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RESOURCE PARTITIONING AMONG THE SNAKES OF THE UNIVERSITY OF KANSAS NATURAL HISTORY RESERVATION: A PRELIMINARY ANALYSIS

Robert W. Henderson

ABSTRACT--Using previously published data, an analysis of resource ırtitioning among 12 species of snakes found on the University of Kansas ıtural History Reservation was conducted. Food, habitat, temperature eference, time of activity, and snake size were the five variables used in e analysis and the following relationship was found among them: snakes the same size tend to have similar food preferences; snakes with similar od preferences are found in the same general habitat at the same time ither diurnal or nocturnal) and are active at approximately the same mperatures. Kinds of prey taken and subhabitat and/or microhabitat eferences seemingly segregate species which, superficially, appear to have nilar ecological requirements.

Ecological segregation in lizards has received considerable tention (e.g., Rand, 1964; Rand and Humphrey, 1968; :hoener, 1968), but snakes have been largely ignored. ırpenter (1952), Fitch (1940, 1941) and Fox (1951, 1952) udied segregating factors in congeners or conspecifics and all orked exclusively with the genus *Thamnophis*. They found ·od and habitat differences which tended to minimize :ological overlap. Pough (1966) found that habitat and evation tended to segregate sympatric species of *Crotalus*. .tch (1949) reported on the relationships of heterogenerics in ılifornia snake populations, but it was only a cursory :amination. Leston and Hughes (1968) discussed resource ırtitioning of a forest cocoa-farm snake fauna in Ghana. Using ıeral habitat, food preference and time of activity they were ɔt always able to segregate species but suggested that "it is :ely that some at present unknown factor segregates them." ıe present study examines the ecological relationships of 12 ecies of snakes found in northeastern Kansas. The relationships :tween potentially segregating variables is examined and a scussion of segregating factors is presented.

Since 1948 H. S. Fitch and several of his students have udied the snakes of the University of Kansas Natural History eservation (and surrounding areas) located 4.5 mi N and 1.5 mi

of Lawrence, Douglas County, Kansas. Most of these studies have been of an autecological nature and many of the common and some of the uncommon) species have received intensive tudy. Specific aspects of their natural histories have also been tudied, such as temperature relations (Fitch, 1956) and home anges and movements (Fitch, 1958). No one has, however, examined the Reservation's entire snake fauna and discussed the cological relationships of its members. Indeed, until now, when letailed accounts of the natural histories of all of the common pecies are available, such a study would have been impossible.

METHODS

Excellent records are available on each snake captured on the Reservation and perhaps, eventually, a statistical analysis of resource partitioning in this snake community will be undertaken. Autecological studies on less common Reservation snakes are in progress and much data that have been collected but are, as yet, unpublished, have been excluded from this analysis.

Four variables considered essential in minimizing resource-use overlap were analyzed: food, habitat, temperature, and time of daily activity (diurnal or nocturnal). One variable physical character of snakes important in resource partitioning was also used: size (range of adult total length).

The food, habitat, and temperature data sources for the 12 species (of 11 genera and two families) of Reservation snakes considered residents follows: *Carphophis vermis* - Clark (1968, 1970), Fitch (1956, 1958, pers. comm.), R. L. Lattis (pers. comm.); *Coluber constrictor* - Fitch (1956, 1963a, pers. comm.); *Diadophis punctatus* - Fitch (1956, pers. comm.), R. L. Lattis (pers. comm.); *Elaphe obsoleta* - Fitch (1956, 1963b, pers. comm.); *Lampropeltis calligaster* - Fitch (1958, pers. comm.); *L. triangulum* - Fitch (1958), Fitch and Fleet (1970); *Natrix sipedon* - Fitch (1958, pers. comm.); *Storeria dekayi* - Fitch (1956, 1958, pers. comm.); *Thamnophis sirtalis* — Fitch (1956, 1965a, pers. comm.); *Virginia valeriae* - Fitch (1956, 1958), G. R. Pisani (pers. comm.); *Agkistrodon contortrix* - Fitch (1960, pers. comm.), R. L. Lattis (pers. comm.); *Crotalus horridus* - Fitch (1958, pers. comm.). Although several other species have been found on the Reservation, they are so rare (e. g., *Tantilla gracilis*), or only hibernate there (e. g., *Pituophis melanoleucus*), that they have been excluded from this report. Information on time of activity was taken from Smith (1956) and snake sizes (total lengths) were taken from Wright and Wright (1957).

By constructing n x m contingency tables I was able to determine the relationship which existed between the 5 variables. Every possible combination of pairs of the 5 variables was compared and, using an Olivetti-Underwood 101 Programma electronic desk computer, a chi-square test for independent assortment (Williams, 1969) was made for statistical significance. The data used for the contingency tables were taken only from those species that have been thoroughly studied and the results published. They are *Carphophis vermis*, *Coluber constrictor*, *Elaphe obsoleta*, *Lampropeltis triangulum*, *Thamnophis sirtalis*, and *Agkistrodon contortrix*. *Diadophis punctatus* was also used because, although a thorough account of its ecology has not been published, it is the most common snake on the Reservation, much is known about it, and data on it are now being processed.

The Reservation may be divided into 3 general habitat types: (1) woodland; (2) prairie-pasture; and (3) pond. Approximately one-half of the Reservation is woodland and the other half grassland (Fitch, 1960). There is a pond located on the Reservation and another on the Rockefeller Experimental Tract (see Fitch, 1965b, for a thorough description and maps).

The results and discussion which follow refer only to Reservation snakes and not to particular genera or species in general.

RESULTS AND DISCUSSION

Figure 1 shows the distribution of food preferences of seven species of Reservation snakes. All except *L. triangulum* are among the most common snakes, and all utilize the woodland general habitat although *Coluber* and *Thamnophis* are more often found in other general habitats. Except for the small earthworm predators (*Carphophis* and *Diadophis*), each species takes a variety of prey species from several prey groups. But each species also exhibits a definite preference for a particular prey group. The greatest amount of prey group overlap occurs among earthworm, frog (*Natrix* also preys mainly on frogs, though not shown in Fig. 1), and mammal predators.

Figure 2 illustrates the preferred temperature ranges for the 6 species of Reservation snakes for which this information is known. There is a great deal of overlap both in preferred range and preferred optimum temperatures.

The results of the contingency table and chi-square analysis are presented in Table 1. Five pairs of variables were found to be independent and 5 pairs dependent. The dependent pairs are summarized in Fig. 3 and can be interpreted as follows: snakes of the same size tend to have similar food preferences (take similar size prey); snakes with similar food preferences are found in the same general habitat at the same time (diurnal or nocturnal) and are active at approximately the same temperatures.

The dependent factors segregate species with similar requirements into groups. Then, within each group there must be additional factors segregating species.

While it is true that most snakes eat a variety of prey species from several prey groups, all of the snakes on the Reservation are restricted to one of five principal prey groups (earthworms, insects, frogs, lizards, or mammals) from which 60-100 per cent of their prey are taken. Burghardt (e.g., 1968) and Burghardt and Abeshaheen (1971) have shown that newborn, naive snakes have innate prey preferences and that one prey group (e.g., frogs or mammals) is usually favored over others.

Of the snake species on the Reservation that share the same prey group in the same general habitat (earthworms: *C. vermis*, *D. punctatus*, *S. dekayi*, and *V. valeriae*; frogs: *N. sipedon* and *T. sirtalis*; mammals: *E. obsoleta*, *A. contortrix*, *C. horridus*), all tend to feed on a common species in their respective prey group. That is, all four worm eaters feed on the same species of earthworm; the frog eaters both feed primarily on *Rana pipiens*; and the first two mammal predators prey most often on the prairie vole (*Microtus ochrogaster*) while the rare *C. horridus* takes squirrels and wood rats.

It seems unlikely that a prey item as seemingly abundant as earthworms would be a limiting factor on the Reservation. Likewise, *N. sipedon* and *T. sirtalis* are syntopic only at the pond where *R. pipiens* is most abundant, and *E. obsoleta* and *A. contortrix* feed most often on the most common Reservation mammal. So there appears to be a system of checks and balances: where there is prey-preference overlap, the prey species tend to be common or where the predators occur together the prey is most abundant.

The kinds of prey taken less frequently may help minimize overlap. For example, *A. contortrix* fed upon a total of 31 prey species of which only 13 were mammals and is probably less

dependent than *E. obsoleta* on endothermic prey. Looking only at the percentages of kinds of mammals preyed on by *E. obsoleta* and *A. contortrix* many similarities are found, but also some significant differences exist. Both took prairie voles about 32 per cent of the time and white-footed mice (*Peromyscus*) about 23 per cent of the time, and there are other similarities among less frequent prey items. But shrews (*Blarina* and *Cryptotis*) comprised 25 per cent of the mammalian diet of *A. contortrix* as compared to only about 3 per cent for *E. obsoleta.* On the other hand, *E. obsoleta* preyed upon wood rats (*Neotoma floridana*) and Eastern cottontails about 13 per cent of the time as contrasted to about 2 per cent for *A. contortrix*. So it appears that *E. obsoleta* takes larger prey more often while *A. contortrix* apparently favors smaller mammals. Also, birds and their eggs comprise about 23 per cent of the diet of *E. obsoleta* whereas they make up only 0.4 per cent of the copperhead's diet. Fitch and Shirer (1971), however, using radiotelemetry, found *E. obsoleta* in trees nearly 50 per cent of the time. This suggests that birds and eggs probably comprise more than just 23 per cent of the rat snake's diet as indicated in Fitch's study (1963b).

Likewise, *N. sipedon* took fish in addition to frogs, but *T. sirtalis* did not. *Natrix* was much more closely associated with water than *T. sirtalis* and the latter was frequently found in prairie habitat where *N. sipedon* was absent.

Among the earthworm eaters, *Storeria* and *Virginia* are more resistant to a dessicating environment than *Carphophis* and *Diadophis* (Elick and Selander, 1972). *Storeria* is found more often under a dense leaf canopy while *Virginia* seems to prefer a more open canopy. *Caphophis* and *Diadophis* are more fossorial than *Storeria* and *Virginia* (Elick and Selander, 1972). *Carphophis* is more fossorial than *Diadophis*, is soil specific whereas *Diadophis* is not, and prefers damper situations than *Diadophis* (Clark, 1968).

There are only two congeners on the Reservation, *Lampropeltis calligaster* and *L. triangulum*, and they are segregated by both prey preference and habitat.

Although Arnold (1972) stated that ". . . available information on snake species and their prey defies any simple notion of resource partitioning by habitat segregation in time or space", it appears that the Reservation snakes do partition resources by habitat and food preference differences. It is, however, necessary to go beyond general habitat and food

classes to determine this. A future analysis of the many thousands of individual records of Reservation snakes should emphasize these segregating factors even more strongly.

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Table 1. Results of the contingency table and chi-square analysis.

INDEPENDENT

Variable Pair	χ^2 .05	df	Computed χ^2
Habitat-Temperature	23.68	14	12.86
Habitat-Size	55.75	40	36.29
Temperature-Time	14.06	7	3.59
Temperature-Size	124.34	140	43.38
Time-Size	31.41	20	4.98

DEPENDENT

Variable Pair	χ^2 .05	df	Computed χ^2
Habitat-Food	21.02	12	96.92
Habitat-Time	5.99	2	9.02
Food-Temperature	58.12	42	72.56
Food-Size	124.34	120	472.48
Food-Time	12.59	6	12.86

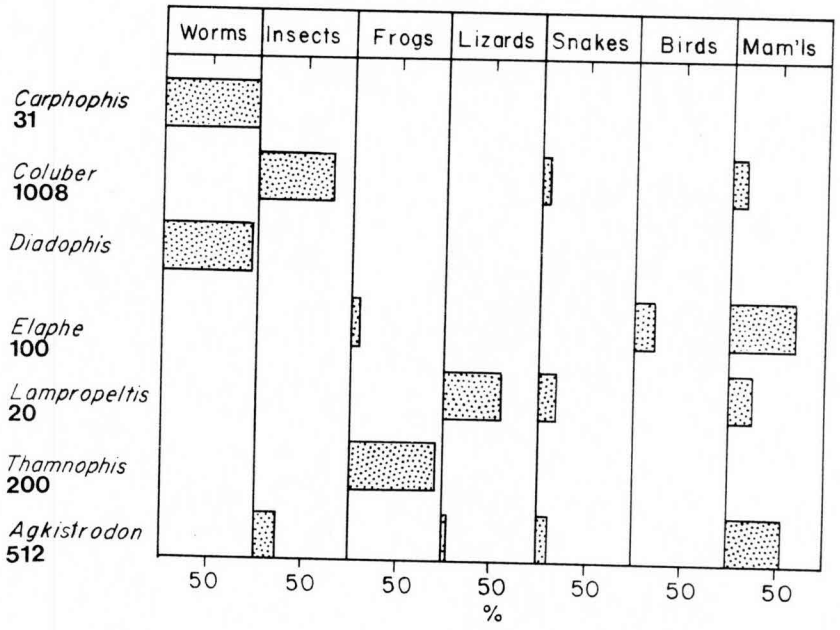

FIGURE 1. Percentages (by occurrence) of prey classes taken by seven species of Reservation snakes. Only prey classes which comprise at least 5 per cent of the species' diet are shown. *Thamnophis* includes records from Harvey County, Kansas. *Diadophis* is based on an estimate by H. S. Fitch. Sample size is listed below each generic name. *Lampropeltis* refers to *L. triangulum*.

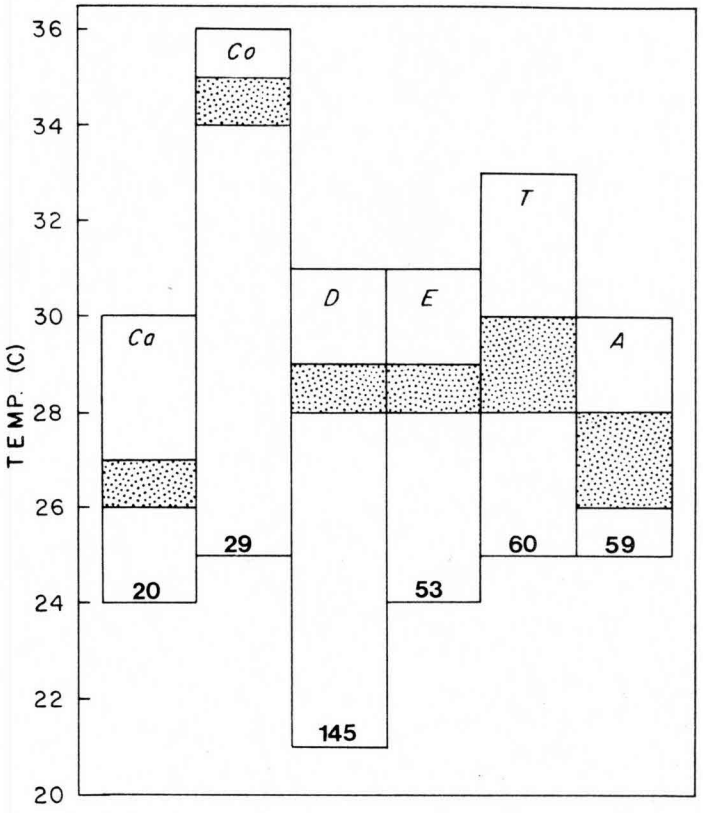

FIGURE 2. Preferred temperature ranges and preferred optimum temperatures (stippled areas) of six species of Reservation snakes. (See Fitch, 1956, for an explanation of preferred range and preferred optimum.) *Ca = Carphophis, Co = Coluber, D = Diadophis, E = Elaphe, T = Thamnophis, A = Agkistrodon.* Sample size appears at the bottom of each bar.

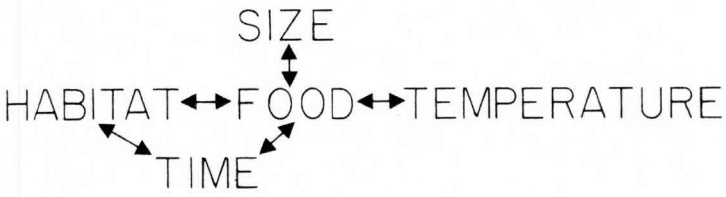

FIGURE 3. Relationship of five variables used in analyzing resource partitioning in Reservation snakes. A two-headed arrow between a pair of variables means that they are dependent; all others are independent.

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