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The Olympic Shrew (*Sorex rohweri*) near Easton, Washington, USA. (Photographed by Jordan Ryckman).

CONTENTS

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The Editors of *Western Wildlife* would like to acknowledge the following biologists for their expert reviews since the inauguration of the journal in 2014. Your efforts, dedication, and professionalism have ensured that *Western Wildlife* continues to be an outlet for the ecology, natural history, management, and conservation biology of animals in western North America.

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NOTES

NEST DESCRIPTIONS FOR BIRDS OF SUB-ALPINE MEADOWS IN THE TRINITY ALPS WILDERNESS, CALIFORNIA

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Abstract.—**Descriptive studies are foundational for ecological models and theories and for conservation efforts, and the lack of accurate descriptive studies on wildlife populations can lead to mismanagement of species. The Trinity Alps Wilderness of northern California lacks any published description of the current breeding bird communities. I found nests opportunistically in sub-alpine meadows by observing behavior, accidental flushing, and systematic searching. Once the nest was inactive, I recorded nest material, nest dimensions, and nest microhabitat. I found 25 nests of seven species. The most common species of nests that I found were Lincoln's Sparrows (*Melospiza lincolnii*) and Dark-eyed Juncos (*Junco hyemalis*). I found Lincoln's Sparrow nests much closer to water than previously described in the literature, and they commonly left one egg unhatched and unviable in the nest. Some of the dimensions of nests differed from what is published in other areas. These data add to our knowledge of bird nesting in the Trinity Alps.**

Key Words.—baseline; birds; meadow; montane; monitoring; subalpine

Descriptive scientific studies have been foundational for ecological models and theories. These types of studies supported development of accepted concepts of biogeography and evolution, and they have helped us understand how communities change over time (Dayton and Sala 2001). As ecosystems are stressed by development, invasive species, and climate change, we are often left without an understanding of what the communities were like prior to their modification (Pitcher 2001). While conducting amphibian monitoring surveys for the California Department of Fish and Wildlife, I often accidentally flushed breeding birds off their nests. I describe the species, microhabitats, and construction materials of the nests I found.

I found nests in various sub-alpine meadows contained in two basins (Echo Lake Basin and Siligo Basin) within the Trinity Alps Wilderness in the Klamath Mountains (Fig. 1). The Klamath Mountains Bioregion ranges from northern California to south-eastern Oregon. In California, it lies between the northern California coast on the west and the southern Cascade Range to the east. The region has the most diverse conifer forests in North America (Skinner et al. 2006). The climate is Mediterranean, which is characterized by cool, wet winters and dry, warm summers. The proximity to the Pacific Ocean creates a moisture and temperature gradient that leads to patterns of precipitation via orographic effects producing occasional summer rains. Precipitation average is 101 cm annually with most rainfall between October and April (Skinner et al. 2006). The average snowpack by 1 April is 259 cm at an elevation of 2,042 m (Skinner et al. 2006). The diverse parent rock types of the region including mixtures of granite and peridotite rock creating vegetation patterns more complex than found in the Sierra Nevada or the Cascade Range (Sawyer and Thornburg 1977). The Upper Montane and Subalpine Forest include tree species such as Shasta Red Fir (*Abies magnifica* var. *shastensis*), Mountain Hemlock (*Tsuga mertensiana*), Western White Pine (*Pinus monticola*), and Foxtail Pine (*Pinus balforiana*). Common understory shrubs are manzanita (*Arcostaphilus* spp.), Huckleberry Oak (*Quercus vaccinifolia*), and Mountain Spiraea (*Spiraea densiflora*). In the meadows, the dominant plant are sedges (*Carex* spp.), interspersed with Cobra Lily (*Darlingtonia californica*) and White Rush Lily (*Hastingsia alba*) growing in the fens.

I conducted surveys at 12 sites in 2016: six sites were in the Echo Lake Basin and six in Silago Basin (Fig. 1). Sites ranged from 1,800 to 2,100 m elevation; Penthouse, Echo Lake, and Snowmelt Pond were at higher elevations. I located most nests while conducting amphibian and reptile Visual Encounter Surveys that involved walking along the perimeter of ponds or streams, and when water was not present, walking in a zig-zag pattern covering the entire meadow. I found most bird nests by accidentally flushing the parent bird off the nest; otherwise, I noticed the behavior of a parent bird and followed it to the nest. These methods are similar to those used by Martin and Guepel (1993) and the Breeding Biology Research and Monitoring Database (BBIRD).

Once I located a nest, I recorded the nest location with a handheld GPS unit (UTM NAD 27 CONUS). I only used flagging if necessary, which I placed 20 m away or more to avoid predator association and increased predation. I approached nests and left them in a different direction and I did not approach an active nest if I knew potential predators were present or watching. For each nest, I recorded species, date, and nesting stage (building, laying, incubation, nestling). To avoid birds abandoning active

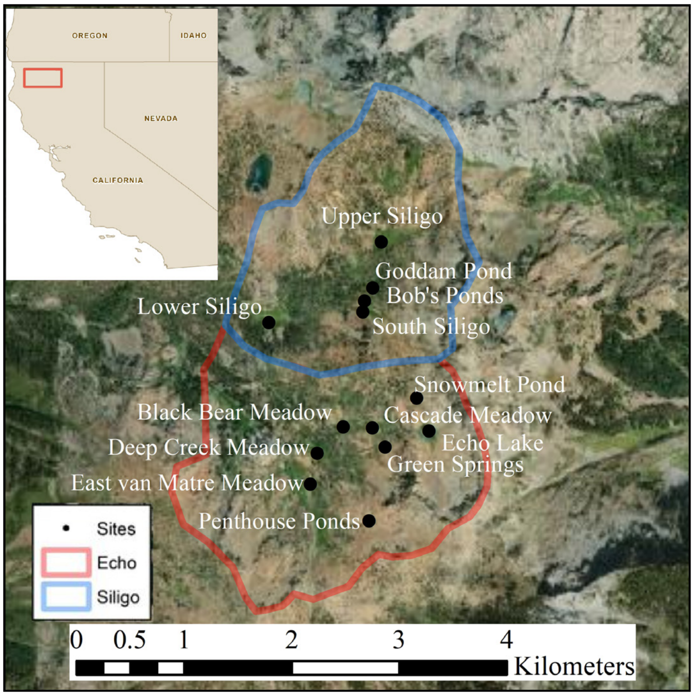

Figure 1. The study area with the names of specific study sites in the Trinity Alps Wilderness, California (insert).

nests, I measured nests after nesting was completed and young were fledged.

After the nest was inactive (e.g., nestlings fledged), I recorded the materials used in nest construction, taking samples of materials for identification when necessary. I measured the width (edge or rim to edge of rim), height (top of nest to base of nest), cup width (inner rim of nest to inner rim), and cup depth (base of nest cup to top rim) using millimeter calipers. I collected data on nest location including nest height (visually estimated) and plant species used as the nest substrate. I recorded the objects concealing the nest (cover type), height of the grass, shrubs or trees the nest was in, distance from trunk, and distance of nest from foliage edge.

I located nests of seven species: Lincoln's Sparrow (*Melospiza lincolnii*), Dark-eyed Junco (*Junco hyemalis*), American Robin (*Turdus migratorius*), Sooty Grouse (*Dendragapus fuliginosus*), Mallard (*Anus platyrhynchos*), Audubon's Yellow-rumped Warbler (*Setophaga coronate auduboni*), and Green-tailed Towhee (*Pipilo chlorurus*). The most nests I found were those of Lincoln's Sparrows and Dark-eyed Juncos (Table 1). I found 15 Lincoln's Sparrow nests between 14 June and 23 July. Most were associated with wet sedge as cover and substrate type, and nest material was composed of dry sedge (Fig. 2). Average distance to water of Lincoln's Sparrow nests was 0.4 m, and average grass height was 45.0 cm around nests (Table 2). The Lincoln Sparrow nests I observed were similar to published studies that reported the nest microsites being wetter than that used by other species, including Dark-eyed Junco (Hadley 1970; Ammon 1995). Even though Ammon (1995) found no significant association of nest

Table 1. Average (± standard deviation) and range (in parentheses) of nest dimensions (except for nests of n = 1) of Lincoln's Sparrow (*Melospiza lincolnii*; LISP), Green-tailed Towhee (*Pipilo chlorurus*; GTTO), Dark-eyed Junco (*Junco hyemalis*; DEJU), Mallard (*Anus platyrhynchos*; MALL), Sooty Grouse (*Dendragapus fuliginosus*; SOGR), American Robin (*Turdus migratorius*; AMRO), and Audubon's Yellow-rumped Warbler (*Setophaga coronate auduboni*; YRWA) in the Trinity Alps, California.

Species	Number Observed	Mean Cup Width (mm)	Mean Cup Depth (mm)	Mean Nest Width (mm)	Mean Nest Height (mm)
AMRO	2	98.0 ± 6.7 (91.3–104.7)	72.2 ± 0/7 (71.5–72.8)	126.7 ± 13.2 (113.5–139.9)	85.3 ± 12.5 (72.8–97.7)
DEJU	3	62.4 ± 8.4 (51.3–72.0)	50.7 ± 13.1 (32.6–63.0)	86.0 ± 5.1 (79.6–92.1)	47.9 ± 6.2 (42.7–56.6)
GTTO	2	61.7 ± 2.5 (59.1–64.2)	51 ± 3 (29.9–35.6)	119.1 ± 19.1 (100.0–138.2)	32.6 ± 3.0 (29.6–35.6)
LISP	15	60.5 ± 5.6 (48.1–71.4)	32.6 ± 12.2 (45.0–90.0)	96.8 ± 8.1 (81.7–105.2)	62. 4 ± 14.7 (45.6–90.2)
MALL	1	170.0	75.5	290.0	76.0
SOGR	1	145.4	71.8	305.0	79.0
YRWA	1	79.5	35.3	139.0	98.0

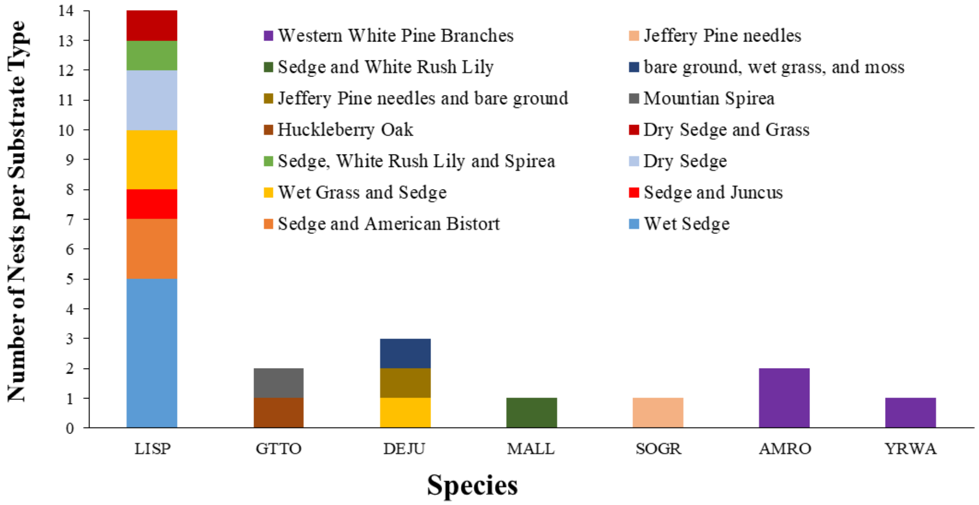

Figure 2. Number of nests of Lincoln's Sparrow (*Melospiza lincolnii*; LISP), Green-tailed Towhee (*Pipilo chlorurus*; GTTO), Dark-eyed Junco (*Junco hyemalis*; DEJU), Mallard (*Anus platyrhynchos*; MALL), Sooty Grouse (*Dendragapus fuliginosus*; SOGR), American Robin (*Turdus migratorius*; AMRO), and Audubon's Yellow-rumped Warbler (*Setophaga coronate auduboni*; YRWA) found the various vegetative substrates in the Echo Lake and Siligo basins in the Trinity Alps, California.

site with perch trees or other microhabitat features, I found Lincoln's Sparrow nests associated with water features such as ponds, lakes, and streams. Heights of grass cover were similar to published data showing shrub cover that is usually < 60 cm (Ammon 1995). The nest measurements of Lincoln's Sparrow (Table 1) did not differ substantially from the published data from Colorado (Ammon 1995).

Of the three Dark-eyed Junco nests I found between 25 May and 10 July, two were in creek cut banks and the other was among rock and Mountain Spiraea on a glacial moraine. All three Dark-eyed Junco nests I found were most associated with wet grass, Jeffrey Pine (*Pinus jeffreyi*) needles, and moss for the substrate type (Fig. 2). Dark-eyed Junco nests were composed of a variety of sedge, pine needles, hair, and fine roots. Dimensions of Dark-eyed Junco nests (Table 1) were larger than those of Peck and James (1987, 1998). This was possibly due to latitudinal effects because published measurements were collected in Ontario, Canada. Differences in nest size could reflect the possible larger size of the individuals in this colder climate (i.e., Bergmann's Rule).

I found two American Robin nests between 5–7 August in the crowns of Western White Pine trees (Fig. 2), and nests were made from Huckleberry Oak twigs, sedges, grasses (Poaceae), and mud. Robins nested higher off the ground than any other species nests I measured (Table 2). The American Robin nests had slightly greater nest widths and nest heights, yet smaller cup depths and cup widths (Table 1), than nests from published data in New York (Howell 1942). I think the nest height differences are related to the stunted tree heights in the Trinity Alps due to elevational effects and heavy snowpack during the winter.

I found one Sooty Grouse nest 25 May at the base of a small Western White Pine and a large Jeffrey Pine on the edge of a small meadow (Fig. 2). The branches and trunk of both trees covered the nest from above and about 50%

Table 2. Average (± standard deviation) and range (in parentheses) of nest microhabitats, (except for nests of n = 1) of Lincoln's Sparrow (*Melospiza lincolnii*; LISP), Green-tailed Towhee (*Pipilo chlorurus*; GTTO), Dark-eyed Junco (*Junco hyemalis*; DEJU), Mallard (*Anus platyrhynchos*; MALL), Sooty Grouse (*Dendragapus fuliginosus*; SOGR), American Robin (*Turdus migratorius*; AMRO), and Audubon's Yellow-rumped Warbler (*Setophaga coronate auduboni*; YRWA) in the Trinity Alps Wilderness, California. Distance from Trunk not applicable (NA) to ground nesting birds. Plant cover height not applicable (NA) for tree nesting birds.

Species	Number Observed	Plant Cover Height (cm)	Nest Height Off Ground (m)	Distance to Water (m)	Distance from Trunk (cm)	Distance to Foliar Edge (cm)	Distance to Nearest Tree (m)
AMRO	2	NA	6.1 ± 1.8 (4.3–7.9)	1.8 ± .65 (4.5–3.2)	12 ± 12 (0–24)	21.5 ± 11.5 (10–33)	0
DEJU	3	120.0 ± 58.2 (10–120)	0	1.4 ± 1.3 (0.5–3.3)	NA	0	5.58 ± 4.7 (2.7–11)
GTTO	2	92.0± 21.2 (77–107)	0.2 ± 0.2 (0.04–0.40)	70.9 ± 20.6 (50.3–91.4)	6.5 ± 1.5 (5–8)	101 ± 51 (50–152)	11.7 ± 13.1 (2.4–21)
LISP	15	45.0 ± 14.1 (23–71)	0.1 ± 0.2 (0–0.9)	0.4 ± 0.5 (0.02–1.5)	NA	0	16.5 ± 7.0 (2.1–24)
MALL	1	7.5	0	0.4	NA	0	6.1
SOGR	1	25.4	0	3.0	NA	0	0.1
YRWA	1	NA	3.1	3.0	79	45.3	0

of the sides (Table 2). The nest itself was built in a small depression and composed of mostly Jeffrey Pine needles and some Western White Pine needles. I found one Mallard nest 10 July in a large meadow on a small island between three ponds that dried by the end of summer (Fig. 2). The mallard and Lincoln's Sparrows nested the closest to standing water than other birds I found (Table 2). The Mallard nest was placed in thick cover of sedges and White Rush Lily that had a maximum height of 7.5 cm (Table 1). The nest was made up entirely of sedge.

I found one nest of an Audubon's Yellow-rumped Warbler 26 June on the fork of a branch of a Western White Pine in a small strip of timber that penetrated East van Matre Meadows along a glacial moraine (Table 2). The nest was 3 m up the 5.2 m tall tree, and the nest was made of a homogeneous mixture of hair, feathers of multiple bird species including Steller's Jay (*Cyanocitta stelleri*), and plant fibers (roots, grasses, and twigs), none of which were > 1 mm thick (Table 1, Fig. 2). The nest had much larger dimensions (Table 1) than those measured by Harrison (1975), but similar to those measured in Ontario by Peck and James (1987). This nest did have some damage, and the young may have fledged for some time before I measured it, and that could account for some differences in size. Elevational effects might also account for the differences with nest from Ontario. The nest I found was in a horizontal branch fork of a conifer (Table 2), which is what has been found before (Peck and James 1987). Nest of Audubon's Warblers were unique by having feathers of other bird species incorporated in the nest material, compared to the other breeding bird nests I studied. What I found has been seen for this warbler in other areas (Mcilwraith 1894).

Lastly, I found two nests of Green-tailed Towhee during their construction 26 July, and both nests were immediately abandoned after I located them. One nest was along a traveling route on a glacial moraine between meadows and was subject to more disturbance by amphibian surveyors while moving from meadow to meadow. The other nest was next to the camping area amphibian surveyors used throughout the 4-mo survey season. Despite our best effort to limit disturbance, the nests were quickly abandoned. I measured the two unfinished nests, and they were both associated with Huckleberry Oak and Mountain Spiraea for cover type and nest material (Fig. 2). Both nests were found in shrubs on glacial moraines that have vegetative community of mostly Huckleberry Oak, prostrate manzanita, and stunted Western White Pine. Compared to the other nests described, these nests were the farthest from water (Table 2). The quick abandonment of these nests suggests that Green-tailed Towhees seem much quicker to abandon their nests than the other birds I observed to be breeding in the area. Green-tailed Towhee nests reported in the literature (Harrison 1978) were just under twice the width and height what I measured (Table 1). They may have been abandoned before they were finished, therefore these nests my not be comparable to data on completed nests.

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A REVIEW OF THE HISTORICAL MARKET: EFFECT OF THE WEST COAST COMMERCIAL FISHERY ON WESTERN POND TURTLES (*ACTINEMYS MARMORATA* AND *A. PALLIDA*)

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***Abstract*.—In the mid to late 1800s and early 1900s, Western Pond Turtles (*Actinemys marmorata* and *A. pallida*) were sought after in California as an ingredient in turtle soups and stews. At the height of the commercial terrapin fishery in California in 1895, about 63,000 Western Pond Turtles were reported in the markets, but agency records are sporadic and a full accounting of the market data remains incomplete. The U.S. Fish and Wildlife Service (USFWS) initiated a review of the status of Western Pond Turtles in 2015 to determine if there is sufficient evidence to warrant their listing as an Endangered or Threatened species. To better understand the magnitude of the commercial terrapin fishery, we reexamined commercial fish landing reports of the USFWS and California Department of Fish and Wildlife (CDFW) and other relevant texts available in digital repositories to determine the Reported (known) market data (262,600 turtles). Then we estimated the Model-fitted (unknown) market data (261,500 turtles) to calculate the overall Estimated market total (524,100 turtles). Because the source material suggests that the market data reported in agency reports underrepresented the overall terrapin fishery, we calculated scaled estimates that suggest as many as a million turtles were captured for human consumption. These numbers demonstrate the magnitude of the historical terrapin fishery and could provide a baseline to inform future listing decisions.**

Key Words.—California; commercial exploitation; commercial fishery; data analysis; endangered or threatened species; historical record; population decline; reptiles.

INTRODUCTION

The Western Pond Turtle (Fig. 1) complex (*Actinemys marmorata* and *A. pallida*) and the Western Painted Turtle (*Chrysemys picta*) are the only freshwater turtles native along the North American Pacific Coast west of the Sierra-Cascade divide between Canada and Baja California (Iverson et al. 2017; Turtle Taxonomy Working Group 2017). Excluding the Sonora Mud Turtle (*Kinosternon sonoriense*) that is now extirpated from locations where its range along the Colorado River once extended into California (Turtle Taxonomy Working Group 2017; Stebbins 2003), *Actinemys* are the only freshwater turtles native to California. Western Pond Turtles (listed as terrapin in the historical record) were once sought after in California as an ingredient in turtle soups and stews served in hotels and restaurants of San Francisco in the mid to late 1800s and early 1900s (Wallace W. Elliot and Co. 1883a, 1883b). At the height of the commercial terrapin fishery in California in 1895, about 63,000 Western Pond Turtles were reported in the meat markets that year alone (Wilcox 1902).

Although the history of the commercial market for Western Pond Turtles was documented previously (Bettelheim 2005), a full accounting of the market data was incomplete. Between 1888 and 1931, intermittently published fishery records of agencies documented the commercial harvest of turtles that were collected throughout the state for sale in the San Francisco market (Bettelheim 2005); however, there are data gaps of as many as 17 y (e.g., 1863–1879) in the historical record between 1863 and 1931. In 1992, the U.S. Fish and Wildlife Service (USFWS) initiated a review of the status of the Western Pond Turtle (considered at that time to be a single species) to determine if there was sufficient evidence to warrant listing as an Endangered or Threatened species under the Endangered Species Act (USFWS 1992). At that time it was determined that the species did not warrant such listing based on the best scientific and commercial information available (USFWS 1993). In 2015, the USFWS initiated a new review of its status (USFWS 2015), and this review is still in progress. A better understanding of the magnitude of the commercial terrapin fishery could provide insight into previous distribution and population sizes and

FIGURE 1. Northwestern Pond Turtle (*Actinemys marmorata*) from the upper Klamath River in southern Oregon, USA. (Photographed by Matthew Bettelheim).

establish a baseline to inform future listing decisions. This paper reexamines the historical terrapin fishery of the west coast of North America to better quantify its magnitude and extent.

Methods

Nomenclature.—The Western Pond Turtle complex includes both the Northwestern Pond Turtle (*A. marmorata*) and Southwestern Pond Turtle (*A. pallida*; Iverson et al. 2017). Because we examined primarily historical source materials that did not recognize two species, we used the name Western Pond Turtles collectively to represent both species throughout their ranges. Based on repeated context clues throughout the literature, the term terrapin was traditionally used in the late 1800s and early 1900s in the commercial fish landing reports of the west coast of North America to refer to any edible, non-marine turtle, while the word turtle was used to refer only to sea turtles. For example, terrapin were sold by the dozen, which was not an observed standard unit of sale for sea turtles. The reported origins of terrapin that were captured included both coastal and inland California counties rather than strictly coastal counties and the reported origins of turtles was strictly limited to Mexico. This usage is consistent with common parlance around this time, which in Webster's New International Dictionary of the English Language in 1939 recognized a terrapin as "any of various edible North American turtles of the family Testudinidae living in fresh or brackish water, esp. any of those constituting the genus *Malaclemys*," and recognized a turtle as "any marine reptile of the order Chelonia." A similar commercial market existed for Diamond-backed Terrapin (*Malaclemys terrapin*), which dates back to the 1500s, and was still active on the east coast of North America during the late 1800s and early 1900s (Brennessel 2006).

Although we found little distinction made between Western Pond Turtles and the Diamond-backed Terrapin in the commercial fisheries, it is unlikely that Diamond-backed Terrapin were regularly imported from the East Coast to the West Coast to supply the San Francisco market. There is no mention in the literature of an attempt to import Diamond-backed Terrapin to support a commercial market on the west coast. Attempts to introduce Diamond-backed Terrapin to the marshlands in the San Francisco Bay Area were made in 1894 (Newspaper 1; Newspaper 2), in 1896 (State Board of Fish Commissioners 1900; Taft 1944; Brown 1971), and in 1943 (Taft 1944; Hildebrand and Prytherch 1947; Brown 1971). There is no evidence that these experimental introductions were successful (Jennings 1983). Therefore, we inferred all references to terrapin in the literature on the West Coast fisheries (e.g., terrapin market, terrapin fishery, terrapin trade), when not explicitly corroborated by name, to be Western Pond Turtles. We considered only commercial fishery data specific to terrapin, rather than turtle, during literature searches.

We collected data for the commercial terrapin market from two primary agencies: the California Department of Fish and Wildlife (CDFW) and the USFWS. Although both agencies underwent several organizational name changes between their inception and the present, and published agency reports accordingly under those various names, for simplicity we refer to each agency in the text by their contemporary name. Similarly, we refer to the California Fish and Game Commission, which is the regulatory body of CDFW.

Source material.—We revisited the commercial terrapin market data from Bettelheim (2005) plus additional resources to fill in missing data that may have been digitized since 2005. This included a review of all available annual/biennial commercial fish landing reports of CDFW, including its biennial reports, the journal California Fish and Game (now, California Fish and Wildlife Journal), select issues of the Fish Bulletin of CDFW that revisit historical commercial fishery data, and assorted USFWS fisheries reports (Table 1). We searched for the key word terrapin using Optical Character Recognition in digital repositories (Table 1)

Table 1. Source materials searched for data on the commercial terrapin market in California. Abbreviations are USFWS = U.S. Fish and Wildlife Service and CDFW = California Department of Fish and Wildlife. Online searches were made with the term terrapin.

Source	Reference
USFWS fisheries reports	Collins (1892), Smith (1895), Wilcox (1895), Wilcox (1898), Townsend (1900), Wilcox (1902), Wilcox (1907), Sette (1928), Fiedler (1932), Fiedler (1933)
CDFW biennial reports	State Board of Fish Commissioners 1886, 1900 California Fish and Game Commission 1910, 1913, 1914, 1916, 1918, 1921, 1923, 1924, 1927, 1929, 1931, 1933
California Fish and Game/ California Fish and Game Journal	Board of Fish and Game Commissioners 1918a,b,c,d, 1919a,b,c,d, 1920a,b,c,d, 1921a,b,c,d, 1922a,b,c,d, 1923a,b,c,d, 1924a,b,c,d, 1925a,b,c,d, 1926a,b,c,d, 1927a,b Division of Fish and Game 1927a, b, 1928a,b,c,d, 1929a,b,c,d, 1930a,b,c,d, 1931a,b,c,d, 1932a,b,c,d
Fish Bulletin	Staff of the Bureau of Commercial Fisheries 1929, 1930, 1935, 1936, 1949
Online	www.escholarship.org, www.hathitrust.org, www.archive.org, www.californiawarden.com, www.biodiversitylibrary.org, www.library.noaa.gov, cdnc.ucr.edu, and chroniclingamerica.loc.gov

and constrained searches to 1848 through 1940, using the California Gold Rush (when there was a sudden influx of prospectors and settlers to California) as a starting point, and as an end point a span of roughly 10 y beyond 1931 when Western Pond Turtles were last reported in the market (Bettelheim 2005).

Units of measurement and abundance.—We reported all units of measure in the metric system, but included the equivalent conversion in the imperial system when describing turtle weight as they were originally reported in the source material for comparative purposes. We reported all commercial terrapin market data by total number (e.g., 3,600 turtles). In select years between 1918 and 1924, CDFW reported the products or yield of the fisheries for the commercial terrapin fishery market data in both pounds and dozens (California Fish and Game Commission 1921, 1923, 1924, 1929; Staff of the Bureau of Commercial Fisheries 1930, 1936), offering an average weight per turtle of 907 g (2 lbs), a number confirmed in later Bureau of Commercial Fisheries records (Staff of the Bureau of Commercial Fisheries 1930). We therefore divided data originally reported in pounds by a factor of two (assuming an average weight per turtle of 907 g = 2 lbs), and multiplied data originally reported in dozens by a factor of 12, to convert pounds/dozens measurements into a total number of turtles.

Data analysis.—To determine the magnitude of the terrapin fishery, we made certain assumptions based on the Reported (known) market data to estimate the Model-fitted (unknown) market data (i.e., data in-between reported years), and then calculate the overall Estimated market totals. Assuming an average weight per turtle of 907 g, we converted all market data into total number of individual turtles and plotted them in Microsoft Excel on a time-series chart (Fig. 2). Next, for years where market data were unavailable between 1862 and 1931, we estimated the total number of turtles for each unreported year based on an ascending exponential fit of Reported data between 1862 and 1895, as follows:

$$y = 2.4068\, e^{0.3133x}$$

where y = number of turtles per year and x = number of years since 1862 (i.e., x = 0 at 1862, x = 1 at 1863, etc.). For unreported years between 1899 and 1931, we estimated numbers based on a descending exponential fit of Reported data between 1899 and 1931 as follows:

$$y = 96433096\, e^{-0.2082x}$$

where y = number of turtles per year and x = number of years since 1862 (i.e., x = 37 at 1899, x = 38 at 1900, etc.). We then combined and plotted the Reported data and the Model-fitted curve together on a single time-series chart (Fig. 2) to examine the overall results. Next, for the single unreported year of 1896 (data were reported for 1895 and 1897) not covered by the two other exponential fits, a linear interpolation based on the 1895 and 1897 values was used to represent an estimate for the year of 1896. Lastly, we used the sum of the Reported data and Model-fitted data (where Reported data were not available) to calculate the Estimated market totals between 1863 and 1931.

RESULTS

History of the San Francisco terrapin fishery.—We include a brief history of the San Francisco terrapin fishery here. A more exhaustive review is available elsewhere (Bettelheim 2005). In 1863, the terrapin fishery of the west coast of North America was first documented through a brief mention describing terrapin

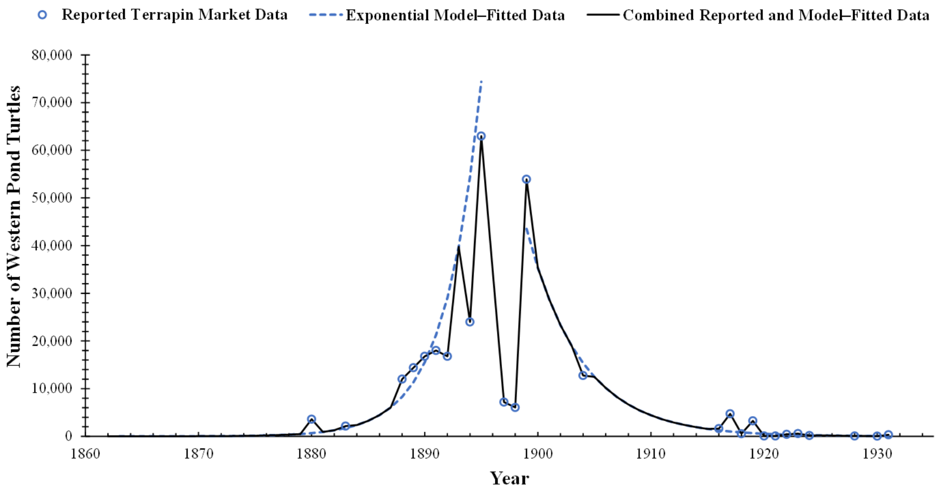


FIGURE 2. Time-series chart depicting the Reported (known) and Model-fitted (unknown) market data for Western Pond Turtles (*Actinemys marmorata* and *A. pallida*) from California for the years 1863 through 1931, based on U.S. Fish and Wildlife Service and California Department of Fish and Wildlife annual/biennial commercial fish landing reports and other relevant texts.

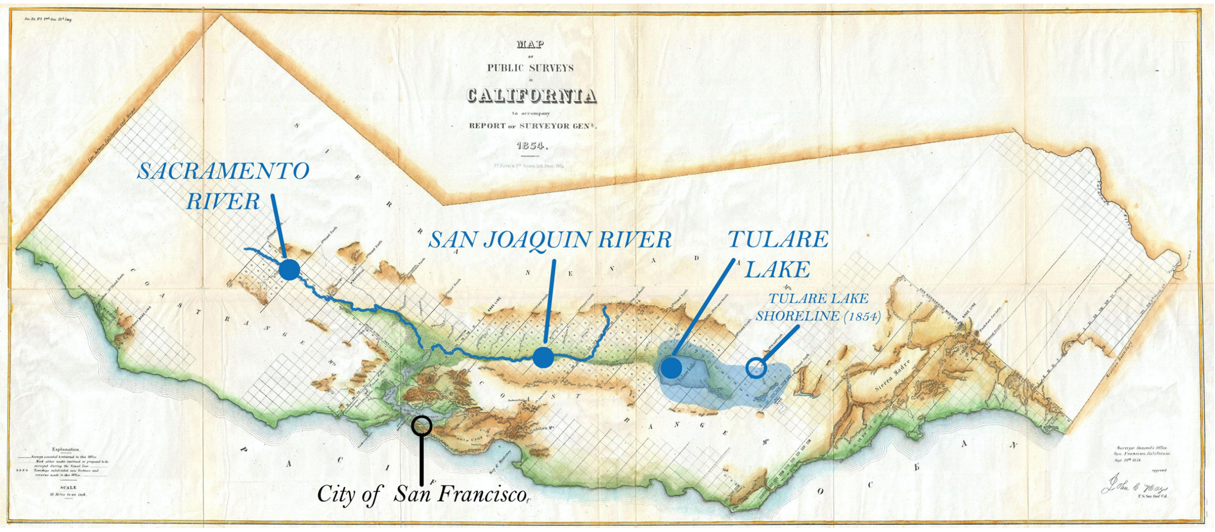


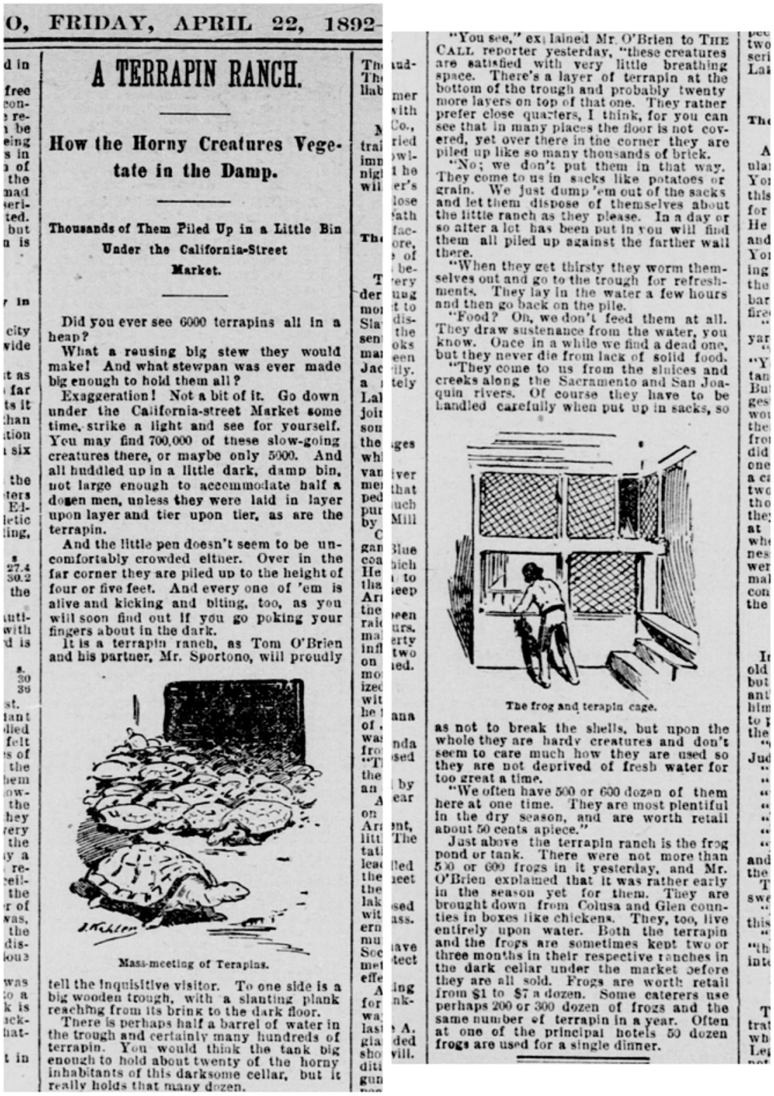
Figure 3. Historical map of California showing the primary water bodies in the Central Valley where the historical terrapin fishery took place. As depicted here, during flood events, Tulare Lake would engulf neighboring water bodies in the southern San Joaquin Valley floor. The outer limits of the lake (blue overlay) represent the reported extent of the shoreline in 1854 (base map adapted from the Map of Public Surveys in California to Accompany Report of the Surveyor General, 1854; http://www.geographicus.com/mm5/cartographers/landoffice.txt).

caught for meat markets (Cooper 1863). A few years later, Cronise (1868) reported that Western Pond Turtles were almost constantly for sale in the markets of San Francisco (Fig. 3).

One trapper in Tulare Lake in the San Joaquin Valley employed a common fishing seine 30 m in length dragged between two men and on a good day, this method would yield as many as 80 or 90 turtles on each set (Wallace W. Elliot and Co. 1883b; Brown and Richard 1940). Another trapper seined Tulare Lake between 1884 and 1894 with a net 400 m long dragged by horses, which yielded an average of several dozen turtles a catch that were packed two dozen to a barley sack and shipped to San Francisco on a Railroad Express car (Newspaper 3; Gist 1976). Two brothers employed a sailing vessel to fish for turtles and in one season they caught as many as 3,600 turtles (Newspaper 3; Wallace W. Elliot and Co. 1883a, 1883b; Mitchel 1970; Haslam 1993).

At the same time, farmers diverted the waters and feeder streams of the San Joaquin Valley for irrigation, and the lakes in the Tulare and Buena Vista basins (Tulare, Buena Vista, and Kern lakes), which during wet years could merge into a giant lagoon, instead dried up, destroying the local fisheries, depriving regional wildlife (waterfowl, beavers, otters, grizzlies, elk) of a key water source, and eliminating the local terrapin fishery (Haslam 1993). By the early 1900s, the once 80,937 ha Tulare Lake was all farmland, with the waters diverted to irrigate cotton and safflowers (Haslam 1993). By 1892, one turtle meat operation was underground beneath the California Street Market of San Francisco (Newspaper 4). There, turtles gathered up from the sluices and creeks along the Sacramento and San Joaquin rivers were "piled up like so many thousands of brick[s]" to be sold for $0.50 apiece (Newspaper 4; Fig. 4). In 1897, another wholesaler reported shipping 7,200 turtles to San Francisco markets (Newspaper 5). Their stock came from the big canyons and high mountain streams of the upper Sacramento River, and was collected at times by Native Americans (Newspaper 5). They also had an additional stock of 9,000 turtles on hand in northern California, with the intent of increasing their stock to 20,000 turtles by hunting on the Klamath Indian Reservation in Oregon the following year (Newspaper 5). Tracy Irwin Storer, Professor at University of California Davis, documented the later years of the terrapin fishery. In 1923, he questioned one trapper who would ship his largest turtles to market in barley sacks with as many as 54 turtles apiece (T.I. Storer, archived field notes, California Academy of Sciences; J.S. Dixon, archived field notes, Museum of Vertebrate Zoology). In 1925, Storer met with a San Francisco turtle dealer who had been in business for 22 y supplying frogs and turtles to colleges and restaurants. His turtles came from the Central Valley (Sacramento and San Joaquin valleys) and were purchased from various trappers at $3.00 to $5.00 per dozen. At the time of the visit by Storer, the dealer had > 50 turtles on hand (T.I. Storer, archived field notes, *op. cit.*). As the terrapin fishery drew to a close, in 1931 Storer interviewed a northern California market hunter who was keeping 1,400 Western Pond Turtles for the market to be sold for $2.50 per dozen in Chinatown of San Francisco (T.I. Storer, archived field notes, *op. cit.*).

Market numbers.—By 1880, a minimum of 3,600 turtles, representing the haul of one trapper in Tulare Lake, was sent to San Francisco in one season (Wallace W. Elliot and Co. 1883a, 1883b; Figs. 2 and 3). Between 1888 and 1894, USFWS records on fisheries of the Pacific Coast reported between 12,000 and 24,000 turtles



O, FRIDAY, APRIL 22, 1892-

A TERRAPIN RANCH.

How the Horny Creatures Vegetate in the Damp.

Thousands of Them Piled Up in a Little Bin Under the California-Street Market.

Did you ever see 6000 terrapins all in a heap?

What a reusing big stew they would make! And what stewpan was ever made big enough to hold them all?

Exaggeration! Not a bit of it. Go down under the California-street Market some time, strike a light and see for yourself. You may find 700,000 of these slow-going creatures there, or maybe only 5000. And all huddled up in a little dark, damp bin, not large enough to accommodate half a dozen men, unless they were laid in layer upon layer and tier upon tier, as are the terrapin.

And the little pen doesn't seem to be uncomfortably crowded either. Over in the far corner they are piled up to the height of four or five feet. And every one of 'em is alive and kicking and biting, too, as you will soon find out if you go poking your fingers about in the dark.

It is a terrapin ranch, as Tom O'Brien and his partner, Mr. Sportono, will proudly tell the inquisitive visitor. To one side is a big wooden trough, with a slanting plank reaching from its brink to the dark floor.

Mass-meeting of Terapins.

There is perhaps half a barrel of water in the trough and certainly many hundreds of terrapin. You would think the tank big enough to hold about twenty of the horny inhabitants of this darksome cellar, but it really holds that many dozen.

"You see," explained Mr. O'Brien to THE CALL reporter yesterday, "these creatures are satisfied with very little breathing space. There's a layer of terrapin at the bottom of the trough and probably twenty more layers on top of that one. They rather prefer close quarters, I think, for you can see that in many places the floor is not covered, yet over there in the corner they are piled up like so many thousands of brick.

"No; we don't put them in that way. They come to us in sacks like potatoes or grain. We just dump 'em out of the sacks and let them dispose of themselves about the little ranch as they please. In a day or so after a lot has been put in you will find them all piled up against the farther wall there.

"When they get thirsty they worm themselves out and go to the trough for refreshments. They lay in the water a few hours and then go back on the pile.

"Food? Oh, we don't feed them at all. They draw sustenance from the water, you know. Once in a while we find a dead one, but they never die from lack of solid food.

"They come to us from the sluices and creeks along the Sacramento and San Joaquin rivers. Of course they have to be handled carefully when put up in sacks, so as not to break the shells, but upon the whole they are hardy creatures and don't seem to care much how they are used so they are not deprived of fresh water for too great a time.

The frog and terapin cage.

"We often have 500 or 600 dozen of them here at one time. They are most plentiful in the dry season, and are worth retail about 50 cents apiece."

Just above the terrapin ranch is the frog pond or tank. There were not more than 500 or 600 frogs in it yesterday, and Mr. O'Brien explained that it was rather early in the season yet for them. They are brought down from Colusa and Glen counties in boxes like chickens. They, too, live entirely upon water. Both the terrapin and the frogs are sometimes kept two or three months in their respective ranches in the dark cellar under the market before they are all sold. Frogs are worth retail from $1 to $7 a dozen. Some caterers use perhaps 200 or 300 dozen of frogs and the same number of terrapin in a year. Often at one of the principal hotels 50 dozen frogs are used for a single dinner.

FIGURE 4. The 22 April 1892 issue of The Morning Call, a San Francisco newspaper, included a description of a terrapin ranch in operation underground beneath California Street Market of San Francisco (Newspaper 4).

per year passing through the San Francisco market alone (Collins 1892; Smith 1895; Wilcox 1895). The 1890s marked the apex of the terrapin fishery. At the apparent height of the terrapin fishery in 1895, 42,864.5 kg (94,500 lbs) of turtles (explained in a footnote to represent 63,000 turtles) were sold in San Francisco originating from the Central Valley and Bay Area (Wilcox 1898). In the years that followed, 7,200 turtles (from northern California), 6,063 turtles (no origin reported), and 53,935 turtles (from the Bay Area and Central Valley) were marketed in 1897, 1898, and 1899, respectively (Newspaper 5; Townsend 1900; Wilcox 1902).

After the turn of the century, records were scarce. Then, starting in 1916, the California Fish and Game Commission began tracking commercial catch (based on what were called landing receipts or fish-tickets) submitted by markets and packing facilities (Table 1). Market numbers between 1916 and 1931 rarely exceeded 500 turtles, with the exception of higher numbers reported in 1916 (1,608 turtles), 1917 (4,728), and 1919 (3,247).

These numbers may underestimate the intensity of the terrapin fishery underway. In 1931, the last year for which commercial terrapin market data was reported, at least one market hunter was storing turtles (T.I. Storer, archived field notes *op. cit.*). That same year, however, official records for the San Francisco terrapin fishery reported only 330 turtles sold (California Fish and Game Commission 1933; Staff of the Bureau of Commercial Fisheries 1935; Staff of the Bureau of Commercial Fisheries 1936; Division of Fish and Game 1932b). Depending on whether the 330 turtles sold that year originated from the 1,400 turtles harvested by the market hunter Storer interviewed (1,400 turtles total harvested in 1931) or were harvested by a second party (1,400 + 330 turtles total harvested in 1931), as many as 1,730 turtles may have been harvested that year. This discrepancy in numbers suggests that the 330 turtles officially reported for sale in the San Francisco market that year may have underrepresented the actual terrapin fishery by an order of five times or greater (Table 2).

Table 2. Estimated underrepresentation (last column) of the actual number of Western Pond Turtles (*Actinemys marmorata* and *A. pallida*) harvested compared to commercial terrapin fishery data based on the reported number sold in 1897, 1904, and 1931. Headings are Sold = reported number of turtles sold, Unsold = reported number of turtles unsold, Harvested = number of turtles sold and unsold, Percentage = number of turtles sold / harvested, and Underrepresentation = number of turtles harvested / sold.

Year	Sold	Unsold	Harvested	Percentage	Underrepresentation
1897	7,200	9,000	16,200	44.44%	2.25 ×
1904	15,770	9,730	25,500	61.84%	1.61 ×
1931	330	1,400	1,730	19.08%	5.24 ×

The potential for underrepresenting the terrapin fishery is further reinforced by two more instances. In 1904, Wilcox (1907) reported 11,567 kg (25,500 lbs) total for the state of California, followed by two entries for the products of Sacramento County (907 kg = 2,000 lbs) and San Joaquin County (10,659 kg = 23,500 lbs). The two county totals equal the sum of the state total, and there is a third entry of just 7,153 kg (15,770 lbs) for what is termed the wholesale fishery trade of San Francisco. Of the 11,567 kg marketed from the Central Valley that year, only a portion of the product, 7,153 kg (roughly 61.8%), reached the San Francisco market to be recorded. Lastly, in 1897 one northern California wholesaler reported shipping 7,200 turtles to San Francisco, with an additional stock of 9,000 turtles on hand (Newspaper 5; Table 2).

Based on commercial terrapin market data, the reported terrapin fishery from 1863 and 1931 was about 262,600 turtles. When plotted on a time-series chart, the Reported data is a curved ascending line and a curved descending line. Based on Model-fitted data for which Reported data were not available for a given year, an additional 261,500 turtles may have been harvested. Therefore, we estimated that a total of 524,100 Western Pond Turtles were harvested between 1863 and 1931 (Table 2).

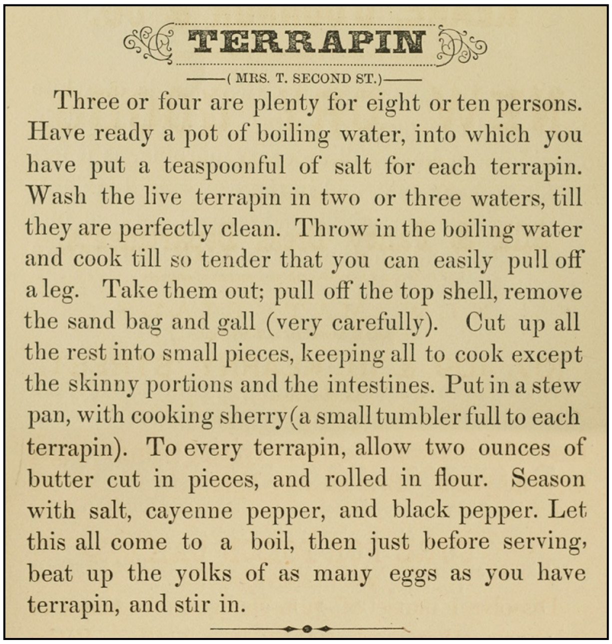
Discussion

We estimate that more Western Pond Turtles were being harvested by trappers in the wild or captivity than were being reported in market receipts, fish-tickets, or fish landing reports. Thus, the number of Western Pond Turtles sold to retailers and consumers in the market each year likely represents a fraction of the number of Western Pond Turtles actually harvested in the wild. This suggests that the actual magnitude of the terrapin fishery may have been much greater than the overall estimated total. The likelihood that the Reported and Model-fitted market data underrepresent the actual magnitude of the overall terrapin fishery is substantiated by two agency reports that state that their numbers reflect only a small part of the turtle catch because most of the turtles caught were handled by dealers not in the regular fish business (Staff of the Bureau of Commercial Fisheries 1936) and most of the catch was not listed on the commercial fish receipts because turtle dealers were not required to submit statistical records (Staff of the Bureau of Commercial Fisheries 1949).

Our analysis assumes that turtles continued to be harvested and sold in years for which no commercial terrapin market data were reported. The historical record includes several instances where trappers were supplying the market with turtles, while holding stocks of turtles on reserve. Further, if we treat the inventory of these three unique dealers in business in 1897, 1904, and 1931 not as isolated occurrences but as a reasonable representation of standard market practice between 1863 and 1931, and assume these and other dealers were operating simultaneously, then the overall magnitude of the terrapin fishery could be over a million turtles (assuming the estimated total of 524,100 Western Pond Turtles was underrepresented by an order of at least two times).

Due to the limitations of intermittent agency fishery records and the uncertainties associated with secondary source material, the analysis we performed required model-fitting that may over- or underestimate the magnitude of the terrapin fishery. Further, the primary basis for the terrapin fishery is limited to commercial terrapin market data reported for a portion of California destined for the San Francisco market. There were reported plans to collect turtles in Oregon, but it is unknown whether similar markets existed for Western Pond Turtles elsewhere in the range of the species. Similarly, there is no mention, nor any evidence to support or dispel, the potential for collecting the Western Painted Turtle, whose native range extends into portions of Oregon and Washington (Turtle Taxonomy Working Group 2017). This potentiality, however, is highly unlikely given the ready availability of Western Pond Turtles closer to California and the San Francisco markets. While care should be taken relying on the accuracy of these numbers, this analysis indicates a significant scale of the historical terrapin fishery and puts the decline of Western Pond Turtles in perspective, especially in the context of risks facing these species today.

After 1931, Western Pond Turtles disappeared from the commercial terrapin fishery records. Much like the Diamond-backed Terrapin on the east coast of North America, the demand for Western Pond Turtles had waned over the years, most likely in response to the same economic, legal, and social factors: the involvement of the U.S. in World War I (1914–1918); the Prohibition Era (1920–1933); the Wall Street Crash (1929); and The Great



TERRAPIN

(MRS. T. SECOND ST.)

Three or four are plenty for eight or ten persons. Have ready a pot of boiling water, into which you have put a teaspoonful of salt for each terrapin. Wash the live terrapin in two or three waters, till they are perfectly clean. Throw in the boiling water and cook till so tender that you can easily pull off a leg. Take them out; pull off the top shell, remove the sand bag and gall (very carefully). Cut up all the rest into small pieces, keeping all to cook except the skinny portions and the intestines. Put in a stew pan, with cooking sherry (a small tumbler full to each terrapin). To every terrapin, allow two ounces of butter cut in pieces, and rolled in flour. Season with salt, cayenne pepper, and black pepper. Let this all come to a boil, then just before serving, beat up the yolks of as many eggs as you have terrapin, and stir in.

Figure 5. An example of a typical recipe for terrapin that includes the requisite alcohol, in this case sherry, as featured in the 1872 edition of the Recipe Book of the Ladies of California (Ladies of California 1872).

Depression (1929–1933; Coker 1920; Hildebrand 1929). If turtle consumption was only considered palatable if cooked in alcohol such as sherry, dry sherry, white wine, Madeira, or brandy (Ladies of California 1872; Coker 1920; Fig. 5), then the prohibition of the manufacture and sale of alcoholic beverages from 1920–1933 may have ended the general consumption of Western Pond Turtles.

These effects would have been further compounded by local changes in the California landscape, especially the conversion of the Tulare Lake basin to farmland by 1900. Prior to 1895, the peak in number of turtles could be attributed to the drawdown of Tulare Lake. If these turtles originated from Tulare Lake (their point of origin is unreported), they may have been easier to collect as the waters receded and turtles became concentrated in the shallow waters of the lake. Then, in the five years leading up to the complete drawdown of Tulare Lake, the number of turtles drops precipitously from 63,000 turtles in 1895 to roughly 7,200 in 1897 and 6,063 in 1898. The direct cause-and-affect implied here is uncertain, however. Between 1895 and 1898, the turtles reported in the market originated not from Tulare Lake, but from the rest of the San Joaquin Valley and Bay Area, plus the upper Sacramento River. 1895 also marks the first year in which agencies recorded the point of origin of turtles by county. While the practice of reporting the county of origin might simply reflect the implementation of better data collection practices, it might also represent a move of the terrapin fishery away from Tulare, Buena Vista, and Kern lakes and the Sacramento and San Joaquin rivers into the waters of the surrounding counties farther north. By 1900, Tulare Lake would have dried up, depleting the terrapin fishery of this invaluable source of turtles, and despite a second peak of 53,935 turtles in 1899 (again, also from the Bay Area and Central Valley), market data post-1899 shows a steady decline thereafter.

Trappers undoubtedly sought out large adult turtles that would yield more meat for sale at market. The harvest of adult turtles reduces reproductive capacity in the population (Close and Seigel 1997). In general, turtles are long-lived, have low reproductive rates, and high juvenile mortality, which makes them vulnerable to collecting (Pough and Janis 2019). Western Pond Turtles attain reproductive maturity at approximately 130 to 135 mm carapace length (CL), which may require 5–10 y to reach this size in more northern portions of their range (Bury et al. 2012), but they can reach maturity as young as 4–5 y in Central Coast of California (Germano and Rathbun 2008) and in the San Joaquin Valley (Germano 2016, 2021). Collecting for the commercial harvest likely had an impact on turtles by removing a greater number of reproductively viable adults and, consequently, acted as an intense population suppressant. Given that turtles throughout Central California exhibit fast growth rates and early maturity (Germano and Rathbun 2008; Germano 2016, 2021) compared to more northern areas of their range, the commercial harvest at Tulare Lake and throughout the valley floor may have permitted the collection of younger adult-sized turtles, functionally increasing the number of turtles acceptable for sale in the commercial market. Demographic studies of other turtle species indicate that population stability is sensitive to changes in adult or juvenile survival (see Congdon et al. 1993, 1994). Across multiple turtle species exhibiting a range of mean annual fecundity, annual survival, and age at maturity, Heppell (1998) demonstrated that adult survival had the greatest influence on the annual population multiplication rate of turtle species. Levell (2000) reports similar patterns in *Clemmys* and *Emydoidea* pond turtles where adult survivorship is central to the long-term persistence of functional wild turtle populations. Accordingly, Bury et al. (2012) reinforced that the recovery of a long-lived and slow-growing turtle species like Western Pond Turtles could be difficult after a population is depleted.

Although the demand for Western Pond Turtles all but disappeared during the post-1929 depression, new risks continue to threaten their populations today, including urbanization and development, water projects, and habitat fragmentation. Other potential (but not yet shown) problems are introduced non-native turtles like Red-eared Sliders (*Trachemys scripta*) and potential non-native predators such as American Bullfrogs (*Lithobates catesbeianus*; Bury et al. 2012), and most recently, the emerging fungal pathogen Shell Disease (*Emydomyces testavorans*; Haman et al. 2019; Woodburn et al. 2019; Adamovicz et al. 2020; Woodburn et al. 2021). The vulnerability of Western Pond Turtles to these threats may have been exacerbated by the commercial terrapin fishery that began more than 150 y ago, and the ability for the populations to recover after more than half of a century of harvest would only be complicated by these emerging risks.

Without an estimate of the overall population sizes of Western Pond Turtles today, it is difficult to quantify the effects the terrapin fishery exacted on population numbers overall. Still, the market numbers from earlier show the magnitude of this terrapin fishery. Now, we need estimates of remaining populations. By establishing a baseline for the magnitude of the terrapin fishery, this information could help inform future listing decisions, and future researchers and resource managers can make more informed management decisions on behalf of the species.

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GENETIC ANALYSIS LEADS TO RANGE EXTENSION OF THE OLYMPIC SHREW (*SOREX ROHWERI*) TO THE EASTERN SLOPES OF THE CASCADE RANGE IN WASHINGTON STATE

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Abstract.—**The documented geographic range of the Olympic Shrew (*Sorex rohweri*) is western Washington, Oregon, and British Columbia; however, during a study on shrews in central Washington in summer 2019, we genetically verified the presence of this species on the eastern slopes of the Cascade Range. Of the 127 terrestrial shrews captured, mtDNA analysis of cytochrome *b* gene sequences identified 41 of them as *S. rohweri*. Most of these live-trapped individuals were misidentified in the field as *S. cinereus* but others were field-identified as Trowbridge's Shrew (*S. trowbridgii*), Montane Shrew (*S. monticolus*), or Vagrant Shrew (*S. vagrans*). This discovery extends the known geographic range of *S. rohweri* to the drier eastern slopes of the Cascade Range in Washington and highlights the importance of collecting genetic samples for field studies of live animals, especially for taxa that are challenging to distinguish in the field.**

Key Words.—distribution; Eulipotyphla; insectivores; mtDNA; populations; small mammals; Soricidae.

INTRODUCTION

Multiple shrew species in the genus *Sorex* often live sympatrically, occupying the same geographic range (Churchfield 1990). Shrews are notoriously difficult to identify in the field during live-trapping studies. Reliable identification to species often requires skull and dental measurements (Rausch et al. 2007; Nagorsen and Panter 2009; Woodman and Fischer 2016). This may be suitable for research on voucher specimens in mammal collections but is not feasible for live-trapping methods that aim to reduce mortality during ecological studies. One of the most accurate ways to identify shrews is through genetic analysis (Rausch et al. 2007). As part of a larger study to determine the habitat preferences and population genetic structure of six sympatric shrew species in central Washington, we sequenced mitochondrial DNA from the cytochrome *b* gene (Dubey et al. 2007; O'Neill et al. 2005; Hope et al. 2012). Here, we report the genetic identification results from these shrew populations, and the discovery of the Olympic Shrew (*Sorex rohweri*) on the east slopes of the Cascade Range in Washington state (Fig. 1).

METHODS

Study site.—Our study area was located within the Okanogan-Wenatchee National Forest in central Washington on the east slopes of the Cascade Range between the southern end of Keechelus Lake and west of Easton. This area of mixed-coniferous forests contains many habitat types including wetlands, talus slopes, and old-growth forests (Washington State Department of Transportation [WSDOT] and U.S. Department of Transportation Federal Highway Administration [USDOT FHWA] 2006). For our study on shrews, we selected three sites (Fig. 2) that straddled Interstate-90 where wildlife crossing structures will be built in the future as part of a larger ecosystem connectivity and highway widening project (WSDOT and USDOT FHWA 2006). Each site encompassed secondary or mature forest through which a stream flowed from north of the highway and through a culvert to the south. Elevations ranged from 732 to 842 m (Table 1). Habitat surveys determined that these sites were dominated by Western Hemlock (*Tsuga heterophylla*), Western Red Cedar (*Thuja plicata*), and Douglas-fir (*Pseudotsuga menziesii*). The forest floor was complex, with abundant leaf litter, woody debris, and nurse logs (fallen trees that foster new vegetative growth). Understory vegetation was dominated by Vine Maple (*Acer circinatum*), Oregon Grape (*Mahonia aquifolium*), and Vanilla Leaf (*Achlys triphylla*). Skunk Cabbage (*Symplocarpus foetidus*) and Devil's Club (*Oplopanax horridus*) were commonly found within or near the streams (Ryckman 2020).

Field methods.—At each site, we placed a trapping transect and a pitfall trapping array 10–15 m away in each of three habitats, both north and south of the highway, for a total of 18 transects and 18 pitfall arrays (three sites × three habitat types × two sides of highway). Streamside habitats were adjacent to a seasonal stream; lowland habitats were relatively flat, forested areas at least 50 m from the stream channel; and upland habitats were in drier forest upslope from the stream. Each transect consisted of 20 Sherman live-traps spaced at 5-m

Figure 1. Field photographs of genetically verified Olympic Shrews (*Sorex rohweri*) captured near Easton, Washington, USA. (Left) Individual originally identified as Montane Shrew (*Sorex monticolus*). (Right) Individual originally identified as Vagrant Shrew (*Sorex vagrans*). (Photographed by Jordan Ryckman).

intervals. Each pitfall array consisted of four 19-L plastic buckets inserted into the ground, level with the surface, and connected by 30-cm-tall metal drift fencing. We also placed up to three aquatic funnel (minnow) traps partially submerged in shallow water in each streamside habitat. We fitted these 60-cm-long wire mesh traps with a cork platform to allow shrews to rest out of the water while trapped. We provided insulation and food (mealworms) in all traps to help sustain shrews overnight. We opened traps for two consecutive nights from dusk until dawn (8–12 h) during two different trapping sessions during summer 2019 (1,772 total trap-nights).

We identified live-captured individuals using a dichotomous key that we derived from multiple sources (Nagorsen 1996; Verts and Carraway 1998; http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.214.2565&rep=rep1&type=pdf) and adapted for species expected in this region. We recorded weight, standard external body measurements (body length, tail length, and hindfoot length), sex, age, and reproductive status. We evaluated body size, pelage color, dentition (observed with a hand lens), and hind feet (fringes and toepads) to identify species. To provide a genetic tissue sample of each individual, we clipped the distal 1–2 mm of the tail. We dipped the end of the tail in coagulant powder (as recommended by a veterinarian) to limit bleeding, then we released the animal at the site of capture. We directly placed each tissue sample into a 0.5-ml microcentrifuge tube filled with 95% non-denatured ethanol and immediately placed samples on ice. We quickly identified recaptured individuals (confirmed by nail polish applied to toes or a clipped tail) to species and then released them. Any shrews that died we collected as whole specimens. We identified all animals other than shrews and released them immediately. For later analysis, we kept tail tissue samples and specimens on ice for 1–2 d in the field and

Table 1. Locations of trapping pitfall arrays and number of Olympic Shrews (*Sorex rohweri*) captured in each habitat at each site in Washington state. Abbreviations are Lat. = latitude, Long. = longitude, Elev. = elevation (m) at the center of the array in each habitat type within each site (also see Fig. 2), and MP = milepost along Interstate-90.

Site	Habitat	North of I-90			South of I-90			Total # *S. rohweri*
		Lat.	Long.	Elev.	Lat.	Long.	Elev.	
Bonnie Creek	Streamside	47.314612	-121.3146	744	47.31280	-121.3164	732	11
	Lowland	47.316041	-121.3157	744	47.31444	-121.3168	740	6
	Upland	47.317373	-121.3176	762	47.31543	-121.3181	740	6
Houle Creek	Streamside	47.300615	-121.2917	741	47.29931	-121.2946	741	10
	Lowland	47.299951	-121.2906	742	47.29856	-121.2947	745	6
	Upland	47.301154	-121.2940	747	47.29847	-121.2938	754	2
MP 67.1 Creek	Streamside	47.269372	-121.2491	815	47.26702	-121.2470	778	0
	Lowland	47.269266	-121.2507	821	47.26754	-121.2433	797	0
	Upland	47.268144	-121.2533	812	47.26705	-121.2412	842	0

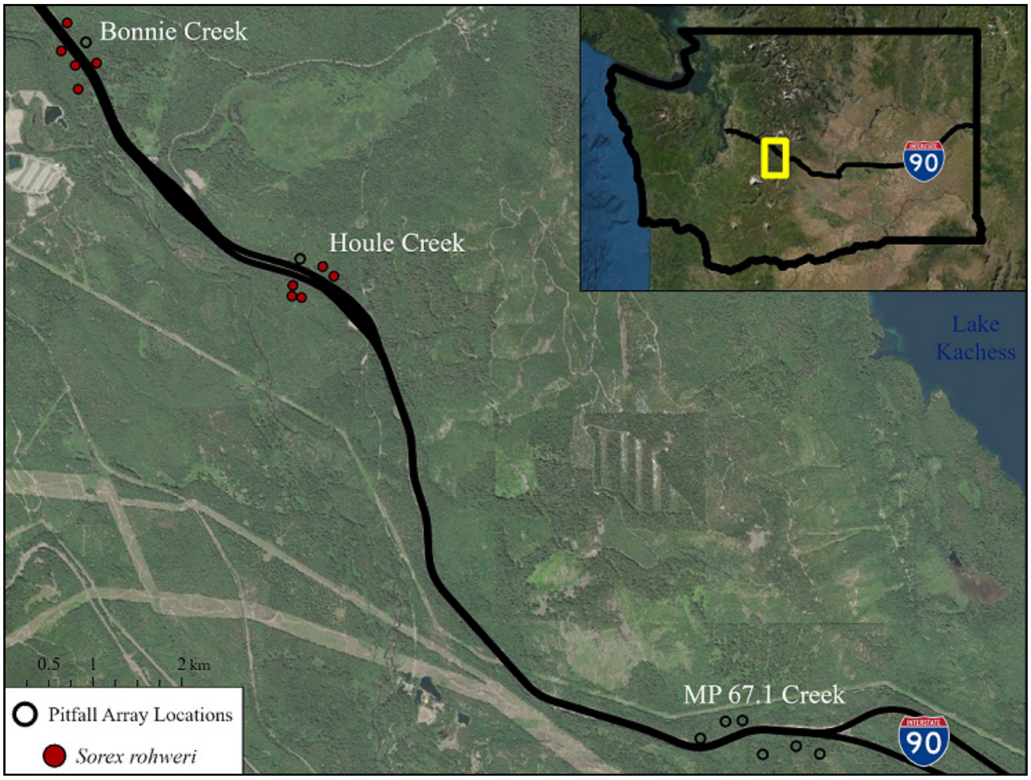

Figure 2. Locations of trapping pitfall arrays (circles) near I-90 in the central Cascades east of Snoqualmie Pass, Washington. Live-trapping took place in and around Bonnie Creek, Houle Creek, and MP 67.1 Creek. These creeks all ran through culverts under I-90. Circles filled in red indicate pitfall arrays where Olympic Shrews (*Sorex rohweri*) were captured.

then placed them in a -20° C freezer. We prepared whole specimens as museum vouchers (dried skins and skulls), and we retained liver samples for DNA extraction.

Genetic analysis.—We sent genetic samples from all individuals of terrestrial species to CD Genomics (New York, New York) for DNA extraction, amplification, and sequencing (the Aquatic Marsh Shrew, *S. bendirii*, and Western Water Shrew, *S. navigator,* were easily identifiable from the other species, so were excluded from genetic analysis). Proteinase K and zirconia beads were added to each sample and vortexed with Qiagen Tissue Lyser II. The tissue was then incubated at 55° C for no less than 3 h. Genomic DNA was extracted from the tissue lysate using the magnetic beads extraction method. The mitochondrial cytochrome *b* gene was amplified using the primers L14723 and H15915 (Nicolas et al. 2012). Cycling conditions were 96° C for 10 min, followed by 35 cycles of 95° C for 30 sec, 50° C for 30 sec, then 72° C for 10 min. Samples were then stored at 4° C. PCR products were purified with the PCR purification kit. The Sanger Sequencing method was used to sequence the mitochondrial cytochrome *b* gene (1140 bp). Two Sanger sequences were performed with both PCR primers and Bigdye 3.1 and run on an ABI 3730XI sequencer. The forward and reverse sequences from the same sample were assembled using the CodonCode Aligner, then consensus sequences were reported to us. Of the 128 samples, 127 were successfully sequenced using this method.

We conducted phylogenetic and molecular evolutionary analyses using MEGA version X (Kumar et al. 2018). Sequences were aligned using ClustalW in MEGA with a Northern Short-tailed Shrew (*Blarina brevicauda*) sequence (sample AB175134.1 from GenBank) as the outgroup. Of the 1140 base pairs in the mitochondrial cytochrome *b* gene, 1,085 base pairs were preserved in the alignment.

We compared all samples to known samples in GenBank using BLAST (Basic Local Alignment Search Tool) and set a species identification criterion as > 99% identical to the sequences of that species. One third of the samples (41) were most closely related (> 99%) to *S. rohweri*. Because this was unexpected based on previous range maps, we performed a maximum likelihood phylogenetic analysis with 100 bootstraps in MEGA to estimate the phylogenetic tree that included individuals identified as *S. rohweri* from this study plus two GenBank samples each of *S. rohweri (*GenBank samples EU088302 and EU088303.1), Trowbridge's Shrew (*S. trowbridgii*; GenBank samples FJ667520.1 and AY014956.1), Montane Shrew (*S. monticolus*; GenBank samples AB100273.1 and AB100272.1), Vagrant Shrew (*S. vagrans*; GenBank samples MK691376.1 and MK691381.1), and Masked Shrew (*S. cinereus*; GenBank samples AY014951.1 and AY014952.1). The tree was rooted by the *Blarina brevicauda* sequence (Fig. 3).

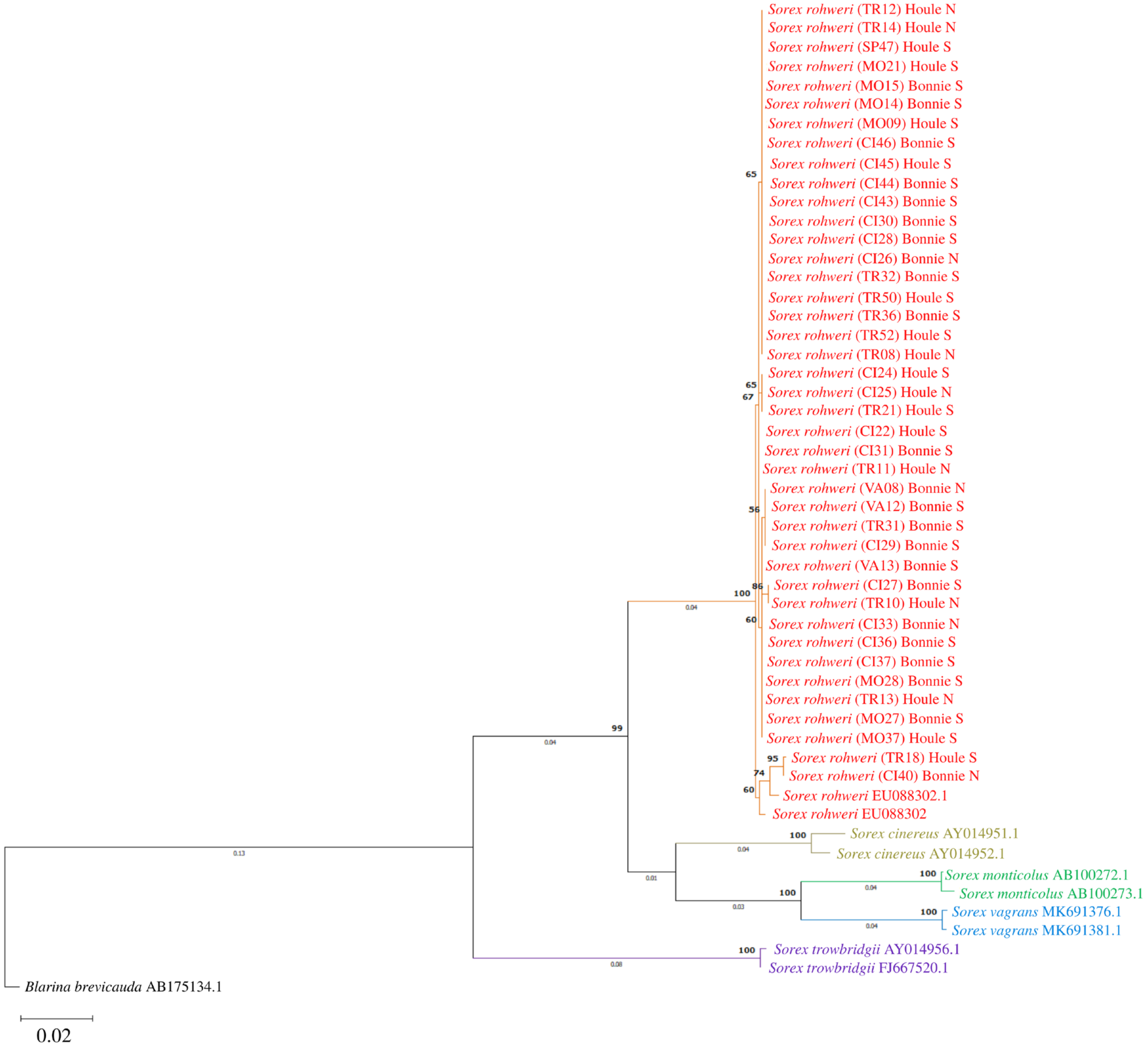

Figure 3. Maximum likelihood phylogenetic tree from 41 Olympic Shrew (*S. rohweri*) samples collected near Easton, Washington, in 2019. A Northern Short-tailed Shrew (*Blarina brevicauda*) sample from GenBank was included to root the tree, and two samples each of Trowbridge's Shrew (*Sorex trowbridgii*), Montane Shrew (*Sorex monticolus*), Olympic Shrew (*Sorex rohweri*), Vagrant Shrew (*Sorex vagrans*), and Masked Shrew (*Sorex cinereus*) from GenBank were included to verify species identifications. The percentage of trees in which the associated taxa clustered together is shown in bold text next to the branches. The tree is color-coordinated by species and drawn to scale, with branch lengths measured in number of substitutions per site (Tamura and Nei 1993; Kumar et al. 2018).

Results

The phylogenetic tree confirmed 41 *S. rohweri*. No shrews were confirmed as *S. cinereus*, and 68% of the individuals identified in the field as *S. cinereus* (n = 17) were genetically identified as *S. rohweri* (the other eight were identified as *S. monticolus* or *S. vagrans*). The remaining individuals confirmed as *S. rohweri* were originally identified in the field as *S. trowbridgii*, *S. monticolus*, *S. vagrans*, or *Sorex* sp. (Table 2). We captured most of the *S. rohweri* individuals in pitfall buckets (n = 37); only four were captured in Sherman traps. We only caught S. *rohweri* at the Bonnie Creek (n = 23) and Houle Creek (n = 18) sites (Fig. 2); none of the 14 shrews captured at the MP 67.1 Creek site, just 4.5 km east of Houle Creek, was genetically identified as *S. rohweri* (all shrews at that site were either *S. trowbridgii* or *S. vagrans*). The capture site farthest east was near Houle Creek (47.298561, -121.293831) at an elevation of about 730 m.

Discussion

Sorex rohweri was first discovered and described by Rausch et al. in 2007 through museum specimens from western Washington and British Columbia that were originally identified as *S. cinereus* or *S. vagrans*. The geographic range of the species was later extended northward into British Columbia (Nagorsen and Panter 2009) and southward into western Oregon (Woodman and

Table 2. Species identifications of 127 *Sorex* shrews captured near Easton, Washington, showing the number of individuals (n) identified to each species in the field and their confirmed genetic identifications. Numbers in bold across the diagonal represent individuals with correct field identifications.

		Genetic Identification				
Field Identification	n	*S. cinereus*	*S. trowbridgii*	*S. monticolus*	*S. vagrans*	*S. rohweri*
Masked Shrew (*S. cinereus*)	25	**0**	0	5	3	17
Trowbridge's Shrew (*S. trowbridgii*)	53	0	**32**	8	0	13
Montane Shrew (*S. monticolus*)	30	0	0	**19**	4	7
Vagrant Shrew (*S. vagrans*)	14	0	0	8	**3**	3
Unidentified (*Sorex* sp.)	5	0	0	3	1	1
Total	127	0	32	43	11	41

Fischer 2016), encompassing areas from the Pacific coast to inland sites around the crest of the Cascade Range in British Columbia, Washington, and Oregon. Most records are from the Coastal Range and western slopes of the Cascade Range in Oregon and Washington, the Olympic Peninsula of Washington, and the Fraser River Basin of southwestern British Columbia (Rausch et al. 2007; Nagorsen and Panter 2009; Woodman and Fisher 2016; Woodman 2018). All Washington records of *S. rohweri* in the University of Washington Burke Museum (207 specimens), U.S. National Museum of Natural History (USNM; 26 specimens), and iDigBio databases came from counties west of the Cascade Range crest: Clallam, Grays Harbor, Jefferson, Kitsap, Lewis, Pacific, Pierce, and Skamania (Burke Museum. 2021. Mammalogy Collection Database. Available from https://www.burkemuseum.org/collections. [Accessed 4 November 2021]; U.S. National Museum. 2021. Division of Mammals Collections. Available from https://collections.nmnh.si.edu/search/mammals/. [Accessed 4 November 2021]; iDigBio. 2021. Integrated Digital Biocollections Portal. Available from https://www.idigbio.org/portal. [Accessed 4 November 2021]). The furthest east longitude of those specimens was -121.5262 (latitude 46.9879) in Pierce County, north of Mt. Rainier, Washington.

Our captures are the first documentation of *S. rohweri* on the east slopes of the Cascade Range in Washington State. All of our sites were within Kittitas County (which extends from the crest of the Cascade Range eastward) and slightly further east (-121.293831) than all previous records (Fig. 4). The elevational limits of *S. rohweri* vary regionally but range from sea level to at least 1,585 m (recently documented in Whatcom County, Washington, 58 km east of the town of Glacier; Woodman and Fisher 2016). Our captures occurred at the midrange (732–762 m) of previously reported elevations. Due to the rain shadow effect, the eastern slopes of the Cascade Range experience increasingly warmer and drier conditions compared with the leeward western slopes. This spatially shifting climate results in a gradual change of forest habitats. Several species of small mammals that have most of their geographic distribution in western Washington extend over the Cascade crest onto the upper eastern slopes of the Cascades and eventually drop out as one continues eastward and downward in elevation; included among them are the shrews *S. bendirii* and *S. trowbridgii*. *Sorex rohweri* appears to follow this geographic pattern.

Some of our identification errors were due to the unexpected occurrence of *S. rohweri* in the study area, as it was not included in our dichotomous key. Other

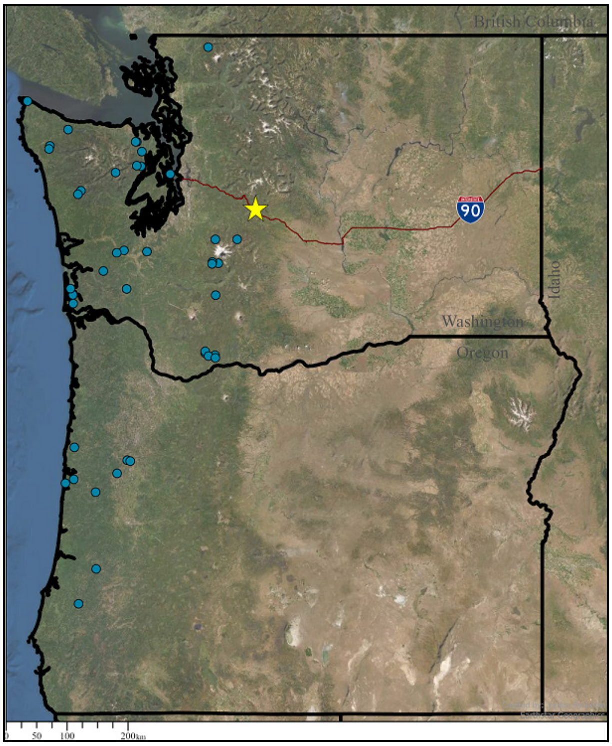

Figure 4. Location of our new Olympic Shrew (*Sorex rohweri*) records (yellow star) and locations of previously documented sites (blue circles) from database records of the University of Washington Burke Museum and the National Museum of Natural History.

errors, however, were most likely caused by the difficulty of scoring small characteristics (e.g., teeth and toepads) on live shrews. Even with a key including all possible species in the Cascade Range of Washington, several species are not reliably keyed out by morphology, especially on live animals. Individual *S. rohweri, S. vagrans,* and *S. cinereus* shrews, especially live ones, cannot be reliably distinguished due to overlapping measurements (Nagorsen and Panter 2009; Woodman and Fisher 2016). Despite an estimated 850,000-y divide (coalescence time, using cytochrome b) between *S. rohweri* and its sister group, the *S. cinereus* complex, these taxa remain morphologically similar (Hope et al. 2012). Genetic analysis proved to be crucial for the accuracy of this study, not only for *S. rohweri* but also for the other shrew species. We highly recommend its use for any field studies on live shrews.

Documentation of the longitudinal and upper elevational limits of a species is important for understanding future impacts of climate change. Future work could include more extensive sampling in this location after wildlife crossing structures are built and in other locations along the eastern slopes of the Cascade Range. We also recommend a review and genetic analysis of museum specimens from the area. Genetic expansion statistics from all samples of S. *rohweri* in Washington, Oregon, and British Columbia may help infer the source and timing of any past range extension.

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Jordan D. Ryckman is a Biologist who spent her undergraduate and graduate career studying small mammals as part of the I-90 Snoqualmie Pass East Project. She has grown a passion for wildlife and conservation and is intrigued by human activities that impact wildlife such as roads and development. After graduation, she worked on a restoration crew in central Washington, and now works with Conservation Northwest, a non-profit that works to protect, connect, and restore wildlife habitat. (Photographed by Kris Ernest).

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IRRUPTIVE MOVEMENTS OF THE BLACK-CHINNED SPARROW (*SPIZELLA ATROGULARIS*) IN RESPONSE TO VARIATIONS IN PRECIPITATION: IMPLICATIONS FOR CLIMATE CHANGE RESILIENCY

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Abstract.—**The Black-chinned Sparrow (*Spizella atrogularis*) is a quintessential southwestern bird, its breeding range restricted to the southwestern U.S., central Mexico, and northernmost Baja California. This species stages sporadic breeding season incursions into northern California, however, and occasionally as far north as southern Oregon. These movements tend to be irruptive, with birds reported at several different locations during those years. We attempted to determine both the source population(s) and the factors influencing these northward irruptions. We tested whether these irruptions derived from birds normally breeding in southern California, and that years with below average precipitation in southern California drove some individuals to move north seeking better breeding conditions. We first looked for evidence of regional song dialects that could be used to identify the source of irruptive birds and found that all northern California breeders used song types of the subspecies *S. a. cana*. We found a significant negative correlation between the numbers of northern California Black-chinned Sparrows reported and southern California precipitation levels in the months prior to each breeding season. Our findings may have implications for the potential of this species to adapt to changing levels of precipitation by expanding its breeding range northward.**

Key Words.—irruption; precipitation; song; song dialect; climate change.

INTRODUCTION

The primary range of the Black-chinned Sparrow (*Spizella atrogularis*; Fig. 1) includes most of the southwestern U.S. (southern California, Arizona, New Mexico, Texas, and southernmost Utah and Nevada) and much of central Mexico and Baja California (Tenney 1997). The species breeds sparsely in central California (San Luis Obispo County north to Monterey County and in the western foothills of the southern Sierra Nevada range) with intermittent breeding in the northern half of the state (e.g., Shuford 1993; Bolander and Parmeter 2000; Roberson 2002; Bousman 2007; Berner 2015). The nature of northern California breeding appears to be irruptive, with reports of birds both numerous and widespread during these years (Beedy and Pandolfino 2013; Rottenborn et al. 2013).

Four subspecies of *Spizella atrogularis* are currently recognized (Clements et al. 2021), *S. a. atrogularis* breeding in central Mexico, *S. a. evura* in northernmost Mexico and from western Texas to southeastern California, *S. a. cana* from Monterey County in California and the west-central Sierra Nevada foothills south to Baja California, and *S. a. caurina* breeding in the interior Coast Range of California from Contra Costa County south to eastern San Benito County. The winter range of *S. atrogularis* is almost entirely within Mexico, with the exception of small areas of southernmost Arizona, New Mexico, and westernmost Texas. The subspecies *S. a. cana* is believed to winter in Baja California Sud, but the non-breeding ranges of each of the subspecies are uncertain (Tenney 1997). The status of *S. a. caurina* is controversial with some considering it synonymous with *S. a. cana* (Phillips et al. 1964; Patten et al. 2003; Pyle 2022). This subspecies was originally described based on just five specimens (Miller 1929) and subsequent physical measurements by others found broad (Van Rossum 1935) or complete (Tenney 1997) overlap with *S. a. cana*.

FIGURE 1. Irruptive Black-chinned Sparrow (*Spizella atrogularis*) in Amador County, California. (Photographed by Don Marsh).

The source of the intermittent breeders in northern California and the factors that may drive these irruptions have not been studied. Some have speculated that these extralimital breeders may include *S. a. cana* or *S. a. caurina*, or both (Miller 1929; Tenney 1997; Bousman 2007) and others suggested that drought conditions in the southern breeding range may be driving some birds to move north to find better conditions during those dry years (Beedy and Pandolfino 2013; Rottenborn et al. 2013). Although we found no studies bearing on these speculations or directly linking precipitation with breeding success for this species, this connection appears to be supported by a cascade of relationships, beginning with prey and habitat type. *Spizella atrogularis* depends largely on adult and larval insect prey during the breeding season and this species is strongly linked to post-fire Chaparral landscapes (Tenny 1997). A key characteristic of this type of habitat is a diverse and abundant herbaceous plant community in the aftermath of fire (Keeley et al. 1981; Quinn and Keeley 2006). The extent of herbaceous cover was significantly correlated with annual rainfall in San Diego County (Keeley et al. 1981), and the extent of herbaceous cover in post-fire chaparral was correlated with insect abundance (Force 1990). Indeed, Force (1990) asserted that flower-visiting insect abundance and diversity is higher in Chaparral than in any other California habitat. Thus, one might reasonably expect that drought years could produce fewer insects and negatively affect *S. atrogularis* breeding success.

We chose to address these questions by testing the predictions that members of the subspecies *S. a. cana* normally breeding in southern California were the source of these irruptions, and that below normal rainfall in southern California was a factor behind these irruptions. Because specimens of these northern extralimital breeders were not available, but recordings of songs of many of these individuals are archived, we chose to examine the songs of *Spizella atrogularis* subspecies to determine if song dialect could be used to identify the source population(s). Many bird species use distinct regional song dialects (Catchpole and Slater 2008). Dialects can be based on qualitative (distinctly different traces on a spectrogram) or quantitative (e.g., pitch, rates of singing, length of songs) characteristics of the songs (Kroodsma 2004; Catchpole and Slater 2008). Tenney (1997) suggested some differences between songs of birds in California (*S. a. cana*) and those in southern Nevada, Arizona, and Texas (*S. a. evura*) with California songs having generally fewer introductory and terminal notes than those of the eastern birds. Thus suggesting that song dialects may exist. This was based on a small number of samples (25 total), however. We tested our prediction that below normal rainfall in southern California was a factor in driving these northward movements by looking for correlation between the number of northern California breeders and southern California rainfall during the eight months prior to each breeding season.

Breeding Bird Survey data show significant declines in the abundance of the *S. atrogularis* since 1966, rangewide and within California (Sauer et al. 2020). This species is particularly sensitive to the effects of urbanization and habitat fragmentation (Bolger et al. 1997; Crooks et al. 2004), both of which are significant factors within the ranges both *S. a. cana* and *caurina*. In addition, this sparrow may face challenges as the climate changes. Most climate change models predict significant increases in temperature but equivocal projections for changes in precipitation for California during coming decades (Cayan et al. 2008; Ackerly et al. 2010; Feldman et al. 2021). Precipitation projections for southern California are particularly variable (Feldman et al. 2021) with some models predicting stable or slightly increasing precipitation and others significant decreases. As noted above, decreases in annual rainfall could lead to lower breeding success for *Spizella atrogularis*.

Irruption is an extreme example of facultative migration (i.e., migration that can occur some years, but not others; Newton 2012). To the extent that individuals of a species can make such movements in response to poor breeding conditions, facultative migration can have important conservation implications. Such extralimital breeding can be the precursor to expansion of the range of a species (Newton 2003). Expansions or shifts in breeding range can provide a basis for adapting to changes in climate or other conditions and such shifts have been documented for many bird species (e.g., Hitch and Leberg 2007; Tingley et al. 2009; Saracco et al. 2019).

Methods

We used song recordings from the full range of *Spizella atrogularis* to look for evidence of distinct regional dialects by examining spectrograms with Raven Pro software (https://ravensoundsoftware.com/). We used all available recordings from the Mark Robbins/Macaulay Library (www.macaulaylibrary.org) and xeno-canto (www.xeno-canto.org) that were of sufficient quality to interpret and that included at least two examples of full song. We used recordings of 147 individuals made from April through July (Appendix 1). We assumed that multiple recordings from the same location and the same year to be of the same individual unless otherwise specified by the recordist. We identified 24 distinct song types (Appendix 2) and the six most common song types (Fig. 2) accounted for more than 83% of all songs recorded. Different song types were characterized based on the introductory notes and the first few notes of the following trill. Because individual *S. atrogularis* used two song types, usually alternated, the dialect assigned was based on the pair of song types used. In each case, the assignment of song types to a given recording was done in a blind manner. That is, the location of the recording was not known by the author

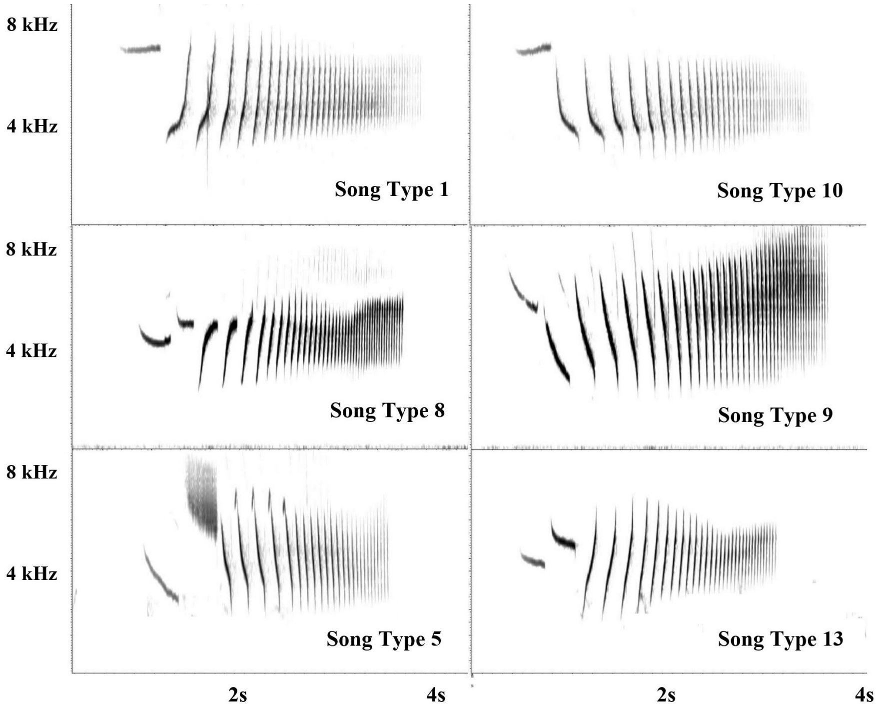


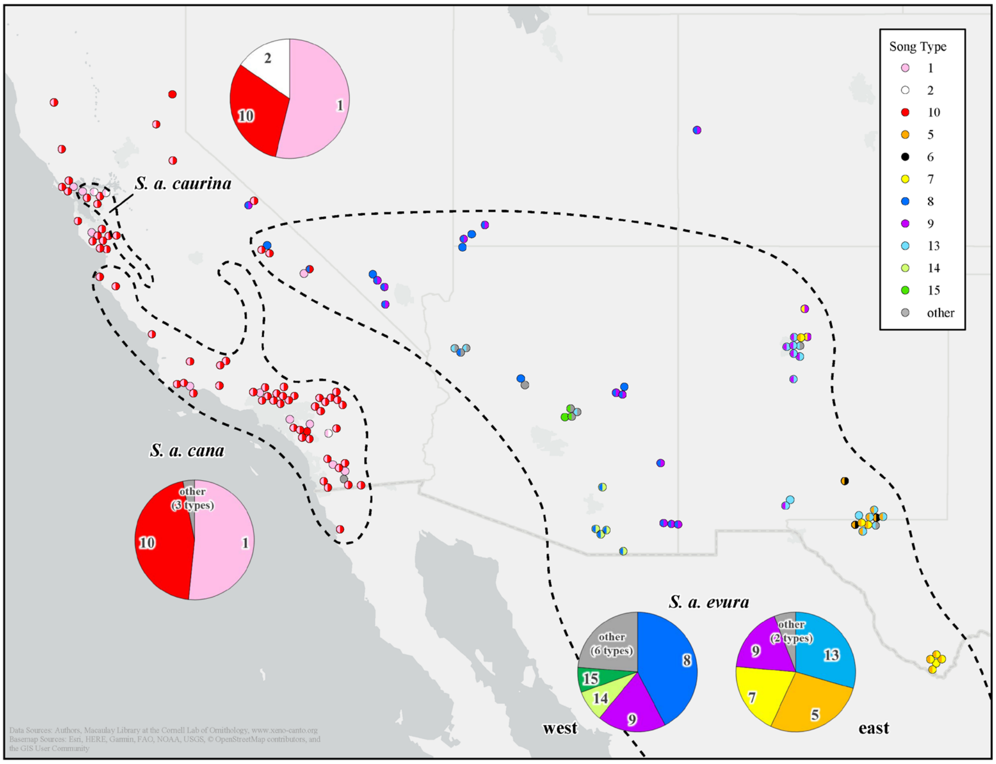
Figure 2. Examples of the six most common song types of the Black-chinned Sparrow (*Spizella atrogularis*).

when assigning the song type to avoid any possibility of unintentional bias.

To quantify precipitation prior to the breeding season (hereafter, pre-breeding precipitation), we used monthly precipitation data (https://www.ncdc.noaa.gov/cdo-web/) from the five counties that encompass the majority of the southern California breeding range of *S. atrogularis* (Santa Barbara, Ventura, Los Angeles, San Bernardino, and San Diego). We averaged total precipitation (cm) across these five counties during the eight months (August through March) prior to each breeding season. The southern California rainfall season in these California Chaparral habitats begins in late August (rare) with most precipitation from late fall through spring (Quinn and Keeley 2006). We chose to include the entire pre-breeding season rainfall period because the condition of the both the herbaceous (Keeley et al. 1981) and shrubby (Quinn and Keeley 2006) plant communities is influenced by annual rainfall.

To index the size of each annual irruption, we compiled reports of *S. atrogularis* in northern California from 1992 through 2021 from Monterey County north, including those within the published range of *S. a. caurina*, using eBird (https://ebird.org) and archives of North American Birds, both published (www.aba.org/north-american-birds/) and unpublished (from Regional Editor records). We tallied occurrences from April through July and eliminated any duplicate reports from the same general location in the same year. We assumed eBird reports or reports from the North American Birds data from the same location in the same season were from a single individual unless the reporter specifically noted the number of separate individuals observed. When multiple individuals were noted by more than one observer in one location, we used the highest total observed by any single observer on a single day in that location for the total number of birds. Because locations of eBird reports are based on where the user chose to start the checklist, we assumed eBird reports within 5 km of each other in the same season were of the same individual. Similarly, we indexed the size of the annual breeding population of *S. a. caurina* by tallying April through July reports of *S. atrogularis* within the range of *S. a. caurina* as approximated by Grinnell and Miller (1944) and Tenney (1997).

The annual irruption index was related to pre-breeding precipitation using negative binomial regression to allow for overdispersion in the positive, integer-valued index (Ver Hoef and Boveng 2007). To fit negative binomial models in the R language for statistical computing (R Core Team 2021), we used function glm.nb from the MASS package (Venables and Ripley 2002). To further account for any excess zeros in the response variable, we used function zeroinfl from the pscl package (Jackman 2020). Within each regression framework, we compared a null (intercept-only) model of our annual irruption index with what we called a precipitation model that contained an intercept and an additive effect of pre-breeding precipitation. Model support was evaluated using Akaike's Information Criterion (AIC) corrected for overdispersion and small sample size, QAIC*c*, and we assumed that a difference in QAIC*c* (ΔQAIC*c*) of more than four units suggests strong support for the model with lower QAIC*c* (Burnham and Anderson 2002).



Data Sources: Authors, Macaulay Library at the Cornell Lab of Ornithology, www.xeno-canto.org
Basemap Sources: Esri, HERE, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors, and the GIS User Community

Figure 3. Locations of recordings used and the song types from each recording. Filled circles indicate that the recording included only one song type and dotted lines indicate the approximate extent of the ranges of the subspecies based on Grinnell and Miller (1944) and Tenney (1997).

Results

Songs and song dialects.—Songs of *Spizella atrogularis* in our sample followed the general form described by Pieplow (2019). Songs had variable numbers of musical, often high-pitched introductory notes, followed by an accelerating trill with notes becoming progressively less musical (progressing from slurred notes into a rapid unmusical trill). None of the individuals in our set showed more than two song types, and most birds alternated between their two types during a singing bout.

We found distinct regional song dialects for *S. atrogularis* recorded in the U.S. (Fig. 3). There were too few recordings (five) from central Mexico to assess dialects within the range of *S. a. atrogularis*. Nearly all birds (> 95%) recorded in the range of *S. a. cana* or *caurina* used song types 1 and 10. These two song types were also used exclusively by birds in the extralimital recordings west of the Sierra Nevada crest in California and were not found in any recording from the range of *S. a. evura* east of California. Among the five birds recorded in Inyo County, California, at the edge of the published range of *S. a. evura* (Grinnell and Miller 1944), four used song type 1 or 10, or both, and two used song type 8, with one individual using both 8 and 10. Within the range of *S. a. evura*, the dominant song types were distinct from those within the range *S. a. cana* or *caurina*. Song types used commonly in the western parts of the range of *S. a. evura* (southeastern California, southernmost Nevada and Utah, and Arizona) differed from those in the eastern range (New Mexico and Texas). Song types 8 and 9 accounted for 61% of all song types in the west, and song types 14 and 15 comprised another 15%. Eastern *S. a. evura* birds used song types 5, 7, or 13 in 76% of recordings, and song type 9 accounted for another 18%.

Irruptions and precipitation.—We found a strong inverse relationship between the annual index of breeding season Black-chinned Sparrows in northern California (excluding those within the range of *S. a. caurina*) and pre-breeding precipitation in southern California (Fig. 4). The negative relationship between our irruption index and precipitation was well supported (QAIC*c* of the precipitation model was 9.65 units lower than QAIC*c* of the null model). In 10 of the 12 y in which a large number (> 14) of *S. atrogularis* was reported in northern California, southern California precipitation was below the 30-y average, ranging from 37% to 63% below average in those years. When we included only those reports within the published range of *S. a. caurina* (Fig. 5), the inverse relationship between our annual irruption index and pre-breeding precipitation was also well supported (QAIC*c* of the precipitation model was 18.92 or 10.08 units lower than QAIC*c* of the null model for negative binomial or zero-inflated negative binomial models, respectively; Table 1). The fitted value of the coefficient of pre-breeding precipitation was quite similar

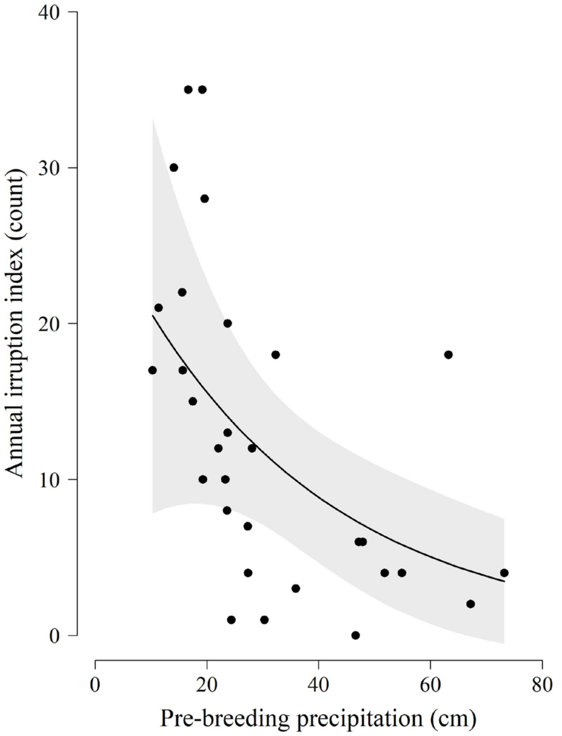


Figure 4. Relationship between an index of irruption (number of extralimital breeders reported outside the range of *Spizella atrogularis caurina*) and southern California precipitation (cm) during the eight months prior to the breeding season, as determined through negative binomial regression (curve) and its 95% confidence interval (shaded region).

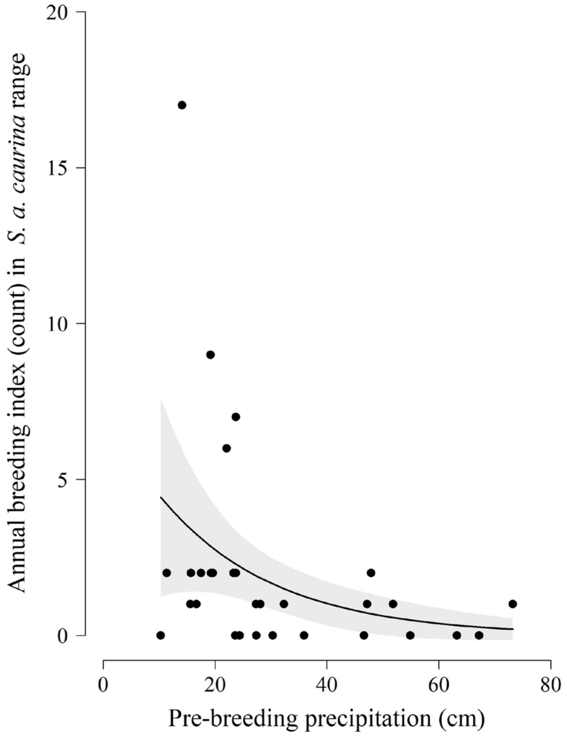


Figure 5. Relationship between an index of breeding population size within the range of *Spizella atrogularis caurina* (number of breeders reported) and southern California precipitation (cm) during the eight months prior to the breeding season, as determined through a negative binomial regression (curve) and its 95% confidence interval (shaded region).

between the model based on all records of extralimital breeders (mean ± standard error = -1.007 ± 0.249) and the model based on only those breeders recorded within the range of *S. a. caurina* (-1.550 ± 0.493).

Discussion

Song dialects.—Tenney (1997) found some regional differences among the songs of *Spizella atrogularis*, with the length of the trill portion of songs significantly longer among birds in California (*S. a. cana* range) than birds in the range of *S. a. evura*, as well as differences in introductory and terminal notes. He also found some regional differences within *S. a. evura* in the highest pitch of notes in that trill, with the notes from birds in the eastern part of the range (New Mexico and Texas) reaching higher pitches than Arizona birds. Those results were based on small samples, however, and could have reflected clinal differences rather than distinct dialects. Thus, our work is the first demonstration of true song dialects in this species.

Confirmation of song dialects is important not only because it is believed to confirm that song is learned rather than innate (Kroodsma 2004; Catchpole and Slater 2008), but also because such dialects can reveal early signs of speciation or sub-speciation (Marler and Tamura 1962; Nottebohm 1969; Baker 1975; Slabbekoorn and Smith 2002; Pandolfino and Pieplow 2015). Additionally, for birds that sing in winter or during migration, well-mapped dialects can be used to reveal migratory connectivity and strategy (DeWolfe and Baptista 1995; Pandolfino and Douglas 2021). There is evidence that *S. atrogularis*

Table 1. Akaike's Information Criterion (AIC) models corrected for overdispersion and small sample size (QAIC*c*) of Black-chinned Sparrow (*Spizella atrogularis*) irruption index across the extralimital range of the species (y), including a fixed effect of southern California precipitation (*precip*) or intercept only (1) and within the range of *S. a. caurina* (y_s), assuming negative binomial (NB) or zero-inflated negative binomial (ZINB) variation in the irruption index and including a fixed effect of southern California precipitation (*precip*) or intercept only (1). The symbol k = number of parameters.

Model	QAIC*c*	ΔQAIC*c*	*k*
Extralimital Range			
$y \sim precip$	70.43	0	3
$y \sim 1$	80.08	9.65	2
Within the Range			
NB, $y_s \sim precip$	84.19	0	3
NB, $y_s \sim 1$	103.10	18.92	2
ZINB, $y_s \sim precip$	166.18	81.99	4
ZINB, $y_s \sim 1$	176.26	92.07	3

sings in migration and winter (Unitt et al. 1995; Williams 1995), and we found one January song recording (https://xeno-canto.org/618609) from Central Mexico.

We found the songs of *S. a. cana* and *evura* distinct. No song types from the range of either subspecies were found in any of the recordings from the range of the other, with the exception of mixed song types in Inyo County, California. Thus, this area, originally mapped as within the range of *S. a. evura* (Grinnell and Miller 1944), may represent a contact zone between *S. a. cana* and *evura*. Indeed, one bird there used both song type 8, associated with *S. a. evura*, and song type 10, associated with *S. a. cana*. Such observations of mixed song types could be the result of individuals of one subspecies learning the song of another, or of intergradation between the subspecies. We also found differences between the songs in the western versus eastern ranges of *S. a. evura*. Combined with the findings of Tenney (1997) on differences in song pitch, our results suggest that *S. a. evura* may show regional variation worthy of more investigation.

We detected no difference in dialect used between the songs of birds in the *S. a. cana* versus *caurina* ranges, or among extralimital breeding birds in northern California. These birds used song types 1 and 10 almost exclusively. Song type 2 was found in two recordings in the range of *S. a. caurina* and one in the southern range of *S. a. cana*; however, this song type is very similar to song type 10 (see Appendix 2) and may be simply a variation on that song type. The extralimital recordings included those from birds that breed somewhat regularly (Bousman 2007) in the Santa Cruz Mountains along the border between Santa Clara and Santa Cruz counties. Unfortunately, there are no specimens of these birds available.

Northern California irruptions and Southern California precipitation.—Our finding of a strong negative relationship between southern California precipitation and the numbers of breeding season reports of *S. atrogularis* in California from Monterey County northward is consistent with an irruptive pattern driven by poor breeding conditions in the southern California breeding range. Most examples and most studies of irruptive migration are based on non-breeding season irruptions and are believed to be influenced by conditions in the usual winter range (Newton 2012). There are examples of breeding season irruptions, however, likely driven by birds seeking better breeding conditions (Shaw 1990; Whitaker et al. 1996; Lindström et al. 2005; Burbridge and Fuller 2007; Pedler and Lynch 2016).

Factors other than, or in addition to, precipitation in southern California may influence this irruptive behavior also. It is possible that unusually high over-winter survival during the preceding winter or high levels of breeding productivity in the breeding season of the year before the irruptions create an excess of breeders beyond the carrying capacity of the southern breeding range. We found no documented examples of either factor implicated in other breeding season irruptions, but movements of some fall/winter irruptive species such as the Pine Siskin (*Spinus pinus*) may be influenced by both breeding and non-breeding range conditions (Strong et al. 2015).

We also found a strong negative relationship between our index of irruption and pre-breeding season southern California precipitation when including only birds reported within the published range of *S. a. caurina*, suggesting that birds breeding in that range are also influenced by breeding season conditions in southern California. This finding, coupled with the use of song dialects identical to those of *S. a. cana*, lends support to recommendations for synonymizing these two taxa (Phillips et al. 1964; Patten et al. 2003; Pyle 2022). Indeed, based on our findings and the significant overlap of morphological measurements, *S. a. caurina* does not meet the requirements for valid subspecies status suggested by Patten and Unitt (2002) and Patten (2015).

Conservation implications.—*Spizella atrogularis* faces a spectrum of challenges, particularly in its core Southern California breeding range. This species is highly susceptible to conversion or fragmentation of habitat (Bolger et al. 1997; Crooks et al. 2004), both of which are continuing threats in this area (EcoAdapt. 2017; Climate change vulnerability assessment for the Southern California Climate Adaptation Project. Available from http://ecoadapt.org/data/documents/EcoAdapt_SoCalVASynthesis_Chaparral_FINAL2017.pdf [Accessed 15 July 2022]). Even in more remote locations, drought in southern California has limited the recovery of the Chaparral habitats of the species from the many recent wildfires (Storey et al. 2020). In addition, projected climate change may reduce the quality of the remaining habitat and increase the frequency and intensity of those fires (EcoAdapt 2017, *op. cit.*).

To persist in the face of declining habitat quality, a species must either adapt to the new conditions or move to areas that offer better options. One or both of these strategies have been observed to be in process among a huge array of organisms (Parmesan and Yohe 2003; Inouye 2022), including plants (Parmesan and Yohe 2003; Corlett and Westcott 2013), insects (Parmesan and Yohe 2003; Forrest 2016; Howe et al. 2022), mammals (Parmesan and Yohe 2003; Inouye 2022), and birds (e.g., Thomas and Lennon 1999; Hitch and Leberg 2007; Tingley et al. 2009; Saracco et al. 2019; Curley et al. 2020) in response to climate change. Many have adjusted migratory or breeding phenology (Forrest 2016; Inouye 2022) or shifted their wintering and/or breeding ranges (Thomas and Lennon 1999; Parmesan and Yohe 2003; Hitch and Leberg 2007). Most birds have shifted ranges poleward, north in the northern hemisphere and south in the southern hemisphere (Thomas and Lennon 1999; Hitch and Leberg 2007). In general, these range shifts have closely tracked the climatic ideal of the species (Tingley et al. 2009; Saracco et al. 2019; Curley et al. 2020), although many are still facing climate mismatches that may pose a threat (Viana and Chase 2022). Most of these range shifts have been ascribed to changing climate; however, Newton (2003) stressed that direct human impacts on habitat could also be a factor in some or most of these examples.

While shifts and expansions of the ranges of species are well-documented, the mechanisms by which they occur remain largely unknown. Both irruptions (sporadic, but regular, movements beyond the typical range) and vagrancy (occasional or rare out-of-range movements) have been proposed as possible precursors to range expansions or shifts (Grinnell 1922; Patten and Marantz 1996; Newton 2003). Confirming this with birds or mammals would require extensive long-term studies, though the expansion of the Cattle Egret (*Bubulcus ibis*) into the western hemisphere (Newton 2003; Telfair 2020) provides an intriguing example. Perhaps the only well-documented case of irruptions leading to range expansion involves the Western Balsam Beetle (*Dryocoetes confusus*) expansion into western Canada (Howe et al. 2022).

The ability of the *S. atrogularis* to stage these irruptions into northern California may offer the species a means to mitigate the effects of climate change and human development in their southern California range. Although the entire state is expected to see increasing temperatures and variable precipitation in the coming decades, the northern California locations used by this sparrow (which include coastal Monterey, Marin, and Santa Clara counties and the foothills of the Sierra Nevada and the Coast Ranges) are projected to remain cooler and wetter than southern California (Cayan et al. 2008). They are also generally further from urbanized areas and likely to see less development impact than most of the southern California Chaparral areas.

It remains to be seen whether these irruptions lead to an actual range expansion. As noted by Newton (2003), such an expansion requires that a number of conditions are met, including: (1) movements of sufficient numbers of irruptive individuals to permit pairs to meet; (2) the ability to breed successfully in the expanded range; and (3) a lack of excessive competition in the new range. If conditions in southern California deteriorate, the first requirement may be met; however, the other requirements suggest the need for further study of the birds occupying these irruptive locations.

***Conclusions*.**—Our results demonstrated distinct regional dialects among the subspecies of the *S. atrogularis*. Nearly every bird recorded in California used identical song dialects, including individuals recorded in the published range of *S. a. cana* and *caurina*, and the northern California irruptive birds. Our finding that these northern irruptions correlated well with years of drought in the southern California range suggests that some individuals may be migrating further north in those years, seeking better breeding conditions. Continued monitoring will be needed to determine if these irruptions lead to a northward expansion of the breeding range of this species.

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Ed Pandolfino received his Ph.D. from Washington State University, Pullman, and has served as president of Western Field Ornithologists, vice-president of the San Francisco Bay Bird Observatory, and on the board of the Institute for Bird Populations. He co-authored Birds of the Sierra Nevada: Their Natural History, Status, and Distribution (University of California Press 2013) and is lead author of Sacramento Breeding Birds: A Tale of Two Atlases and Three Decades of Change (Central Valley Bird Club 2021). Much of his past research covered status, distribution, and conservation of western birds, with particular emphasis on the Central Valley of California. Many of his recent publications involve bird vocalizations and their application to studies of taxonomy, migration, and breeding phenology. (Photographed by Kathleen Lynch).

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APPENDICES

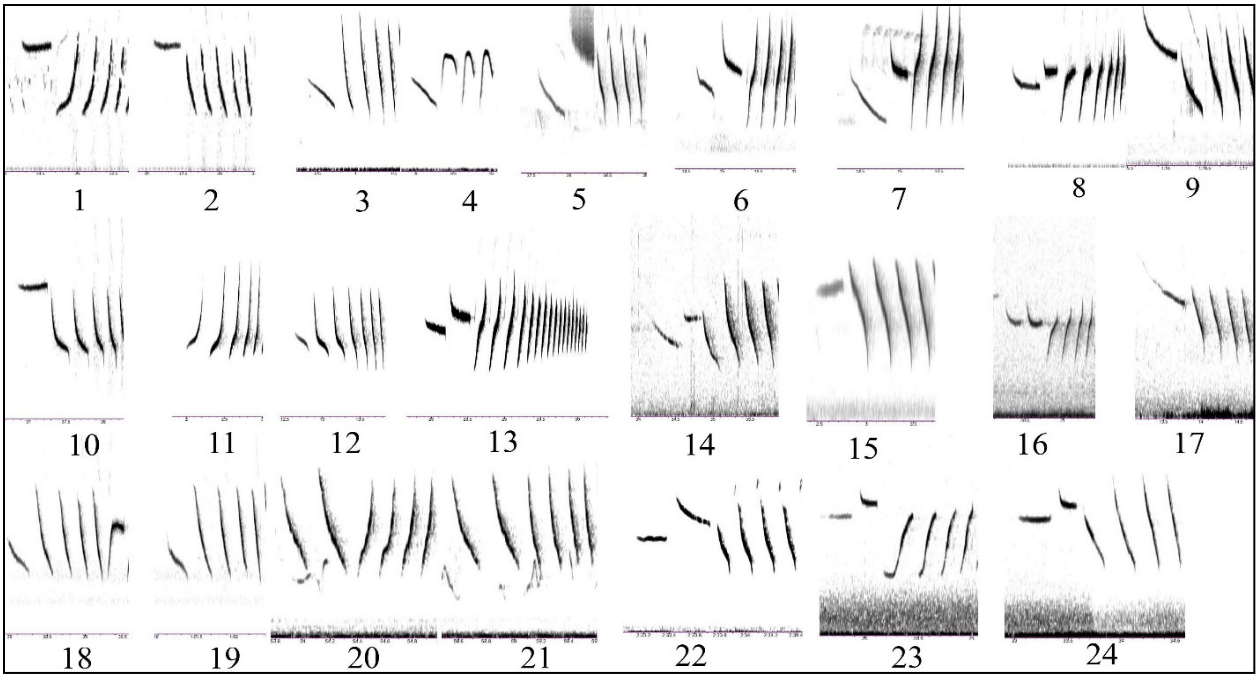
APPENDIX 1. Metadata for all recordings used for our analyses. The asterisk (*) indicates catalog numbers that are preceded by "xc" are from xeno-canto, all others from Macaulay Library.

Catalog No.*	State	Latitude	Longitude	Date	Recordist
15398	Oaxaca	18.90	-97.24	02 June 1961	L. Irby Davis
39322	Arizona	31.92	-109.20	18 April 1987	Oliver H. Hewitt
40631	Texas	31.90	-104.82	09 May 1986	Geoffrey A. Keller
45062	Texas	31.97	-104.81	23 April 1986	Geoffrey A. Keller
56879	California	33.61	-116.83	09 May 1991	Geoffrey A. Keller
64226	Arizona	31.93	-109.37	10 May 1979	William W. H. Gunn
147801	Texas	31.98	-104.75	13 May 2008	Benjamin Clock
147804	Texas	31.99	-104.76	13 May 2008	Benjamin Clock
215898	Durango	23.97	-104.61	26 June 1991	Steve N. G. Howell
224467	California	39.65	-120.30	19 June 2000	Gregory Budney
27237461	California	33.64	-117.39	17 April 2016	Julie Szabo
30050001	New Mexico	32.72	-105.34	10 June 2016	Bob Nieman
30616601	Arizona	31.72	-110.77	26 June 2016	David Stejskal
30862081	Arizona	31.75	-110.80	03 July 2016	Laurens Halsey
32309861	Texas	31.91	-104.85	27 July 2016	Jay McGowan
56033941	California	37.97	-122.63	28 April 2017	Mark Forney
57014421	New Mexico	32.34	-106.59	06 May 2017	Wyatt Egelhoff
57934581	California	33.64	-117.39	13 May 2017	Julie Szabo
58300691	California	33.65	-117.40	16 May 2017	Greg Cross
60738361	California	37.88	-121.91	10 June 2017	Steve Lombardi
60762621	New Mexico	32.37	-106.56	10 June 2017	Bill Tollefson
60934901	California	34.86	-119.24	30 May 2016	Ed Thomas
61315251	California	32.96	-116.58	17 June 2017	Eve Martin
77282271	Utah	37.10	-113.82	12 May 2013	Kenny Frisch
96838851	California	36.93	-118.32	27 April 2018	Rosie Howard
97023421	New Mexico	34.60	-106.48	28 April 2018	Nancy Hetrick
98281091	New Mexico	35.28	-106.48	05 May 2018	Spencer Follett
99699371	California	32.96	-116.58	11 May 2018	Eve Martin
101411471	California	37.10	-121.85	21 May 2018	Ryan Phillips
103556271	California	33.68	-117.50	06 June 2018	Brad Dawson
103789261	Utah	37.13	-113.82	03 June 2018	Kenny Frisch
103885601	California	34.22	-117.71	09 June 2018	Lance Benner
105077381	California	37.72	-118.61	20 June 2018	Rosie Howard
107220181	California	37.85	-121.93	05 May 1976	Darrell Peterson
129975381	California	37.89	-122.23	09 June 2012	Ken Schneider
152114651	New Mexico	35.09	-106.43	19 April 2019	David Buckley
152135651	Arizona	33.92	-111.44	15 April 2019	John Bjorkman
152545651	New Mexico	35.14	-106.48	21 April 2019	TJ Hathcock
154726381	Utah	37.21	-113.64	25 April 2019	Matt Cahill
156786071	California	36.51	-117.37	04 May 2019	Chris Howard
157745991	California	37.72	-118.61	19 June 2018	Joshua Stacy
161787001	California	34.53	-120.04	30 May 2019	Glenn Kincaid
162592431	Arizona	34.62	-112.55	01 June 2019	Susan Drown
163105731	California	34.53	-120.04	07 June 2019	John Callender
163543491	California	34.53	-120.06	09 June 2019	George Chapman
163800411	California	39.51	-122.94	02 June 2019	Bryan McIntosh
166015291	New Mexico	35.14	-106.48	11 June 2019	Liam Wolff
167602791	Texas	29.25	-103.31	27 April 2019	Max Wilson
181069741	Arizona	31.40	-110.27	23 April 2015	Brian Henderson
226058201	Arizona	32.61	-110.73	21 April 2020	Tim DeJonghe
227687331	California	32.69	-116.91	26 April 2020	Paul Marvin

Catalog No.*	State	Latitude	Longitude	Date	Recordist
228180741	California	33.87	-117.69	26 April 2020	brendan galvin
229785731	California	32.64	-116.10	25 April 2020	Justyn Stahl
231183491	California	36.51	-117.37	04 May 2020	Chris Howard
231448321	California	34.86	-119.24	03 May 2020	Ed Thomas
233243501	Arizona	34.50	-112.46	08 May 2020	Janine McCabe
234456381	California	32.91	-116.46	10 May 2020	Hans Petermann
234585541	California	37.10	-121.85	14 May 2020	Jason Vassallo
235452091	California	34.48	-119.25	16 May 2020	Rick Ridgeway
235642271	California	34.42	-118.27	16 May 2020	Naresh Satyan
237407481	California	34.36	-118.35	21 May 2020	Naresh Satyan
237578451	New Mexico	35.22	-106.49	25 May 1983	Arch McCallum
239160261	California	37.10	-121.85	27 May 2020	Garrett Lau
240202501	California	34.93	-119.91	31 May 2020	Anonymous
240360221	California	37.44	-122.40	01 June 2020	Malia DeFelice
240645541	Texas	31.99	-104.77	02 June 2010	Arch McCallum
241301801	California	37.85	-122.20	05 June 2020	Teale Fristoe
242862691	California	32.60	-116.84	12 June 2020	Paul Marvin
243982011	New Mexico	35.29	-106.44	17 June 2020	Spencer Follett
244853031	California	34.27	-116.73	20 June 2020	George Chapman
245381141	Texcoco	19.50	-98.85	24 June 2020	Anuar López
246758061	Baja California	31.81	-116.57	09 May 2020	Antonio Maldonado
264866981	Texas	29.25	-103.31	18 May 2009	Andrew Spencer
313549581	California	37.97	-122.63	06 May 2017	Connor Cochrane
325706481	Texcoco	19.50	-98.82	12 April 2021	Anuar López
326627911	California	34.10	-117.12	15 April 2021	Mikael Romich
326905781	California	35.42	-120.76	16 April 2021	Jay Carroll
331684751	California	34.21	-118.31	29 April 2021	Andrew Birch
332557321	California	37.19	-121.55	01 May 2021	Mike Ambrose
332616521	California	34.54	-120.05	30 April 2021	John Callender
332990401	California	34.36	-118.40	01 May 2021	Becky Kitto
333953001	California	36.93	-118.32	04 May 2021	Nancy Overholtz
334094421	California	34.22	-117.75	01 May 2021	Naresh Satyan
335206671	California	38.70	-122.76	06 May 2021	Bob Hasenick
338630551	California	33.65	-117.45	12 May 2021	Ron Overholtz
339240351	California	37.10	-121.85	16 May 2021	Carter Gasiorowski
341374131	California	34.21	-118.31	22 May 2021	Andrew Birch
342372351	California	37.10	-121.85	25 May 2021	Cindy Cummings
342505511	Texas	29.25	-103.31	04 May 2021	Jason Vassallo
342565251	Utah	37.37	-113.35	23 May 2021	V. Schneggenburger
343417871	California	37.10	-121.85	29 May 2021	Emilie D
343858501	California	34.02	-117.00	29 May 2021	Gary McLarty
344726951	New Mexico	35.37	-106.17	02 June 2021	Chris Chappell
344811351	Arizona	34.33	-110.29	02 June 2021	Eric Hough
345174711	New Mexico	35.88	-106.23	04 June 2021	T. Jay Adams
346406511	California	37.10	-121.85	24 May 2021	Bill Pelletier
346845751	California	36.45	-121.92	10 June 2021	Bill Hubick
348140831	California	32.97	-116.60	15 June 2021	Gary Leavens
349166831	California	37.85	-121.93	25 May 2021	Teale Fristoe
350307531	Arizona	33.92	-111.41	17 April 2021	Damon Haan
351036271	New Mexico	35.14	-106.48	28 June 2021	Aidan Place
355789081	Nevada	36.27	-115.58	20 July 2021	Jan Hansen
362300631	Arizona	34.36	-110.43	07 July 2021	Eric Hough
362301701	Arizona	34.32	-110.29	20 July 2021	Eric Hough
421840981	California	34.34	-117.98	21 May 2021	Diana Doyle
421844781	California	33.70	-116.65	27 May 2021	Diana Doyle

Catalog No.*	State	Latitude	Longitude	Date	Recordist
xc125082	California	34.19	-116.90	03 June 2001	Richard Webster
xc125085	California	34.19	-116.90	03 June 2001	Richard Webster
xc125088	California	34.26	-116.71	22 May 2001	Richard Webster
xc125089	California	34.19	-116.90	03 June 2001	Richard Webster
xc125726	California	34.25	-116.75	05 May 2006	Richard Webster
xc135973	California	36.29	-121.56	01 June 2013	Brian Sullivan
xc136118	Arizona	31.91	-109.14	04 July 1990	Dan Lane
xc153422	California	32.80	-166.48	12 April 2012	Paul Marvin
xc153436	Texas	29.27	-103.30	07 April 2012	Paul Marvin
xc153437	Texas	31.88	-104.87	16 June 2011	Paul Marvin
xc179725	Arizona	33.99	-111.44	26 May 2014	Tim Marquardt
xc181407	California	34.30	-118.01	07 June 2014	Lance Benner
xc246100	Arizona	35.09	-113.89	24 May 2015	Bobby Wilcox
xc247517	Arizona	35.09	-113.89	24 May 2015	Jarrod Swackhamer
xc314118	California	37.10	-121.84	28 April 2016	Alex Rinkert
xc325723	Arizona	31.72	-110.77	04 July 2016	Nick Komar
xc34034	Texas	31.91	-104.88	10 May 2009	Andrew Spencer
xc34134	Texas	31.91	-104.88	15 May 2009	Andrew Spencer
xc34135	Texas	31.91	-104.88	15 May 2009	Andrew Spencer
xc34571	Texas	29.25	-103.31	18 May 2009	Andrew Spencer
xc366792	California	38.14	-122.59	28 April 2017	Derek Lecy
xc368284	California	37.97	-122.63	16 May 2017	Jim Holmes
xc408008	California	32.75	-116.45	15 May 2015	Frank Lambert
xc418264	Nevada	36.42	-115.76	08 May 2018	Bobby Wilcox
xc418279	Nevada	36.39	-115.74	10 May 2018	Bobby Wilcox
xc428178	California	34.22	-117.71	08 June 2018	Lance Benner
xc444605	California	38.50	-120.29	28 May 2014	Ed Pandolfino
xc475295	Nevada	35.96	-115.56	11 May 2019	Bobby Wilcox
xc483157	Arizona	33.92	-111.42	16 April 2018	Keith Corliss
xc551165	California	34.46	-117.82	26 April 2020	Lance Benner
xc553310	Arizona	35.09	-113.89	01 May 2020	Bobby Wilcox
xc5803	California	37.88	-121.91	07 May 1977	Darrell Peterson
xc611125	Arizona	33.06	-109.44	29 May 2020	Richard Webster
xc6143	Guanajato	20.92	-100.75	04 June 2006	Manuel Grosselet
xc618609	Cuidad	19.32	-98.97	30 January 2021	Manuel Grosselet
xc639459	California	33.14	-116.85	08 April 2021	Paul Marvin
xc645514	California	36.94	-118.30	04 May 2021	Ron Overholtz
xc647005	California	34.22	-117.71	10 May 2021	Ethan Van Arnam
xc648850	California	33.67	-117.46	12 May 2021	Ron Overholtz
xc655752	California	39.13	-120.66	10 June 2021	Ed Pandolfino
xc76071	Colorado	39.03	-108.63	17 April 2011	Nathan Pieplow

Appendix 2. Examples of all 24 Black-chinned Sparrow (*Spizella atrogularis*) song types we identified from our review all recordings.



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PEER-EDITED NOTE

PREDATION OF A SMALL RODENT BY A BLUNT-NOSED LEOPARD LIZARD (*GAMBELIA SILA*)

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***Abstract*.—The Blunt-nosed Leopard Lizard (*Gambelia sila*) is a relatively large predatory lizard found in the San Joaquin Desert of California. The food habitats of this species have been previously studied, and primary diet components include orthopterans (mainly grasshoppers) and coleopterans (various beetle groups). Here, I report the predation of a small rodent by a radio-collared Blunt-nosed Leopard Lizard. To my knowledge, this is the first report of predation by a Blunt-nosed Leopard Lizard of a mammal, although the congeneric Long-nosed Leopard Lizard (*G. wislizenii*) is known to eat small rodents. Because of differences in activity times, I believe it is unlikely that Blunt-nosed Leopard Lizards regularly predate or consume rodents.**

Key Words.—diet; food habits; mammals; prey.

The Blunt-nosed Leopard Lizard (*Gambelia sila*) is a relatively large predatory lizard found in the San Joaquin Desert (Germano et al. 2011). It can reach 120 mm snout-vent length (SVL) and weigh 45 g (Montanucci 1965; Germano 2009). As a member of the family Crotaphytidae, Blunt-nosed Leopard Lizards are opportunistic carnivores that mainly eat insects and other lizards (Conant and Collins 1991; McGuire 1996; Stebbins 2003). Specific food habitats of Blunt-nosed Leopard Lizards have been previously assessed and orthopterans (mainly grasshoppers) and coleopterans (various beetle groups) were the primary food items in both stomachs and scats (Meek 1905; Montanucci 1965, 1967; Germano et al. 2007). Hymenopterans (bees, wasps, and ants) and dipterans (flies and relatives) were also part of their diet (Montanucci 1965, 1967; Germano et al. 2007). Other diet components that tend to be less prominent include lizards, hemipterans (true bugs: cicadas, aphids, etc.), insect larvae, spiders, mites, scorpions, and plant matter (Montanucci 1965, 1967; Germano et al. 2007).

There is no documentation of predation of mammals by Blunt-nosed Leopard Lizards, nor have mammals been recorded in stomach contents or scats, although the Little Pocket Mouse (*Perognathus longimembris*) has been documented as part of the diet of the congeneric Long-nosed Leopard Lizard (*G. wislizenii*; Pietruska et al. 1981). Food habitat studies on Long-nosed Leopard Lizards have otherwise shown a similar diet pattern to Blunt-nosed Leopard Lizards, with orthopterans and coleopterans dominating the diet (Pack 1922; Knowlton and Thomas 1936; McCoy 1967; Parker and Pianka 1976; Lemos-Espinal et al. 2000). Similarly, small rodents have infrequently appeared in stomachs of the Eastern Collared Lizard (*Crotaphytus collaris*), which are in the same family (Crotaphytidae) as leopard lizards (McAllister and Trauth 1982; McAllister 1985).

In 2015, I was tracking Blunt-nosed Leopard Lizards as part of radio-telemetry study in the Semitropic Natural Area, Kern County, California. I was tracking a female lizard (snout-vent length 103 mm; weight 38 g) and had just spotted her and planned to take a GPS location when a small rodent ran out from an adjacent shrub. The rodent ran toward the female radio-collared Blunt-nosed Leopard Lizard and she immediately ran to the rodent and captured it in her mouth. The lizard then retreated under a shrub and held the rodent in her mouth. I watched her for over 10 min and took several photographs of the predation event (Fig. 1). I was never able to determine whether she ate the rodent or not. I think it is unlikely she would be able to swallow the rodent, especially while wearing a radio collar. I am unsure what species of rodent she captured, but, based on nocturnal rodents known to be present on the site, it may have been a juvenile Tipton Kangaroo Rat (*Dipodomys nitratoides nitratoides*) or Heermann's Kangaroo Rat (*Dipodomys heermanni*) or an adult San Joaquin Pocket Mouse (*Perognathus inornatus*).

In June 2022, I received another report of a Blunt-nosed Leopard Lizard capturing a small rodent. I received a photograph of a male Blunt-nosed Leopard Lizard in full breeding colors with a small rodent in its mouth. The photograph was taken by Andy McCory along a fence line at Pixley National Wildlife Refuge, Tulare County, California (Bill Vanherweg, pers. comm.). The head of the rodent was in the mouth of the lizard and only the hind end and hind legs were in view. The consensus of several biologists who viewed the photograph was that the rodent may have been a North American Deermouse (*Peromyscus maniculatus*) based on the bicolored tail. It is unknown whether the lizard ate the rodent or not. I attempted to contact the photographer but did not receive a response.

Based on observations of Blunt-nosed Leopard Lizards over the course of my study as well as observations by

Figure 1. Female Blunt-nosed Leopard Lizard (*Gambelia sila*) with a small rodent in her mouth at Semitropic Natural Area, Kern County, California. (Photographed by Erin N. Tennant).

other researchers, this lizard seems to be an opportunistic predator that will eat almost anything available that it can catch (also see Germano et al. 2007). Thus, if a rodent is caught and can be swallowed, it is likely it will be eaten. These instances are likely very rare, however, because small rodents are nocturnal in the desert habitats where Blunt-nosed leopard lizards are found. One aspect of the diet of Blunt-nosed Leopard Lizards that needs further study is determining their food consumption in comparison to prey availability on specific sites where they are found (Germano et al. 2007).

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NOTES

INVERSE RELATIONSHIP BETWEEN SIZE AND MOVEMENT DISTANCES OF THREE KANGAROO RAT SPECIES ON A GRID

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Abstract.—**For 24 y we trapped at a site on the west side of the San Joaquin Valley that harbored the Federally and State-listed as endangered Giant Kangaroo Rat (*Dipodomys ingens*), the Short-nosed Kangaroo Rat (*D. nitratoides brevinasus*), a Species of Special Concern, and the un-protected and wide-spread Heermann's Kangaroo Rat (*D. heermanni*). Of the three species, *D. ingens* is the largest and *D. n. brevinaus* the smallest. Knowing distances that each species may move daily can help determine if the current buffer distance of 15.2 m (50 ft) from the edge of a development project is adequate to protect these species. Average movement distances between traps of the large *D. ingens* during a trapping session was < 9 m, although some moved up to 80 m. Average distance moved daily for *D. heermanni* was under 13 m (up to 43.6 m) and was almost 22 m for the small *D. n. brevinasus*. We also found that *D. ingens* is highly philopatric with individuals we caught between sessions found almost at the same trap, on average, from previous trapping sessions. In contrast, male *D. n. brevinasus* were caught almost 22 m, on average, from previous sessions. Based on average daily movements between traps within a session, a buffer of 15.4 m is adequate to protect *D. ingens* from project effects, but *D. n. brevinasus* moves too far on average during a day to avoid project boundaries.**

Key Words.—*Dipodomys heermanni*; *Dipodomys ingens*; *Dipodomys nitratoides brevinasus*; Giant Kangaroo Rat; Heermann's Kangaroo Rat; Short-nosed Kangaroo Rat.

Understanding the movements and home ranges of animals is an important metric in minimizing the direct and indirect effects of habitat disturbances on animals. Portions of the San Joaquin Desert of California are occupied by the Federally and State-listed as endangered Giant Kangaroo Rat (*Dipodomys ingens*), the Short-nosed Kangaroo Rat (*D. nitratoides brevinasus*), a Species of Special Concern, and the un-protected and wide-spread Heermann's Kangaroo Rat (*D. heermanni*). The three species vary in size from the large *D. ingens* (120–150 g) to the small *D. n. brevinaus* (35–40 g) and co-occur in some localities on the west side of the San Joaquin Valley (U.S. Fish and Wildlife Service 1998). Previous studies have identified differences in home range sizes between these kangaroo rat species (Braun 1985; Cooper and Randall 2007; Tennant and Germano 2013). The San Joaquin Desert continues to be subject to many human activities that degrade or remove native habitat that supports these species. Biological consultants generally conduct trapping surveys to determine the presence of these listed kangaroo rat species in areas that are potentially impacted by surface disturbing projects such as oil well pads, pipelines, powerlines, roads, facilities, highway construction, communication sites, and water infrastructure. If protected species are found in project areas, mitigation measures must be employed to minimize harm to these species. Trapping surveys are typically designed to cover the project footprint and a surrounding buffer area of 15.2 m (50 ft; Randi McCormick, pers. comm.; pers. obs.). Traps are usually spaced at 10–15 m intervals. We considered our twice-yearly trapping study on a permanent survey grid from 1993 to 2016 (Germano and Saslaw 2017) to be an opportunity to quantify daily and inter-session movement distances among these three species and to evaluate whether the 15.2 m buffer distance is an adequate distance from project boundaries to avoid interaction with these species.

We trapped kangaroo rats on the west side of the San Joaquin Valley in Kern County, California. The site (35°25'43"N, 119°37'06"W; 100 m elevation) was a 40 ha (99 acre) parcel of federal land managed by the U.S. Bureau of Land Management. The site was surrounded on three sides by irrigated agriculture and bordered on the east by the California Aqueduct (see Germano and Saslaw 2017 for site map). The study site was a remnant saltbush (*Atriplex* spp.) scrubland typical of the San Joaquin Desert (Germano et al. 2011). Depending on the year, the soil surface was either covered by a moderate to dense growth of native and non-native forbs and grasses or was bare between the perennial shrubs.

In August 1993, we established a 144-trap plot (12 × 12 lines) at the study site. We placed wooden stakes at 10-m intervals and placed an extra-large Sherman live trap (Model XLF, H.B. Sherman Traps, Tallahassee, Florida) at each stake. For 24 y, from August 1993 to May 2016, we trapped rodents during six consecutive days, twice each year during spring (March-May) and fall (August-October). We baited the traps with Parakeet Mix bird

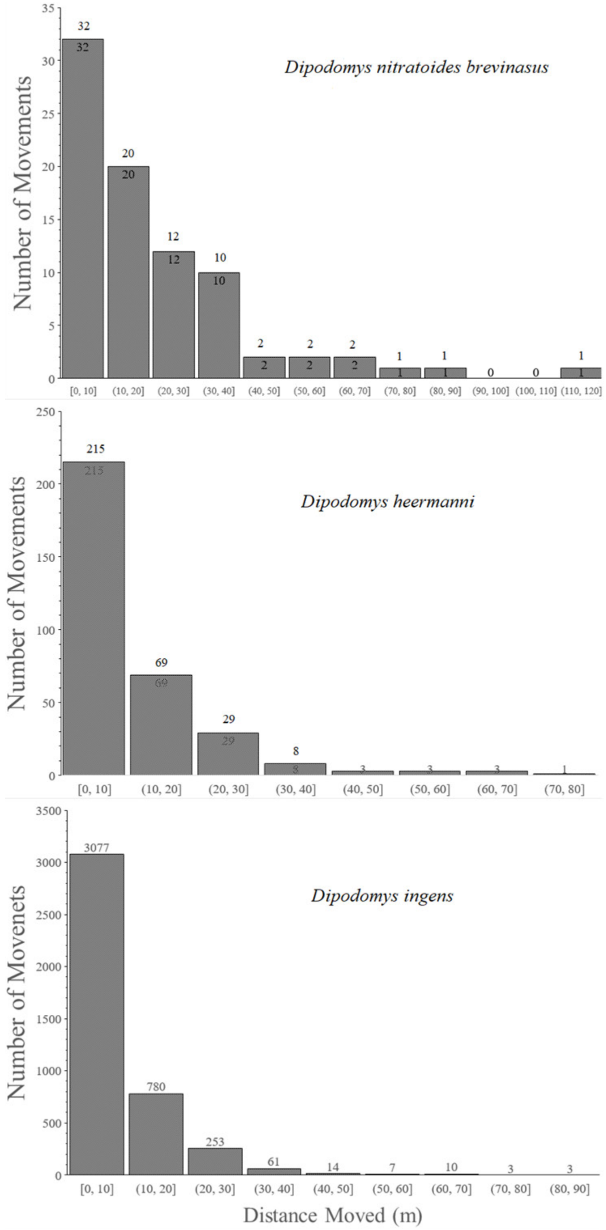

Figure 1. The range of movement distances (m) within a session on a 144 trap grid (10 m spacing) trapped biannually over 24 y in North Lokern, Kern County, California. The movement distances are for Short-nosed Kangaroo Rats (*Dipodomys nitratoides brevinasus*), Heermann's Kangaroo Rats (*D. heermanni*), and Giant Kangaroo Rats (*D. ingens*).

seed, which is a mixture of several different small seeds, and we included one or two sheets of brown paper towels that we wadded tightly as bedding material. We opened the Sherman traps in late afternoon, and we checked them at dawn the next morning. We used ear tags and PIT tags to permanently mark all kangaroo rats we caught.

We analyzed movements of individual *Dipodomys ingens*, *D. heermanni*, and *D. n. brevinasus* by species, within a session and between sessions. We estimated movements of kangaroo rats as the distances between trap locations on the X, Y stations of the trap grid. Distances between traps were 10 m. We calculated diagonal distances between traps based on the hypotenuse of a right triangle. For movement distances within a session, we used successive trap locations of individual animals, which may have been over two or more days within a trapping session, to calculate average movement distances per individual. We analyzed the average movements of an individual within a session. We calculated between session movements of an individual as the minimum distances between trap locations between successive trapping sessions. If any of the same trap locations were used between successive sessions, or if there was an overlap of the outlined area of traps used between successive trapping sessions, we used zero as movement distance. Because variances were significantly different than equal and transformation did not equalize variances, we used a Kruskal-Wallis test ($\alpha = 0.05$) to compare mean distances moved within a session (averages of individuals) and between sessions by species and sex (six groups). If there were group differences, we used Dunn's multiple range test with Bonferroni corrections.

The mean movement distances per day for *D. ingens* was 8.96 m for males and 9.47 m for females, and 91.7% (3,857 of 4,208) of movements were within 10–20 m (Fig. 1). The mean movement distances of *D. heermanni* was 13.19 m for males and 12.32 m for females and was 21.41 m for male and 23.29 m for female *D. n. brevinasus* (Table 1). The average distance moved on the plot within a session was inversely related to the size of the kangaroo rat, with the small *D. n. brevinasus* moving about 2.5 times farther than *D. ingens* (Table 1). The average distance moved among groups differed significantly ($H = 145.4$, df $= 5$, $P < 0.001$). Average distances moved within a session differed significantly among species but not by sex of a species (Table 1).

Between sessions, the average distance moved from the last location from the previous session showed the same pattern of size and distance seen within sessions, although average distances were lower (Table 1). The average distance moved among groups between sessions differed significantly ($H = 87.65$, df $= 5$, $P < 0.001$). Average distances moved between sessions differed significantly between both male and female *D. ingens* and *D. n. brevinasus* sexes but not *D. heermanni* sexes (Table 1). Intersession movements of *D. heermanni* were not significantly different than female *D. nitratoides* but did differ significantly from male *D. nitratoides*. Although not significantly different, male *D. nitratoides* moved almost twice as far from the last location in the previous session as females (Table 1), a pattern not seen in the other two species.

Dipodomys ingens showed close affinity for a particular spot on the plot, both during a session and between sessions. On average, distances individuals moved were less than the distance between traps (10 m), even for successive trapping sessions. This species moved much less on the plot than the much smaller *D. nitratoides*. This likely occurred because *D. ingens* is tied closely to its burrow

Table 1. Sample size (n), mean (in meters), 95% confidence interval (CI), and range of movements of male and female Giant Kangaroo Rats (*Dipodomys ingens*), Heermann's Kangaroo Rats (*Dipodomys heermanni*), and Short-nosed Kangaroo Rats (*Dipodomys nitratoides brevinasus*) within and between trapping sessions at our North Lokern study grid in Kern County, California. Within session movements are based on the average distance moved of an individual. Movements are based on trap locations on the plot. Distances between traps were 10 m. Significant differences (Dunn's test with Bonferroni corrections) indicated by different letter superscripts (means with the same letter are not significantly different). Range of values are all movements, not average movements.

	Within Session Average Movements				Between Session Minimum Movements			
Species/Sex	n	Mean	95% CI	Range	n	Mean	95% CI	Range
D. ingens								
Males	627	8.96^{a}	0.60	0–100.0	634	2.61^{a}	0.60	0–92.0
Females	629	9.47^{a}	0.63	0–72.1	689	2.30^{a}	0.48	0–76.0
D. heermannii								
Males	201	13.19^{b}	1.35	0–60.8	93	8.50^{a,b}	3.76	0–72.0
Females	152	12.32^{b}	1.48	0–41.2	73	7.08^{a,b}	4.05	0–72.8
D. nitratoides brevinasus								
Males	50	21.83^{c}	4.45	10–86.0	27	20.89^{c}	8.08	0–72.0
Females	42	23.29^{c}	5.79	5–111.8	13	11.85^{b,c}	10.13	0–40.0

system (precinct) to defend its underground seed stores and they have an extensive social system based on kinship (Meshriy et al. 2011). *Dipodomys nitratoides* is a scatter hoarder that does not defend large stores underground (Jacobs 1992). The relative movement distances that we found among *D. ingens*, *D. heermanni*, and *D. nitratoides* are reflective of the sizes of the home ranges reported for these species and other similar-sized *Dipodomys*. For *D. ingens*, Braun (1985) found that the mean home ranges of six individuals was 239.3 m^2. The radius of 239.4 m^2 is 8.73 m, a linear distance very similar to the mean movement distances of male and female *D. ingens* within a session that we found. Cooper and Randall (2007) calculated home ranges of 0.02 ha for males and females in the non-breeding season, which gives a radius of 7.98 m, although male home range size in the breeding season (but not females) was 0.1 ha, on average, which gives a radius of 17.85 m. The average home ranges of five radio-telemetered *D. heermanni* was 602.2 ± 334.1 m^2 (radius = 13.85 ± 10.31 m) and five Tipton Kangaroo Rats (*D. n. nitratoides*) was 1,606.1 ± 926.1 m^2 (radius = 22.62 ± 17.17 m; Tennant and Germano 2013), with the radii linear distances also similar to our within session movement distances. Schroder (1979) determined that *D. spectabilis*, similar in weight (98–130 g; Kays and Wilson 2002) to *D. ingens*, defended a home range of 0.05 ha (225 m^2). *Dipodomys heermanni* arenae had mean home range sizes of 373 m^2 for females and 962 m^2 for males (Shier and Randall 2004), whereas Jones (1989) calculated the home ranges of five small-sized male *D. merriami* to be 7,413 m^2 and for females 2,644 m^2. In all cases, the smallest kangaroo rats had the largest size of home ranges.

The mean movement distances for *D. ingens* of 8.96 m for males and 9.47 m for females is within the 15.2 m buffer distance. Movements > 50 m were for kangaroo rats that were caught only twice (one movement value) in the 24 y of trapping and may represent peripheral *D. ingens* drawn in because of the bait seeds. They probably do not represent *D. ingens* that were established on the grid. These individuals would not likely move these distances on the edge of a project without a valuable resource drawing them in. The average movement distances for *D. n. brevinasus* of 20.16–21.57 m, however, is beyond the 15.2 m buffer distance and means that the buffer distances for this species need to be expanded to decrease the likelihood of including the home ranges of individuals within the project footprint and buffer.

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REPRODUCTION AND WEIGHTS OF GIANT KANGAROO RATS OVER 24 YEARS OF TRAPPING IN THE SAN JOAQUIN DESERT

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***Abstract.*—Because of its endangered status, recovery of the Giant Kangaroo Rat (*Dipodomys ingens*) will benefit from increased information about its basic biology. During a 24-y study of a rodent community in the Lokern area of Kern County, California, we collected data on the reproductive status and weights of male and female *D. ingens* during twice yearly 6-d censuses (48 sessions) on a 12 × 12 trap plot. We found that females occasionally were reproductive during our April or May sessions but were not in reproductive condition in our late summer/fall sessions. Finding females in reproductive condition in the spring varied greatly depending on the year. We found similar variability in male reproductive condition, although some males showed signs of being reproductive in late summer/fall censuses. We caught young-of-the year in most spring sessions, and occasionally in late summer and fall sessions. Adult weights varied markedly across the 24-y study, and with one exception, the average weight of adult males in a year always was greater than the average weight of adult females. Yearly average weights of adult males varied from 113.6 g to 138.8 g, and for adult females the average weight varied from 108.6 g to 130.1 g. The average weight of adult males across all years (124.7 g, n = 657) was significantly higher than the average weight (117.9 g, n = 610) of all adult females.**

Key Words.—Dipodomys ingens; females; males; offspring; young-of-the-year.

INTRODUCTION

The Giant Kangaroo Rat (*Dipodomys ingens*; Fig. 1) is state and federally listed as Endangered (U.S. Fish and Wildlife Service 1998). It occupies a portion of the San Joaquin Desert along the bajada of the western edge of the San Joaquin Valley from Panoche south to Maricopa and west into the Carrizo and Elkhorn plains and the Cuyama Valley (Williams and Kilburn 1992). Conservation of this species relies, in part, on understanding its biology so that management actions are based on reliable information. In 1993, we initiated a 24-y study of a rodent community in the Lokern area of Kern County, California (Germano and Saslaw 2017). The rodent community at the site was dominated by *D. ingens*. Besides the information we published on population numbers, sex ratios, age classes, longevity, and survivorship (Germano and Saslaw 2017), we also recorded information on reproduction and weights of male and female *D. ingens* across the 24-y study. We report this information here.

METHODS

***Study site*.**—We trapped *D. ingens* on the west side of the San Joaquin Valley in Kern County. The site (35°25’43” N, 119°37’06” W; 100 m elevation) was a 40-ha (99-acre) federal parcel of land managed by the U.S. Bureau of Land Management. The site was surrounded on three sides by irrigated agriculture and bordered on the east by the California Aqueduct (see Germano and Saslaw 2017 for site map). The study site was a remnant saltbush (*Atriplex* spp.) scrubland typical of the San Joaquin Desert (Germano et al. 2011). Depending on the year, the soil surface was either covered by a moderate to dense growth of native and non-native forbs and grasses or was bare between the perennial shrubs.

***Field methods*.**—In August 1993, we established a 144-trap plot (12 × 12 lines) at the study site. We placed wooden stakes at 10-m intervals and placed an extra-large Sherman live trap (Model XLF, H.B. Sherman Traps, Tallahassee, Florida) at each stake. For 24 y, from August 1993 to May 2016, we trapped rodents during six consecutive nights, twice each year during spring (March-May) and fall (August-October). We baited the traps with Parakeet Mix bird seed, which is a mixture of several different small seeds, and we included one or two sheets of brown paper towels that we wadded tightly as bedding material. We opened the

FIGURE 1. Giant Kangaroo Rat (*Dipodomys ingens*) from the North Lokern study site, Kern County, California. (Photographed by David J. Germano).

Sherman traps in late afternoon, and we checked them at dawn the next morning.

For each *D. ingens* we captured, we recorded its trap location on the grid, its sex and weight (using a spring scale), and its reproductive condition, and we permanently marked kangaroo rats with passive integrated transponder (PIT) tags (Model TX1400 series, Biomark, Boise, Idaho) inserted subcutaneously on the back with a hypodermic needle (Schooley et al. 1993; Williams et al. 1997). We judged reproductive condition of males as non-reproductive (scrotal sac not enlarged), questionable (scrotal sac partially enlarged), or reproductive (scrotal sac enlarged and presumed capable of insemination). For females, we scored them as non-reproductive, estrous (swollen vagina with or without a vaginal plug), lactating (nipples enlarged and pink or red), or pregnant (enlarged nipples, distended abdomen, and of a heavy weight). For all kangaroo rats, we determined age classes of individuals as adult or young. We determined young kangaroo rats by their low body mass, lack of guard hairs, grayish color of pelage, and relatively large head and feet for their body size. In practice, however, some animals that had these juvenile characteristics had attained adult weights and sometimes were reproductive, so for all analyses we classified *D. ingens* that were > 90 g as adults. Over the 24 y, the number of *D. ingens* that were > 90 g yet exhibited some juvenile characteristics added either no or just a few additional young in most years and up to 4–5 times more possible young in a few years.

Analyses.—We used Pearson's Product Moment Correlation to determine if there was an association between the number of young (only those < 90 g) caught in a year to the total number of *D. ingens* caught the previous fall and the total number of all kangaroo rats (including Heermann's Kangaroo Rats, *D. heermanni*, and Tipton Kangaroo Rats, *D. n. nitratoides*) caught the previous fall. We made the same correlation comparisons for total number of young caught in year but including those judged to be young even if they weighed > 90 g. We used t-tests to compare average weights between sexes and the upper decile (10%) weights between sexes. We also used Pearson's Product Moment Correlation to determine if there was an association between the average weight of males and the average weight of females to the average number of *D. ingens* caught in that year, to yearly (July-June) rainfall, to the amount of residual dry matter (RDM) measured in that year, and to RDM measured in the previous year. The method of collecting RDM is in Germano and Saslaw (2017). For all tests $\alpha = 0.05$.

RESULTS

Because our aim was to track population sizes and not specifically reproduction, we did not trap during the main reproductive period of *D. ingens* in January-March (Williams et al. 1993). Our spring trapping, however, was effective to note the ending of reproduction and when young of the year were being added to the population. From 1993 to 1997 (before the 1998 total population crash; Germano and Saslaw 2017), a high percentage of males were either scrotal or their scrotal sacs were partially inflated, in both spring and fall sessions (Table 1). After the crash, the proportion of males exhibiting active reproductive status when we trapped was much lower, even in years of high *D. ingens* abundance (Germano and Saslaw 2017). Our trapping in spring and late summer/fall did not often show females in a reproductive state, although there were exceptions, especially if trapping occurred in April or May (Table 1). In some spring trapping sessions, we found females in estrous, pregnant, and lactating, often all in the same session. Also, in August 1997 and 1999 (just before and after the population crash), we caught several females who were lactating (Table 1). We did not see any other signs of reproduction in females in late summer or fall in any other year.

We caught young-of-the year in most spring sessions, and occasionally in late summer and fall sessions (Table 1). The number of young of the year (< 90 g) was significantly negatively correlated with the total number of *D. ingens* caught the previous fall ($r = -0.482$, $t = 2.33$, df = 18, $P = 0.032$), and the total number of all kangaroo rats caught the previous fall ($r = -0.466$, $t = 2.23$, df = 18, $P = 0.038$). The total number of young of the year, including those judged young but > 90 g, was not significantly correlated with the total number of *D. ingens* caught the previous fall ($t = 1.81$, df = 18, $P = 0.087$), but was significantly negatively correlated with the total number of all kangaroo rats caught the previous fall ($r = -0.453$, $t = 2.16$, df = 18, $P = 0.045$).

Adult weights of *D. ingens* varied across years, but, except for 2008, males always weighed more on average than adult females (Fig. 2). In 2008, males weighed an average of 125.9 g and females weighed 125.6 g. Yearly average weights of males varied from 113.6 g in 2016 to 138.8 g in 1994. Yearly average weights of females varied from 108.6 g in 2015 to 130.1 g in 1994. The average weight of adult males across all years (124.7 g, n = 657) was significantly higher than the average weight (117.9 g, n = 610) of all adult females ($t = 8.88$, df = 1,262, $P < 0.001$). The heaviest 10% of adult males (upper decile weight) was 149.4 g (n = 66) was significantly greater than that of females (140.3 g, n = 61; $t = 8.02$, df = 124, $P < 0.001$). The same relationship was true of weight comparisons when comparing only non-reproductive *D. ingens*. Average weight of all non-reproductive males (123.9 g, n = 612) was significantly greater than that of non-reproductive females (117.6 g, n = 598; $t = 8.13$, df = 1,197, $P < 0.001$) as was upper decile weight of males (148.2 g, n = 62) to that of females (139.3 g, n = 60; $t = 8.17$, df = 117, $P < 0.001$). The heaviest male we caught weighed 176 g (non-reproductive) from 2013

Table 1. The reproductive condition of female (E =estrous, P = pregnant, L = lactating, NR = non-reproductive) and male (S = scrotal, Q = partially scrotal, NR = non-reproductive) Giant Kangaroo Rats (*Dipodomys ingens*) and the number of offspring captured during spring and fall trapping sessions from 1993 to 2016 at the North Lokern study site in the San Joaquin Desert of California. The reproductive condition is for both adult and young individuals. The number of young captured is given as individuals ≤ 90 g (a conservative designation of young) and all young, which includes any individual up to 120 g that we assessed were young in the field based on pelage characteristics and head to body proportions (see text). The number of reproductive kangaroo rats is sometimes fewer than the total number caught because reproductive condition was occasionally not recorded. No information is presented for the spring and fall trapping sessions in 1998 because we caught no rodents either time (Germano and Saslaw 2017).

	Females				Males			Young		Total
Session	E	P	L	NR	S	Q	NR	≤ 90 g	All	Caught
17–22 August 1993	0	0	0	38	4	40	9	0	0	96
4–9 April 1994	0	0	6	48	12	30	13	8	12	113
25–30 August 1994	0	0	0	49	11	23	8	0	3	91
23–27 April 1995	1	7	15	17	21	8	10	5	20	81
23–28 August 1995	0	0	0	47	2	31	26	0	3	106
6–11 May 1996	0	0	0	33	1	22	11	2	15	67
27–31 August 1996	0	0	0	20	0	6	5	0	0	32
9–14 May 1997	0	1	0	11	5	10	1	1	7	28
18–23 August 1997	0	0	3	2	5	1	1	2	2	12
14–19 April 1999	2	2	0	0	3	2	1	2	2	11
18–22 August 1999	0	0	2	6	1	2	2	3	3	14
11–16 May 2000	1	1	0	14	3	1	9	11	12	29
6–11 September 2000	0	0	0	8	1	0	5	0	1	18
26–31 March 2001	1	0	2	4	1	2	2	2	3	14
8–13 August 2001	0	0	0	30	1	1	19	3	16	53
2–7 May 2002	0	0	0	45	0	0	35	0	2	81
9–14 August 2002	0	0	0	27	0	2	25	0	0	55
29 April-6 May 2003	0	0	0	18	1	1	22	12	12	48
5–10 August 2003	0	0	0	24	1	0	31	1	1	56
13–18 April 2004	0	0	3	33	0	2	28	4	4	67
30 July-4 August 2004	0	0	0	25	0	0	19	0	0	45
25 April-1 May 2005	1	0	10	7	6	5	9	6	11	41
7–12 September 2005	0	0	0	27	0	3	22	0	0	52
25 April-1 May 2006	0	0	2	38	0	0	39	9	13	80
17–22 September 2006	0	0	0	42	0	1	44	0	0	86
20–25 March 2007	0	0	0	32	0	1	44	0	0	79
9–14 October 2007	0	0	0	17	0	2	14	0	0	34
15–19 April 2008	0	0	0	30	0	1	28	11	14	60
1–6 September 2008	0	0	0	29	0	0	15	0	0	44
25–29 May 2009	1	0	14	34	6	5	31	24	45	97
24–29 August 2009	0	0	0	62	1	1	46	4	11	112
3–8 May 2010	0	0	2	69	0	0	70	6	13	148
4–10 October 2010	0	0	0	75	0	0	65	1	1	142
26 April-3 May 2011	0	2	4	90	0	0	74	9	19	172
26 Sept-1 October 2011	0	0	0	75	0	3	75	0	0	153
23–28 April 2012	0	0	0	64	0	3	78	0	0	145
17–22 September 2012	0	0	0	40	0	7	41	0	0	90
8–13 April 2013	0	1	0	51	0	1	50	10	12	103
30 Sept-5 October 2013	0	0	0	13	0	1	15	0	0	31
7–12 April 2014	0	0	0	6	0	0	7	1	1	13
22–27 September 2014	0	0	0	2	0	0	0	0	0	2
13–18 April 2015	2	4	4	6	0	5	7	1	1	29
31 Aug-5 Sept 2015	0	0	0	18	0	0	11	0	0	29
25–30 May 2016	0	0	0	24	0	0	25	15	22	49

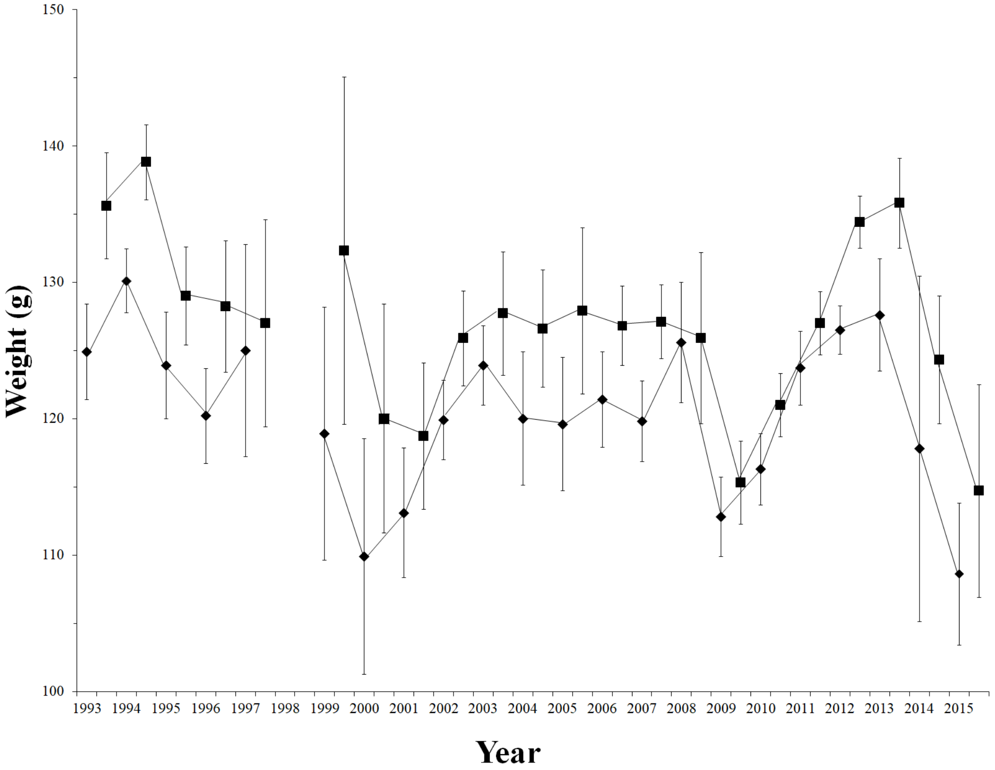

Figure 2. Average weights of female (diamonds) and male (squares) adult Giant Kangaroo Rats (*Dipodomys ingens*) from the North Lokern study site, Kern County, California, 1993 to 2015. No rodents of any species were caught in the two trapping sessions in 1998. The error bars are the 95% confidence intervals.

and the heaviest female caught was pregnant in 2011 and weighed 176 g. The heaviest non-reproductive female we caught was 166 g in 2004 trapping. There was no association between average weight of adult males (t = 0.970, df = 21, P = 0.343) or average weight of adult females (t = 1.55, df = 21, P = 0.136) and the average number of *D. ingens* caught in a year or between average weight of adult males (t = 0.891, df = 20, P = 0.385) or average weight of adult females (t = 0.803, df = 20, P = 0.432) and yearly rainfall. Levels of RDM in the same year also were not associated with male (t = 0.728, df = 19, P = 0.728) or female (t = 1.552, df = 19, P = 0.823) weight, nor was the level of RDM from the previous year with male (t = 1.756, df = 19, P = 0.094) or female (t = 0.672, df = 19, P = 0.510) weight.

Discussion

In some years, we found male and female *D. ingens* in reproductive condition in April and May. Female *D. ingens* have been reported to be in reproductive condition from January to May (Grinnell 1932; Williams et al. 1993). Grinnell (1932) caught three pregnant females in February and one pregnant female 18 May. Shaw (1934) caught a female lactating 3 March, and Williams and Kilburn (1992) reported a museum specimen that was caught 16 February contained three fetuses. By far, the most comprehensive data set of timing of female reproduction of *D. ingens* and the appearance of young-of-the year is from a report by Williams et al. (1993). They trapped *D. ingens* on the Elkhorn Plain in San Luis Obispo County from 1987 to 1991. Between July 1987 and April 1989, trapping for reproductive condition occurred bimonthly or monthly on two plots. From November 1988 through August 1991, trapping occurred monthly for two to three nights on a third plot (Williams et al. 1993). Based on this extensive trapping, females were found in estrous in February 1988, January to February 1989 and 1990, and in 1991, from February through August. Pregnant females were caught from January to March in 1988, in February 1989, March 1990, and March through August 1991. Lactating female *D. ingens* were found on the Elkhorn Plain from February to April 1988, March to April 1989, April 1990, and March to August 1991 (Williams et al. 1993). Young-of-the-year (< 90 g) followed a similar pattern with young caught from February to May in 1988, March to April 1989, April 1990, but from April to August in 1991 (Williams et al. 1993).

Although we did not trap at the most appropriate times to fully determine timing of reproduction, we did find females in reproductive condition in some spring trapping sessions, similar to the yearly variability found by Williams et al. (1993). We also captured young *D. ingens* in many spring trapping sessions across the 24-y study. Rainfall patterns varied widely during our 24 y of trapping with progressively higher rainfall from 1993 to 1998, dry conditions until higher rainfall started in 2009, and then dry conditions again in 2012 (Germano and Saslaw 2017). The number of young (< 90 g) was negatively associated with the number of *D. ingens* and the total number of all kangaroo rat species the preceding fall, suggesting that space and food levels over the winter may limit reproductive output of *D. ingens* (i.e., too many adults for the available food). On the Elkhorn Plain, rainfall was above average in 1987–1988, but was well below average in 1986–1987 and from 1988 through 1990, culminating in the almost total absence of herbaceous cover in 1990 (Williams et al. 1993; Germano et al. 1994; Germano and Williams 2005). This is reflected in the increasingly more restricted time when females were reproductive. The highly unusual extended period of reproduction (and young found) from February through August in 1991 appears to be due to the breaking of the drought when high amounts of rain fell in March 1991 (Williams et al. 1993; Germano et al. 1994; Germano and Williams 2005). This rain led to high levels of herbaceous plant material (Williams et al. 1993; Germano et al. 1994; Germano and Williams 2005) to which *D. ingens* immediately responded reproductively. On our Lokern study site, high amounts of rainfall and high levels of ground cover culminated in a population collapse in 1998, although an increase in rainfall and higher levels of herbaceous cover after a prolonged dry period increased numbers of *D. ingens* until a severe drought once again led to a crash in numbers (Germano and Saslaw 2017).

No data have been published on the timing of reproductive readiness in male *D. ingens*. We found that a high percentage of male *D. ingens* were either scrotal or partially scrotal during both spring and late summer/fall trapping sessions from August 1993 until March 2001. Thereafter, except for April 2005, we found no males or a low percentage of males that were in some level of reproductive condition. As with females, we did not trap in late fall or winter when most males in every year likely are reproductive to match female receptiveness. At least some male Merriam's Kangaroo Rats (*D. merriami*) have been found to be reproductive all year (Bradley and Mauer 1971; Kenagy and Bartholomew 1985) and Behrends et al. (1986) found 60% of males scrotal in November, 60–100% in December, and 100% from January through May. Some male Ord's Kangaroo Rats (*D. ordii*) also have found to be reproductive all year (Garner 1970; Hoditschek and Best 1983), and we suspect that *D. ingens* follow this same pattern.

Average weights of *D. ingens* on our study plot varied widely over the 24-y study period, similar to the 5-y study on the Elkhorn Plain (Williams et al. 1993). On the Elkhorn Plain, average weight of adult males varied from 121.0 g to 143.0 g and for females 116.0 g to 135.8 g (Williams et al. 1993), and we found average male weight varied from 113.6 g to 138.8 g and female weight from 108.6 g to 130.1 g. The earliest data on weights of *D. ingens* found much higher averages than more recent work, although sample sizes and length of study were much less than either our study or that by Williams et al. (1993). Grinnell (1932) reported an average weight of 15 males as 157.0 g with a range of 140.0 g to 174.2 g and for seven females, an average of 151.4 g (range, 130.8–180.0). For five adult *D. ingens* (two females, three males), average weights were 147.4 with a range of 125 g to 159 g (Shaw 1934). These higher average weights are similar to the upper decile weights we found: 149.4 g for males and 140.3 g for females. Perhaps the average weights of *D. ingens* have decreased in the past 60–70 y, although the much lower sample sizes of these early studies may have skewed these results. Our maximum weights of males (176 g) and of females (176 g pregnant, 166 g non-reproductive) are similar to that found by Grinnell (1932) but higher than that of Shaw (1934). The highest weights reported by Williams et al (1993) were 166 g for a male and 158.0 g for a female. Previously (Germano and Saslaw 2017), we found no association between average weights of *D. ingens* and the number of *D. ingens* on the plot, the amount of yearly rainfall, or levels of RDM. Here we analyzed the average weight of males and females separately but also found no association of these weights with *D. ingens* numbers, rainfall, or RDM.

The information we collected on reproduction and weights of *D. ingens* is similar to previous studies but was collected over a much longer time period than before. We show the first data for timing of reproduction for male *D. ingens* although a focused study of monthly or bimonthly trapping is needed to fully understand when males become reproductive and for how long. Long-term studies such as ours shed light on how environmental variability affects the basic biology of *D. ingens*. As a listed endangered species, the recovery of *D. ingens* will be advanced with a fuller understanding of its basic biology because this may allow for the prediction of changes to populations due to climate change that is happening across the planet.

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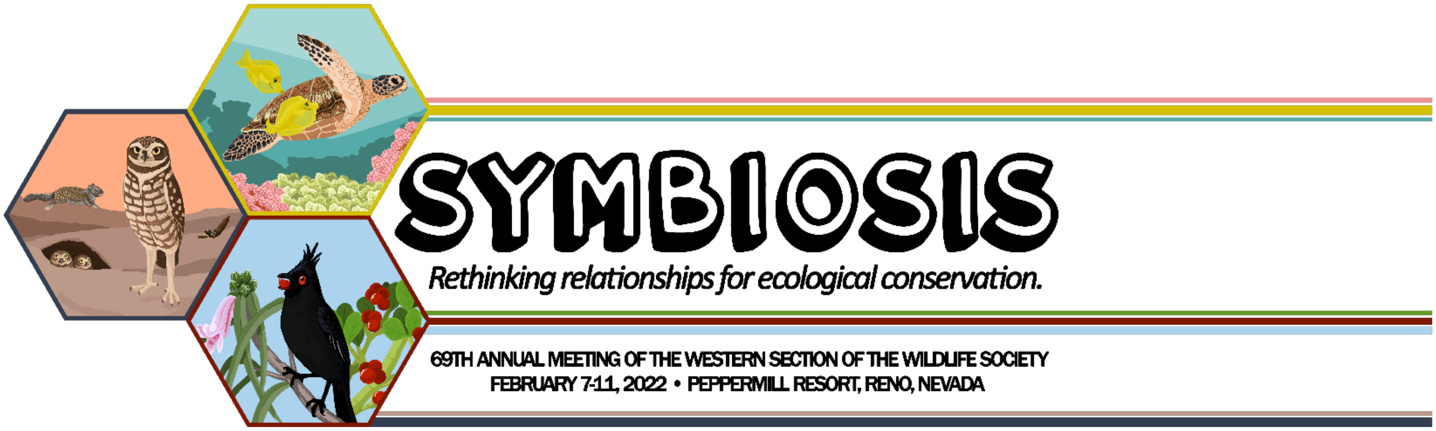
David J. Germano is a Professor Emeritus of Biology at California State University, Bakersfield. He earned a B.A. in Biology, a M.S. in Wildlife Ecology, and a Ph.D. in Biology, and is a Board Member and Section Editor of *Herpetological Conservation and Biology* and is the Editor of *Western Wildlife.* His research interests involve population ecology, life-history analysis, and the conservation of small mammals, reptiles, and turtles. He has conducted long-term studies of Blunt-nosed Leopard Lizards, Western Pond Turtles, North American tortoises, Desert Box Turtles, and various species of kangaroo rats including a 24-y study of a rodent community dominated by the Giant Kangaroo Rat. (Photographed by Larry Saslaw).

Larry R. Saslaw worked as a Wildlife Biologist in the Bureau of Land Management Bakersfield Field Office between 1985 and 2011 where he collaborated on studies that investigated the effects of livestock grazing, fire, and oil and gas activities on several San Joaquin Valley listed species. Larry is currently working part-time for the Endangered Species Recovery Program assisting on San Joaquin Desert listed species and habitat surveys for landscape conservation. He is currently serving on the Board of Directors for the Tulare Basin Watershed Network and Sequoia Riverlands Trust. (Photographed by Katie Heffernan).

2022 Annual Meeting Review

69th Annual Meeting, Hybrid



Program Chair: **Katie Smith** - WRA, Environmental Consultants

Attendance: 590 participants including 114 students and 47 Early Career Professionals

Plenary Theme: Symbiosis: Rethinking relationships for ecological conservation

Plenary Speakers: **Tiana Williams-Claussen**, Director, Yurok Wildlife Department; **Luka Zavas**, Outreach Associate, American Bird Conservancy; **Marcus Blum**, Post-Doctoral Researcher, University of Nevada, Reno

Keynote Address: ***Heather Reich**, Bear Biologist, Nevada Department of Wildlife*

Capstone Presentation: ***Dr. Chris Schell,** Department of Environmental Science, Policy, and Management, UC Berkeley; **Dr. Christine Wilkinson,** Post-Doc Researcher, Schell Lab, UC Berkeley; **Tyus Williams,** Doctoral Student, Schell Lab, UC Berkeley*

2022 Pre-Conference Workshops:
- Symposium: Connecting People who Connect Wildlife: Crossings, Corridors and More!
- R Bootcamp
- Wildlife Biologist Construction Awareness Training (WildCAT)
- Major Environmental Regulations: Practical Knowledge for Biologists
- Wilderness First Aid

Awards Bestowed:
- In Memoriam: **Bob Nelson**, 1933-2021, and **Geoff Monk**, 1954-2021
- The Raymond F. Dasmann Award for the Professional of the Year went to **Dr. Kelley Stewart**
- The Conservationist of the Year Award went to **Ducks Unlimited-Western Region**
- The Chapter of the Year Award went to the **California Southern California Chapter**
- The James D. Yoakum for Outstanding Service and Commitment to The Western Section of The Wildlife Society went to **Dr. Marshall White** AND **Dr. Reginald H. Barrett**
- The Barrett A. Garrison Mentor of the Year Award went to **Wendell Gilbert**
- The TWS Fellows Award went to **Mike Chapel**
- The TWS Distinguished Service Award went to **Karen Swaim**

Student Presentation Awards

ORAL PRESENTATION:

1st: Maria Costantini
Honeycreeper hosts: Testing the effects of diet, environment, and genetic relatedness on the gut microbiome using a classic example of adaptive radiation

1st: Jackson Tenney
Modeling Plasticity in Rodent Responses to the Lunar Cycle Following Habitat Modification

2nd: Chelsea Andreozzi
Investigating Drivers of Summer Bat Activity in California Redwood Forests

3rd: Kate McGinn
The role of forests as microclimates for spotted owls

POSTER:

1st: Olivia Wang
Insights into the Nest Site Characteristics of Pueo (Hawaiian Short-eared Owl; *Asio flammeus sandwichensis*) on O'ahu

2nd: Salix Scoresby
Multi-Species Presence Concurrent with Red Tree Vole (*Arborimus longicaudus*) Nest Use in Managed Forests of the Oregon Coast Range

3rd: Julia Owen-Ramos
Use of Whole Genome Sequencing to Investigate the Evolutionary History of Island Spotted Skunks

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2022 Western Section Membership

Retired – 51
Regular – 725
Lifetime-full – 49
Lifetime-partial – 2
Student – 184
New Professional – 144

Contributing – 2
Supporting – 10
Youth – 0
Honorary – 2

Total (excluding honorary) – 1,167