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ABSTRACT -- Winterkill occurs when drought conditions expose hibernating turtles to desiccation and lethally cold temperatures. Winterkill is thought to represent a major source of mortality in northern populations of the painted turtle (*Chrysemys picta*), but few field observations are available. We herein reported on catastrophic winterkill among western painted turtle (*C. picta bellii*) at Limestone Butte Lake (LBL) in western South Dakota during the winter of 2003-2004. Additionally, we used the carcasses of winterkilled turtles (n = 86) to estimate the standing crop biomass of the painted turtle at LBL (0.6 kg/ha). This was the only estimate of biomass available for a painted turtle population in South Dakota and one of only two for the Great Plains; furthermore, it was the lowest estimate from anywhere in North America. We attributed this to several factors, including the painted turtle probably began emigrating from LBL in response to receding water levels before the winterkill event of 2003-2004.

Key words: biomass, *Chrysemys picta*, drought, South Dakota, western painted turtle, winterkill.

The abiotic environment is a strong selective force in the evolution of life history characteristics (Grant and Grant 1995). Ectotherms such as turtles are especially susceptible to extreme abiotic fluctuations owing to a lack of intrinsic

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thermoregulatory ability, and consequently might suffer significant mortality as a result (Gregory 1982, Bodie and Semlitsch 2000). In particular, winterkill has been suggested as a major source of mortality among northern populations of the painted turtle (*Chrysemys picta*) (Christiansen and Bickham 1989, St. Clair and Gregory 1990). Winterkill most often occurs among hibernating turtles and is thought to result from an interaction between drought conditions and low temperatures (Christiansen and Bickham 1989). However, field observations of winterkill in turtle populations are notable for their paucity in the literature (Bodie and Semlitsch 2000). We herein reported on catastrophic mortality as a result of winterkill among a population of the western painted turtle (*C. picta bellii*) in southwestern South Dakota. Additionally, this event presented us with the opportunity to estimate the minimum standing crop biomass of the western painted turtle on the study site. Biomass estimates are essential to understanding the role of turtles in community organization, energy flow, and ecosystem productivity, but are not widely available, even for many well-studied species such as the painted turtle (Iverson 1982a, Congdon and Gibbons 1989, Vogt and Villarreal Benitez 1997, Dodd 1998).

STUDY AREA and METHODS

Our study was conducted at Limestone Butte Lake (LBL; 43° 09' 36"N; 103° 09' 47"W), an isolated 34.4 ha man-made impoundment on the Buffalo Gap National Grassland, approximately 5 km southeast of Olerichs, Fall River County, South Dakota. Prior to extreme drought conditions in 2004, this shallow (< 1.5 m) lake was characterized by dense stands of cattails (*Typha* sp.) along the shoreline, but otherwise contained little aquatic vegetation. Water levels dramatically declined during 2003 (S. Platt, personal observation) owing to rainfall that was 50% below normal throughout most of western South Dakota (Nelson-Stastny 2004), and by early May 2004 the lakebed was completely dry. During a visit on 26 May 2004, numerous dead painted turtles were found scattered throughout the lakebed. Turtle carcasses retained drying and decayed flesh indicating the mortality was a recent occurrence and did not represent an accumulation of shells from previous years. We made repeated visits to LBL from late May through September 2004 to search the dry lakebed and surrounding shoreline, and collect turtle carcasses. Calipers were used to measure the straight-line carapace length (CL) of each shell to the nearest 1.0 mm. Because CL is correlated significantly with body mass (BM) (Iverson, 1982a), we used the equation BM = 0.4377(CL 2.542) of Iverson (1982b) to estimate the BM (in grams) of each turtle. We then summed the BM of each turtle, converted this value to kilograms, and divided it by the area of LBL to estimate the minimum standing crop biomass (kg/ha) of painted turtles at LBL. Mean values are presented as ± 1 SD.

RESULTS

We found 86 dead painted turtles (density = 2.5 turtles/ha) at LBL in 2004, and attributed this mortality to drought conditions that exposed hibernating turtles to lethally low ambient temperatures during the winter of 2003-2004. The mean CL and BM for this population were 11.6 ± 3.2 cm (range = 4.5 to 20.3 cm) and 257.0 ± 187.9 g (range = 20.0 to 922.2 g), respectively. A size distribution is presented in Figure 1. Summing the BM for each turtle yielded a composite mass of 22.1 kg or an estimated standing crop biomass of 0.6 kg/ha.

DISCUSSION

Populations of painted turtle in the central and northern United States and southern Canada appear particularly susceptible to winterkill (Christiansen and Bickham 1989, St. Clair and Gregory 1990), but there are few reports of this phenomenon in the literature. Christiansen and Bickham (1989) recovered 186 winterkilled turtles of five species from a lake in Iowa, of which 132 (71.0%) were painted turtle. Although only 16 painted turtles occurred among 144 winterkilled turtles of five species found in central Missouri, Bodie and Semlitsch (2000)

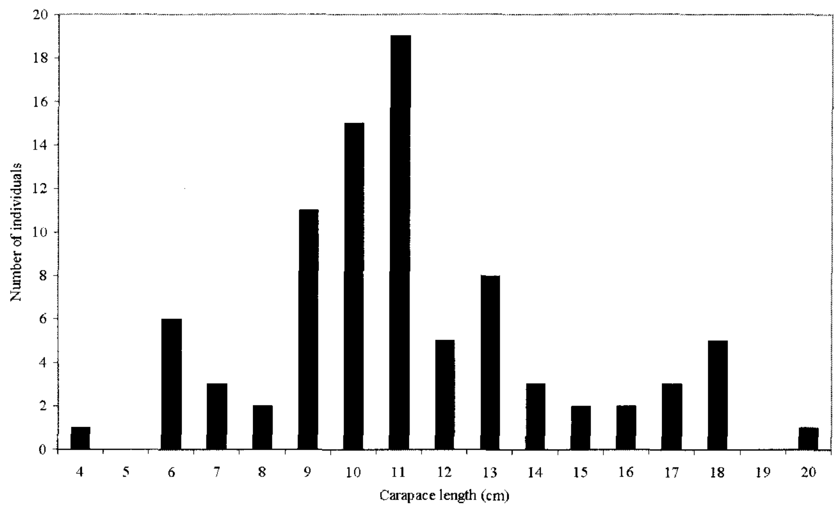

Figure 1. Size distribution of winterkilled individuals of the western painted turtle (n = 86) found at Limestone Butte Lake, Fall River County, South Dakota (May through September 2004).

concluded that based on their proportional representation in the sample, the painted turtle was much more likely to perish from winterkill than other species. Finally, St. Clair and Gregory (1990) observed an unspecified number of painted turtle shells at a study site in southeastern British Columbia and attributed these to winterkill. The painted turtle overwinters in shallow (< 2 m) water, ensconced within common muskrat (*Ondatra zibethicus*) and American beaver (*Castor canadensis*) lodges, under overhanging banks, and buried beneath or resting on the surface of the mud (Gregory 1982, St. Clair and Gregory 1990, Ernst et al. 1994). Our observations and those of others (Christiansen and Bickham 1989, St. Clair and Gregory 1990, Bodie and Semlitsch 2000) indicate that winterkill occurs when low water levels expose overwintering turtles to desiccation and lethally cold temperatures.

Population and community level effects of winterkill on the painted turtle are not well understood. Like most chelonians, the painted turtle possesses a unique suite of life history traits (e.g., delayed onset of sexual maturity, low juvenile but high adult survivorship, long lifespan) that severely constrain the ability of populations to recover from episodes of increased adult mortality (Congdon et al. 1993, 1994). Thus, in the Great Plains and other semi-arid regions where droughts result in occasional catastrophic winterkill, shallow wetlands that provide a suboptimal hibernation environment might represent population sinks (Watkinson and Sutherland 1995) in the local metapopulation dynamics of the painted turtle. Furthermore, by decreasing the relative abundance of freeze susceptible species such as the painted turtle, winterkill might act as a strong selective force in structuring freshwater turtle assemblages in these habitats (Christiansen and Bickham 1989).

The painted turtle, occurring from the Atlantic to Pacific coasts and north from the Gulf Coast states into southern Canada, is one of the most widely distributed freshwater chelonians in North America (Ernst et al. 1994). Despite this extensive distribution, estimates of standing crop biomass are available only for painted turtle populations in the eastern United States (Table 1). Our study provided the only estimate of biomass for a painted turtle population in South Dakota, and was one of only two estimates for the Great Plains (see also Iverson et al. 2006). In general, estimates of standing crop biomass in turtle populations are extrapolated from population estimates and are influenced by the same sampling biases that affect the latter (Dodd 1998). For example, variation in the susceptibility to capture, habitat use, and activity patterns of different age/size classes represent potential sources of error in estimates of both population size and standing crop biomass (Dodd 1998). Additionally, estimates of population size that have not been adjusted for unequal sex ratios and sexual size dimorphism, either of which can be substantial for many species, are often used to calculate biomass (Congdon et al. 1986). We largely avoided these potential sources of bias by basing our calculations of biomass on the measurement of every individual in the population we observed rather than on an estimate of population size.

Table 1. Estimates of density and biomass for painted turtle populations in lacustrine habitats. NR = not reported.

Location	Density (turtles/ha)	Biomass (kg/ha)	Source
Indiana	48.8	11.2	Wade and Gifford 1965, Iverson 1982a
Michigan	576.0	28.2	Gibbons 1968
	89.5	16.6	Congdon et al. 1986
	39.9	7.2	Congdon et al. 1986
	41.6	7.2	Congdon et al. 1986
Nebraska	149.0	54.7	Iverson et al. 2006
New York	137.0	28.3	Zweifel 1989
Pennsylvania	591.0	106.4	Ernst 1971, Iverson 1982a
South Dakota	2.5	0.6	Our study
Virginia	NR	28.3	Mitchell 1988

The painted turtle often attains high densities with correspondingly high biomass in lacustrine habitats (Ernst et al. 1994), but the values that we found at LBL are the lowest yet reported from anywhere within the extensive distribution of the species (Table 1). Possibly the biomass of the painted turtle at LBL simply reflects the low overall primary productivity of the region, but we regard this as unlikely and attribute our results to several factors. First, it is likely that turtles began emigrating from LBL as water levels receded during the summer and fall of 2003 and before the onset of hibernation. Increased overland emigration in response to drought conditions has been reported in other painted turtle populations (McAuliffe 1978, Gibbons et al. 1983, Christiansan and Bickham 1989, Lindeman and Rabe 1990). Moreover, some large adults possibly overwintered successfully and departed the site after emerging from hibernation in the spring of 2004. Bodie and Semlitsch (2000) found that larger individuals exhibit a higher tolerance for freezing and desiccation than smaller individuals, and larger turtles might also engage in different overwintering behaviors that render them less susceptible to winterkill. Second, although we conducted a thorough search of the study site and most carcasses proved readily obvious, we cannot dismiss the likelihood that some dead turtles, particularly small juveniles, were overlooked. However, small to medium sized turtles are well represented in our sample and the few that we might have over-looked are unlikely to constitute a significant source of error. Lastly, it is likely that scavengers such as coyote (*Canis latrans*), red fox (*Vulpes vulpes*), turkey vulture (*Cathartes aura*), and American crow (*Corvus brachyrhynchos*) removed some turtle carcasses from the study site prior to and during our investigation.

In conclusion, our observations suggested that winterkill might be a major source of mortality for painted turtle populations on the northern Great Plains, particularly those inhabiting shallow wetlands vulnerable to occasional drought. Moreover, population and community level effects of winterkill remain poorly understood and warrant further investigation. Finally, our study highlighted the need for additional biomass estimates from painted turtle populations in western North America.

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