Massasauga

Sistrurus catenatus (Rafinesque 1818)

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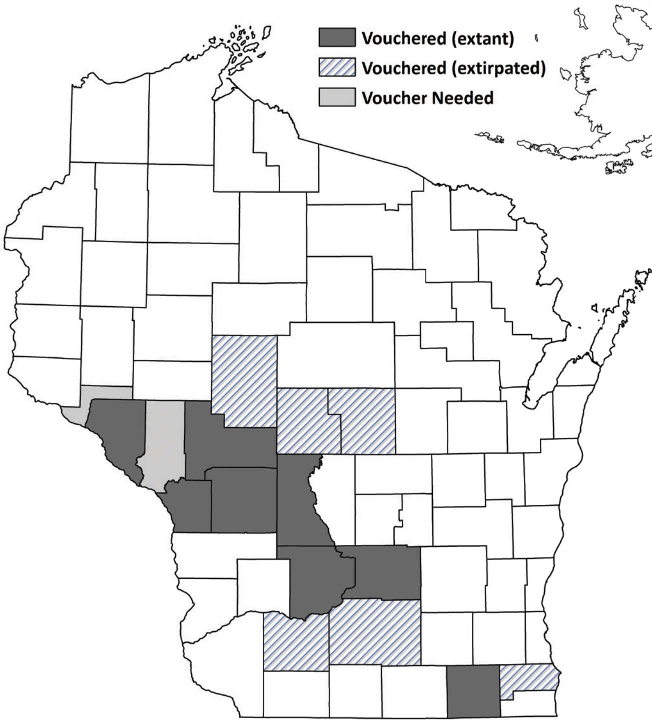

Adult Massasauga (Buffalo County; photo by R. Paloski).

AT A GLANCE

Massasaugas (a.k.a. 'swamp rattlesnakes') are one of two venomous snakes found in Wisconsin. They can be identified as venomous by their elliptical pupils, obvious rattle on the end of the tail, and presence of a heat-sensing pit between the eyes and nostrils on either side of the head. Their dorsal pattern consists of numerous saddle-shaped chocolate-colored blotches over a gray background that run along the back. Two broad brown stripes bordered by white occur on each side of the head: one that runs from the back of the eye to the back corner of the jaw, and another that runs parallel to the mouth. Massasaugas frequent wet or swampy habitats, including damp meadows, fens, and wet prairies. They are active in Wisconsin from mid-April to mid-October. The period when adults breed in the state is somewhat difficult to determine, based on past reports. Some indicate that breeding mostly occurs in summer or autumn, while others suggest that it occurs in spring and summer. Regardless, females give birth to live young from early August to mid-September. Their diet in Wisconsin consists almost entirely of small mammals, while the snakes are likely eaten by various birds and mammals found in wetland habitats. Although Massasauga populations are much smaller and more isolated than those of Wisconsin's other venomous snake, the Timber Rattlesnake, this species was once widespread and locally abundant in southern Wisconsin. Habitat loss and human persecution, including a state-paid bounty for Massasaugas from 1903 to 1973, have contributed to its decline. Massasaugas are now among Wisconsin's rarest vertebrates and only reliably found in a handful of locations from the western and central portions of the state. It remains unclear if the species will persist in Wisconsin. The Massasauga has been listed as Endangered in the state since 1975 and was listed as Threatened in the US under the Endangered Species Act in 2016.

SYSTEMATICS

The phylogenetics of *Sistrurus catenatus* (Massasauga) have been extensively studied. The species belongs to a group of snakes (genus *Sistrurus*) collectively known as pigmy rattlesnakes. There are three species in the genus: *S. catenatus* (Rafinesque 1818), *S. miliarius* (Pigmy Rattlesnake; Linnaeus 1766), and *S. ravus* (Mexican Pigmy Rattlesnake; Cope 1865). *S. miliarius* is widely distributed across the southeastern and south-central United States. *S. catenatus* occurs from Arizona to New York and Ontario. *S. ravus* has a relatively small range, limited to southern Mexico.

Until recently, *Sistrurus catenatus* was thought to encompass three subspecies, including *S. c. catenatus* (Eastern Massasauga), *S. c. tergeminus* (Western Massasauga), and *S. c. edwardsii* (Desert Massasauga). Extensive genetic research (Anderson et al. 2010, Gibbs and Chiucchi 2011, Ray et al. 2013, Ryberg et al. 2015) indicates that only *S. c. catenatus* occurs in Wisconsin, and this subspecies should be considered a separate species. Among Wisconsin snakes, *S. catenatus* is one of only two species in the family Viperidae, the other being *Crotalus horridus* (Timber Rattlesnake).

DESCRIPTION

Adults: In Wisconsin, Massasaugas have 26–40 prominent middorsal blotches that are chocolate brown to very dark brown or nearly black. The blotches are overlaid on a ground color that ranges from light gray to gray brown (Vogt 1981, Oldfield and Moriarty 1994; Figure 299). Each side of the body has two or three

Figure 299. Two adult Massasaugas showing the slight color variation that can occur in Wisconsin (Juneau County; photo by R. Hay).

Figure 300. Massasauga head pattern (Buffalo County; photo by R. Paloski).

rows of smaller alternating blotches, the lowest often merging with the ventral scales. The blotches can be faintly bordered by a very thin white line (Ditmars 1907). The ventral surface is dark gray to black and mottled with yellow, cream, or white, but it can also be mostly black. The dorsal body scales are keeled.

The head is noticeably wider than the neck and has nine large plate-like scales between the eyes (Figure 300). The top of the head also has two broad dark brown and irregularly shaped bands running from behind the parietal scales on top of the head onto the neck (Figure 300). The sides of the head have two short broad brown stripes bordered with white: one that runs from the eyes to the back of the head, and another that runs along the labial scales (Figure 301). This snake has a pit between the nostril and eye on both sides of the head that detects radiant heat (Bakken and Krochmal 2007). Both of Wisconsin's rattlesnakes have vertical pupils, unlike Wisconsin's nonvenomous snakes, which have round pupils (Ernst and Ernst 2003). The tail has dark dorsal bands that alternate against the ground color, giving it a ringed pattern. Males have a longer tail than females, with five to seven tail rings, whereas females have fewer than five or exactly five rings (Vogt 1981). The anal plate and subcaudal scales are undivided. The rattle consists of horny caudal scales that are loosely connected. After every shedding cycle a new scale or segment is added to the rattle. A special muscle in the tail allows the snake to elevate the rattle vertically while quickly vibrating it from side to side, producing a distinct rattling sound (Friederici 2008). The number of rattle segments is not indicative of age, as they can shed more than once a year, and the rattles can also break off (Steen 2011; Figure 302).

Above, top: Figure 301. Photograph highlighting the broad brown stripes bordered by white on the side of the head. Note that the green tint on the rattle is due to paint used as a short-term identifying mark by researchers (Buffalo County; photo by J. Kapfer).

Above, bottom: Figure 302. A close-up of the rattle from a Massasauga (Buffalo County; photo by R. Paloski).

Massasaugas in Wisconsin are medium-sized, stout-bodied snakes ranging from 50 to 75 cm TL (19.5 to 29.5 in; Vogt 1981), although individuals as large as 100 cm TL (39 in) have been reported (Ditmars 1907, Conant and Collins 1998). The largest known wild specimen from Wisconsin came from

Juneau County and measured 85.2 cm TL (33.5 in, UWZM 23946). Wild males sampled from a three-county area of west-central Wisconsin ranged from 56.5 to 73.5 cm SVL (22.2 to 28.9 in), and tail length ranged from 5.3 to 8.5 cm (2.0 to 3.3 in, $n = 24$). Female SVL and tail length ranged from 53 to 71 cm (20.9 to 28.0 in) and 4.0 to 5.8 cm (1.6 to 2.3 in, $n = 24$), respectively. Weights for adult males ranged from 195 to 550 g (6.9 to 19.4 oz), nongravid females ranged from 220 to 380 g (7.8 to 13.4 oz), and gravid females ranged from 225 to 510 g (7.9 to 18.0 oz; Robert Hay, Turtles for Tomorrow, unpublished data).

Preadult stages: Neonates look similar to adults in pattern but usually have a lighter ground color and are born with a distinctly yellow tail tip (ca. the last centimeter of the body; Figure 303). This tail color fades somewhat quickly as the snake grows and becomes dark like the dorsal blotches. Mean TL of neonates from Buffalo County was 22.0 cm (8.66 in, SD = 0.1 cm [0.04 in], $n = 207$) and mean weight was 9.7 g (0.349 oz, SD = 0.1 g [0.004 oz]; Keenlyne and Beer 1973b). King et al. (2004) reported that captive-born Wisconsin neonates from wild-caught females in Juneau and Monroe Counties had a mean weight of 8.3 g (0.29 oz, SD = 0.7 g [0.02 oz], $n = 32$). Hileman et al. (2017) indicated that the weights reported by King et al. (2004) were the lowest for any Massasauga population and that across the species' range, neonate mass was positively correlated with mean annual precipitation.

Figure 303. A neonate Massasauga. Note the yellowish tail (Buffalo County; photo by J. Kapfer).

Variation: No significant variation in appearance is known in Wisconsin, although dorsal blotches can range from light to dark brown (see Figure 299), and juveniles have a yellow tail tip (see Figure 303). There is no apparent sexual dimorphism in color or pattern (R. Hay, unpublished data), but adult males are likely longer and heavier than females.

Diagnosis: Massasaugas can be characterized by the presence of verticle pupils, one or more rattle segments on the end of the tail, a heat-sensing pit between the eye and nostril, and large plate-like scales on the top of the head. They also possess strongly keeled dorsal scales in 21–27 rows at midbody and 139–160 ventral scales. Their tail anterior to the rattle segments is banded, while the anal plate is undivided, and most subcaudal scales are undivided. There are 2 prefrontal scales, and each side of the head has 11–12 supralabial scales, 11–13 infralabial scales, 2 preocular scales, and 3–4 postocular scales. Massasaugas are distinguishable from Wisconsin's other venomous snake, the Timber Rattlesnake, because the latter is beige with dark brown or black bands that cross the dorsal surface, has a mostly unpatterned head, and has a solid black tail. Timber Rattlesnakes possess many small head scales (reviewed by Ernst and Ernst 2003), as opposed to the nine large scales on the head of the Massasauga. The scale counts of Timber Rattlesnakes also differ from those of Massasaugas, with 13–15 supralabial scales, 14–16 infralabial scales, and 154–183 ventral scales. Although Bailey (1942) reported a natural Massasauga × Timber Rattlesnake hybrid, the rate of incidence in the wild is likely low, and no reports of hybridization exist from Wisconsin.

Five Wisconsin snake species are considered 'rattlesnake mimics,' since they often vibrate the end of their sharply pointed tail when disturbed, which confuses differentiation from Massasaugas. These include Eastern Foxsnakes (*Pantherophis vulpinus*), Gophersnakes (*Pituophis catenifer*), Eastern Milksnakes (*Lampropeltis triangulum*), Gray Ratsnakes (*Pantherophis spiloides*), and North American Racers (*Coluber constrictor*). Eastern Foxsnakes and Eastern Milksnakes, for example, have somewhat similar dorsal blotch patterns. Yet adult Eastern Foxsnakes have little to no pattern on an orange or copper-colored head, whereas Massasaugas have a prominently patterned head. Juvenile Eastern Foxsnakes, on the other hand, do have a heavily patterned head but possess round pupils and patterned ventral surfaces, unlike Massasaugas. Eastern Milksnakes possess blotches that are brown or reddish but with a narrow black border, while the Massasauga's blotches are usually bordered by a faint white line. Eastern Milksnakes also typically have a light-colored V- or Y-shaped mark on the nape of the neck, while Massasaugas have two somewhat parallel brown bands behind the eyes that run onto the neck (Vogt 1981). Gophersnakes possess many poorly defined dorsal blotches, with variegated spots between them (unlike the Massasauga's well-defined blotches), while North American Racers and Gray Ratsnakes do not have obvious dorsal patterns as adults. Eastern Hog-nosed Snakes (*Heterodon platirhinos*) are another potentially confusing species, although they do not vibrate their tails when threatened. They are thick-bodied, like Massasaugas, and some adults possess prominent dark dorsal blotches (although many have a more uniform tan or olive dorsal surface). The Eastern Hog-nosed Snake's rostral scale is pointed and upturned. This snake also often flares its neck when approached, a behavior not typical in Massasaugas. As stated previously, all nonvenomous snakes in Wisconsin have round pupils and a sharply pointed tail, unlike venomous species.

DISTRIBUTION AND HABITAT

Global distribution: Massasaugas occur in a southwest to northeastern swath across North America. Their range extends from Arizona and Texas in the South, north through Oklahoma, and into southern Kansas (with an isolated pocket in Colorado). A gap in the distribution occurs across much of Missouri and Iowa, after which they range into the Upper Midwest across Illinois, into Wisconsin and east across Ohio, Indiana, and the Lower Peninsula of Michigan, and into western New York, Pennsylvania, and southern Ontario.

Distribution in Wisconsin: Vogt (1981) reported that Massasaugas could only be found with regularity at a handful of sites through the 1970s. Today they are even rarer in Wisconsin and perhaps the state's most endangered reptile (Christoffel et al. 2008). At best, they occur at fewer than ten locations, and the species' future in the state is uncertain (Faust et al. 2011). Massasaugas are currently reported from 16 counties, although cataloged specimens are either missing or do not exist for two of these. For example, Vogt (1981) included Pepin County in the snake's range, but no vouchered specimen from that county is known. Casper (1993b) included an anecdotal observation from Pepin County by "R. Hoffman" in 1987, but no further anecdotes are documented.

Several additional voucher specimens reported in support of county records are either missing or suspect. Recent inquiries into the existence of the voucher for Trempealeau County (UWEC 1455, presumably the specimen listed as "UWEC Unnumbered" in Casper [1993b]) revealed that it is currently lost (Joshua Kapfer, UW–Whitewater, personal communication). The voucher specimen for Dane County (UWZM 17584) submitted in 1962 by "R. K. Nelson" includes the note "died at birth in captivity," and it is unclear if Dane County is the location of collection or captivity. No other specimens from Trempealeau or Dane County are known. Casper (1993b) submitted an observational report by "J. Ramsey" in Trempealeau County, while R. Hay (personal observation) and R. S. King (personal observation) have also observed them in this county. Several counties with records supported by historic vouchers may no longer represent extant populations. For example, the specimens taken from Racine County were collected in the 1800s by P. Hoy (USNM 524–525), and no recent substantiated reports from that county are known.

Localities of possible occurrence: A review of various sources provides insight into the historical range of this species in Wisconsin. For example, Schorger (1967–68) compiled anecdotal historical reports of Massasaugas from 26 Wisconsin counties, which did not include Portage County, where they have since been documented via museum specimen (CM 70492; Casper 2015). Schorger's review also revealed some surprising locations for purportedly occupied sites, which included several that are now considered major urban centers and unlikely to have extant populations.

For example, although museum specimens from Milwaukee County are not known, the area of the current city of Milwaukee was once apparently home to a substantial Massasauga population. Olin (1930) described a Massasauga site in Milwaukee as "the marsh where Mason Street now strikes the river." This wetland was likely destroyed long ago, as the area is now the site of residential and commercial buildings. Historic accounts also indicate that the Madison area had at least two Massasauga populations: one near the outlet of Lake Monona (Schorger 1967–68) and the other on the marshes that once covered most of the area between the Yahara River and the state capitol building (Vogt 1981). Currently, both locations are largely urban or residential, although a small wetland (Paunack Marsh) remains near the outlet of Lake Monona.

Schorger (1967–68) compiled further historical records from additional counties where this species apparently no longer exists, which include (but are not limited to) Chippewa, Dunn, Grant, Jefferson, and Vernon Counties. The WDNR has also compiled a handful of more recent observational reports of this species from counties without known voucher specimens, including Adams, Green, and Crawford Counties (WDNR 2016b). Casper (1993b) reported reliable observational records from 1991 in additional counties that currently lack voucher specimens, including Rock, Green, and Grant Counties. Casper (1996) also included an observation from Kenosha County in 1987 that additional surveys could not verify.

Habitat: Massasaugas generally inhabit a mosaic of open wetland habitat interspersed with pockets of drier uplands and floodplain forest (e.g., Keenlyne 1968, Marshall et al. 2006, Moore and Gillingham 2006, Harvey and Weatherhead 2006a; see descriptions in Amphibians and Reptiles in Wisconsin Plant Communities chapter). Knudsen (1954b) described Massasauga habitat in Wisconsin as "marshy areas of the southwestern one-quarter of the state." Vogt (1981) identified mesic and lowland areas along rivers, lakes, and marshes as characteristic habitats for this species. Other historical accounts provide a similar picture of the habitats once occupied in Wisconsin. For example, Hoy (1883) wrote: "This species inhabits marshy, grassy prairies where meadow mice live, on which they almost exclusively subsist." Higley (1889) wrote: "Not rare, in grassy marshes throughout the state." Pope (1926) located specimens at a farm near Portage and described the area as the "Massasauga swamp." However, based on a photograph in Pope (1926), this area could be referred to as an open, perhaps mesic, meadow.

These historic descriptions of Massasauga habitat are consistent with locations where it still occurs in Wisconsin. Research on five of the remaining Massasauga sites in the state describe the associated habitat as meadows in low-lying wet areas (such as sedge meadows) and adjacent wet or mesic prairies (McCumber and Hay 2003, King et al. 2004, Durbian et al. 2008). Suitable habitat is frequently described as open canopy, and individuals tracked using radio telemetry in Buffalo County were located in areas with 26.5%–44.9% mean tree canopy cover (McCumber and Hay 2002, 2003). Unfortunately, many of these meadows are now dominated by invasive Reed Canary Grass (*Phalaris arundinacea*) or have succeeded to habitats overrun with woody vegetation that may not be suitable for this species (see Conservation section).

McCumber and Hay (2002, 2003) recorded microhabitat associations for individuals from Buffalo County for two years ($n = 6$ and 10 in 2002 and 2003, respectively). Their findings indicate that Massasaugas are frequently found in leaf litter ($\bar{x}$ litter coverage centered on snake location = 37%–40.8%) and herbaceous vegetation ($\bar{x}$ coverage = 34%–44.9%), compared to rock ($\bar{x}$ = 9.3%–11%) and woody debris ($\bar{x}$ = 14%–17.9%) cover. Harvey and Weatherhead (2006a) reported that Massasaugas in Ontario were always within ca. 0.5 m (1.6 ft) of retreat sites and frequently found near shrubs. The authors suggested this might be due to a combination of the cover from predators and thermoregulatory opportunities provided by both. They also reported variation in microhabitat preference among gravid females, which selected sites that were rockier, with more open canopies than males and nongravid females.

Given the length of hibernation in Wisconsin, habitat used for overwintering is of equal importance to that used during the active season. Wetlands with relatively stable winter water levels are critical

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for Massasauga hibernation. Massasaugas must descend below the frost line to overwinter and typically hibernate underwater or at groundwater level. A variety of hibernacula are reportedly used, such as below-ground channels associated with tree and shrub roots (Conant 1951, Johnson 1995, King et al. 2004), small mammal and crayfish (Cambaridae) burrows (Maple and Orr 1968, Hallock 1991), and even anthropogenic structures (Ravesi et al. 2015). Several authors have mentioned that crayfish burrows near the water table line, in particular, are important hibernacula for this species in Wisconsin (Keenlyne 1968, Vogt 1981, McCumber and Hay 2003). Maple and Orr (1968) reported that Massasaugas in Ohio overwintered at depths of 30–90 cm (11.8–35.4 in). Research in Ontario found Massasaugas rarely used the same hibernacula in consecutive years but often overwintered within 100 m (328 ft) of a previously selected hibernaculum (Harvey and Weatherhead 2006b).

Without a relatively stable water supply within the hibernacula, snakes can die of exposure if the water level drops and frost penetrates into the soil. This threat could be a defining characteristic that limits the northern edge of their range and may partially explain the species' North American distribution. An examination of locations across the eastern range of this species illustrates the importance of wetlands with stable water levels. For example, all of Canada's extant populations are less than 50 km (31.1 mi) from the Great Lakes. While the Great Lakes water levels do fluctuate, this fluctuation is typically minimal during the course of one winter. The majority of extant populations in the US are found in Michigan (Szymanski 1998), where they often associate with wetlands known as fens (Moore and Gillingham 2006, Bailey et al. 2012). Fens are similar to mesic or wet meadows or marshes but are groundwater driven and therefore have a stable water supply that fluctuates little in the winter (Marshall et al. 2006).

REPRODUCTION AND DEVELOPMENT

There are reported differences in when Massasaugas breed. Vogt (1981) claimed Wisconsin populations mated in spring and late summer but provided no evidence to support this. Spring breeding in Ohio was speculated by Crawford (1936) and recorded in Iowa (Guthrie 1927) based on a single captive pair. Other reports, however, suggest Massasaugas breed during summer or autumn and that reproduction is biennial throughout much of their range, including Pennsylvania (Reinert 1981), New York (Johnson 1995, 2000), Illinois (Aldridge et al. 2008), and Michigan (Degregorio et al. 2011a). In Wisconsin, Keenlyne (1978) indicated that adults reproduced annually, but more recent studies support that females reproduce biennially (McCumber and Hay 2002, 2003). It is noteworthy that Johnson et al. (2016a) concluded that some females in New York reproduced on a triennial schedule, which could also occur in Wisconsin.

Adult males are longer and heavier than females (see Description section). Evolutionarily, this sexual size dimorphism is likely a result of intraspecific male-male competition for breeding opportunities with females (Shine 1978, 1994). Male-male combat (VanDeWalle 2005) and aggression (Shepard et al. 2003, E. McCumber, WDNR, personal observation) preceding copulation has been documented. After summer or autumn copulation, females store sperm in the oviduct over winter (ca. eight months) until the following spring, when fertilization occurs (Aldridge et al. 2008). In a range-wide analysis, Hileman et al. (2017) found the proportion of gravid females in Massasauga populations ranged from 23% to 82%. Communal gestation sites have been documented in Pennsylvania (Reinert and Kodrich 1982), while communal parturition sites have been observed in Wisconsin (R. King, personal observation) and Michigan (Eric Hileman, Northern Illinois University, personal observation). In Wisconsin, parturition occurs from early August to mid-September, and snakes are born live, with an average litter size of 11.1 ($n = 58$; Keenlyne 1978). Multiple paternity is widespread in snakes (Jellen and Aldridge 2010) and was recently identified in Massasaugas from Michigan, Illinois, and Pennsylvania (Stedman et al. 2016).

After parturition, females maintain close proximity to their young until completion of the neonates' first ecdysis cycle, which lasts ca. one to two weeks (Butler et al. 1995). During this time neonates may be particularly vulnerable to predators due to visual impairment and possible impairment of the heat-detecting pit (Greene et al. 2002, Durbian

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et al. 2008). This form of parental care or 'maternal attendance' is common among pit vipers (Butler et al. 1995) and is documented in Massasaugas from Michigan (Hileman et al. 2015a), Pennsylvania (Reinart and Kodrich 1982), and Wisconsin (R. Hay, personal observation, R. King, personal observation). During this time, neonates actively maintain mother-offspring associations using chemical cues and scent trailing. However, neonates are unable to distinguish between maternal scent and scent of unrelated conspecifics (Hileman et al. 2015a).

In Michigan, individual growth rates are most rapid during the first and second seasons of life and decrease with each passing year thereafter (King and Hileman 2013). Hileman et al. (2017) reported that among nine Massasauga sites (none from Wisconsin), neonate growth rates in their first year ranged from 2.2 to 8.5 cm/year (0.87 to 3.35 in/year). Age of male sexual maturity is largely unknown and likely varies geographically. Based on growth rates of individuals from the Chicago area, Pope (1944) suggested that both sexes reach sexual maturity at three years of age. Motile sperm was detected in one two-year-old male (SVL = 43.7 cm [17.2 in]), but male sexual maturity is probably more common at three years of age in Michigan (E. Hileman, unpublished data). In Wisconsin, females typically show follicular growth in their second season and reproduce for the first time in their third or fourth season (Keenlyne 1978). Although longevity records for free-ranging individuals are lacking, a captive male from the Staten Island Zoo reportedly lived for 20 years and 5 days (Snider and Bowler 1992).

ACTIVITY

Massasaugas in Wisconsin are primarily active from mid-April to mid-October, although variation can occur. Timing of spring emergence varies annually and geographically but is apparently triggered by increasing soil temperature (Smith 2009, King and Hileman 2013). Wisconsin Massasaugas typically emerge from hibernation when soil temperatures at a depth of 15 cm (6 in) reach 10.6°C (51°F; E. McCumber, personal observation). King (1999) observed emergence from hibernation in Wisconsin as early as 4 April, although individuals used for a repatriation experiment in Wisconsin emerged slightly later than this (King et al. 2004).

Both Western Massasaugas (Seigel 1986) and Desert Massasaugas (Hobert et al. 2004) are primarily diurnal except in summer, when they are primarily nocturnal. A similar pattern was documented for Massasaugas in Clinton County, Illinois (Mike Dreslik, Illinois Natural History Survey, unpublished report). Seigel (1986) reported that in northwestern Missouri, spring and autumn activity was greatest from noon to 4:00 p.m., while summer activity was slightly later (i.e., 4:00 to 8:00 p.m.). Ernst and Ernst (2011) indicated that activity increases after summer rain showers. The mean body temperature of ten Buffalo County individuals tracked with radio telemetry was 23.9°C (75°F; McCumber and Hay 2003). Peak active body temperatures for a population in Illinois were high but also differed by sex and gravidity: males (30°C–34°C [86°F–93.2°F]), gravid females (29°C–33°C [84.2°F–91.4°F]), and nongravid females (26°C–28°C [78.8°F–82.4°F]; Dreslik 2005).

Published estimates of home range size for Wisconsin Massasaugas show large variability. Mean home range size (based on minimum convex polygon estimates) was 2.4 ha (5.9 ac) for a Monroe County population ($n = 10$), 135.8 ha (335.6 ac) for a Juneau County population ($n = 4$; Durbian et al. 2008), and 8.9 ha (22 ac) for a Buffalo County population ($n = 10$; McCumber and Hay 2003). Range length (i.e., the distance between the most widely separated locations within an individual's home range) averaged 272.1 m (992.7 ft) and 1,378.6 m (4,523.0 ft) for populations in Monroe and Juneau Counties, respectively (Durbian et al. 2008). In comparison to other midwestern states, Wisconsin home ranges are larger than those reported from Illinois (Dreslik 2005, Dreslik et al. 2016a), Indiana (Marshall et al. 2006), and southern Michigan (Moore and Gillingham 2006) but smaller than those reported from northern Michigan (Degregorio et al. 2011a).

Massasauga movement patterns are apparently affected by the severity of habitat disturbance, particularly in areas between summer foraging grounds and winter hibernacula (Weatherhead and Prior 1992, Johnson 2000a, Durbian et al. 2008). These patterns also appear to vary by sex. Several studies found home range sizes and movements of males were greater than those of females (e.g., Dreslik 2005, Moore and Gillingham 2006, Durbian et al. 2008, Bieser 2008, Degregorio et al. 2011a). This disparity could be related to the mate-searching behavior of males and its influence on reproductive success. In fact, Jellen et al. (2007) demonstrated that travel distance and body mass of males from southern Illinois were positively correlated with mating success.

In Wisconsin, Massasaugas hibernate for ca. six months. They enter hibernacula by mid- to late October when mean surface water temperature exceeds mean air temperature (McCumber and Hay 2003, King et al. 2004). In autumn, individuals move between openly basking under warm conditions and remaining submerged when temperatures drop. As an example, on warm October days, King et al. (2004) noted the midday emergence of Massasaugas from the hibernacula they selected. These snakes quickly became tannin-stained (brown) from the subsurface water and continued this behavior until temperatures dropped enough to trigger hibernation. During October floods, radio-tracked Massasaugas in Wisconsin were observed thermoregulating while submerged at their hibernation sites. They remained coiled in areas of shallow water with high light penetration and surfaced occasionally to breathe (McCumber and Hay 2003). This behavior has also been noted in Canada (Kent Prior, Canada Ministry of Natural Resources, personal communication). The latest observation of active Massasaugas in Wisconsin was 1 November (King 1999). Maple and Orr (1968) reported that mean body temperature of overwintering snakes monitored in Ohio was 2.6°C (36.7°F).

PREY AND PREDATORS

The diet of Massasaugas has received extensive attention. Past reports indicate this species is an opportunistic, generalist feeder and is able to adapt to whatever appropriately sized prey items are available (reviewed by Ernst and Ernst 2011). Examples of prey include insects, crayfish, frogs, toads, birds, mammals, snakes, and lizards (Holycross and Mackessy 2002). They are also reported to occasionally consume carrion (reviewed by DeVault and Krochmal 2002). The Massasauga's venom is highly toxic to small mammals (Gibbs and Mackessy 2009), which consequently make up the majority of adult diet regardless of geographic location. Among small mammals, shrews (*Sorex* and *Blarina* spp.) appear to be an important food item (Hallock 1991, Shepard et al. 2004, Weatherhead et al. 2009). Furthermore, Keenlyne and Beer (1973a) collected and euthanized 323 Massasaugas from a population in Buffalo County in 1967 to analyze their stomach contents. They found that Meadow Voles (*Microtus pennsylvanicus*) constituted more than 85% of all prey items. All other prey species individually represented less than 5% of the total food items collected and included White-footed Mice (*Peromyscus leucopus*), Meadow Jumping Mice (*Zapus hudsonius*), a Masked Shrew (*Sorex cinereus*), gartersnakes (*Thamnophis* spp.), and one fledgling Red-winged Blackbird (*Agelaius phoeniceus*). Shepard et al. (2004) found that wild neonates consumed mostly Southern Short-tailed Shrews (*Blarina carolinensis*), but neonates in laboratory feeding trials preferred snakes, which indicates that both may be important prey types. Neonates in some regions will also wave their bright yellow tail to lure anuran prey, although there is apparently geographic variation in the likelihood that such behavior is employed (reviewed by Shepard et al. 2004). Massasaugas are generally ambush hunters that lie in wait for unsuspecting prey. After potential prey is detected through a combination of olfaction, thermal reception, and vibrations, it is struck and injected with venom (Bakken and Krochmal 2007, Friedel et al. 2008). Although the envenomated prey often leaves the vicinity, the snake follows via olfaction and consumes it.

Predation is an apparently important source of mortality in Massasauga populations (Szymanski 1998, King et al. 2004, Durbian et al. 2008, Baker et al. 2016). Numerous confirmed and suspected predators are reported from Wisconsin (McCumber and Hay 2002, King et al. 2004, Durbian et al. 2008), Michigan (Bailey et al. 2011), Illinois (Anton 1993, Baker et al. 2016), and Pennsylvania (Jellen and Kowalski 2007). In some cases, specific species are identified, such as American Mink (*Mustela vison*; McCumber and Hay 2002) and Coyotes (*Canis latrans*; Harvey et al. 2013). Yet reports of predators are often more general, including "owl" (Durbian et al. 2008), "bird" (Moore and Gillingham 2006), and "mammal"

(Moore and Gillingham 2006, Bailey et al. 2011). Although not Massasauga predators, humans are also a leading cause of mortality both directly and indirectly (e.g., Keenlyne 1968, Dreslik 2005; see Conservation section).

Massasaugas typically rely on their cryptic coloration to avoid threats (Robillard and Johnson 2015) and are generally considered mild-mannered (reviewed by Keenlyne 1968). Avoidance tactics often involve either crypsis or flight (Harvey and Weatherhead 2006a). Massasaugas can also warn potential threats of their presence by producing a rattling sound with their specialized tail scales. Yet Keenlyne (1968), who collected hundreds of Massasaugas in Buffalo County, noted that only two individuals he encountered rattled before they were visually detected. Similarly, <40% of Massasaugas monitored in Ontario rattled in response to human disturbance, but snakes with higher body temperatures were more likely to rattle (Prior and Weatherhead 1994). Massasaugas that feel especially threatened could bite and possibly envenomate perceived threats. Yet some studies suggest that this strategy is rarely employed. Prior and Weatherhead (1994) observed that Massasaugas never struck during 174 trials during which researchers approached snakes to within 0.5 m (1.6 ft). Due to their small size, Massasaugas administer a smaller volume of venom compared to larger rattlesnake species and confirmed incidences of Massasaugas envenomating people are rare (see Snakebite Envenomation in Wisconsin and the Northern Upper Mississippi River Valley chapter).

CONSERVATION

Status: Globally, the Massasauga (including the Eastern, Western, and Desert subspecies) is listed as a Least Concern species by the IUCN. However, this ranking could change if the subspecies are elevated to separate species (see Systematics section). In the US, the Eastern Massasauga was listed as Threatened under the Endangered Species Act in 2016 (*Federal Register* 31, no. 190). Wisconsin listed the Massasauga as a State Endangered species in 1975 and considers it a Species of Greatest Conservation Need (WDNR 2005b).

Populations: Rigorous estimates of population sizes from Wisconsin do not exist (Faust et al. 2011). Annual abundance estimates from 1999 to 2010 in Carlyle Lake, Illinois, varied across years ranging from 18 to 70 individuals, depending on the estimator used (Dreslik et al. 2016b). Population estimates for Beausoleil Island in southeastern Georgian Bay, Canada, ranged from 35 to 77 individuals from 1993 to 2007 (Jones et al. 2017). Johnson et al. (2016a) estimated that the number of gravid females in Cicero, New York, ranged from 9 to 46 individuals from 2006 to 2014. Using the year with the largest estimated number of gravid females and assuming a 1:1 ratio of gravid to nongravid females and a 1M:1F sex ratio, Johnson et al. (2016a) suggested a maximum population size of 164 individuals for their Cicero Swamp Wildlife Management Area study site.

Using conditional likelihood and full likelihood closed population models, Bradke et al. (2013, 2015) estimated adult density for a population in Barry County, Michigan. Density was calculated using the upper and lower 95% CIs of their abundance estimate divided by the total area surveyed (ca. 19.9 ha [49.2 ac]). This resulted in adult female density estimates of 1.4–3.5 snakes/ha (0.57–1.42 snakes/ac) in 2013 and adult male and female density estimates of 1.8–4.5 and 2.5–3.2 snakes/ha (0.73–1.82 and 1.01–1.30 snakes/ac), respectively, in 2015. As this method did not include a boundary strip (i.e., the area just outside of the study area that is periodically occupied), the density estimates may be positively biased. Based on number of captures and confidence interval width, the best estimate for this population was 101 adults (95% CI = 86–143; Bradke et al. 2015).

Local extinction risk has been evaluated multiple times through simulations and population viability analyses (Seigel and Sheil 1999, Brennan and Tischendorf 2004, Middleton and Chu 2004, Bissell 2006, Bailey 2010). Several of these reports found that populations may be particularly sensitive to juvenile mortality (Brennan and Tischendorf 2004, Baily 2010). Bailey et al. (2011) estimated an adult (8 males and 19 females) active season survival rate of 0.9472 (95% CI = 0.8518–1.0000) in Michigan. In the most complete Massasauga survival analysis to date, Jones et al. (2012) characterized range-wide

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geographic patterns of adult survival for 16 locations across the species' range. This study used known fate models for 499 telemetered snakes from 21 radio telemetry datasets. Although unable to detect differences in survival between sexes, Jones et al. (2012) provided evidence that annual adult survival ranged from 0.35 to 0.95 and increased along a southwest to northeast geographic axis. Adult annual survival estimates in Cicero, New York (females = 0.78, 95% CI = 0.67–0.86; Johnson et al. 2016a), and Beausoleil Island, Georgian Bay, Canada (males = 0.74, 95% CI = 0.67–0.80, females = 0.73, 95% CI = 0.64–0.80; Jones et al. 2017), based on capture-recapture methods fall within the range-wide annual survival estimates based on radio telemetry (Jones et al. 2012). Realized population growth rate (λ) estimates are only available for the Beausoleil Island population and suggested the population was stable from 1992 to 2008 (λ = 1.02; Jones et al. 2017).

Threats: The large-scale conversion of landscapes from natural to anthropogenic use throughout Wisconsin has almost certainly taken a toll on Massasaugas (see Past, Present, and Potential Future Landscapes of Wisconsin chapter). As such, many general concerns associated with the conservation of wetlands and adjacent prairies potentially apply to this species (see Introduction to Conservation and Management of Wisconsin's Amphibians and Reptiles chapter). The impacts of habitat alteration and degradation are more subtle than those of outright habitat destruction but nonetheless lead to sizable conservation concerns. For example, the effects of habitat degradation via encroachment of woody vegetation into otherwise open areas can be particularly important, given the Massasauga's association with open habitats. Seigel (1986) suggested that extensive habitat degradation during the 1960s at a site in northern Missouri had drastic effects on the resident Massasauga population, which did not "stabilize" until the late 1980s despite continued protection.

Past research further suggests indirect connections between habitat loss and declining Massasauga populations also exist. For example, Durbian et al. (2008) proposed that Massasauga movement patterns were influenced by habitat fragmentation in Juneau County. The authors indicated the large home range sizes they recorded were related to limited and widely dispersed patches of suitable habitat. They also found evidence that individual snakes traveling large distances could be more prone to mortality. The authors regularly located a radio-tracked male in what are often considered unsuitable habitats, such as "closed canopy forests, pastures, and residential areas," the latter being particularly hazardous due to a higher threat of human interactions. As habitat dwindles, populations could also become more concentrated in small remaining pockets of suitable habitat or be forced to use risky open areas (e.g., grassy road shoulders), which increases their vulnerability to mortality (e.g., predation and vehicle collisions) and collection (Szymanski 1998, Durbian et al. 2008, Shepard et al. 2008b, reviewed by Ernst and Ernst 2011). Durbian et al. (2008) provide an example of this from Monroe County, where gravid females were concentrated on the only available open-canopy upland habitat (a railroad corridor) and the remains of at least four Massasaugas (three neonates and one adult) were found in one owl pellet.

Several studies have noted that road mortality is an important anthropogenic factor affecting Massasauga populations (e.g., Seigel 1986, Shepard et al. 2008b). Baker et al. (2016) even determined that vehicle strikes were the most prominent source of mortality (32% of 155 dead snakes observed) for an Illinois population studied from 2000 to 2011. Along these lines, Durbian et al. (2008) found road-killed individuals at a Juneau County study site and suggested the use of open roadsides was caused by the dominance of closed-canopy forests at this location. On the other hand, Shepard et al. (2008a) found that roads were avoided by Massasaugas in Illinois, a phenomenon that could fragment and disrupt populations.

Natural and anthropogenic-induced changes in hydrology, such as water flow and depth, along rivers in Wisconsin likely have negative impacts on Massasaugas (but see the discussion of the potential benefits of dams that are implemented appropriately below). Many populations in Wisconsin were once associated with wetlands along rivers, such as the Black, Yellow, Chippewa, Fox, Yahara, and Mississippi (Vogt 1981). All of these rivers have been greatly altered by dams, and associated Massasauga populations have probably either been extirpated or experienced substantial declines since the mid-1900s. Such impacts are evidenced by anecdotal observations. For example, in Juneau County radio-tracked individuals were observed swimming during flood events to search for dry ground (R. King, personal observation). Although this did not result in direct mortality (King 1999), snakes are more susceptible to mortality when concentrated in small dry areas, as could be the result of high water. As another anecdotal example, a population in Buffalo County was subjected to unusually high water levels that began prior to emergence from hibernation in spring 2003 and lasted for eight to ten weeks. After the flood subsided, no Massasaugas were found at survey locations on-site where they had been previously observed for several years (E. McCumber and R. Hay, unpublished report). Water-level fluctuations during the winter could be particularly problematic. In theory, a dam closed during the winter will lead to a drop in downstream water levels, which facilitates the penetration of ice into newly exposed damp soils. If snakes overwintering at or below the water table are unable to retreat to below the frost line as water recedes, mortality could occur as a result of exposure to freezing conditions. Although the full effect of this is unknown, the impacts to Massasauga populations could be severe. As an example, winter drawdowns to replace water-control structures were conducted in 1989 at a Wisconsin wildlife management area where Massasaugas had, to that point, been well-documented. Yet post-drawdown surveys yielded no Massasaugas for ca. 27 years (R. Hay, unpublished data, R. King, personal observation, Rori Paloski, WDNR, personal communication).

Lack of genetic variation due to restricted migration between Wisconsin populations could be another cause for concern. Chiucchi and Gibbs (2010) investigated the genetic composition of largely separated populations from Ohio, Pennsylvania, and Ontario and (perhaps predictably) found high genetic similarity among individuals within each population. Yet their results indicate that recent habitat fragmentation was not the primary cause of low intrapopulation genetic variation. Rather, the authors believed that Massasaugas historically existed in smaller isolated populations with limited potential for dispersal. As such, they suggested that high genetic similarity among individuals within populations may naturally occur; therefore, this species has adapted and is resistant to long-term impacts of genetic isolation. Still, the possible effects of inbreeding and low genetic variability within Wisconsin populations are worthy of additional investigation.

The influences of climate change on Massasaugas should also be considered. Climate change could impact snake thermoregulatory opportunities and cause changes in available habitat. Using spatially explicit climate change vulnerability assessment models, Pomara et al. (2014) found that drought, flooding, and other extreme events have increased in frequency and severity over time and are contributing to long-term range contractions and population declines in Massasaugas. Moreover, they provided evidence that these climatic events are good predictors of historic extirpations (Pomara et al. 2014). King and Niiro (2013) modeled the future effects of climate change on this species in the Midwest. Their results indicate that by the year 2080, if climate change continues on its current trajectory, suitable conditions for this species will have shifted away from the locations in Wisconsin where they currently persist. Further research on the potential impacts of climate change and mechanisms to offset them would be useful for proactive conservation of Massasaugas.

There is little doubt that direct human persecution has always been a prominent threat to this species in Wisconsin. Historic accounts suggest that since the mid-1800s, Wisconsin residents have killed thousands of Massasaugas, which has almost certainly contributed to its current rare status in the state (see Natural History Box: The History of Massasauga Persecution and Conservation in Wisconsin). For example, reports from the 1800s indicate that both Milwaukee and Columbia Counties had sizeable Massasauga populations, but due to heavy human persecution these populations are either extirpated or so small that they are no longer viable. Although this species is protected by state and federal law so that direct killing is less common than in the past, even the subtle impacts of human presence are an important consideration. Middleton and Chu (2004) reported that populations could be sensitive to even

NATURAL HISTORY BOX: The History of Massasauga Persecution and Conservation in Wisconsin

Early in Wisconsin's history and even prior to achieving statehood, Massasaugas were apparently plentiful in many locations. Although exact numbers are not known, Schorger (1967–68) reviewed numerous Massasauga reports from the 1800s and early 1900s, which conjure an image of a historically abundant species. For example, an important historical location in Wisconsin was the canoe portage between the Fox and Wisconsin Rivers (present-day city of Portage, Columbia County). This famous portage route had been used by French, British, and American traders for hundreds of years and by Native Americans for millennia. In 1826, on his way to sign the Treaty of Fond du Lac, Thomas McKenney walked the short portage between these rivers and wrote of Massasaugas, "This whole country is full of them; and so constant is the noise of their rattles . . . that the ear is kept half the time deceived by what seems to be the ticking of watches, in a watch-makers window" (McKenney 1827). The anxiety of potentially stepping on a rattlesnake must have made carrying supplies and canoes across this three-mile portage even more difficult! Unfortunately, many past Massasauga tales not only indicate abundance but also reveal the heavy persecution this species endured from early Wisconsin residents. In 1849 hundreds of Massasaugas were reportedly killed per day in the Portage area (Schorger 1967–68). Furthermore, Olin (1930) wrote of this species in Milwaukee during the mid-1830s: "The first day we mowed we killed a quantity of rattlesnakes. I will not say a thousand for fear someone will think it a snake story." These early attitudes and practices, which did not abate for many decades, almost certainly contributed to this species' substantial decline and current rarity in the state.

In the mid-1800s, the Daniel Muir family moved from Scotland to a farm on the Fox River not far from the previously mentioned portage. It was on this farm that Daniel's son, John Muir, developed a connection with the natural world (Muir 1913). This connection later inspired him to advocate for the establishment of the National Park System and Sierra Club and challenge people to reconnect with wild places and the creatures found in them. Muir used rattlesnakes to question contemporary utilitarian views of nature. "Nevertheless, again and again, in season and out of season, the question comes up, 'What are rattlesnakes good for?' As if nothing that does not obviously make for the benefit of man had any right to exist; as if our ways were God's ways. Long ago, an Indian to whom a French traveler put this old question replied that their tails were good for toothache, and their heads for fever. Anyhow, they are all, head and tail, good for themselves, and we need not begrudge them their share of life" (Muir 1901).

Unfortunately, Muir's challenge to utilitarian views of nature made no difference for Massasaugas in his lifetime. In the 1900s, perhaps not too long after the time of Muir's writings, Wisconsin established a bounty for rattlesnakes. The bounty system lasted approximately 70 years and resulted in the mortality of innumerable snakes (see Natural History Box: Historical Anecdotes Describing Human Interactions with Reptiles in Early Wisconsin in the Introduction to Conservation and Management of Wisconsin's Amphibians and Reptiles chapter). The true impact of the bounty on Massasauga populations is unknown for various reasons, which includes poor record-keeping. To make matters more difficult, while some counties maintained detailed rattlesnake bounty records, these generally did not distinguish between bounties paid for Massasaugas or Timber Rattlesnakes. However, we can assume that the bounty's effect on Massasaugas was substantial from records in counties where it was likely the only rattlesnake species present. Numbers from a small area in Juneau County, where Timber Rattlesnakes can effectively be ruled out, indicate that more than 4,000 rattlesnakes were killed in 20 years (R. Theil, WDNR, unpublished data). One can only imagine the sizeable negative influence this level of mortality had on populations of a species with relatively low reproductive output and slow development (see Reproduction and Development section).

Although early research on Massasauga populations in Wisconsin was limited (Keenlyne 1968), the likely impacts of human persecution had already become apparent by the 1920s. At this time, Pope (1926) described the substantial effort required to find these snakes in areas where they were previously common. The prevalent view of Massasaugas as a nuisance species lasted well into the latter half of the 1900s. One need only review Keenlyne's (1968) thesis to find support for this contention. He conducted research on a population from Buffalo County, for which he killed 323 wild individuals during a single active season and 207 neonates born to wild females in captivity. His primary justification for conducting the work was that "more ecological information will be necessary on the life history of the Massasauga if for some reason it is found necessary to eradicate it as a menace to human life or to manage it as a sport animal" (Keenlyne 1968).

Attitudes apparently changed dramatically in the 1970s, when the rattlesnake bounty was discontinued in Wisconsin. The bounty's termination probably reduced the intensity of direct killing by Wisconsin citizens, given that rattlesnake hunters could no longer profit by actively harvesting Massasaugas. Yet Massasauga persecution certainly continued. Many landowners and outdoor recreationists surely killed them during incidental encounters, whether the bounty was active or not. Their preferred habitat was also under heavy pressure from Wisconsin's expanding human population, which required conversion of natural landscapes to suit anthropogenic needs (i.e., agricultural and urban/suburban development). Active conservation initiatives and research focused on the Massasauga in the state would also remain uncommon for years after the bounty ended. Although Richard C. Vogt began his master's degree at UW–Madison in the early 1970s with the intention of studying this species, the high human-related mortality he observed, which he knew would influence sample size, caused him to change his mind (see Some Prominent Figures in Wisconsin Herpetology chapter). In 1975 the WDNR listed Massasaugas as an endangered species in Wisconsin, which afforded it legal protection, although as Vogt (1981) noted, this action may have come "too late." Throughout the 1980s and early 1990s, greater effort was expended on conservation of this species, which was primarily channeled into field surveys to better delineate its current range in Wisconsin. During that time a clear picture came into focus; the species was distressingly rare in former locations once considered strongholds, and it had completely disappeared from several others (Szymanski 1998). It appeared this snake was currently affected by a general lack of preferred early successional habitat (i.e., mesic prairies and other open-canopy habitat within and adjacent to wetlands; see Habitat subsection). Research intensified in the latter half of the 1990s, which included radio telemetry investigations of habitat selection, movement, mortality, and the effectiveness of translocation. Unfortunately, the Massasauga's rarity and the small, isolated nature of its populations in Wisconsin hampered the ability of these projects to achieve large sample sizes, a problem that continues to limit the potential for future research endeavors. Generally, despite current efforts, the future of this species in Wisconsin remains uncertain.

Once so abundant to be considered a pest in Wisconsin, the Massasauga has dwindled to a point that conservationists must make difficult decisions regarding preservation of the species. Despite a long conservation history, limited data exist to construct sound management strategies for Massasaugas in the state, and few options for effective conservation are apparent. At this current point, perhaps more than any other, this species' fate in the state could be the best measure of Wisconsin's ability to conserve a nongame species. As eminent Wisconsin conservationist Aldo Leopold wrote, "The last word in ignorance is the man who says of an animal or plant, 'What good is it?' If the land mechanism as a whole is good, then every part is good, whether we understand it or not. If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering" (Leopold 1972).

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small incidental levels of mortality caused by vehicular strikes along roads or direct killing by humans. Prior and Weatherhead (1994) reported that Massasaugas also do not habituate to repeated disturbance by humans. In fact, past research indicates this species will alter its movement patterns at sites where disturbance from humans is more frequent (e.g., outdoor recreation at nature preserves or parks). Parent and Weatherhead (2000) reported that Massasaugas in areas where human disturbance was common moved less often and for shorter distances. However, they cautioned that accurately assessing how this disturbance ultimately influences Massasauga life history is complicated and difficult to ascertain.

Massasauga populations are susceptible to diseases such as the keratinophilic fungus *Ophidiomyces ophiodiicola*, the cause of snake fungal disease (SFD; Allender et al. 2011, Lorch et al. 2015, 2016; see Introduction to Conservation and Management of Wisconsin's Amphibians and Reptiles chapter). Massasaugas collected in Wisconsin and temporarily used for a repatriation experiment (King et al. 2004) were transferred to the National Mississippi River Museum and Aquarium, where they were later diagnosed with this fungal disease (L. Jackson, National Mississippi River Museum & Aquarium, personal communication). The disease was also detected in Illinois (Allender et al. 2011, 2016a) and Michigan (Tetzlaff et al. 2015, Allender et al. 2016b, Tetzlaff et al. 2017) populations. Lorch et al. (2016) did not detect SFD in Massasaugas from various Wisconsin locations. Yet, later work found SFD was present in Massasaugas biopsied from Buffalo County (Richard Staffen, WDNR, personal communication). It is noteworthy that Jaeger et al. (2014) identified four putative functional major histocompatibility complex (MHC) loci in Massasaugas. As MHC is important in immune response, future research in this area may provide important insights into this pathogen-host interaction. Continued monitoring of Wisconsin populations for outbreaks of this fungal infection should be considered until more transmission and population-level effects data are gathered.

Management: Because Massasaugas are sensitive to population-level perturbations, continued legal protection that guards against rampant persecution will be critical to promote their persistence in Wisconsin. Additionally, Faust et al. (2011) conducted an expert opinion-based range-wide population viability analysis that suggested that most populations are imperiled and would benefit from active management. General habitat management considerations for herpetofauna in wetlands and mesic or wet prairies apply to Massasaugas, as do strategies to offset road mortality (see Introduction to Conservation and Management of Wisconsin's Amphibians and Reptiles chapter). Although specific recommendations

NATURAL HISTORY BOX: Repatriation and Population Augmentation as Possible Tools for Massasauga Conservation

Massasaugas are currently protected in Wisconsin by the State Endangered and Threatened Species Law (Statute 29.604) and were recently listed as federally Threatened under the Endangered Species Act (see Conservation section). The new protection granted may require the implementation of additional conservation tactics in Wisconsin. For example, as part of a recovery plan it could be necessary to attempt strategies that involve repatriation or augmentation of existing populations. This could even require that remaining populations be brought into captivity to preserve the species and potentially protect unique genes present in populations across its range. As was the case with other federally protected species, including Red Wolves (*Canis rufus*; USFWS 1989) and California Condors (*Gymnogyps californianus*; USFWS 1996), at some point, removing all remaining wild Massasaugas from Wisconsin might represent the best option to achieve safeguards against extinction. In this hypothetical scenario, wild individuals would be placed into facilities and used for captive breeding, with the goal of bolstering numbers for future establishment or augmentation of populations through repatriation or reintroduction. This very difficult conservation decision is typically made only if three criteria are met: (1) if nothing is done all remaining wild individuals will be lost anyway; (2) placing individuals in captivity will preserve their genetics; and (3) captive-bred individuals can effectively be used to restore populations once conditions are met that allow reintroduction.

There are currently no Massasaugas from Wisconsin in captive populations. However, zoos accredited through the Association of Zoos and Aquariums (AZA) have already enacted captive breeding strategies to promote a stable demographic structure (i.e., stable ratios of males to females and juveniles to adults), and strong genetic diversity in zoo populations to ensure captive breeding can continue in perpetuity. Genetic analyses indicate that 17 unique haplotypes exist among captive Massasaugas (Ray et al. 2013). A consortium of facilities within the AZA called the Eastern Massasauga Rattlesnake Species Survival Plan (EMR SSP; Lentini and Earnhardt 2013) are coordinating the captive breeding program, as well as ongoing in-situ research in southwestern Michigan.

The use of wild-born or captive-born individuals to repatriate formerly occupied or restored habitat remains a controversial issue (Burke 1991, Reinert 1991, Germano and Bishop 2009). Part of the reason reptile reintroductions or repatriations remain contentious is that they are widely viewed as ineffective (Dodd and Seigel 1991), are poorly studied (King and Stanford 2006), and often lack enough released individuals to be successful (Germano and Bishop 2009). King et al. (2004) conducted a Massasauga repatriation experiment in Juneau County in 1999 and 2000. This experiment involved headstarting neonates in captivity for one or two years and briefly releasing them at a location where Massasaugas no longer occurred in the state. This project made no attempt to establish a population but instead was focused on assessing if repatriated Massasaugas could find food, avoid predators, and survive a single hibernation period. King et al. (2004) radio-tracked repatriated individuals and found they had smaller home ranges than wild (never captive) Massasaugas (Durbian et al. 2008), and while the mortality rate among one-year-old individuals was very high, most two-year-old snakes survived during the observation period (including hibernation).

Studying repatriated, headstarted Massasaugas in Michigan, Bieser (2008) found very similar results to King et al. (2004) in regard to lower movement rates and high mortality rates of repatriated snakes compared to resident wild individuals. Bieser (2008) also found that older repatriated Massasaugas fared much better than younger individuals. The results of King et al. (2004) and Bieser (2008) support repatriation to augment populations as a potentially useful conservation tool. However, establishing new populations would likely require sustained efforts over many years, including numerous translocations and intense monitoring. Unfortunately, such projects necessitate substantial resources and often come with an unclear likelihood of success. Yet debate regarding repatriation as a viable conservation tool in Wisconsin matters little at this point because the factors that led to the extirpation or decline of the state's populations have not been reversed. Therefore, without additional habitat restoration and management, augmentation of existing populations or attempts to repatriate formerly occupied locations are likely not prudent conservation measures at this time.

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for habitat management strategies exist, these are often based on limited research or anecdotal observations. Therefore, additional rigorous work is warranted to determine the best management practices for Massasaugas, particularly as it pertains to habitat. It is noteworthy that Durbian et al. (2008) reviewed past studies and warned researchers against the use of populations at small study sites to model space and habitat requirements for management. Yet strategies that create and maintain open-canopy habitat by removal of woody vegetation are likely beneficial to Massasaugas (see suggestions by Seigel and Pilgrim 2002, Dreslik 2005, Moore and Gillingham 2006).

Radio telemetry research on Wisconsin populations in Juneau and Buffalo Counties (McCumber and Hay 2002, 2003, King et al. 2004, Durbian et al. 2008) and capture-recapture research on a population in La Crosse and Trempealeau Counties (R. Hay, unpublished report) illustrate the importance of habitat management that appropriately juxtaposes suitable hibernacula and adjacent open-canopy habitat. At these locations, suitable open-canopy habitat is often separated from hibernacula by unsuitable or degraded habitat. Individuals are, therefore, forced to emerge from hibernation and travel through unsuitable habitat in search of open-canopy areas to thermoregulate (King 1999, Durbian et al. 2008). A hypothetically beneficial scenario includes a landscape with open-canopy summer habitat and overwintering locations that are connected by a contiguous swath of suitable open habitat, which can be achieved through active management. Using a robust Missouri population as a model, Durbian et al. (2008) suggested that maintenance of easy travel corridors to hibernacula (less than 400 m [1,312 ft] long) was desirable. They further determined that if habitat restoration is the goal, then a minimum of 100 ha (247 ac) of suitable habitat should be the target for natural resource managers who hope to sustain Massasauga populations.

Despite this, research on how various management strategies affect Massasaugas is limited. Johnson and Leopold (1998) found some evidence that Massasaugas in New York preferred areas where woody vegetation was removed, indicating that this management strategy could be effective (although a small sample size makes their results somewhat inconclusive). Johnson et al. (2016b) found that gravid females in New York preferred gestation sites where brushy vegetation was mechanically shortened. They found that basking was less frequent on shrubs that approached 0.5 m (1.6 ft) in height and recommended they be kept at ≤0.25 m (0.8 ft) tall.

Poorly timed application of prescribed fire or mowing operations to manage vegetation results in Massasauga mortality (Seigel 1986, Durbian 2006, Cross et al. 2015). Several published studies recommend that land managers consider restriction of habitat

NATURAL HISTORY BOX: Massasauga Conservation in Wisconsin through Public Outreach

Public outreach is an important tactic that can be employed to promote conservation initiatives for Massasaugas. It is more difficult to endear this venomous snake species to the average member of the public than is the case for charismatic endothermic organisms. Therefore, outreach initiatives must occur across a broad array of professional institutions and take many forms to be impactful. The Milwaukee County Zoo conducts outreach efforts designed to expand public understanding and appreciation of this very rare snake in an effort to promote its conservation value to Wisconsin's populace. These outreach endeavors include training docents to interact with zoo guests near snake exhibits and educate them, as well as encourage a respectful and positive attitude toward the species. Zoo staff members even don a Massasauga mascot costume during special events to engage the public of all ages and showcase the importance of these animals in the ecosystem (Figure 304).

Through the Partners for Fish and Wildlife Program, US Fish and Wildlife Service staff contacted private landowners with Massasauga populations to offer technical assistance and financial support for habitat management/restoration that would benefit this species (Pultz 2001). Wisconsin (via the WDNR) was one of only two states to develop a Candidate Conservations Agreement with the USFWS for Massasaugas. The goal of this agreement is to manage and restore sufficient habitat to maximize the potential for maintenance and protection of a population in western Wisconsin. With these conservation measures in place, this particular Massasauga population represents Wisconsin's best chance to maintain this rare snake. Research conducted by natural resource regulators at the state and federal levels, as well as by academics, has helped shape these strategies.

Figure 304. Milwaukee County Zoo staff interact with visitors to promote positive attitudes toward Massasaugas (Milwaukee County; photo by C. Berg).

Despite all of the outreach and conservation efforts noted in this account, Massasaugas have all but disappeared from Wisconsin. Only seven extant populations may remain within the state. Among them, six will likely disappear, if they are not already extirpated. The remaining population is not secure despite measures in place to protect it. This population, Wisconsin's most robust, appears to have a 15% chance of disappearing in 25 years (Faust et al. 2011).

Richard S. King, Robert W. Hay, Turtles for Tomorrow, Billie C. Harrison, Milwaukee Public Museum, and Craig S. Berg, Milwaukee County Zoo (retired) management with prescribed fire or heavy equipment to periods when snakes hibernate (Johnson et al. 2000, Baker et al. 2016). Based on observations in Missouri, Seigel (1986) indicated that Massasaugas were more susceptible to mortality from prescribed burns under warm environmental conditions, when they were likely to be active aboveground. Durbian (2006) also recorded high mortality rates in the summer after completion of mowing regimens to manage habitat in northern Missouri.

Brush piles created as the result of woody vegetation removal are frequently burned on-site by habitat managers as opposed to hauling debris to an ex-situ location. Massasaugas have been observed colonizing brush piles in Trempealeau County (R. King, personal observation). As a result, it is recommended brush piles be left unburned or burned immediately after construction (so that snakes do not have time to occupy them) or during the inactive season (Cross et al. 2015). The removal of brush piles prior to conducting prescribed burns is also recommended (Cross et al. 2015).

Use of dams to regulate water movement should maintain consistent water levels and flow rates in late autumn, winter, and early spring to avoid mortality of overwintering Massasaugas. It is also noteworthy that installation of dams or water control structures to restore wetland habitat might benefit this species, so long as stable water levels are maintained during hibernation. This was the case at Illinois's Carlyle Lake (Shepard et al. 2008b), where dam installation led to flooded fields that were ultimately used by Massasaugas for hibernation. Translocated snakes tracked as part of a repatriation experiment in Juneau County also used impounded areas to successfully hibernate (King et al. 2004). Given the heavy toll road mortality takes on some populations during specific times of year, it may also be wise to periodically close road sections that cause heavy mortality during autumn migration to hibernacula (Seigel 1986, Baker et al. 2016) or create underpass travel corridors for snakes below the roads.

Despite the conservation concerns and population declines noted previously, Wisconsin has been a leader in Massasauga conservation through implementation of various research projects and outreach endeavors over the last two decades. These include studies focused on the habitat use and ecology of the few remaining populations (e.g., King 1999, McCumber and Hay 2002, 2003, Durbian et al. 2008), as well as research on the viability of conservation strategies such as captive breeding and repatriation (Natural History Box: Repatriation and Population Augmentation as Possible Tools for Massasauga Conservation). Furthermore, a critical component for garnering support of effective conservation and management could be landowner and public outreach efforts, which are also ongoing in Wisconsin (Natural History Box: Massasauga Conservation in Wisconsin through Public Outreach).