Butler's Gartersnake

Thamnophis butleri (Cope 1889)

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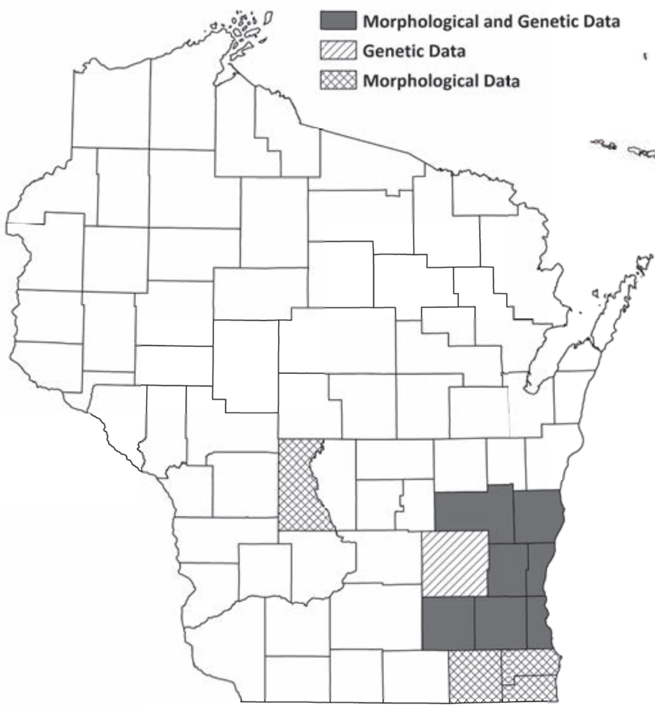

Adult female Butler's Gartersnake (Waukesha County; photo by J. Kapfer).

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AT A GLANCE

Butler's Gartersnakes are the smallest of five gartersnakes that occur in Wisconsin. They are largely restricted to the southeastern part of the state and are often found in open moist habitats such as prairies, wet meadows, wetlands, old fields, and vacant lots. This species is stout with a small narrow head and almost no discernible neck. The characteristic most often used to distinguish Butler's Gartersnakes from sympatric gartersnake species is the position of the lateral stripes. Anteriorly, the lateral stripes cover the third dorsal scale row and typically a portion of scale rows two and four. Butler's Gartersnakes are potentially active from late March to the beginning of November in Wisconsin, and reproduction probably occurs soon after egress from hibernation. Females do not lay eggs but instead give birth to live young from July to early September. This snake feeds primarily on earthworms. However, before European settlers introduced earthworms in the mid-1800s, the snake was likely restricted to habitats supporting leeches. A variety of animals probably prey on Butler's Gartersnakes, including crayfish, snakes, birds, shrews, and other small to midsized carnivorous mammals, ranging from weasels to Red Foxes. When threatened, Butler's Gartersnakes are more prone to flee than strike. This species is closely related to the Plains Gartersnake, and the two species are known to hybridize at some sites where they co-occur in southeastern Wisconsin. Butler's Gartersnake is considered a species of Special Concern and a Species of Greatest Conservation Need by the WDNR.

SYSTEMATICS

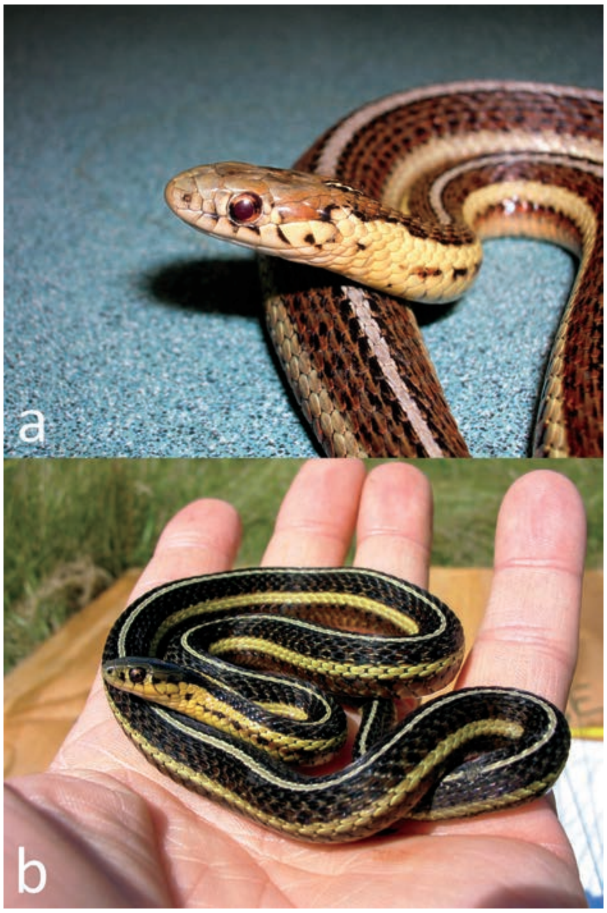
Thamnophis butleri (Butler's Gartersnake) is closely related to *T. radix* (Plains Gartersnake) and *T. brachystoma* (Short-headed Gartersnake). Morphological and molecular evidence supports *T. butleri* and *T. radix* as sister species that diverged from *T. brachystoma* (de Queiroz and Lawson 1994, Alfaro and Arnold 2001, de Queiroz et al. 2002, Pyron et al. 2013, McVay et al. 2015). Rossman et al. (1996) hypothesized that *T. butleri* is a reduced derivative of *T. radix*.

According to mitochondrial DNA sequence and amplified fragment length polymorphism data (Burghardt et al. 2006, Placyk et al. 2012), Wisconsin *Thamnophis butleri* populations are genetically distinct from those in Ohio, Michigan, and Ontario. Genetic analyses also support hybridization between *T. butleri* and *T. radix* along the Wisconsin southern range limit (Burghardt et al. 2006, Fitzpatrick et al. 2008, Placyk et al. 2012). Fitzpatrick et al. (2008) demonstrated that the two species have maintained distinctive species-specific characteristics in Wisconsin despite hybridization. Placyk et al. (2012) suggested that this hybrid zone predates European settlement and is not a consequence of anthropogenic factors (e.g., habitat modification). In Wisconsin, *T. butleri* may also hybridize with *T. sirtalis* (Common Gartersnake), but this phenomenon appears to be rare (see Distribution in Wisconsin subsection; Kapfer et al. 2013a).

DESCRIPTION

Adults: This species is stout with a small narrow head and almost no discernible neck (Figure 267). It has keeled scales with a black, brown, reddish-brown, or olive dorsum and three stripes varying from pale yellow to orange (Figure 268). The stripes run longitudinally, one along the dorsal midline and one on either side of the body. The lateral stripes cover the third scale row, bleeding onto scale rows two and four (Figure 269). Occasionally, a checkerboard pattern

Figure 267. Adult Butler's Gartersnake. Note the small head in comparison to the body (Ozaukee County; photo by E. Hileman).



Above, top: Figure 268. Color variation among Butler's Gartersnakes in Ozaukee County, Wisconsin. (a) Adult (Ozaukee County; photo by G. Mayer). (b) Adult (Ozaukee County; photo by E. Hileman).

Above, bottom: Figure 269. Anterior body pattern typical of Butler's Gartersnake. Note the placement of the lateral stripe and only thin dark bars on few supralabial scales, which are important characteristics used in recognizing this species (Ozaukee County; photo by E. Hileman).

Figure 270. Butler's Gartersnake littermates less than one week old. Note similarities of pattern and coloration to adults (Waukesha County; photo by R. Paloski).

of alternating spots is visible between the stripes on either side of the body. The yellow labial scales may be finely speckled with brown or orange, with occasional thin short bars on the back edge of some posterior labial scales, and there are usually two small yellow markings on the parietal scales. The venter varies from grayish yellow to pale green and commonly has black spots present along the outer edges; occasionally some medial spotting is also present. The Butler's Gartersnake is the smallest of five gartersnakes (*Thamnophis* spp.) that occur in Wisconsin (Vogt 1981). In a study of three Wisconsin populations, one in Ozaukee County and two in Waukesha County, females were typically longer ($\bar{x}$ SVL = 39.9 cm [15.7 in], $n = 605$) than males ($\bar{x}$ SVL = 35.2 cm [13.9 in], $n = 193$; Eric Hileman, Northern Illinois University, personal data). Females (nongravid) were also heavier ($\bar{x} = 38.7$ g [1.4 oz], $n = 206$) than males ($\bar{x} = 24.0$ g [0.8 oz], $n = 192$; E. Hileman, unpublished data). See Rossman et al. (1996) for an exhaustive species description.

Preadult stages: Neonates and juveniles look similar to adults (Figure 270). Neonates born to 11 females captured in Milwaukee County averaged 12.1 cm SVL (4.8 in) and 1.2 g (0.04 oz, $n = 112$; Albright 2001). However, some females were maintained in the lab prior to pregnancy, potentially affecting maternal

Figure 271. Albino female neonate Butler's Gartersnake (15.0 cm SVL [5.9 in]) found underneath a plywood board on 13 September 2009 (Waukesha County; photo by E. Hileman).

and offspring body condition. Additionally, some of the individuals in the study may have been hybrids, as they were captured in southern Milwaukee (Albright 2001) near a known area of hybridization (Fitzpatrick et al. 2008, Placyk et al. 2012). In southeastern Michigan, mean neonate sizes for 28 litters ranged from 10.1 to 12.5 cm SVL (4.0 to 4.9 in) and 0.9 to 1.7 g (0.03 to 0.06 oz; Ford and Killebrew 1983). In Ohio, 22 neonates born to 3 females ranged from 12.7 to 18.1 cm TL (5.0 to 7.1 in; Conant 1938). In Ozaukee and Waukesha Counties, young of the year measured 10.4–23.3 cm SVL (4.1–9.2 in) and 0.8–8.0 g (0.03–0.3 oz, $n = 1{,}489$; E. Hileman, unpublished data). Juveniles from these counties measured 14.0–40.7 cm SVL (5.5–16.0 in, $n = 861$) and 2.0–42.0 g (0.07–1.5 oz, $n = 862$; E. Hileman, unpublished data).

Variation: Albinism is rare but was observed in one individual collected from Milwaukee County on 11 October 1938 (Dyrkacz 1981) and in one neonate captured on 13 September 2009 in Waukesha County (E. Hileman and Julia Robson, Milwaukee County Parks, unpublished data; Figure 271). Melanistic individuals were found in Amherstburg, Ontario (Catling and Freedman 1977), but have not been reported elsewhere. In Wisconsin, males of all age classes have a greater tail-to-body-length ratio ($\bar{x} = 23.3\%$, $n = 165$) than females ($\bar{x} = 21.2\%$, $n = 221$; E. Hileman, personal data). However, adult males tend to be more slender and shorter than adult females (E. Hileman, personal observation).

Diagnosis: Butler's Gartersnakes possess keeled scales that occur in 19 or fewer scale rows at midbody, an undivided anal plate, and divided subcaudal scales. There are 2 prefrontal scales, while each side of the head contains 1 loreal scale, 1 preocular scale, 2–3 postocular scales, 7 (sometimes 6–8) supralabials, and 8–9 infralabials. There are 129–154 ventral scales that possess no obvious pattern. The lateral stripe either partially or fully covers scale rows two, three, and four. Butler's Gartersnakes are similar in appearance to other gartersnake species, and the characteristic generally used to separate them is the scale row position of the lateral stripe. In Butler's Gartersnakes, lateral stripes typically cover part of scale row two, all of three, and part of four. The Common Gartersnake's lateral stripes typically cover part (or all) of scale row one and all of scale rows two and three. The Plains Gartersnake's lateral stripes are usually narrow and cover only scale row three and some proportion of row four. Plains Gartersnakes also typically have thicker bars along the posterior edge of the labial scales than Butler's Gartersnakes. The Eastern Ribbonsnake (*Thamnophis saurita*) and Western Ribbonsnake (*T. proximus*) are much more slender, with white labial scales and white preocular scales, and their lateral stripes include only scale rows three and four. The head of Butler's Gartersnake also appears superficially shorter and narrower (i.e., similar in width to the neck) than the head of other gartersnake species in Wisconsin. Unfortunately, distinguishing Butler's Gartersnakes from Plains Gartersnakes is extremely difficult in areas of geographic overlap and possible hybridization. In these regions, the use of typical characteristics could be unreliable for rapid field identification.

DISTRIBUTION AND HABITAT

Global distribution: Butler's Gartersnakes have a small global geographic distribution and are found only in the Great Lakes region of the US and southern Canada. This species ranges from central Indiana to central Ohio, northward through eastern Michigan and the southernmost edge of Ontario, with isolated populations in central southern Ontario and southeastern Wisconsin (Rossman et al. 1996).

Distribution in Wisconsin: The distribution of Butler's Gartersnakes in Wisconsin is difficult to delineate because they hybridize with other gartersnake species (*Thamnophis* spp.; see Systematics section). Recognized counties of occurrence for this snake have changed over time based on the results of genetic and morphological investigations. Vogt (1981) used morphology to report Butler's Gartersnakes from Fond du Lac, Washington, Waukesha, Milwaukee, Walworth, Racine, and Kenosha Counties. Casper (1996) also reported Butler's Gartersnakes in Ozaukee County based on morphological assessments but questioned records from Fond du Lac, Washington, Walworth, Racine, and Kenosha Counties. Later mitochondrial DNA analyses by Burghardt et al. (2006) supported the occurrence of Butler's Gartersnakes in Fond du Lac, Washington, and Ozaukee Counties while also identifying this species in Sheboygan County. Their analyses further illustrated a lack of concordance between morphology and genetics in snakes sampled from Racine and Kenosha Counties, providing evidence that hybridization with the Plains Gartersnake may be common in that area. Kapfer et al. (2013a) provided genetic and morphological evidence to support the presence of Butler's Gartersnakes in Jefferson County. Recent analysis of nuclear DNA also identified genetic markers of Butler's Gartersnakes in a population of snakes from Dodge County; however, all individuals examined in this population had morphological characteristics suggestive of Plains Gartersnakes (Sloss 2011; Rori Paloski, WDNR, personal communication). In total, genetic analyses have revealed suspected hybrid Butler's × Plains Gartersnakes, or lack of concordance between morphological and genetic data from snakes sampled, in Dodge, Dane, Jefferson, Waukesha, Milwaukee, Walworth, Racine, and Kenosha Counties (Burghardt et al. 2006, Sloss 2011, Placyk et al. 2012, Paloski et al. 2017; R. Paloski, unpublished data). Putative Butler's × Common Gartersnakes have been identified through analysis of nuclear DNA from snakes in Dane, Dodge, Washington, Ozaukee, Waukesha, and Milwaukee Counties (R. Paloski, unpublished data see Common Gartersnake, *Thamnophis sirtalis* species account).

Numerous studies and reports have contributed to the understanding of this species' distribution in Wisconsin (Vogt 1981, Casper 1996, Burghardt et al. 2006, Casper 2008d, Fitzpatrick et al. 2008, Sloss 2011, Placyk et al. 2012, Kapfer et al. 2013c, WDNR 2014b, also R. Paloski, personal communication). However, there is apparent discordance between the morphological traits and genetic markers proposed to differentiate Butler's Gartersnakes and Plains Gartersnakes, with no standardized criteria for distinguishing them when encountered in areas of range overlap. As such, the creation of a definitive county-level range map for Wisconsin is challenging. County records supported by both morphological and genetic data (i.e., counties from which assessed specimens had both morphological characteristics and genetic markers consistent with Butler's Gartersnake) include Fond du Lac, Sheboygan, Washington, Ozaukee, Jefferson, Waukesha, and Milwaukee (shaded black on the range map). Reports from Dodge County are based on genetic data only (i.e., snakes sampled in that population were morphologically consistent with Plains Gartersnakes despite having genetic markers indicative of Butler's Gartersnakes; shaded with black diagonal bars). Several counties have produced records or specimens not corroborated via genetic or morphological analyses, although some specimens are morphologically suggestive of Butler's Gartersnakes, including Juneau, Walworth, Racine, and Kenosha (shaded with crosshatching; Vogt 1981, Casper 1996; Natural History Box: Unusual Butler's Gartersnake Records in Wisconsin: A Historical Perspective).‡ It is noteworthy that both 'pure' Butler's Gartersnakes and putative hybrid Butler's × Plains Gartersnakes have been reported in Dodge, Jefferson, Waukesha, and Milwaukee Counties based on genetic analyses (Fitzpatrick et al.

‡ Note that Dodge and Sheboygan County records have not been published or have been published only in technical government reports (e.g., Burghardt et al. 2006, Casper 2008d, Sloss 2011). It is also noteworthy that not all reported voucher specimens for published county records have been confirmed through genetic analysis (see the Appendix).

NATURAL HISTORY BOX: Unusual Butler's Gartersnake Records in Wisconsin: A Historical Perspective

Recent genetic and morphological studies have not addressed Butler's Gartersnake specimens collected from Juneau County in the 1960s (e.g., UWSP 546, MPM 11791). Casper (1996) suggested that these were part of an "introduced" population. However, the collector of the Juneau County specimens believed the associated population was native, and aside from its disjunct position relative to the known range in Wisconsin, no evidence to support introduction was known (Tom Johnson, Missouri Department of Conservation [retired], personal communication). Regardless, additional work is necessary to both reconfirm the presence of this Juneau County population and determine its genetic relationship to populations in southeastern Wisconsin. If nontranslocated populations are documented in Juneau County, then Butler's Gartersnakes could further occur in adjacent counties (e.g., Adams, Marquette, Green Lake, Columbia).

This species was also reported in Dane County by Threlfall et al. (1973), but the record is suspect because no corroborating specimens or additional observations are known. Still, recent genetic analyses of closely related Plains Gartersnakes from Dane County found evidence of Butler's Gartersnake genetic markers (Rori Paloski, WDNR, personal communication). These findings could support the proposition that the distribution of Butler's Gartersnakes in Wisconsin was historically larger but that perhaps past populations in peripheral locations were genetically overwhelmed through hybridization with the Plains Gartersnake. This could also explain the presence of putative hybrid and pure Butler's Gartersnakes identified in Dodge County and the old specimens collected from Juneau County.

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2008, R. Paloski, personal communication). Further work is necessary to clarify this species' distribution in Wisconsin.

Localities of possible occurrence: Reports of disjunct populations in Wisconsin may support that this species' state distribution was once broader, encompassing more counties than are currently known (Natural History Box: Unusual Butler's Gartersnake Records in Wisconsin: A Historical Perspective). Kapfer et al. (2013a) postulated that 'pure' Butler's Gartersnakes could occur in areas of Walworth County based on the presence of genetically and morphologically confirmed individuals found ca. 1 km (0.62 mi) north of the county border into Jefferson County. This is consistent with reports of the species from Walworth County by Vogt (1981). Furthermore, Butler's Gartersnakes could occur in Calumet and Manitowoc Counties, given the proximity of known populations in Sheboygan County. 'Pure' Butler's Gartersnakes may also be present in some populations from Racine and Kenosha Counties. Confirmation of additional county records would require a combination of morphological and genetic analyses due to the potential for hybridization in Wisconsin.

Habitat: In Wisconsin, Butler's Gartersnakes can be found in mesic to wet prairies, sedge meadows, open wetlands, old fields, and vacant lots (Vogt 1981, Hileman 2010; see Amphibians and Reptiles in Wisconsin Plant Communities chapter). Open upland habitat adjacent to wetlands is particularly important for this species during the active season (Joppa and Temple 2005). For example, at three study sites in Wisconsin, Butler's Gartersnake captures were highest in open grassy upland areas near wetlands when compared to other upland and wetland habitat types (Kapfer et al. 2013b). Similarly, in southwestern Ontario, these snakes were most common in dry upland habitat (Catling and Freedman 1980b). Wetlands provide foraging and overwintering locations, and those dominated by native sedges (e.g., *Carex* spp.) are used more heavily than those with large stands of cattail (e.g., *Typha* spp.) or invasive species (Kapfer et al. 2013a). Closed canopy and shrubby habitats appear to be avoided in Wisconsin (Kapfer et al. 2013b, E. Hileman, personal observation) and Michigan, which suggests that wooded habitats could serve as a dispersal barrier (Carpenter 1952a). This species is frequently found beneath debris such as old logs, bark, or even discarded anthropogenic structures of wood or metal (E. Hileman, personal observation). Because its distribution includes several counties with extensive developed lands in southeastern Wisconsin, Butler's Gartersnakes are sometimes found in green space or undeveloped plots in disturbed landscapes (see Conservation section). For example, Rossman et al. (1996) collected this species "in old house foundations near urban areas" in Wisconsin, while Shonfield et al. (2019) frequently found radio-tracked snakes from Ontario in semi-open to open human-altered habitats.

Butler's Gartersnakes overwinter in a variety of hibernacula. Shonfield et al. (2019) followed four snakes to winter hibernacula and found two in crayfish burrows, one below a wood pile, and another along a "creek drain." In Wisconsin, they are more abundant at sites with crayfish burrows (Sarah Orlofske, UW–Stevens Point, personal communication) and may use crayfish burrows for overwintering and shelter during the active season (Joppa and Temple 2005, WDNR 2014b). Rossman et al. (1996) recounted collecting them "on 5 April 1955 in an old dump near Waukesha, Wisconsin. Most of the snakes were taken on the south face of a dirt bluff that appears to be their overwintering site. Others were basking on piles of bricks or matted grass." In Michigan, Butler's Gartersnakes were found communally overwintering in an ant mound (depth 35.6–68.6 cm [14–27 in]; Carpenter 1953). On another occasion, Carpenter (1953) excavated a number of amphibians and reptiles, including one Butler's Gartersnake, hibernating in a probable Meadow Vole (*Microtus pennsylvanicus*) burrow at a depth of 15.2–38.1 cm (6–15 in).

REPRODUCTION AND DEVELOPMENT

Copulation in wild individuals has not been observed in Wisconsin, but a single observation was recorded in Ohio on 4 April 1930 (Conant 1938). Finneran (1949) described an aggregation comprised of several males courting a female in Michigan on 19 April 1948. Other instances of multiple males pursuing a single female have been documented in captivity (Ruthven 1912, Noble 1937), and captive mating has been observed between late March and late April (Pope 1944). The typical breeding period for wild Butler's Gartersnakes is likely consistent with these observations, since other gartersnake species in the northern US and Canada typically mate soon after spring emergence; however, autumn mating also reportedly occurs in some species (reviewed in Rossman et al. 1996).

Males purportedly find females for reproduction via pheromone trails and exhibit preference for trails left by conspecifics over those produced by Common Gartersnakes (Ford 1982b). When given the option between conspecific and Plains Gartersnake female scents, male Butler's Gartersnakes could not differentiate between the two (Ford 1982b). However, individuals included in the latter experiment may have been hybrids, limiting interpretation of the results (Neil Ford, University of Texas–Tyler, personal communication). In courtship prior to copulation, the male climbs atop the female, moving over her in an anterior direction while contacting her dorsum with his chin and tongue. Once his head reaches her neck, he pushes his cloaca under her and produces high-frequency caudocephalic waves before inserting one of his hemipenes into her cloaca (see Noble [1937] for a more detailed account). After ejaculation, the male deposits a copulatory plug, which likely prevents other males from successfully mating with that female until the plug is expelled (Devine 1975). Additionally, Devine (1977) found that females with a copulatory plug were less likely to be pursued by males. Despite these deterrents, Albright (2001) documented multiple paternity in Milwaukee County.

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Among three sites studied in Ozaukee and Waukesha Counties, the proportion of adult females gravid at each site in 2008 and 2009 ranged from 50.4% to 95.6% (E. Hileman, unpublished data). However, these reproductive rates are likely positively biased, as the coverboards used in this study created a favorable gestation environment (E. Hileman, personal observation). Reported reproductive rates from Michigan may be less biased, where visual searches were conducted without coverboards, and 67% of captured females were gravid (Carpenter 1952a). In Waukesha County, 40.0% of individual adult females were gravid consecutively in 2008 and 2009, 55.6% were gravid only one year, and 4.4% were not gravid either year ($n = 45$; E. Hileman, unpublished data), demonstrating that reproduction is not strictly biennial. In contrast, Carpenter (1952a) found that only 7% of Butler's Gartersnakes recaptured over time were gravid for consecutive years at a site in Michigan.

Butler's Gartersnakes are viviparous and have the lowest fecundity among the five gartersnake species that occur in Wisconsin (Carpenter 1952a, Vogt 1981). Albright (2001) reported litter sizes for captive and wild-bred females from Milwaukee County of 5–20 ($\bar{x} = 11.3$, $n = 9$), and Rossman et al. (1996) reported a mean litter size of 11.9 for Wisconsin. However, some individuals sampled in these studies may have been hybrid Butler's × Plains Gartersnakes (Placyk et al. 2012; N. Ford, personal communication). Despite this, similar litter sizes have been documented in Michigan. In Washtenaw County (Michigan), four females produced a mean of 11 offspring (Carpenter 1952a). Additionally, a range of 6–20 ($\bar{x} = 11.4$) offspring were produced by 28 females in southeastern Michigan (Ford and Killebrew 1983). Smaller litters were reported in Ontario, where six females produced 4–11 neonates ($\bar{x} = 8.5$; Freedman and Catling 1978).

In Wisconsin, both female weight and length were positively correlated with number of offspring produced (Albright 2001, Kirby 2005), but individual neonate weight decreased as litter size increased (Albright 2001). The findings of Albright (2001) and Kirby (2005) corresponded with those of Ford and Killebrew (1983; southeastern Michigan), who also noted this negative relationship and demonstrated that longer females have more offspring and heavier litters. Additionally, Ford and Killebrew (1983) provided evidence that relative clutch mass, as quantified by total litter mass / female mass, does not vary with female size. However, relative clutch mass per offspring decreases as female size increases. Thus, as adult female size increases, the influence of litter size on neonate mass decreases (Ford and Killebrew 1983). Vogt (1981) suggested that parturition occurs from 2 July through 18 September. Of three populations studied in Wisconsin, the earliest dates of neonate observation ranged from 18 July to 12 August (E. Hileman, unpublished data).

In Michigan, Carpenter (1952b) observed that growth rates slow with age and that male growth declined more rapidly than female growth. Due to this decrease in growth rates and variation in individual growth, young of the year and juveniles are easier to age than adults (Carpenter 1952b). In Wisconsin, females generally obtain adult size after the breeding period of their second active season (E. Hileman, unpublished data). Therefore, the earliest mating opportunity is likely in their third growing season (i.e., second spring). Carpenter (1952b) found a sexually mature male and three sexually mature females in Michigan that were comparable in length to snakes in their second spring, but he speculated that many individuals likely remain sexually immature until their third spring. In Wisconsin, the smallest gravid female found in Ozaukee and Waukesha Counties was 30.8 cm SVL (12.0 in; E. Hileman, unpublished data). In comparison, the smallest gravid female found in eastern Michigan was slightly longer (34.5 cm SVL [13.6 in]; Carpenter 1952b). Longevity in the wild has not been reported for this species.

ACTIVITY

Spring emergence is likely triggered after shallow soil temperatures (10 or 30 cm [3.9 or 11.8 in] belowground) exceed deeper soil temperatures (60 or 100 cm [23.6 or 39.4 in] belowground) for several days (Smith 2009, King and Hileman 2012, 2013). In Michigan, Butler's Gartersnakes were observed emerging from overwintering in an ant mound between 27 March and 24 May (Carpenter 1953). Carpenter (1952a) estimated an active season of 215 days in Michigan. Minton (1972) reported that

Butler's Gartersnakes are active from mid-March through the first week of November in northern Ohio and southern Michigan. Vogt (1981) suggested that Wisconsin populations likely have a similar phenology.

Cloacal temperatures of individuals in a Michigan population increased over the active season from 25.7°C (78.3°F) from April to June to 29.5°C (85.1°F) from July to September, with an overall active season mean cloacal temperature of 26.1°C (79.0°F; Carpenter 1956). Cloacal temperatures were typically higher than environmental temperatures in cooler weather and lower than environmental temperatures in warmer weather, and Carpenter (1956) attributed this to behavioral thermoregulation. Doughty (1994) demonstrated under laboratory conditions that critical thermal minimum (CTmin, defined as the inability of a snake placed on its back to right itself) generally decreased with latitude in five gartersnake species, including Butler's Gartersnake. Excluding neonates, the CTmin for Butler's Gartersnakes was 5.8°C (42.4°F; Doughty 1994).

Data on Butler's Gartersnake movement patterns are particularly sparse. Using 2009 capture-recapture data from a population in Waukesha County, adult females had a mean home range of 0.0654 ha (0.1616 ac, $n = 29$, MCP estimator), and individual snakes moved a mean of 2.2 m/day (7.1 ft/day, $n = 82$; E. Hileman, unpublished data). Based on typical distances traveled, Carpenter (1952a) estimated that the 'activity range' of Butler's Gartersnakes at a study site in Michigan was ca. 0.8 ha (2 ac). A radio telemetry study in Ontario reported that mean female home range size was 0.9 ha (2.23 ac, $n = 12$), while the home range size of the single male tracked was 0.26 ha (0.64 ac, MCP estimators; Shonfield et al. 2019). Carpenter (1952a) estimated minimum travel distances of 120.0 m (393.6 ft, $n = 11$) in >200 days and 114.8 m (376.7 ft, $n = 15$) in <200 days. One individual traveled a minimum distance of 121.9 m (400 ft) in two hours (Carpenter 1952a). In Amherstburg, Ontario, minimum travel distances over 70 days ranged from 10 to 433 m (33 to 1,421 ft, $n = 5$) for males and 10 to 517 m (33 to 1,696 ft, $n = 19$) for females (Freedman and Catling 1979). However, >50% of all snakes captured in this study moved <50 m (164 ft) from their initial capture location. Shonefield et al. (2019) reported movement rates of ca. 14 m/day (46 ft/day) for individuals tracked with radio telemetry equipment in Ontario.

Autumn ingress is likely initiated after late-season soil temperatures invert once again, and deeper soil temperatures (60 or 100 cm [23.6 or 39.4 in] belowground) become warmer than shallow soil temperatures (10 or 30 cm [3.9 or 11.8 in] belowground; Smith 2009, King and Hileman 2012, 2013). Carpenter (1952a) estimated a hibernation period of 150 days in Michigan.

PREY AND PREDATORS

Butler's Gartersnakes are well adapted to feed on earthworms, which are their primary food source. In Ohio, earthworms were the only prey item disgorged upon capture (Conant 1938), and in Ontario earthworms comprised 96% of regurgitated meals (Catling and Freedman 1980a). In Michigan, forced regurgitation revealed a diet composed of earthworms (83%) and leeches (10%), with the remaining material unrecognizable (Carpenter 1952a).

Dietary preferences may have influenced the North American distribution of this species. Relevant to this discussion is the fact that the earthworms (Lumbricidae) commonly encountered in the Great Lakes region today are of European origin and presumably introduced by settlers in the mid-1800s (Hale 2007). Historically, Butler's Gartersnakes likely persisted along the periphery of the Wisconsin Ice Sheet and invaded the Great Lakes region soon after the Quaternary glaciation (Conant et al. 1945, Smith and Minton 1957, Minton 1972). If native earthworms (Megascolecidae) occurred in this region, they were probably extirpated prior to the post-glacial invasion of the region by Butler's Gartersnakes (Hale 2007). Therefore, this annelid specialist could have been restricted to an alternate food source, such as leeches, which limited the snake to wetland habitats, until the introduction of European earthworms (Lumbricidae). The expansion of this new and eventually widespread food source then presumably expanded the range of the Butler's Gartersnake.

Butler's Gartersnakes likely use scent trailing as their principal means to locate prey and are able to capture earthworms while foraging underground

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(Catling and Freedman 1980a). Catling and Freedman (1980a) also observed this species foraging for leeches underwater. The vomeronasal system used to detect chemical cues left by prey is likely functional at birth (see Special Remarks section), and Carpenter (1952a) observed that neonates in Michigan consume their first meal within hours of parturition.

Despite a clear specialization in annelid prey, Test (1958) documented consumption of a Spring Peeper (*Pseudacris crucifer*) by a wild Butler's Gartersnake in Michigan, and forced regurgitation yielded the first record of a Western Chorus Frog (*Pseudacris triseriata*) as prey in Ontario (Catling and Freedman 1980a). Additionally, a variety of laboratory experiments have demonstrated that Butler's Gartersnakes opportunistically consume amphibians and minnows in captivity (e.g., Carpenter 1952a, Halloy and Burghardt 1990) and can exhibit plasticity in prey preferences (Lyman-Henley and Burghardt 1995, see Special Remarks section for more detail). These phenomena may be a consequence of the species' close phylogenetic relationship with the Plains Gartersnake, which is more of a generalist predator (Burghardt 1993; see Systematics section).

A variety of animals likely include Butler's Gartersnakes in their diets. In three Butler's Gartersnake populations studied in Wisconsin, Eastern Milksnakes (*Lampropeltis triangulum*, Ozaukee County) and Northern Short-tailed Shrews (*Blarina brevicauda*, Waukesha and Ozaukee Counties; Natural History Box: Predation Event) were the most common predators found under coverboards (Hileman 2010). Carpenter (1953) provided evidence of crayfish predation on unidentified species of gartersnakes. Crayfish likely consume Butler's Gartersnakes, as this snake is known to use crayfish burrows as refugia in Wisconsin (Joppa and Temple 2005, WDNR 2014b). Throughout the Great Lakes region, additional predators probably include birds of prey and numerous small to midsized carnivorous mammals, ranging from weasels (*Mustela* spp.) to Red Foxes (*Vulpes vulpes*; Vogt 1981, Harding 1997).

When threatened, Butler's Gartersnakes are more prone to flee than strike (Herzog and Burghardt 1986, Herzog et al. 1992, Bowers et al. 1993, Albright 2001). In fleeing, they often thrash their body laterally while making limited forward movement. In response to simulated predator threats in the lab, Butler's Gartersnakes also exhibit tail waving, which is likely intended to redirect attacks away from the head (Bowers et al. 1993). If handled, this snake may secrete a foul-smelling musk containing the same volatile compounds found in musk of other North American gartersnakes (Wood et al. 1995).

Despite the overall tendency of this species to flee, neonates more frequently struck defensively at moving stimuli than stationary stimuli in laboratory experiments (Herzog et al. 1989a). Additionally, neonate males struck more often than females regardless of whether stimuli were moving (Herzog and Burghardt 1986, Herzog et al. 1989a). Juveniles, on the other hand, were equally unlikely to strike whether or not a stimulus was moving (Herzog et al. 1989b). Kirby (2005) conducted antipredator tests and compared Butler's Gartersnakes from Wisconsin, Michigan, and Ohio to Plains Gartersnakes from Illinois at 2 days old and 22–25 days old. Overall, she found that Wisconsin Butler's Gartersnakes (many from counties now known to have hybrids; Placyk et al. 2012) displayed antipredator behaviors more similar to those of Plains Gartersnakes from Illinois than to those of Butler's Gartersnakes from Michigan and Ohio. Specifically, at two days old, Wisconsin Butler's Gartersnakes were less likely to flee or tail wave when exposed to simulated threats than individuals from Michigan and Ohio. Similarly, at 22–25 days old, Wisconsin Butler's Gartersnakes were more prone to strike and less likely to flee than snakes from Michigan and Ohio. Additionally, Kirby (2005) found that Butler's Gartersnakes from Racine County behaved more aggressively (similar to Plains Gartersnakes) than Butler's Gartersnakes from Ozaukee County. For instance, individuals from Racine County were more likely to strike and less prone to flee than those from Ozaukee County. As previously mentioned, hybrids have since been identified in Racine (see Systematics and Distribution and Habitat sections).

CONSERVATION

Status: Globally, Butler's Gartersnake is listed as a Least Concern species by the IUCN. In Ontario and Indiana, it is listed as Endangered (COSEWIC 2010a, Indiana Legislature 2011). It is currently

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NATURAL HISTORY BOX: Predation Event

On 14 March 2010, while removing plywood coverboards used for a capture-recapture study of Wisconsin Butler's Gartersnakes, I discovered a shrew cache of ten young Butler's Gartersnakes under one of the boards (Figure 272a). Seven of the ten snakes were fresh kills, with their heads chewed off but their bodies still writhing (Figure 272b). The shrew was not present at the time, but based on the nest, prey cache, and ubiquity of the species, it was most likely a Northern Short-tailed Shrew (*Blarina brevicauda*) or, less likely, a Masked Shrew (*Sorex cinereus*). These voracious predators likely pose a threat year-round, but hibernating snakes may be at greatest risk, since shrews remain active throughout winter (Jackson 1961). Moreover, the Northern Short-tailed Shrew has the added advantage of subduing its prey with venom secreted from its submaxillary salivary glands (Pearson 1942).

Figure 272. (a) Shrew cache of young Butler's Gartersnakes found under a plywood coverboard (Ozaukee County; photo by E. Hileman). (b) Photograph documenting the carnage inflicted by the shrew on individual snakes (Ozaukee County; photo by E. Hileman).

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considered a species of Special Concern and a Species of Greatest Conservation Need in Wisconsin by the WDNR (Natural History Box: A Brief History of Butler's Gartersnake Protection in Wisconsin).

Populations: Little is known about the population ecology of Butler's Gartersnake in Wisconsin. Hileman (2010) provided population estimates for three study sites in Ozaukee and Waukesha Counties; however, the methods used to make these estimates are unreliable. Carpenter (1952a) estimated a population size of 121 individuals on a 19.4 ha (48 ac) study plot in Washtenaw County, Michigan. Freedman and Catling (1978) conducted a capture-recapture study from 14 May to 24 July 1976 on a 40 ha (99 ac) abandoned quarry in Amherstburg, Ontario. They pooled age classes and sexes (excluding neonates) to estimate population size (900 snakes) and density (23/ha [57/ac]) with traditional closed-capture models. Using data provided by Catling and Freedman (1980b),

NATURAL HISTORY BOX: A Brief History of Butler's Gartersnake Protection in Wisconsin

The history of Butler's Gartersnake conservation in Wisconsin is rife with conflict and controversy. Originally listed as state Endangered in 1972 (Wisconsin Administrative Code NR 27.01), Butler's Gartersnake was delisted in 1975 after significant populations were found in the greater Milwaukee area. Habitat loss and fragmentation caused by human development and encroachment of woody vegetation, in addition to concerns of hybridization with the Eastern Plains Gartersnake, resulted in relisting the species in 1997, this time as state Threatened (Hyde et al. 2007).

The protection afforded to Butler's Gartersnake as a Threatened species caused intense debate and conflict between conservationists, politicians, landowners, and land developers over how to balance economic development with preservation of the species and its habitat (Bergquist 2005, Schultze 2005, Enriquez 2006, Lydersen 2006, Sheeley 2007). This is not surprising, given that the core of the snake's range falls within the greater Milwaukee metropolitan area, the most densely populated and urbanized region in Wisconsin. The conflict came to a head in 2006 when a state legislative committee voted to delist the snake (Bergquist 2006b). According to Burghardt et al. (2009), "Only political change through recent elections prevented politicians from, for the first time in U.S. history, delisting an endangered species without even a superficial reliance on scientific data." This political change resulted in the vote being rescinded by the Joint Committee for Review of Administrative Rules (by a vote of seven to two), and the snake's Threatened status was preserved (Bergquist 2006a).

Protection for Butler's Gartersnake was threatened again on 16 May 2008, when the Wisconsin Department of Natural Resources (WDNR) issued a proposed regulatory framework regarding authorization and the definition of 'incidental take' (hereafter, 'take') under Wisconsin's Endangered and Threatened Species Law (Wisconsin Statutes 29.604). (The WDNR currently considers 'incidental take' to be the unintentional loss [or take] of species that are listed as endangered or threatened at the state level [Rori Paloski, WDNR, personal communication]. 'Take,' then, is defined as "shooting, shooting at, pursuing, hunting, catching or killing any wild animal" [Wisconsin Administrative Code NR 27.01].) Presidents of the American Society of Ichthyologists and Herpetologists, the Herpetologists' League, the Society for the Study of Amphibians and Reptiles, and the Canadian Association of Herpetologists argued that the proposed regulatory framework reinterpreted the WDNR's authorization and the definition of 'take' and substantially weakened protection of Butler's Gartersnake as a Threatened species. This interpretation authorized agency programs to approve development projects on the snake's critical upland habitat as long as mortality would likely not occur. Recognizing that destruction of overwintering habitat would result in indirect mortality, society presidents urged officials to reconsider its new interpretation of the state statute in a letter on 1 October 2008. The WDNR contended that agency programs already had this authority and that the regulatory framework adhered to the definition of 'take' as defined in the state statute. It therefore maintained its position. Citing species stability in Wisconsin based on new information on abundance, range, and hybridization, the WDNR downgraded Butler's Gartersnake from Threatened to Special Concern per administrative rule ER–27-11 on 1 January 2014 (Hyde et al. 2012; WDNR 2014b).

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Parker and Plummer (1987) estimated density for this same site as 13–40 adults/ha (32–99/ac) and reported SE (26–42/ha [64–104/ac]) as a percentage of the population estimate. Using Carpenter's (1952a) population estimate, Parker and Plummer (1987) also estimated a density of 6.2 individuals/ha (15.3/ac). However, this is likely an underestimate, as the area used for density estimation incorporated all habitat within the plot, including a wooded area where snakes were never found (Carpenter 1952a). Hileman (2014) also estimated adult density and abundance at a Wisconsin site from 2011 to 2013 by employing spatially explicit capture-recapture models for two trapping areas within this same site. Density ranged from 291 to 609/ha (719 to 1,505/ac). Based on SE, the most reliable density estimates from these two study areas in 2011 were 309/ha (764/ac, 95% CI = 257–362/ha [635–895/ac]) and 437/ha (1,080/ac, 95% CI = 316–558/ha [781–1,379/ac]). Combining the two trapping areas (0.4 ha [1.0 ac]), the 2011 adult abundance estimate was 439 (95% CI = 409–485; Hileman 2014). Density estimates reported in Wisconsin are much higher than those reported for Michigan and Ontario; however, because estimation methods varied widely between studies, they may not be comparable. Using Cormack-Jolly-Seber models and a composite of males and females age one year or greater, Hileman (2014) estimated apparent survival for a Milwaukee County population. Apparent survival ranged from 0.42 to 0.55 across years (2007–2013), but the annual estimate of 0.55 (95% CI = 0.38–0.70) had the lowest SE. Annual recapture probabilities varied from 0.04 to 0.21 across years.

Threats: Habitat loss and fragmentation from agriculture, development, natural succession, and proliferation of invasive plant species pose significant threats to Butler's Gartersnakes (see Introduction to Conservation and Management of Wisconsin's Amphibians and Reptiles chapter). Interestingly, over 20 years ago, Rossman et al. (1996) reported that Butler's Gartersnakes were a suburban species with relatively stable populations. Citing Minton (1968) and Vogt (1981), Ernst and Ernst (2003) also suggested that urbanization may be beneficial to Butler's Gartersnakes. However, Minton suggested that this benefit might be temporary, and Vogt merely stated that the snakes inhabit city lots and that "excellent populations of Butler's garter snakes can still be found within the city limits." More recently, however, this species' use of anthropogenically disturbed sites has raised concerns. For example, its association with suburban landscapes in Wisconsin is likely a by-product of a restricted distribution that naturally coincides with the heavily populated southeastern counties. Consequently, Butler's Gartersnake populations in southeastern Wisconsin are often limited to small disturbed plots and green spaces within urban landscapes, which perhaps give the false impression that they are urbanophiles. Populations in urban areas are likely more susceptible to the effects of habitat degradation, vehicular strike, and human persecution. Furthermore, Freedman and Catlin (1979) pointed out this species' tendency to avoid roads, which could fragment urban populations. Rossman et al. (1996) noted that fragmented Butler's Gartersnake populations could be more heavily impacted if isolated subpopulations occur on landscapes faced with habitat loss due to heavy development pressure. Conversely, Rossman et al. (1996) cited evidence via personal communication with J. Harding that indicates that this species does not appear to avoid roads in Michigan. These conflicting reports suggest that the impact of roads on this species is complex and warrants further investigation.

Research in Wisconsin supports the negative impacts of invasive vegetation. For example, Kapfer et al. (2013b) captured fewer Butler's Gartersnakes in wetland areas dominated by the invasive Reed Canary Grass (*Phalaris arundinacea*) than in areas dominated by native wetland sedges. Given the pervasiveness of Reed Canary Grass, extensive degradation of habitat will likely continue if this invasive grass is not controlled. While hybridization with Plains Gartersnakes could be a historical and nonanthropogenic phenomenon (Placyk et al. 2012), the long-term conservation impacts of this are unknown. Recent molecular work provides evidence that Wisconsin Butler's Gartersnake populations have unique haplotypes from populations in other states and are especially important in maintaining overall genetic diversity for this species (Burghardt et al. 2006, Placyk et al. 2012; see Systematics section).

Climate change poses a threat to reptiles and amphibians worldwide. Using maximum entropy ecological niche modeling, King and Niiro (2013) evaluated the effects of climate change on 11 reptile species of conservation concern in the midwestern United States. Butler's Gartersnake was predicted to be one of the least affected species as measured by reductions in climatically suitable habitat. In addition, their results suggest that climatically suitable habitat for Butler's Gartersnake might actually expand into new localities. However, this expansion would not necessarily lead to a range expansion for Butler's Gartersnakes due to the widespread threats of habitat loss and fragmentation described above.

Management: Preserving open wetlands and adjacent open uplands is critical to maintaining suitable habitat for this species. As such, general management concepts associated with these habitat types are relevant, as are considerations of habitat connectivity and timing of management activities (see Introduction to Conservation and Management of Wisconsin's Amphibians and Reptiles chapter). Protection of upland buffer zones around wetlands is important (Kapfer et al. 2013a), although the ideal width of these zones remains in question. At six sites studied in southeastern Wisconsin, Joppa and Temple (2005) found snakes in adjacent uplands as far as 122 m (400 ft) from the wetland edge. Additionally, Kapfer et al. (2013a) cited R. Hetzel (via personal communication) as finding Butler's Gartersnakes up to 182 m (597 ft) from wetland habitat. These reports and other information on movement (see Activity section) could help in the design and implementation of appropriate wetland buffers to protect this species. It is also important to preserve suitable overwintering sites for population persistence. Therefore, potential hibernacula (e.g., crayfish burrows) should be identified prior to land development or management activities. Given that Butler's Gartersnakes do not frequently use shrubby habitats (Kapfer et al. 2013b), mitigating the spread of woody vegetation in preferred wetlands is an important consideration. Management strategies for this species should also consider strategies to control the invasive plants, such as Reed Canary Grass (Kapfer et al. 2013b). Road underpasses have been used in attempts to mitigate road mortality at several sites in Wisconsin (R. Paloski and Lisie Kitchel, WDNR, personal communication). However, the effectiveness of road underpasses as a management tool for Butler's Gartersnakes has not been demonstrated.

SPECIAL REMARKS

In laboratory conditions, Butler's Gartersnakes voluntarily consumed a Northern Leopard Frog (*Lithobates pipiens*), a Spring Peeper, an American Toad (*Anaxyrus americanus*), an Eastern Red-backed Salamander (*Plethodon cinereus*), and small minnows (Carpenter 1952a). Snakes as young as two months old were able to capture and ingest fish in the lab but exhibited difficulty doing so (Halloy and Burghardt 1990). Others have also observed captive Butler's Gartersnakes consuming small frogs and fishes in addition to earthworms (Ruthven 1904, Ruthven 1908, Conant 1938, Lyman-Henley and Burghardt 1995). Burghardt (1993) speculated that the ability of this species to recognize fishes as prey items is a consequence of its ancestral lineage to the Plains Gartersnake. Additionally, he hypothesized that while this prey recognition is still intact, Butler's Gartersnake has evolved morphological traits better suited to annelids. Cunningham and Burghardt (1999) noted that captive individuals provided with earthworms groomed themselves after 95% of feedings by rubbing their labial and rostral scales against various surfaces.

Laboratory experiments have also revealed details about dietary preferences and sensory function in neonates. Inexperienced captive-born individuals from a wild-caught Michigan female displayed significant tongue flicking and attack responses when presented with surface chemicals extracted from worms, leeches, fishes, and amphibians but not slugs, mice, or a water control (Burghardt 1967, 1969). Additionally, Lyman-Henley and Burghardt (1995) demonstrated plasticity in prey preference. In their experiments, naive ten-day-olds born to wild-caught Michigan females showed preference for worm surface extracts over fish extracts. However, after 149 days, neonates that were fed a strict Mosquito Fish (*Gambusia affinis*) diet shifted their preference to fish extracts, while neonates fed only earthworms (*Lumbricus terrestris*) did not. Burghardt and Pruitt (1975) reported that neonate Common Gartersnakes with tongues completely removed did not attack swabs containing prey extracts. Moreover, in comparison to snakes with tongues intact, those without tongues showed significantly lower interest in the extract swabs (Burghardt and Pruitt 1975). Based on these results, the vomeronasal system seems to be functional at birth and likely mediates chemical cue responses (Burghardt and Pruitt 1975, Holtzman 1993). These findings extend to Butler's Gartersnakes because the vomeronasal system is structurally identical to the Common Gartersnake's throughout development (Holtzman and Halpern 1990). Olfaction may also contribute to chemical cue recognition by newborns (Holtzman 1993).

Kirby (2005) performed a series of experiments comparing neonate Butler's Gartersnakes from Wisconsin (Milwaukee, Ozaukee, Racine, and Waukesha Counties), Michigan, and Ohio to neonate Plains Gartersnakes from Illinois. In chemical cue choice tests, Butler's Gartersnakes from Wisconsin were more likely to respond to fish extracts than Butler's Gartersnakes from Michigan and Ohio. Based on these results, Kirby (2005) concluded that Wisconsin Butler's Gartersnakes share greater feeding response similarities to Plains Gartersnakes than to other Butler's Gartersnakes across their range. Additionally, when compared to Ozaukee County, Butler's Gartersnakes from Racine County were more prone to attack fish extracts. These results are consistent with recent genetics work, which has identified hybrids in Racine and pure Butler's Gartersnakes in Ozaukee (see Systematics and Distribution and Habitat sections).