REPTILES & AMPHIBIANS

Occurrence of the Red-bellied Snake (*Storeria occipitomaculata*) on the Margins of a Disjunct Range

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Abstract.—The Red-bellied Snake (*Storeria occipitomaculata*) can be found throughout much of eastern North America, though two notable disjunct populations exist in the Black Hills of southwestern South Dakota and the Central Platte River Valley in southcentral Nebraska, west of the species' core range. While literature continues to be added on the Red-bellied Snake and its natural history, it remains largely understudied in Nebraska. Throughout much of this species' range, it is considered associated with woodland and wetland habitat features. On 28 September 2021, we detected one Red-bellied Snake near a treeless playa wetland in the Rainwater Basins ecoregion of southcentral Nebraska. Using a Grubbs Test to determine significant outliers, we found that this record was further from the Platte River than other previous accounts of this species in the state. This observation suggests this species may be found in other portions of the Rainwater Basins and considerably further from the Platte River than previously believed. Our observation along with other recent work indicates that Red-bellied Snakes may persist in herbaceous habitats lacking established woodland that include sufficient wetland features to support their primary food sources, including gastropods and other soft-bodied invertebrates. Due to the fragmentation of suitable habitats in the Rainwater Basins, coupled with the low dispersal of Red-bellied Snakes, populations persisting in the region are likely to be isolated.

Introduction

The range of the Red-bellied Snake (*Storeria occipitomaculata*) extends over much of the eastern United States and southeastern Canada but becomes more fragmented moving west across North America (Ernst and Ernst 2003). The two most westerly populations exist within the central Great Plains in the Black Hills of South Dakota and the Central Platte River Valley (CPRV) of Nebraska and are disjunct from the snake's larger eastern range (Ernst and Ernst 2003; Dieter and Ronningen 2017; Tye et al. 2017). Additionally, in the northern Great Plains a population exists as far west as southern Saskatchewan (Cook and Nero 1961; Cairns et al. 2018). Estimating the contours of a species' geographical range entails significant uncertainty, especially near the periphery (Rocchini et al. 2011). This is particularly challenging when considering disjunct populations that may represent remnants from a different climatological period (Bisbal-Chinesta and Blain 2018) and demonstrate regionally-specific habitat associations (Martino et al. 2012).

Disjunct populations, as well as individuals at the edge of a species' range, can be biologically important as they occasionally develop unique physical traits and behaviors that may prove adaptive in a changing world (Macdonald et al. 2017). However, these species often face increased risks of local or regional extirpation as a result of extreme environmental conditions (e.g., drought, cold), reduced habitat quality, interspecific competition with closely related species, and genetic isolation, which generally increases species' sensitivity to habitat fragmentation (Keinath et al. 2017). Regional herpetofauna research indicates that *Storeria occipitomaculata*'s disjunct range within southcentral Nebraska is restricted to the CPRV (Peyton 1989; Ballinger and Beachly 1999; Ballinger et al. 2010; Fogell 2010; Geluso 2012; Geluso and Harner 2013; Tye et al. 2017). Herein we report the first detection of this species within the neighboring Rainwater Basin ecoregion of Nebraska. We examine the distance of this record from the main channel of the Platte River relative to other publicly available records to determine if it represents an outlier extending beyond the periphery of this disjunct population's estimated range. We also assess the implications of detecting a *S. occipitomaculata* near an isolated prairie-wetland complex a significant distance from other protected habitats.

Methods

We estimated the locations of 56 *Storeria occipitomaculata* from the main channel of the Platte River using the "ruler" tool in Google Earth Pro Version 7.3 (Google 2017; Table 1). Data was derived from Crane Trust internal records and all publicly available data sources including Peyton (1989), Ballinger and Beachly (1999), Geluso (2012), Geluso and Harner (2013), Tye et al. (2017), the Harvard University Museum of Comparative Zoology (HUMCZ; 2021), Sternberg Museum of Natural History (FHSM; 2021), and the University of Nebraska State Museum (UNSM; 2021). In total we included just eight records not detailed in Tye et al. (2017). However, we reassessed all locational information from the original sources, and only report decimal degrees to the level of certainty indicated by the original sources. We measured the distance of each record from the respective north or south bank of the main channel of the Platte River as delineated by Caven et al. (2020). Channel banks were estimated following active channel width definitions proposed by Caven et al. (2019). We used imagery from April of 1999 as this represented the closest year imagery was available to the mean year of records in our database ($\bar{x}$ = 2001) considering that active channel widths and locations have remained relatively stable over recent decades in the CPRV (Google 2017; Caven et al. 2019). This also provided a consistent path from which to assess distances to *S. occipitomaculata* occurrences.

We calculated basic univariate sample summary statistics for distance to the main channel of the Platte River for *Storeria occipitomaculata* records including mean, median, range, standard deviation, standard error, and quartile values. We used the open-source statistical software program R version 3.6.3 to conduct all analyses (R Core Team 2020). We conducted a Grubbs' Test using the "outliers" package (version 0.14) to determine if our detection of a *S. occipitomaculata* in the Rainwater Basins represented a distributional outlier in terms of its distance to the Platte River relative to other records (Grubbs 1950; Komsta 2011). We also used the "ggplot2" package (version 3.3.5) to create a histogram of distance to the main channel of the Platte River for *S. occipitomaculata* records to better visualize the univariate distribution of this variable and highlight additional ostensibly outlying values (Wickham 2009). We also calculated multiple metrics to determine the degree to which each observation deviated from mean values. We calculated a *z*-score for each observation, which represents the number of standard deviations an observation is above or below the mean [$z = (x - \mu)/\sigma$] with values of $\geq$ 2.5 representing outliers (Rousseeuw and Hubert 2011). Additionally, we calculated percent variation from the mean for each *S. occipitomaculata* distributional record.

Finally, to estimate how isolated this population was we measured the Euclidean distance from Johnson Waterfowl Production Area ("WPA"; 40.560712°, -99.322880°; 693 m elev.; 236 ha, 43% wetland, USFWS 2017) to the two nearest significant areas (> 10 ha) of habitat in apparently natural condition per the most recent aerial imagery (4/2017) using the "ruler" tool in Google Earth Pro Version 7.3 (Google 2017). We also measured the proportion of that straight-line distance that included small segments of habitat in a "natural" condition (i.e., including "woodland," "grassland," and "wetland," while excluding "row crop agriculture" and "human development" such as roads) to estimate the permeability of the intervening matrix (Row et al. 2010, Caven et al. 2017).

Results

At 1030 h on 28 September 2021, we observed a *Storeria occipitomaculata* while driving down a gravel road that bisects Johnson WPA within the Rainwater Basin ecoregion of Nebraska approximately 13.3 km south of the main channel of the Platte River (Schneider et al. 2011; Table 1, Fig. 1). Digital pictures of the specimen were deposited into the University of Kansas Biodiversity Institute and Natural History Museum, Lawrence, Kansas, USA (KUDA numbers 013858 – 013859). Conditions were fair during the observation (26 °C temperature, 6 kph winds, 48% humidity, 20% cloud cover; Weather Underground 2021) and the snake was sunning close to the road's edge < 10 cm from the nearest vegetation. We estimated the snake to be 16–17 cm total length via post-hoc photographic measurements (Fig. 1). Site photographs indicated dominant plants in the immediate area of the capture included Smooth Brome (*Bromus inermis*), Big Bluestem (*Andropogon gerardii*), Canada Goldenrod (*Solidago canadensis*), and Annual Sunflower (*Helianthus annuus*), with a couple scattered Plains Cottonwoods (*Populus deltoides*) along a roadside ditch about 80 m away. The snake was captured < 140 m from palustrine emergent wetland habitat best described as Western Great Plains Closed Depression Wetland per Rolfsmeier and Steinauer (2013).

The mean distance *Storeria occipitomaculata* were detected from the main channel of the Platte River was 802 m, the standard deviation was 1,788 m, the standard error was 239 m, the minimum distance was 7 m, and the maximum distance was our observation from Johnson WPA, which was 13,282 m. The first quartile value was 440 m, the median was 542 m, and third quartile was 576 m. Ninety percent of values were lower than 936 m, and 95% were below 1,281 m. The Grubbs Test indicated that the Johnson WPA *S. occipitomaculata* detection represented a strong outlier (*G* = 6.980, *U* = 0.098, *p* < 0.001). The *z*-score associated with the Johnson WPA observation (*z* = 6.980) also indicated that it was a statistical outlier as it well exceeded the > 2.5 threshold (Table 1). Though *z*-score values suggest that the Johnson WPA was the only outlying distance to river value, the graphical histogram visually indicated that three relatively high values notably exceeded what was otherwise a relatively

Table 1. Red-bellied Snake (*Storeria occipitomaculata*) records from the disjunct Platte River population in Nebraska including the month, year, county, latitude, and longitude associated with each observation or collection. We also present the distance in meters ("Dist. (m)") each snake was detected from the main channel of the Platte River as delineated by Caven et al. (2020), the associated z-score indicating the number of standard deviations each distance measurement was above or below the sample mean, and the percent variation ("% Var.") of each distance measurement relative to the mean. Finally, we provide all available identifiers for each unique observation include notation in any publication, collection number from any museum, and the collector or observer of the snake.

No.	Month	Year	County	Latitude	Longitude	Dist. (m)	z-score	% Var.	Publication, Collection No., Collector/Observer
1	–	~1850s	Douglas	41.3	-96.4	237	-0.316	-70.4%	Somma (2022), HUMCZ R-135, Hull
2	September	1967	Buffalo	40.6850	-99.2560	1964	0.650	144.9%	Peyton (1989), UNK 161
3	September	1987	Dawson	40.884	-100.124	147	-0.366	-81.7%	Tye et al. (2017), UNSM 9290, Peyton
4	August	1987	Dawson	40.8852	-100.1464	1053	0.140	31.3%	Peyton (1989), UNK 423, Peyton
5	August	1987	Dawson	40.8852	-100.1464	1053	0.140	31.3%	Peyton (1989), UNK 424, Peyton
6	August	1988	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 9781, Peyton
7	August	1988	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 9782, Peyton
8	August	1988	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 9783, Peyton
9	August	1988	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 9784, Peyton
10	August	1988	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 9785, Peyton
11	May	1988	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 9786, Peyton
12	September	1989	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 9883, Peyton
13	September	1989	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 9884, Peyton
14	September	1989	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 9885, Peyton
15	September	1989	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 9886, Peyton
16	September	1989	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 9887, Peyton
17	September	1989	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 9888, Peyton
18	September	1989	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 9889, Peyton
19	September	1989	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 9890, Peyton
20	September	1990	Dawson	40.874	-100.119	580	-0.124	-27.7%	Tye et al. (2017), UNSM 9956, Peyton
21	July-August	1991	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 15015, Peyton
22	July-August	1991	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 15016, Peyton
23	July-August	1991	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 15017, Peyton
24	July-August	1991	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 15018, Peyton
25	July-August	1991	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 15019, Peyton
26	July-August	1991	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 15020, Peyton
27	July-August	1991	Dawson	40.883	-100.129	542	-0.145	-32.4%	Tye et al. (2017), UNSM 15021, Peyton

28	April	1997	Phelps	40.646	-99.412	3921	1.744	388.9%	Tye et al. (2017), UNSM 19189, Friskopp
29	April	1999	Hall	40.75	-98.58	31	-0.431	-96.1%	Ballinger and Beachly (1999), UNSM 16282, Beachly
30	June	2009	Hall	40.7941	-98.4007	40	-0.426	-95.0%	Tye et al. (2017), FHSM 14700, Geluso
31	July	2009	Hall	40.7941	-98.4007	39	-0.427	-95.1%	Tye et al. (2017), Geluso
32	September	2009	Hall	40.7941	-98.4007	39	-0.427	-95.1%	Tye et al. (2017), Geluso
33	October	2009	Hall	40.7877	-98.4652	555	-0.138	-30.8%	Tye et al. (2017), Geluso
34	April	2010	Hall	40.7924	-98.4451	455	-0.194	-43.3%	Tye et al. (2017), FHSM 15628, Geluso
35	May	2010	Hall	40.7968	-98.4456	936	0.075	16.7%	Geluso and Harner (2013b), Geluso
36	May	2010	Hall	40.7968	-98.4456	936	0.075	16.7%	Geluso and Harner (2013b), Geluso
37	September	2010	Hall	40.7968	-98.4456	936	0.075	16.7%	Geluso and Harner (2013b), Geluso
38	September	2010	Hall	40.7842	-98.4691	207	-0.333	-74.2%	Geluso and Harner (2013b), Geluso
39	July	2010	Hall	40.7950	-98.4464	748	-0.030	-6.7%	Geluso and Harner (2013b), Geluso
40	April	2010	Hall	40.7941	-98.4007	39	-0.427	-95.1%	Tye et al. (2017), Geluso
41	April	2010	Hall	40.7951	-98.4434	728	-0.041	-9.2%	Tye et al. (2017), Geluso
42	May	2010	Hall	40.7899	-98.4662	810	0.004	1.0%	Tye et al. (2017), Geluso
43	October	2011	Hall	40.7985	-98.3978	289	-0.287	-64.0%	Tye et al. (2017), FHSM 16163, Geluso
44	October	2011	Kearney	40.6549	-99.1245	573	-0.128	-28.6%	Geluso (2012), FHSM 16161, Geluso
45	September	2012	Merrick	41.1853	-97.8244	7	-0.445	-99.1%	*FHSM 16498, Duffey
46	July	2013	Hall	40.8082	-98.3803	575	-0.127	-28.3%	Tye et al. (2017), FHSM 16543, Wright
47	March	2016	Buffalo	40.6680	-98.8897	73	-0.408	-90.9%	Tye et al. (2017), Pearson
48	October	2016	Buffalo	40.6699	-98.8860	54	-0.418	-93.3%	Tye et al. (2017), Pearson
49	October	2016	Buffalo	40.6699	-98.8860	54	-0.418	-93.3%	Tye et al. (2017), Pearson
50	October	2016	Dawson	40.8825	-100.1293	542	-0.145	-32.4%	Tye et al. (2017), Peyton
51	April	2017	Hall	40.7887	-98.4653	671	-0.073	-16.3%	Schaaf and Caven (In Rev), Wiese
52	October	2018	Hall	40.788	-98.465	587	-0.120	-26.8%	Schaaf and Caven (In Rev), Caven
53	September	2021	Phelps	40.5607	-99.3229	13282	6.980	1556.1%	Schaaf and Caven (In Rev), Schaaf
54	April	2021	Hall	40.7875	-98.4553	440	-0.202	-45.1%	Schaaf and Caven (In Rev), Malzahn
55	April	2021	Hall	40.7875	-98.4553	440	-0.202	-45.1%	Schaaf and Caven (In Rev), Malzahn

Figure 1. Dorsal (top) and ventral views of a Red-bellied Snake (*Storeria occipitomaculata*) captured at Johnson Waterfowl Production Area approximately 13.3 km south of the Platte River within the Rainwater Basin region of Nebraska. We estimated the snake to be 16–17 cm total length via post-hoc photographic measurements. Photographs by Matthew Schaaf.

clustered and continuous data distribution at < 1,100 m distance (Fig. 2). The 2021 Johnson WPA record from Phelps County reported here was 1,556% above the mean distance to river (No. 53, Table 1), the April 1997 collection made by D. Friskopp and reported by Tye et al. (2017) also from Phelps County was 389% above the mean distance (No. 28, Table 1), and the 1967 collection from Buffalo County deposited in the Kearney State College Herptile Collection (No. 2, Table 1) and reported by Peyton (1989) was 145% higher than the mean (Table 1). The next highest value was only 31% above the mean.

The nearest significant natural landscape was a > 850 ha private ranch that appeared to be an isolated Sandhills Mixed-grass Prairie remnant south of the Platte River (40.640056°, -99.331569°; 691 m elev.) and approximately 7.2 km north of Johnson WPA (see Kaul et al. 2012). We estimated that just 2% of the direct path between the ranch and Johnson WPA included natural habitat to facilitate dispersal. The next
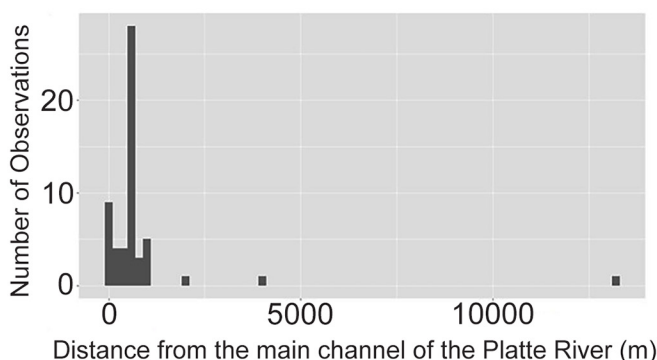

Figure 2. Red-bellied Snake (*Storeria occipitomaculata*) observations and distances to the main channel of the Platte River.

closest significant natural habitat, Funk WPA (40.504112°, -99.224502°; 679 m elev.), was 9.0 km to the southeast of Johnson WPA. Funk WPA is about 787 ha and comprised of about 58% wetland landcover (USFWS 2017). About 3% of the direct path between Johnson and Funk WPAs represented relatively "natural" landcover, predominantly in the form of roadside ditches supporting herbaceous vegetation.

Discussion

The vast majority of *Storeria occipitomaculata* records for the disjunct CPRV population have occurred within a short distance of the Platte River (< 1,300 m, Table 1). However, this *S. occipitomaculata* population may extend further to the south than previously expected in Phelps County in particular. The second furthest record from the Platte River in Nebraska also comes from a collection made in Phelps Co. by D. Friskopp nearly 4 km south of the Platte River (UNSM 19189; Tye et al. 2017; No. 28, Table 1). Similar to our Johnson WPA observation, this specimen was collected from an isolated and relatively large tract (> 125 ha) of herbaceous habitat that included extensive wetland features ("slough wetland", see Meyer and Whiles 2008) and very little tree cover per Google Earth imagery from April 1999 (Google 2017). However, habitat connectivity is currently limited moving south of the Platte River into the Rainwater Basins as a result of intensive agricultural development (Dappen et al. 2008; Verheijen et al. 2018). Though 70-80% of the lowland prairie and wet meadow habitat had been lost from CPRV by the 1980s, restoration has measurably improved conditions in areas with high conservation ownership and protection over recent decades (Currier et al. 1985; Sidle et al. 1989; Krapu et al. 2014; Caven et al. 2019). Significant effort has also been dedicated to improving habitat in the adjacent Rainwater Basins, but conditions remain comparatively fragmented therein. The number of wetlands in the Rainwater Basins has decreased by over 90%, and many of those that remain have limited ecological functionality (Tang et al. 2012; Verheijen et al. 2018). Verheijen et al. (2018) also demonstrated a 150% increase in the mean distance to the nearest wetland in the Rainwater Basins ecoregion.

Inadequate literature exists on the subject, but *S. occipitomaculata* dispersal capabilities appear relatively limited. Lang (1969) suggested that a sample of 12 individuals in northern Minnesota moved about 490 m on average from dens during the active season, but only 150–305 m in any one direction. Blanchard (1937) indicated that marked *S. occipitomaculata* were recaptured within distances ranging from 30–400 m over a 1-week period. In all cases estimates of *S. occipitomaculata* dispersal capabilities are small compared to the approximate distance from Johnson WPA to the nearest significant natural landscape (~7.2 km). Several Colubridae species, as well as many other snakes and small-bodied reptiles, demon-

strate limited dispersal capabilities, small home range sizes, and therefore relatively high sensitivity to habitat fragmentation compared to other more mobile taxa (Macartney et al. 1988; Henle et al. 2017; Keinath et al. 2017). Additionally, genetics research suggests that herpetofauna may be more vulnerable to habitat fragmentation on the periphery compared to the core of their range, indicating that *S. occipitomaculata* populations in the Rainwater Basins [if present] may be particularly at risk of local extirpation (Henle et al. 2017). Nonetheless, the effects of habitat fragmentation on species movements and population connectivity are ultimately moderated by the suitability of the surrounding landscape matrix as well as the distances between quality habitat patches (Row et al. 2010).

High densities of row crop agriculture in addition to moderate levels of residential and industrial development likely create a relatively hostile matrix for *Storeria occipitomaculata* dispersal within the Rainwater Basin ecoregion (Jochimsen et al. 2004; Willson and Dorcas 2004; Dappen et al. 2008; Row et al. 2010; Biaggini and Corti 2015). *S. occipitomaculata* have regularly been recorded using gravel roads and trails for thermoregulation, but these can also pose a significant mortality risk for the species (Cahoe and Troelstrup 2004; Jochimsen et al. 2004; Shepard et al. 2008; Busby et al. 2014; Cairns et al. 2018). Additionally, agricultural monocultures tend to provide little habitat for herpetofaunal movements (Willson and Dorcas 2004; Shepard et al. 2008, Row et al. 2010; Martino et al. 2012; Biaggini and Corti 2015). Vegetative (often "riparian") buffer strips within agricultural monocultures can provide valuable dispersal corridors, however, this practice is not extensively implemented in the Rainwater Basin ecoregion or Great Plains at large (Row et al. 2010; Smith et al. 2011; Biaggini and Corti 2015; Malzahn et al. 2021). Drainage ditches, generally on the margins between agriculture fields and roads, likely present the most abundant corridors for dispersal between suitable habitats for *S. occipitomaculata* throughout most of the Rainwater Basin ecoregion based on studies of other snake species in agricultural landscapes (Row et al. 2010; Plummer et al. 2020a). A persistent population of *S. occipitomaculata* at Johnson WPA is likely to be genetically isolated considering heavy landscape fragmentation, limited movement corridor availability regionally, and the species' modest dispersal abilities. If *S. occipitomaculata* persists in other remnant sites within the Rainwater Basin ecoregion they may only demonstrate long-term viability in patches large enough to support a robust and resilient population.

Very limited literature exists regarding home range sizes for *S. occipitomaculata* and close relatives (Smith and Stephens 2003). Freedman and Catling (1979) reported home ranges of < 0.12 ha for two individual DeKay's Brown snakes (*S. dekayi*), which are closely related to *S. occipitomaculata*. Pisani (2009) estimated a population size of 160 *S. dekayi* in a 5-ha

study area (32/ha) in northeastern Kansas. Additionally, Fitch (1993) recorded a *S. dekayi* density of 12.7/ha in Kansas. In northwestern Pennsylvania, Gray (2014) reported a total population of 122–130 *S. dekayi* and a density of 244–260/ha on a 0.5 ha vegetated slope with 3.25 ha palustrine woodland to its west. The small home range sizes and apparently high densities associated with *S. dekayi* suggest that somewhat modestly sized wetlands could support a sizeable *S. occipitomaculata* population. However, as Busby et al. (2014) notes, the *S. occipitomaculata* has a specialized diet that focuses on comparatively low-density prey (i.e., gastropods) in contrast to the *S. dekayi* which has a more generalized diet that occasionally includes small insects in addition to soft-bodied invertebrates. Also, the site of our observation exists on the extreme periphery of the species' range where population density is likely significantly lower (Henle et al. 2017; Keinath et al. 2017). Other small fossorial Colubridae such as the Ringnecked Snake (*Diadophis punctatus*) have significantly larger estimated home range sizes than *S. dekayi* (Fitch 1975). Based on mark recapture data (n = 433 movements) Fitch (1975) suggested that the diameter of a *D. punctatus* home range was likely about 70 m, with some individuals having extended home ranges reaching 140 m. Assuming a relatively circular spatial form, *D. punctatus* home ranges would be 0.38 ha on average and range up to 1.54 ha per Fitch (1975).

A key uncertainty in estimating the potential carrying capacity of Johnson WPA for *S. occipitomaculata* is the degree to which their home ranges overlap. Patterns of home range overlap can vary widely for Colubrid snakes by species, season, sex, and habitat availability (Bauder et al. 2016; Plummer et al. 2020b). Presuming moderate overlap (40%) of individual home ranges with adjacent conspecifics as well as home range sizes varying from larger *S. dekayi* (0.12 ha) to average *D. punctatus* (0.38 ha) estimates, we conjecture that *S. occipitomaculata* density could vary from roughly 4.4 to 13.9 individuals per ha in south-central Nebraska (Fitch 1975; Freedman and Catling 1979: Fitch 1993; Bauder et al. 2016; Henle et al. 2017; Plummer et al. 2020b). Extrapolating on these density estimates and assuming ~60% habitat availability at Johnson WPA (i.e., the driest portions may not support gastropods and the wettest portions often pond water), it is possible that this site could support between 621–1,967 *S. occipitomaculata*. This extrapolation represents a coarse hypothesis, but it could provide a useful guide for prioritizing sampling sites throughout the Rainwater Basins given the number of wetland complexes in the region (Verheijen et al. 2018). Research demonstrates that smaller populations within more isolated and restricted ranges have higher rates of extirpation (Flather et al. 2011; Frankham et al. 2014). The minimum number of individuals necessary to sustain a population varies by allelic diversity within the extant population, species life history (*r* vs. *K* selected), habitat availability,

and the number and nature of threats (e.g., stochastic events, predation) (Brook et al. 2006; Kuro-o et al. 2010; Flather et al. 2011; Schou et al. 2017). Nonetheless, several studies suggest that a population of > 1,000 individuals is generally needed to maintain long-term genetic fitness and viability for vertebrate populations (Brook et al. 2006; Frankham et al. 2014). Future searches for *S. occipitomaculata* within the region may benefit from surveying habitats that could theoretically support at least 1,000 individuals following the upper range of densities suggested as probable regionally therein (i.e., ~13.9/ha) and a reasonable estimate of habitat availability (e.g., ~60%). This would roughly equate to Rainwater Basin Wetland Complexes > 120 ha in total size.

Though several publications indicate that *Storeria occipitomaculata* occurrence is associated with woodland and woodland edge habitat (Ford et al. 1991; Pisani and Busby 2011; Fogell 2010) some papers from the northern and western Great Plains on the periphery of the species' range suggest it principally uses mesic herbaceous habitats such as wet meadows (Cahoe and Troelstrup 2004; Brown and Phillips 2013; Cairns et al. 2018). Broadly speaking, the literature clearly links *S. occipitomaculata* occurrence to the presence of wetland features regardless of habitat structure (woody vs. herbaceous), which may be related to their dependence on wetland associated gastropods as a primary food source (Semlitsch and Moran 1984; Brown and Phillips 2013; Dieter and Ronningen 2017). Ultimately, it is possible that the perceived association between woodland and *S. occipitomaculata* occurrence is relatively spurious as trees (e.g., Plains Cottonwood - *Populus deltoides* ssp. *monilifera*) are generally concentrated around water sources in the Great Plains (West and Rurak 2004). This hypothesis is bolstered by the fact that *S. occipitomaculata* are adapted to using ant-formed mounds as overwintering refugia in herbaceous landscapes (Busby et al. 2014, Cairns et al. 2018; Harris and Savage 2020). Our observation would indicate that *S. occipitomaculata* can persist in herbaceous landscapes with relatively little tree cover in Nebraska. However, it is important to note that even though trees were never dominant within the Rainwater Basin landscape, the U.S. Fish and Wildlife Service Wetland Management District cleared a significant number of invasive trees off Johnson WPA from 2003–2009 (pers. comm., B. Krohn, formerly USFWS, Rainwater Basin Wetland Management District, Funk, NE, USA; Fogarty et al. 2020). It is possible that these trees or their remnant stumps provide(d) some value for *S. occipitomaculata* in the area over recent decades (Bridger and Geluso 2021).

Our detection of a *Storeria occipitomaculata* in the Rainwater Basin ecoregion, recent unpublished documentation of the species east of its suggested range in the CPRV (April 2022, Bader Park, Merrick Co.; pers. comm., S. Bailey,

Prairie Plains Resource Institute, Aurora, NE, USA), and recent affirmation of a 170-year-old record from the Lower Platte River Valley via a museum specimen (Somma 2022) indicate the margins of the disjunct CPRV population may be more expansive and opaque than previously understood. One *S. occipitomaculata* (AMNH R-3380) was collected from Phillips County, Kansas (39.949°, -99.536°, 631.5 m elev.) in 1894 (AMNH 2022). This record was rejected by Miller and Collins (1993) and Collins et al. (2010) due to its significant disjunction from the rest of the Kansas population, the age of the record, the voucher specimen's need for corroboration, and because the habitat of detection was believed to include insufficient woodland for the species. Lynch (1985) and Peyton (1989), due to specimens collected along the western CPRV in south-central Nebraska, have suggested that AMNH R-3380 may be valid. Our observation is nearer to AMNH R-3380 (dist. = ~70 km) than any previous record and was similarly found in a wetland habitat devoid of established woodland. Documentation of the *S. occipitomaculata* in the southern portion of the western Rainwater Basins near the Republican River Valley could provide additional support for the validity of the Phillips County, Kansas record (AMNH R-3380).

Conclusions

Our documentation of a *Storeria occipitomaculata* > 13 km south of the Platte River Valley in the Rainwater Basin ecoregion along with recent validation of museum records east of the species' known disjunct range within Nebraska indicates *S. occipitomaculata* may be more widespread regionally than previously thought. It also indicates that its habitat preferences may be more variable in the central Great Plains than formerly understood. We suggest the need for a comprehensive survey of the Rainwater Basin ecoregion to determine how widespread and abundant *S. occipitomaculata* is regionally. Given the high level of fragmentation within the landscape we suggest starting with larger remnant wetland complexes that likely had a higher probability of sustaining isolated populations of the species throughout the last century of intensive agricultural development.

Acknowledgements

Literature Cited

American Museum of Natural History (AMNH). 2022. *Vertebrate Zoology Collection Database – Herpetology Collection. Storeria occipitomaculata*, AMNH R-3380. American Museum of Natural History, New York, NY, USA. <https://www.amnh.org/research/vertebrate-zoology>.

Ballinger, R.E. and W. Beachly. 1999. Geographic distribution: *Storeria occipitomaculata. Herpetological Review* 30: 236–237.

Ballinger, R.E., J.D. Lynch, and G.R. Smith. 2010. *Amphibians and Reptiles of Nebraska.* Rusty Lizard Press, Oro Valley, AZ, USA.

Bauder, J.M., D.R. Breininger, M.R. Bolt, M.L. Legare, C.L. Jenkins, B.B. Rothermel, and K. McGarigal. 2016. The influence of sex and season on conspecific spatial overlap in a large, actively-foraging colubrid snake. *PLoS One* 11: e0160033. https://doi.org/ 10.1371/journal.pone.0160033.

Biaggini, M. and C. Corti. 2015. Reptile assemblages across agricultural landscapes: where does biodiversity hide? *Animal Biodiversity and Conservation* 38: 163–174. https://doi.org/ 10.32800/abc.2015.38.0163.

Bisbal-Chinesta, J.F. and H.A. Blain. 2018. Long-term changes in composition and distribution patterns in the Iberian herpetofaunal communities since the latest Pleistocene. *Quaternary Science Reviews* 184: 143–166. https://doi.org/10.1016/j.quascirev.2017.06.010.

Blanchard, F.N. 1937. Data on the natural history of the red-bellied snake, *Storeria occipito-maculata* (Storer), in northern Michigan. *Copeia* 1937: 151–162. https://doi.org/10.2307/1436135.

Brook, B.W., L.W. Traill, and C.J. Bradshaw. 2006. Minimum viable population sizes and global extinction risk are unrelated. *Ecology letters* 9: 375–382. https://doi.org/10.1111/j.1461-0248.2006.00883.x.

Brown, L.E. and C.A. Phillips. 2013. Distribution, habitat, and zoogeography of the semifossorial red-bellied snake *Storeria occipitomaculata* (Storer) in Illinois. *Illinois Natural History Survey Bulletin* 39: 297–322. https://doi.org/10.21900/j.inhs.v39.104.

Bridger, T. and K. Geluso. 2021. Importance of woodland patches as hibernacula for gartersnakes in a prairie river floodplain of central Nebraska. *Transactions of the Nebraska Academy of Sciences* 41: 71–87. https://doi.org/10.32873/unl.dc.tnas.41.7.

Busby, W.H., G.R. Pisani, E.T. Peterson, and N. Barve. 2014. *Ecological Studies of the Smooth Earth Snake and Redbelly Snake, and Niche Modeling of Forest Species in Eastern Kansas.* Kansas Department of Wildlife, Parks and Tourism, Pratt, Kansas.

Cahoe, R.D. and N.H. Troelstrup. 2004. Habitat use and population biology of the Northern Redbelly Snake at Oaklake Field Station, SD. *Proceedings of the South Dakota Academy of Science* 83: 137–147

Cairns, N.A., P.L. Rutherford, and D.J. Hoysak. 2018. Morphology, reproduction, habitat use, and hibernation of Red-bellied Snake (*Storeria occipitomaculata*) near its northern range limit. *The Canadian Field-Naturalist* 132: 150–162. https://doi.org/10.22621/cfn.v132i2.2054.

Caven, A.J., E.M. Brinley Buckley, K.C. King, J.D. Wiese, D.M. Baasch, G.D. Wright, M.J. Harner, A.T. Pearse, M. Rabbe, D.M. Varner, B. Krohn, N. Arcilla, K.D. Schroeder, and K.F. Dinan. 2019. Temporospatial shifts in Sandhill Crane staging in the Central Platte River Valley in response to climatic variation and habitat change. *Monographs of the Western North American Naturalist* 11: 33–76. https://doi.org/10.3398/042.011.0104.

Caven, A.J., K.C. King, J.D. Wiese, E.M. Brinley Buckley. 2017. A descriptive analysis of Regal Fritillary (*Speyeria idalia*) habitat utilizing biological monitoring data along the Big Bend of the Platte River, NE. *Journal of Insect Conservation* 21: 183–205. https://doi.org/10.1007/s10841-017-9968-0.

Caven, A.J., D.M. Varner, and J. Drahota. 2020. Sandhill Crane abundance in Nebraska during spring migration: making sense of multiple data points. *Transactions of the Nebraska Academy of Sciences* 40: 6–18. https://doi.org/10.32873/unl.dc.tnas.40.2.

Collins, J.T., S.L. Collins, and T.W. Taggart. 2010. *Amphibians, reptiles and turtles in Kansas.* Eagle Mountain Publishing, Eagle Mountain, Utah, USA.

Cook, F.R. and R.W. Nero. 1961. The Green Snake and the Red-bellied Snake in Saskatchewan. *Blue Jay* 19: 134–135. https://doi.org/10.29173/bluejay2509.

Currier, P.J., G.R. Lingle, and J.G. VanDerwalker. 1985. *Migratory bird habitat on the Platte and North Platte Rivers in Nebraska.* Platte River Whooping Crane Critical Habitat Maintenance Trust, Grand Island, Nebraska, USA.

Dappen, P.R., I.C. Ratcliffe, C.R. Robbins, and J.W. Merchant. 2008. Mapping agricultural land cover for hydrologic modeling in the Platte River Watershed of Nebraska. *Great Plains Research* 18: 39–52.

Dieter, C.D. and T. Ronningen. 2017. A survey of Redbelly Snakes in the Black Hills of South Dakota. *Proceedings of the South Dakota Academy of Science* 96: 25–32.

Ernst, C.H. and E.M. Ernst. 2003. *Snakes of the United States and Canada.* The Smithsonian Institute, Washington, D.C., USA.

Fitch, H.S. 1975. A demographic study of the ringneck snake (*Diadophis punctatus*) in Kansas. *University of Kansas Museum of Natural History Miscellaneous Publications* 62: 1–53.

Fitch, H.S. 1993. Relative abundance of snakes in Kansas. *Transactions of the Kansas Academy of Science* 1903: 213–224.

Flather, C.H., G.D. Hayward, S.R. Beissinger, and P.A. Stephens. 2011. Minimum viable populations: is there a 'magic number' for conservation practitioners? *Trends in Ecology & Evolution* 26: 307–316. https://doi.org/10.1016/j.tree.2011.03.001.

Fogell D. 2010. *A field guide to the amphibians and reptiles of Nebraska.* Conservation and Survey Division, School of Natural Resources, University of Nebraska-Lincoln, Lincoln, NE. 156 pp.

Ford, N.B., V.A. Cobb, and J. Stout. 1991. Species diversity and seasonal abundance of snakes in a mixed pine-hardwood forest of eastern Texas. *The Southwestern Naturalist* 32: 171–177.

Frankham, R., C.J. Bradshaw, and B.W. Brook. 2014. Genetics in conservation management: revised recommendations for the 50/500 rules, Red List criteria and population viability analyses. *Biological Conservation* 170: 56–63.

Freedman, B. and P.M. Catling. 1979. Movements of sympatric species of snakes at Amherstburg, Ontario. *Canadian Field-Naturalist* 93: 399–404. https://doi.org/10.1016/j.biocon.2013.12.036

Geluso, K. 2012. Sixteen county records of herpetofauna from south-central Nebraska. *Collinsorum* 1: 3–6.

Geluso, K. and M.J. Harner. 2013. Reexamination of herpetofauna on Mormon Island, Hall County, Nebraska, with notes on natural history. *Transactions of the Nebraska Academy of Sciences* 33: 7–20.

Google. 2017. Google Earth Pro (Version 7.3) [Computer program]. Aerial imagery of the Central Platte River Valley, 4/2000. Alphabet Inc., Mountain View, CA, USA.

Gray, B.S. 2014. Natural history of Dekay's Brownsnake, *Storeria dekayi* (Holbrook, 1836), at a site in northwestern Pennsylvania. *Journal of North American Herpetology* 2014: 28–39. https://doi.org/10.17161/jnah.vi1.11891.

Grubbs, F.E. 1950. Sample Criteria for testing outlying observations. *The Annals of Mathematical Statistics* 21: 27–58. https://doi.org/10.1214/aoms/1177729885.

Harris, S.A. and A.M. Savage. 2020. Observations of Snakes Associated with Active Nests of Allegheny Mound Ant (*Formica exsectoides*) in Northeastern Pennsylvania. *Northeastern Naturalist* 27: 585–595. https://doi.org/10.1656/045.027.0317.

Henle, K., C. Andres, D. Bernhard, A. Grimm, P. Stoev, N. Tzankov, and M. Schlegel. 2017. Are species genetically more sensitive to habitat fragmentation on the periphery of their range compared to the core? A case study on the sand lizard (*Lacerta agilis*). *Landscape Ecology* 32: 131–145. https://doi.org/10.1007/s10980-016-0418-2.

Kaul, R.B., D. Sutherland, and S. Rolfsmeier. 2012. *The Flora of Nebraska.* Second Edition. School of Natural Resources, University of Nebraska–Lincoln, Lincoln, NE, USA.

Keinath, D.A., D.G. Doak, K.E. Hodges, L.R. Prugh, W. Fagan, C.H. Sekercioglu, S.H. Buchart, and M. Kauffman. 2017. A global analysis of traits predicting species sensitivity to habitat fragmentation. *Global Ecology and Biogeography* 26: 115–27. https://doi.org/10.1111/geb.12509.

Krapu, G.L., D.A. Brandt, P.J. Kinzel, and A.T. Pearse. 2014. Spring migration ecology of the mid-continent Sandhill Crane population with an emphasis on use of the Central Platte River Valley, Nebraska. *Wildlife Monographs* 189: 1–41. https://doi.org/10.1002/wmon.1013.

Komsta, L. 2011. *Outliers: Tests for outliers. R package version 0.14.* <https://CRAN.R-project.org/package=outliers>.

Kuro-o, M., H. Yonekawa, S. Saito, M. Eda, H. Higuchi, H. Koike, and H. Hasegawa. 2010. Unexpectedly high genetic diversity of mtDNA control region through severe bottleneck in vulnerable albatross *Phoebastria albatrus. Conservation Genetics* 11: 127–137. https://doi.org/10.1007/s10592-009-0011-1.

Lang, J.W. 1969. Hibernation and movements of *Storeria occipitomaculata* in northern Minnesota. *Journal of Herpetology* 3: 196–197.

Lynch, J.D. 1985. Annotated checklist of the amphibians and reptiles of Nebraska. *Transactions of the Nebraska Academy of Sciences* 13: 33–57.

Macartney, J.M., P.T. Gregory, L.W. Larsen. 1988. A tabular survey of data on movements and home ranges of snakes. *Journal of Herpetology* 22: 61–73.

Macdonald, S.L., J. Llewelyn, C. Moritz, and B.L. Phillips. 2017. Peripheral isolates as sources of adaptive diversity under climate change. *Frontiers in Ecology and Evolution* 5: 88. https://doi.org/10.3389/fevo.2017.00088.

Malzahn, J.M., A.J. Caven, S. Warren, B.L. Ostrom, and D.M. Ferraro. 2021. Habitat associations and activity patterns of herpetofauna in the Central Platte River Valley, Nebraska, with notes on morphometric characteristics. *Transactions of the Nebraska Academy of Sciences* 41: 88–105. https://doi. org/10.32873/unl.dc.tnas.41.8.

Martino, J.A., R.G. Poulin, D.L. Parker, and C.M. Somers. 2012. Habitat selection by grassland snakes at northern range limits: implications for conservation. *The Journal of Wildlife Management* 76: 759–767. https://doi.org/10.1002/ jwmg.313.

Miller, L.L., and J.T. Collins. 1993. *History, Distribution, and Habitat Requirements for Three Species of Threatened Reptiles in Eastern Kansas*. Kansas Department of Wildlife and Parks. Pratt, Kansas, USA.

Meyer, C.K., and M.R. Whiles. 2008. Macroinvertebrate communities in restored and natural Platte River slough wetlands. *Journal of the North American Benthological Society* 27: 626-639. https://doi.org/10.1899/07-086.1.

Harvard University Museum of Comparative Zoology [HUMCZ]. 2021. MCZBASE: The Database of the Zoological Collections, Herpetology Collection. *Storeria occipitomaculata occipitomaculata*, Herpetology R-135. Harvard University, Cambridge, MA, USA. <https://mczbase.mcz.harvard. edu/guid/MCZ:Herp:R-135>.

Jochimsen, D.M., C.R. Peterson, K.M. Andrews, J.W. Gibbons, and E. Drawer. 2004. *A Literature Review of the Effects of Roads on Amphibians and Reptiles and the Measures Used to Minimize Those Effects*. Idaho Fish and Game Department, USDA Forest Service.

Peyton, M.M. 1989. Geographic distribution: *Storeria occipitomaculata* (Redbelly Snake). *Herpetological Review* 20: 13.

Pisani, G.R. 2009. *Virginia valeriae* and *Storeria dekayi* in a northeast Kansas grassland community – Ecology and conservation implications. *Journal of Kansas Herpetology* 32: 20–36.

Pisani, G.R. and W.H. Busby. 2011. Ecology of the Smooth Earth Snake (*Virginia valeriae*) and Redbelly Snake (*Storeria occipitomaculata*) in northeastern Kansas. Open-file Report No. 172. Kansas Biological Survey, Lawrence, Kansas.

Plummer, M.V., C.S. O'Neal, S.M. Cooper, R. Stork, N.E. Mills, and A.B. McKinney. 2020a. Leave or Die: Dispersal of Red-Bellied Mudsnakes (*Farancia abacura*) from their Home Ranges in an Isolated Wetland. *Wetlands* 40: 2489–2498. https://doi.org/10.1007/s13157-020-03162-w.

Plummer, M.V., C.S. O'Neal, S.M. Cooper, and R. Stork. 2020b. Red-bellied Mudsnake (*Farancia abacura*) home ranges increase with precipitation in an isolated wetland. *Herpetological Conservation and Biology* 15: 160–168.

R Core Team. 2020. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Fogarty, D.T., C.P. Roberts, D.R. Uden, V.M. Donovan, C.R. Allen, D.E. Naugle, M.O. Jones, B.W. Allred, and D. Twidwell. 2020. Woody plant encroachment and the sustainability of priority conservation areas. *Sustainability* 12: 8321. https://doi.org/10.3390/su12208321.

Rocchini, D., J. Hortal, S. Lengyel, J.M. Lobo, A. Jimenez-Valverde, C. Ricotta, G. Bacaro, and A. Chiarucci. 2011. Accounting for uncertainty when mapping species distributions: the need for maps of ignorance. *Progress in Physical Geography* 35: 211–226. https://doi.org/ 10.1177/0309133311399491.

Rolfsmeier, S., and G. Steinauer. 2013. *Nebraska Natural Heritage Program state vascular plant list*. Nebraska Game and Parks Commission, Lincoln, NE, USA.

Rousseeuw, P.J., and M. Hubert. 2011. Robust statistics for outlier detection. *Wiley interdisciplinary reviews: Data mining and knowledge discovery* 1: 73–79. <https://doi.org/ 10.1002/widm.2>.

Row, J.R., G. Blouin-Demers, and S.C. Lougheed. 2010. Habitat distribution influences dispersal and fine-scale genetic population structure of eastern foxsnakes (*Mintonius gloydi*) across a fragmented landscape. *Molecular Ecology* 19: 5157–5171. https://doi.org/10.1111/j.1365-294X.2010.04872.x.

Schou, M.F., V. Loeschcke, J. Bechsgaard, C. Schlötterer, and T.N. Kristensen. 2017. Unexpected high genetic diversity in small populations suggests maintenance by associative overdominance. *Molecular Ecology* 26: 6510–6523. https://doi.org/ 10.1111/mec.14262.

Semlitsch, R.D., and G.B. Moran. 1984. Ecology of the redbelly snake (*Storeria occipitomaculata*) using mesic habitats in South Carolina. *American Midland Naturalist* 111: 33–40.

Schneider, R., K. Stoner, G. Steinauer, M. Panella, and M. Humpert. 2011. *The Nebraska Natural Legacy Project: State Wildlife Action Plan*. 2nd ed. The Nebraska Game and Parks Commission, Lincoln, NE, USA.

Shepard, D.B., M.J. Dreslik, B.C. Jellen, and C.A. Phillips. 2008. Reptile road mortality around an oasis in the Illinois corn desert with emphasis on the endangered eastern massasauga. *Copeia* 2008: 350–359. https://doi.org/10.1643/ CE-06-276.

Smith, B.E. and N. Stephens. 2003. *Conservation assessment for the redbelly snake in the Black Hills National Forest South Dakota and Wyoming*. United States Department of Agriculture, US Forest Service, Custer, South Dakota, USA.

Smith, L.M., D.A. Haukos, S.T. McMurry, T. LaGrange, and D. Willis. 2011. Ecosystem services provided by playas in the High Plains: potential influences of USDA conservation programs. *Ecological Applications* 21: S82–S92. https://doi.org/10.1890/09-1133.1.

Sidle, J.G., E.D. Miller and P.J. Currier. 1989. Changing habitats in the Platte River Valley of Nebraska. *Prairie Naturalist* 21: 91–104.

Somma, L.A. 2022. Providence of the red-bellied snake, *Storeria occipitomaculata* (Storer) (Squamata: Natricidae), collected from eastern Nebraska, USA, in the 19th century. *Breviora* 575: 1–10.

Sternberg Museum of Natural History (FHSM). 2021. Herpetology Collection. *Storeria occipitomaculata*, FHSM 14700, 15628, 16161, 16163, 16498, 16543. Fort Hays State University, Hays, KS, USA. <https://sternberg.fhsu. edu/research-collections/zoology/herpetology.html>.

Tang, Z., X. Li, N. Zhao, R. Li, and E.F. Harvey. 2012. Developing a restorable wetland index for rainwater basin wetlands in south-central Nebraska: A multi-criteria spatial analysis. *Wetlands* 32: 975–984. https://doi.org/10.1007/ s13157-012-0320-x.

Tye, S.P., K. Geluso, and M.J. Harner. 2017. Early emergence and seasonality of the Red-bellied Snake (*Storeria occipitomaculata*) along the Platte River in south-central Nebraska, USA. *Transactions of the Nebraska Academy of Sciences* 37: 11–17.

U.S. Fish and Wildlife Service [USFWS]. 2017. *Waterfowl Production Areas*. National Wildlife Refuge System, Rainwater Basin Wetland Management District, Funk, Nebraska, USA. <https://www.fws.gov/refuge/Rainwater_ Basin_WMD/wildlife_and_habitat/WPA.html>.

University of Nebraska State Museum [UNSM]. 2021. Amphibians and Reptiles Collection. *Storeria occipitomaculata*, UNSM 19189, 16282, 15015-15021, 9956, 9883-9890, 9781-9786, 9290. University of Nebraska-Lincoln, NE, USA. <https://museum.unl.edu/collections/zoology/index.html>.

Verheijen, B.H., D.M. Varner, and D.A. Haukos. 2018. Effects of large-scale wetland loss on network connectivity of the Rainwater Basin, Nebraska. *Landscape Ecology* 33(11): 1939–1951. https://doi.org/10.1007/s10980-018-0721-1.

Weather Underground. 2021. Kearney, NE, Weather History, 9/28/2021. Kearney Regional Weather Station (40.71°, -99.08°; 663 m elev.). <https://www.wunderground.com/history/daily/us/ne/kearney/KEAR/date/2021-9-28>.

West, E. and G. Rurak. 2004. A long, long time ago…: Historical evidence of riparian forests in the Great Plains and how that knowledge can aid with restoration and management. *Journal of Soil and Water Conservation* 59: 104A–110A.

Wickham, H. 2009. ggplot2: elegant graphics for data analysis. Springer-Verlag, New York, New York, USA.

Willson, J. D., and M. E. Dorcas. 2004. Aspects of the ecology of small fossorial snakes in the western piedmont of North Carolina. *Southeastern Naturalist* 3: 1–12. https://doi.org/10.1656/1528-7092(2004)003[0001:AOTEOS]2. 0.CO;2.