu.pdf.

USFDA [United States Food and Drug Administration]. 1975. Control of communicable diseases: turtles intrastate and interstate requirements. Code of Federal Regulations 1975;21CFR1240.62.

USFWS [United States Fish and Wildlife Service]. 1993. Endangered and Threatened Wildlife and Plants; notice of 1-year petition finding on the Western Pond Turtle. 50 CFR, Part 17; 58(153):42717–42718.

USFWS [United States Fish and Wildlife Service]. 2015. Notice of petition findings and initiation of status reviews. Federal Register 80(69):19259–19263.

USFWS [United States Fish and Wildlife Service]. 2023a. Endangered and Threatened Wildlife and Plants: Threatened Species Status with Section 4(d) Rule for the Northwestern Pond Turtle and Southwestern Pond Turtle. Proposed Rule. Federal Register 88(190):68370–683999. https://www.regulations.gov/document/FWS-R8-ES-2023-0092-0001.

USFWS [United States Fish and Wildlife Service]. 2023b. Species status assessment report for the Northwestern Pond Turtle (*Actinemys marmorata*) and Southwestern Pond Turtle (*Actinemys pallida*), Version 1.1. Ventura, CA: U.S. Fish and Wildlife Service, Ventura Fish and Wildlife Office, 139 pp. https://www.regulations.gov/document/FWS-R8-ES-2023-0092-0028.

USFWS [United States Fish and Wildlife Service]. 2025. Endangered and Threatened wildlife and plants; Threatened Species Status with Section 4(d) Rule for the Northwestern Pond Turtle and Southwestern Pond: Long-term Actions. RIN: 1018-BH08. https://www.reginfo.gov/public/do/eAgendaViewRule?pubId=202504&RIN=1018-BH08&operation=OPERATION_PRINT_RULE.

Vander Haegen, W.M., Clark, S.L., Perillo, K.M., Anderson, D.P., and Allen, H.L. 2009. Survival and causes of mortality of head-started Western Pond Turtles on Pierce National Wildlife Refuge, Washington. Journal of Wildlife Management 73:1402–1406.

Vogt, R.C. and Bull, J.J. 1982. Temperature controlled sex-determination in turtles: ecological and behavioral aspects. Herpetologica 38:158–164.

White, A., Giannetto, M., Mulla, L., Del Rosario, A., Lim, T., Culver, E., Timmer, M., Bushell, J., Lambert, M.R., and Hernández-Gómez, O. 2023. Bacterial communities of the threatened Western Pond Turtle may be impacted by land use. FEMS Microbiology Ecology 99:fiad143, 11 pp.

Wilcox, J.T. 2019. *Actinemys marmorata* (Northern Pond Turtle). Diet. Herpetological Review 50:553.

Wilcox, J.T. and Alvarez, J.A. 2023. Turtles (*Actinemys marmorata*) under ice. Western Wildlife 10:42–46.

Woodburn, D.B., Miller, A.N., Allender, M.C., Maddox, C.W., and Terio, K.A. 2019. *Emydomyces testavorans*, a new genus and species of onygenalean fungus isolated from shell lesions of freshwater aquatic turtles. Journal of Clinical Microbiology 57:10.1128/jcm.00628-18, 11 pp.

Woodburn, D.B., Kinsel, M.J., Poll, C.P., Langan, J.N., Haman, K., Gamble, K.C., Maddox, C., Jeon, A.B., Wellehan, J.F., Ossiboff, R.J., and Allender, M.C. 2021. Shell lesions associated with *Emydomyces testavorans* infection in freshwater aquatic turtles. Veterinary Pathology 58:578–586.

Woodruff, S.M., Grasso, R.L., Halstead, B.J., and Todd, B.D. 2025. Effects of American Bullfrogs and their removal on Northwestern Pond Turtles. Biological Conservation 305:111090.

Wright, T.L., Gjeltema, J., Wack, R.F., Woodburn, D., and Tell, L.A. 2021. Plasma voriconazole concentrations following single- and multiple-dose subcutaneous injections in Western Pond Turtles (*Actinemys marmorata*). Journal of Zoo and Wildlife Medicine 52:538–547.

Wu, Z., Li, Y., Wang, Y., and Adams, M.J. 2005. Diet of introduced Bullfrogs (*Rana catesbeiana*): predation on and diet overlap with native frogs on Daishan Island, China. Journal of Herpetology 39:668–674.

Yamamoto, Y. 2010. Contribution of bioturbation by the Red Swamp Crayfish *Procambarus clarkii* to the recruitment of bloom-forming cyanobacteria from sediment. Journal of Limnology 69:102–111.

Yarnal, C. 2019. Best management practices for the conservation of Western Pond Turtle populations in California. M.S. Thesis, University of San Francisco, California.

Yntema, C.L. 1970. Observations on females and eggs of the Common Snapping Turtle, *Chelydra serpentina*. American Midland Naturalist 84:69–76.

Zaragoza, G., Rose, J.P., Purcell, K., and Todd, B.D. 2015. Terrestrial habitat use by Western Pond Turtles (*Actinemys marmorata*) in the Sierra foothills. Journal of Herpetology 49:437–441.

Citation Format for this Account:

Bury, R.B., Germano, D.J, and Ashton, D.T. 2026. *Actinemys marmorata* (Baird and Girard 1852) – Northwestern Pond Turtle. In: Rhodin, A.G.J., Iverson, J.B., van Dijk, P.P., Stanford, C.B., Goode, E.V., Buhlmann, K.A., and Mittermeier, R.A. (Eds.). Conservation Biology of Freshwater Turtles and Tortoises: A Compilation Project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group. Chelonian Research Monographs 5(20):135.1–36. doi: 10.3854/crm.5.135.marmorata.v2.2026; www.iucn-tftsg.org/cbftt/.