Variation in Distribution and Abundance of Four Sympatric Species of Snakes at Amherstburg, Ontario

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Catling, P. M. and B. Freedman. 1980. Variation in distribution and abundance of four sympatric species of snakes at Amherstburg, Ontario. Canadian Field-Naturalist 94(1): 19–27.

Mapping of the local distribution and abundance of four sympatric species of snakes in a 40-ha study area near Amherstburg, Ontario, revealed four strikingly different patterns. No seasonal variations in these distribution patterns were observed. The most widespread and abundant species in the study area was Butler's Garter Snake (*Thamnophis butleri*), which had a large portion of its population in a seasonally dry upland area. The restricted distribution of the Eastern Garter Snake (*Thamnophis s. sirtalis*) corresponded well with the distribution of standing water and amphibian prey. The Brown Snake (*Storeria dekayi*) occurred primarily in moist areas of dense vegetation where slugs were common, but extended further into the dry upland than *T. s. sirtalis*. The Fox Snake (*Elaphe vulpina gloydi*) was widespread but uncommon in both dry and moist portions of the study area. The existing literature has associated *T. butleri* and *E. vulpina gloydi* more often with moist situations. Competition with both *T. s. sirtalis* and *S. dekayi* may explain the scarcity of *T. butleri* in a relatively moist area where all three occurred together. The absence or rarity of *T. s. sirtalis* and *S. dekayi* in the dry upland where *T. butleri* was abundant may result from an inability of the former two species to withstand drought and/or a competitive advantage of *T. butleri* in this seasonally dry habitat. The suite of characteristics which adapt *T. butleri* to earthworm prey are also functionally useful in drought avoidance.

Key Words: *Thamnophis butleri, Thamnophis sirtalis sirtalis, Storeria dekayi, Elaphe vulpina gloydi,* sympatry, ecology, distribution, habitat, competition, drought, southwestern Ontario.

During the summers of 1976 and 1977 we studied four species of snakes co-existing in a 40-ha area 2.4 km NE of Amherstburg (42°07′N, 83°05′W) in Essex County, Ontario (Catling and Freedman 1977, 1979; Freedman and Catling 1978, 1979). A large part of our field work at Amherstburg was directed toward collecting data on local distribution and abundance; there are few previous studies done on a local basis. Such information provides the basis for an understanding of the various factors affecting local sympatry in closely related and/or similar species.

This report documents the patterns of local distribution and abundance of the Eastern Garter Snake (*Thamnophis s. sirtalis*), the Butler's Garter Snake (*Thamnophis butleri*), the Brown Snake (*Storeria dekayi*), and the Fox Snake (*Elaphe vulpina gloydi*). It also considers some of the ways in which these patterns may relate to sympatry through the effects of prey availability, competitive interaction, and adaptation to seasonal drought.

Study Area

The dominant features of the study area are illustrated in Figure 1. Most of the western portion is comprised of an old limestone quarry and waste beds belonging to Allied Chemical Ltd. It is relatively high and rocky, and has irregular topography in contrast to the lower and flat eastern portion. The quarry, which has been abandoned for at least 15 yr, is bounded on the west by a frequently-used north-south gravel road, 10 m wide, and on all other sides by a narrower and little-used gravel road 4–5 m across. Some smaller areas to the west of the quarry have been abandoned for several years but much of this peripheral area has been disturbed by bulldozing, dumping, quarrying, and other activities.

Essentially flat and lower in elevation, the eastern portion of the study area is mainly comprised of abandoned industrial and agricultural lands, last occupied for these purposes more than 5 yr previous to our study. Several derelict buildings, as well as piles of scrap and rubble remaining from a previous smelter facility, are situated in the west-central section of the study area. The wooded valley of Big Creek cuts across the far eastern portion. There are a few areas of recently cultivated (within the last few years) ground, and presently cultivated fields of corn exist along the southern boundary.

Although vegetation and substrate are very patchy and variable over distances of only a few metres, it is readily observed that there are three major biophysiographic regions in the study area (Figure 1). In addition to these, there are minor areas of disturbed barren ground, scrub, cultivated, and recently cultivated

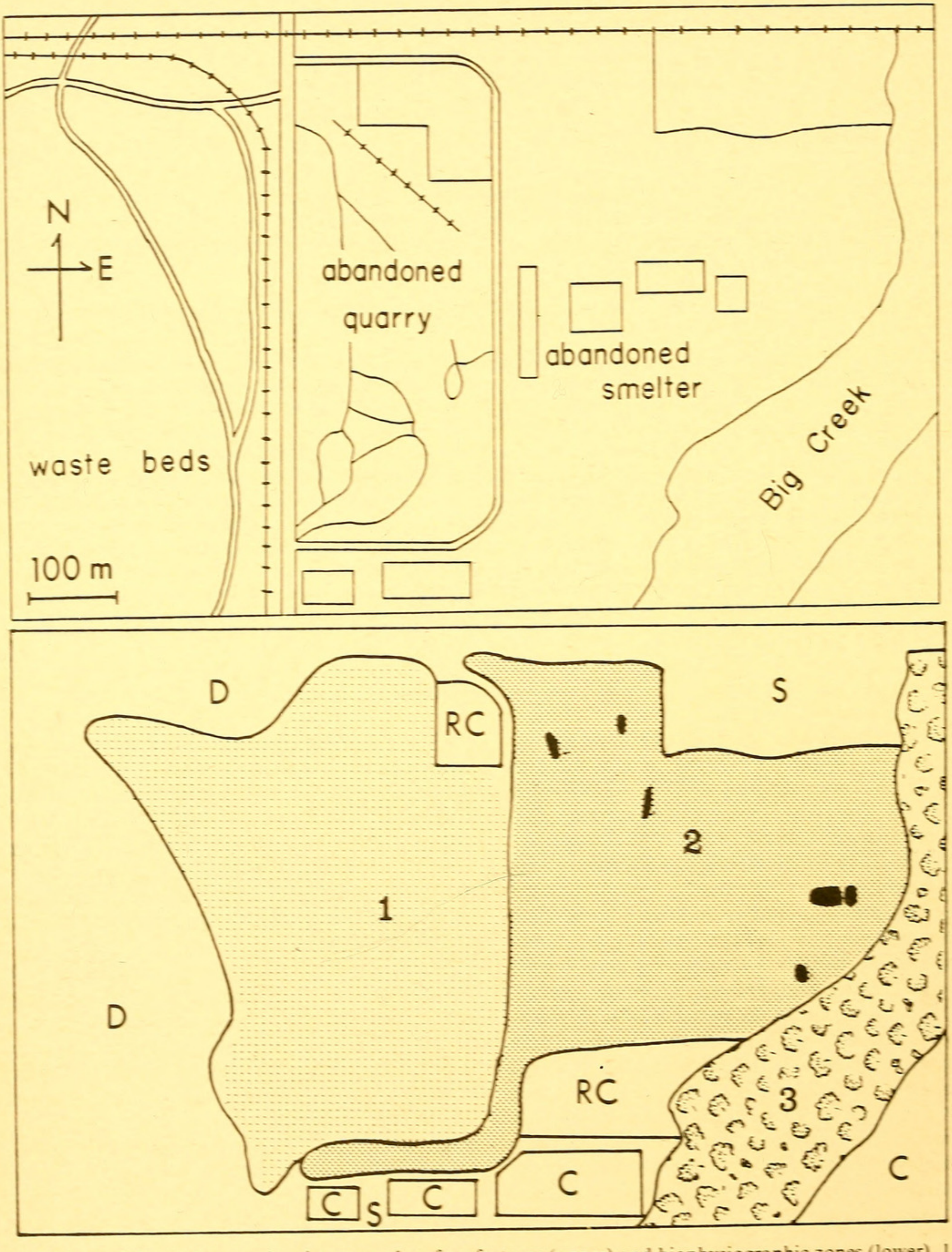

FIGURE 1. Maps of the study area showing general surface features (upper) and biophysiographic zones (lower). 1 = dry, well-drained upland with relatively low vegetation cover values; Cottonwood and Hawthorn clumps with much dry grassland and rocky ground with sparse vegetation cover, limestone bedrock at the surface, ephemeral pools in the spring only. 2 = low flat area with rank cover of grasses and forbs, in many places permanently moist, with ditches and wetlands having *Typha* spp. and permanent pools scattered throughout. 3 = Oak-Hickory woodland on slopes of Big Creek valley. D = disturbed ground (bulldozed within last 2 yr); RC = recently cultivated; C =presently cultivated; S = scrub.

ground. Area 1 (Figures 1 and 2) consists of the rocky, topographically irregular quarry area representing the highest elevations on the site (ca. 225 m). This area may be wet in spring and fall with small temporary pools, but it dries out by June, and is very dry with no standing water in July and August. Deeper soils in localized areas are composed of fine clay (pH 7.6–7.8) that hardens upon drying and cracks into deep fissures. In most places the soil is shallow, and rocky substrate ranging from outcroppings of bedrock to piles of boulders or smaller stones is frequent. The area is essentially sparse open grassland. Much of it has been used as an unmanaged garbage dump and numerous fires started to burn trash have helped to maintain the open grassland.

Area 2 is lower in elevation (ca. 183 m) and essentially flat, without rock in the form of either outcropping or piles. The vegetation is generally a dense cover of grasses and forbs, but drier areas of sparse vegetation, not unlike that characteristic of Area 1, occur in a few places. Throughout there are pockets of soil that remain moist during the summer, as well as six permanent pools (Figure 3). In addition, the numerous ephermeral pools in this area last much longer than those in Area 1, still having water in late June or early July.

Area 3 consists of the wooded (Oak-Hickory) valley and banks of Big Creek (elevation 180 m).

Methods

During spring and summer of 1976 and 1977, 10 visits were made to the study area. These were, in 1976: 14 May, 30 May, 15 June, 10 July, and 24 July,

FIGURE 2. Dry rocky upland with scattered Cottonwoods (*Populus deltoides*), Sumacs (*Rhus typhina*, *R. glabra*), and Dogwood (*Cornus drummondii*). The sparse open grassland is dominated by *Poa compressa*, *Poa pratensis*, *Bromus japonica*, *Sporobolus neglectus*, *Diplotaxis tenuifolia*, *Daucus carota*, *Pastinaca sativa*, *Vitis riparia*, and *Parthenocissus vitacea*.

FIGURE 3. Permanent pond surrounded by Cattail (*Typha* spp.) with Bur Oak (*Quercus macrocarpa*) to the right, in Area 2. The plant community in the foreground and behind the pool is dominated by *Melilotus alba, Daucus carota, Poa pratensis, Agropyron repens, Phleum pratense,* and *Dactylis glomerata.*

and in 1977: 11 April, 6 May, 26 May, 15 June, and 20 July. On each of these visits the 40-ha study area was systematically searched for snakes over a 1- or 2-d period. Searching included wandering through vegetation, and turning over rocks and debris. The study area was divided into 50-m squares on aerial photographs, and the numbers of snakes of each species found in each square on each visit was recorded.

The distributions of various prey species observed in the study area during these searches were also mapped, as were the general surface features and vegetation, so that these patterns could be compared with the local distribution and abundance of snakes.

Results and Discussion

Distribution and Abundance of Snakes

Figures 4 and 5 indicate that each of the four species of snakes had different patterns of local distribution and abundance. *Thamnophis butleri* was the most common and widespread snake in the study area. Pockets of abundance appeared in the center of Area 1 and along the western extension of Area 2. Unlike the other three snake species, *T. butleri* was abundant in Area 1, and in fact was most abundant in this dry upland area. It was exceeded in abundance by both *T. s. sirtalis* and *S. dekayi* in the eastern portion of Area 2. There was relatively little overlap between *T. butleri* and the congeneric *T. s. sirtalis* in our study area.

Thamnophis butleri is generally associated with moist habitat (Ruthven 1908; Schmidt and Davis 1941; Carpenter 1952; Wright and Wright 1957). Prior to this study the only reference to *T. butleri* inhabiting dry areas was that of Logier (1939).

In contrast to *T. butleri, S. dekayi* and *T. s. sirtalis* were more or less restricted to the lower and more moist Area 2, where pockets of abundance occurred. Interestingly, *S. dekayi* and *T. butleri* both occupied

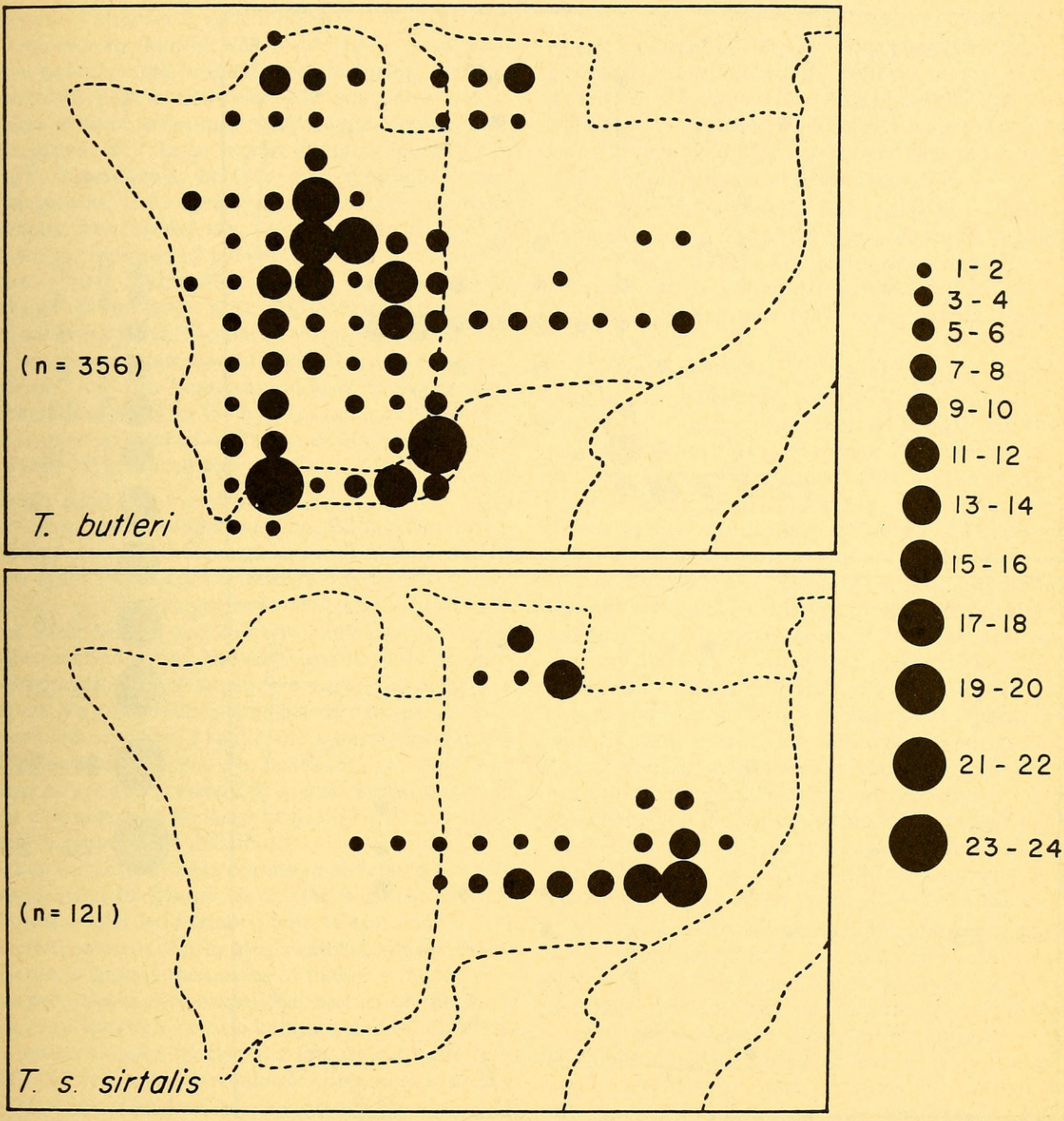

FIGURE 4. Distribution and abundance of *Thamnophis butleri* and *Thamnophis s. sirtalis* in the study area. Data are a summary of 10 visits in 1976 and 1977. n = total number of snakes. The relationship between spot size and total number of snakes captured in a 50 x 50 m quadrat is illustrated to the right.

moist ditches comprising the southwestern extension of Area 2, but *T. s. sirtalis* was never found here. *Storeria dekayi* occupied the entire area of distribution of *T. s. sirtalis*, and a part of the area of distribution of *T. butleri*, but was less common than either of these in the area of overlap. *Storeria dekayi* is generally reported in the literature to occupy a great variety of habitats (Wright and Wright 1957).

Carpenter (1952) found *T. s. sirtalis* in his study area to be widespread in a variety of habitats, and he compared this to the relatively restricted distributions of *T. butleri* and the Eastern Ribbon Snake (*T. s. sauritus*). In general, the literature reports *T. s. sirtalis* from a wide variety of habitats, but associates the snake with wet places; "It prefers to be near water, but also wanders far from it into high and dry places" (Logier 1958). Wright and Wright (1957), in a review of numerous references to its habitat, suggested that

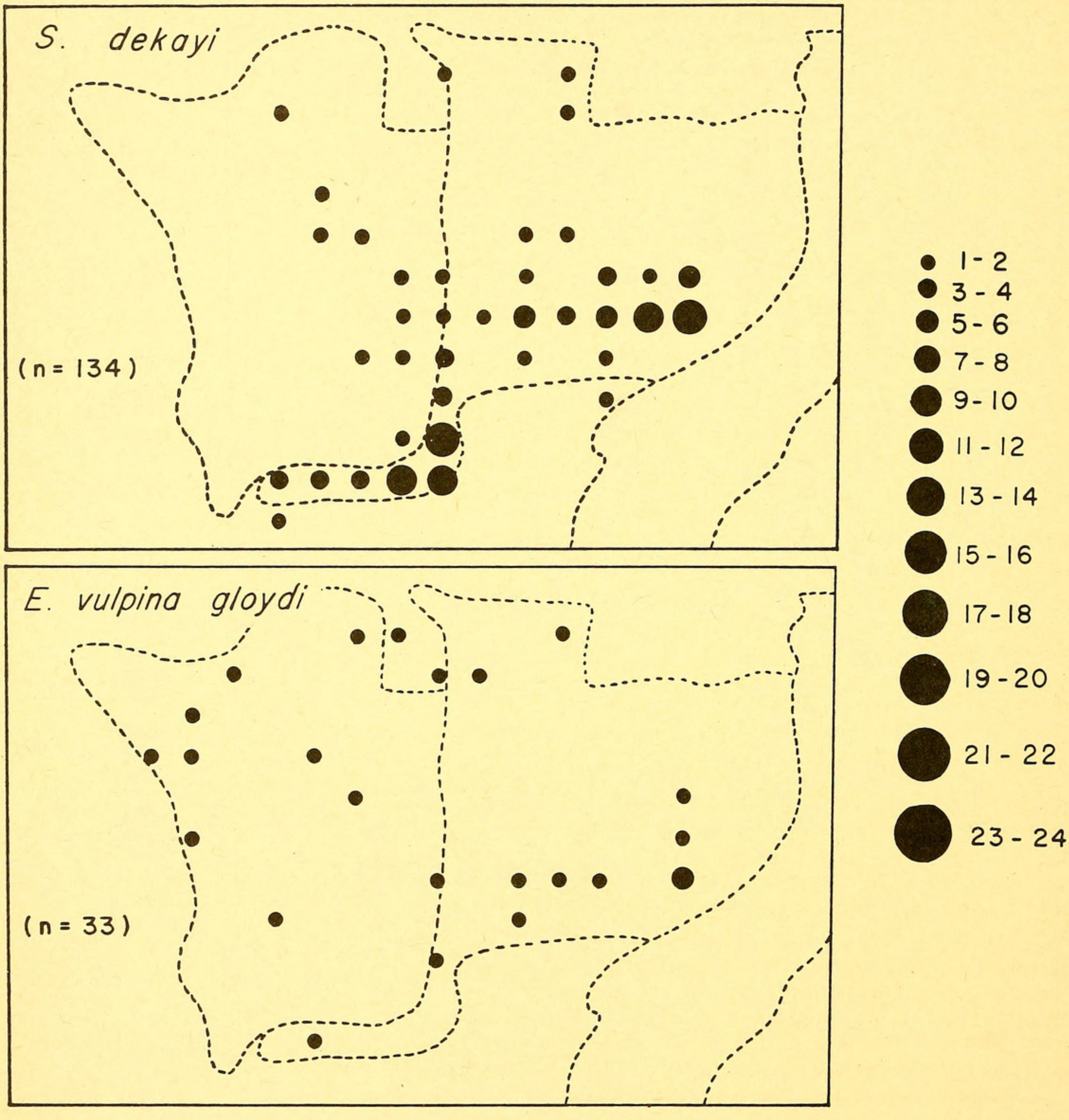

FIGURE 5. Distribution and abundance of *Storeria dekayi* and *Elaphe vulpina gloydi* in the study area. Data are a summary of 10 visits in 1976 and 1977. n = total number of snakes. The relationship between spot size and total number of snakes captured in a 50 x 50 m quadrat is illustrated to the right.

T. s. sirtalis is semi-aquatic. Considering these references (see also Fitch 1965), it is not surprising that we found it confined to the relatively moist Area 2, where there were several permanent pools of water.

Elaphe vulpina gloydi was widespread but relatively uncommon in both Areas 1 and 2 with no obvious pockets of concentration (Figure 5). Conant (1938) and Logier (1958) suggested that this constrictor occurs in and near extensive lakeside marshes. Rivard (1976) found it in a variety of open habitats, but frequently within 10 m of a marsh shoreline. Interestingly, several *E. vulpina gloydi* were found in Area 1 in midsummer, at least 500 m from the nearest standing water.

Seasonal Variation in Distribution

Thamnophis butleri was found to be somewhat more concentrated in local areas in spring, and less concentrated in the summer. The concentrations of snakes in some areas may have resulted from spring emergence of a large group simultaneously from nearby hibernacula, or they may represent sexual aggregations, for example a large number of males attracted by a few females. Sexual aggregations of *T. butleri* are reported by Finneran (1949). But observations in both spring and summer were widespread throughout the study area, and overall distribution did not differ much. Similarly, the other three species did not demonstrate any differences in distribution at different seasons. Seasonal changes in distribution were not expected on the basis of the relatively short movements of marked snakes, most of which travelled less than 50 m (Freedman and Catling 1979).

Factors Affecting Distribution

Jordan (1967) thought that vegetation cover or factors limiting vegetation cover determined the distributions of the Plains Garter Snake (*Thamnophis radix*) and *T. s. sirtalis* in a praire-forest ecotone in Minnesota. Both Areas 1 and 2 of our study area are essentially open and grassy, but very variable in the amount and composition of vegetative cover (as described above). No direct relationship between the presence of a particular species of snake and a particular vegetative cover was apparent. For instance, *T. s. sirtalis* was frequently found in Area 2 in sparse vegetation of the type characteristic of large portions of Area 1. Distinctive patterns of distribution and abundance of snakes in our study area appear to be related to some combination of factors associated with the general features of the landscape. These factors include (1) different patterns of prey availability accompanied by differences among the species of snakes using the various prey species, (2) competitive interactions between species of snakes in certain habitats, and (3) differences between snake species in adaptation to different microenvironments, particularly differences in ability to withstand drought. These factors will be considered separately.

1) *Distribution of prey*

The basis for differences between the snake species in prey usage has been considered (Catling and Freedman 1979). Here we will focus upon prey distribution as it relates both to food actually taken, and to local distribution and abundance of the different snake species.

Both the literature and our data from Amherstburg (Catling and Freedman 1979) suggest that *S. dekayi* feeds largely on slugs and earthworms. The distribution of this snake in our study area corresponds well with the areas of abundance of the former prey.

The pattern of distribution and abundance of *T. s. sirtalis* corresponds closely with the distribution of Leopard Frogs (*Rana p. pipiens*) and American Toads (*Bufo a. americanus*) in our study area. Amphibians are reported to comprise a significant portion of the prey of *T. s. sirtalis*, and they did so in our study area (Catling and Freedman 1979).

Elaphe vulpina gloydi is reported to feed chiefly on mammals, birds, and birds' eggs (Conant 1938; Logier 1958; Rivard 1976). The widespread occurrence of Meadow Voles (*Microtus pennsylvanicus*) in our study area corresponds well with the distribution of *E. vulpina gloydi*.

Thamnophis butleri, T. s. sirtalis, and *S. dekayi* all prey upon earthworms, but these seem to be most important in terms of total diet to *T. butleri* (Catling and Freedman 1979). The species of earthworm eaten by *T. butleri* appear not to account for the unusually large population of this snake in our study area (Freedman and Catling 1978; Catling and Freedman 1979). All of these earthworms are more or less widespread in Ontario (Reynolds 1977). It is quite possible that the variety of earthworm species present, and the abundance of debris at the study site makes this prey more available than is usually the case. Beneath such widespread debris as rocks, decaying wood, mattresses and furniture, tins, rubber, and tar paper, and within dumped garden refuse and decomposing paper and cardboard, worms are available that otherwise do not come to the surface. Although it seems reasonable to explain the large population of *T. butleri* in the study area partially on the basis of prey and prey availability, the pattern of distribution and local abundance of this snake is not so easily explained.

No marked differences in abundance of earthworms were noted in Areas 1 and 2 in late April and early May. As the spring progressed much of Area 1 began to dry out, and by midsummer earthworms were rarely seen there. Earthworms could, however, be found under piles of trash and in moist ditches in many parts of Area 2 until late summer, when some of these areas also began to dry out. Thus, availability of earthworms to snakes appeared to last much longer into the summer drought in Area 2 than in Area 1. Although none of the snakes in our study area were directly associated with overall earthworm distribution, *T. s. sirtalis*, and to a lesser extent *S. dekayi*, were associated with areas of more continuous earthworm availability, while *T. butleri* was associated with an area of relatively ephemeral earthworm availability.

Thus, the distribution and abundance of the "preferred prey combination" (i.e., prey taken most frequently under natural circumstances) is correlated with the distribution of three of the four species of snakes. But the complete exclusion of *T. s. sirtalis* and partial exclusion of *S. dekayi* from Area 1 is not explained by the absence of prey *per se*, because earthworms are seasonally present here and both of these snakes are capable of utilizing earthworms as a significant portion of their diets (Catling and Freedman 1979). The distribution and abundance of *T. butleri* is apparently not explained by the distribution and abundance of prey. This snake was relatively scarce in Area 2, where earthworms are abundant and available for a relatively long period.

2) *Competitive interactions*

Various authors have presented evidence that *T. butleri* is better adapted to feeding on earthworms than *T. s. sirtalis* (see Catling and Freedman 1979). Relatively small size, activity periods corresponding to earthworm activity, and physiological and behavioral adaptations of *T. butleri* may all contribute to its better adaptation to earthworm prey. R. J. Planck and J. T. Planck (1977, unpublished report to the Department of Supplies and Services) speculated that *T. butleri* displaces the ecologically more general *T. s. sirtalis* (see also Fitch 1965, p. 506) to areas of less competition and to prey species for which competition is decreased. They reported areas where *T. butleri* was more abundant than *T. s. sirtalis*, but they did not find any areas where *T. butleri* occurred to the total exclusion of *T. s. sirtalis*. This latter situation is very obvious in parts of our study area (Figure 4), and may be partly owing to a competitive advantage of *T. butleri* in the dry upland where only earthworm prey is available. On the other hand, *S. dekayi* and *T. s. sirtalis* might have a competitive advantage in Area 2 where prey in addition to earthworms is available, and where earthworm availability is prolonged, thereby partially displacing *T. butleri*.

3) *Ability to withstand drought*

Thamnophis butleri, which had a large portion of its population permanently centered in the dry upland of Area 1, and *S. dekayi*, which was also present there in low numbers, must have been able to withstand the severe midsummer drought that occurred there. *Elaphe vulpina gloydi* also had a large portion of its population in this area. Desiccation might be avoided by aggregation and aestivation during hot, dry weather, by nocturnal activity, or it may be tolerated.

Both *T. butleri* and *S. dekayi* are found in aggregations at times of the year other than early spring and late fall (Noble and Clausen 1936; Finneran 1949). Apparently snakes can follow trails left by the skin of conspecifics (Noble and Clausen 1936). This could lead to aggregations and might assist newcomers in an area to find appropriate cover. Aggregation may be facilitated in snakes that are scent-oriented with respect to prey, and it would be a distinct advantage in a seasonally-dry habitat because water loss through the skin and through ventilation is decreased in members of an aggregated group (Noble and Clausen 1936). Summer aggregation and aestivation would not only help them to avoid drought, but would also result in activity periods corresponding to those of earthworm prey.

The relative scarcity of *T. butleri* in our study area in June and July did not appear to be the result of emigration (Freedman and Catling 1979). Rather it appeared that *T. butleri* or a large proportion of its population was hiding.

Continued activity of *T. butleri* in permanently moist sites during the summer may help to explain the frequent association of *T. butleri* with wet sites, reported in most of the literature (e.g., Carpenter 1952). Although this snake may be readily apparent in moist situations, it could still be very abundant yet inconspicuous in sites that are dry in midsummer. Its presence in an extensive dry upland area indicates that *T. butleri* does not necessarily require areas of continuous earthworm activity, contrary to the suggestion of Planck and Planck (*op. cit.*). In fact it may have an advantage over other species (e.g., *T. s. sirtalis* and *S. dekayi*) in summer-dry situations.

Evidence for nocturnal activity of *T. butleri* and *S. dekayi* has been presented previously (Catling and Freedman 1979). All of the 33 *E. vulpina gloydi* seen during our study were found under cover, suggesting that this snake also may avoid drought by nocturnal activity. No information on relative drought tolerance is available for the snake species discussed here.

Both *T. butleri* and *E. vulpina gloydi* are biogeographically associated with the summer-dry prairie environment and are presumably adapted to coping with drought stress. *Thamnophis butleri* is endemic to the prairie peninsula region. It may have emigrated from the west with the extension of the grasslands into the eastern peninsula region 8000 to 4000 years ago, later persisting in isolated pockets during the reinvasion of forests (Transeau 1935; Schmidt 1938; Sears 1942; Smith 1957; Wright 1968). *Elaphe vulpina gloydi* is also thought to have extended its range eastward through the post-Wisconsin prairie peninsula region, with the later reinvasion of forests isolating the eastern and western populations (Schmidt 1938; Conant 1940; Smith 1957; Bleakney 1958). Considering the affinities of *T. butleri* and *E. vulpina gloydi* to the western summer-dry regions, it does not come as a surprise that these species should be able to withstand the extreme midsummer dryness of Area 1.

Interestingly, Kirtland's Water Snake (*Natrix kirtlandii*), which has a prairie peninsula distribution similar to that of *T. butleri*, occupies relatively small open grassy areas that have ephemeral pools in spring and become dry in midsummer, at which time the snakes are very scarce and are known to aggregate (Conant 1943). Conant noted that *N. kirtlandii* feeds chiefly on earthworms and that its periods of apparent abundance were associated with periods of rain. We postulate that *T. butleri* is ecologically very similar, being adapted to earthworm prey and able to withstand drought. Possibly the character suite that aids in the utilization of earthworm prey (Catling and Freedman 1979) is also functionally useful in drought avoidance. For example, a scent-oriented approach to foraging may increase efficiency of capturing earthworms, (which are most likely to be available in the dark). Through allowing nocturnal activity and facilitating aggregation, it may also enhance drought avoidance. Similarly, it is possible that small size and seasonal activity both increase the efficiency of feeding on earthworms, and at the same time the former may make hiding easier, while the latter permits drought avoidance by summer aestivation.

Acknowledgments

We are grateful to F. R. Cook of the National Museum of Natural Sciences, Ottawa, P. T. Gregory of the University of Victoria, and C. A. Campbell of Waterloo, Ontario for their critical reading of the manuscript. The assistance of K. L. McIntosh and S. M. McKay in the field is gratefully acknowledged.

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Received 5 April 1979
Accepted 7 July 1979