Feeding habits and diet overlap of three species of garter snakes (*Thamnophis*) on Vancouver Island

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Closely related, sympatric species of organisms often show resource partitioning. In this study, diet partitioning is examined in three sympatric species of garter snakes (*Thamnophis*) on Vancouver Island. *Thamnophis sirtalis* feeds mainly on amphibians and earthworms, *Thamnophis ordinoides* on earthworms and slugs, and *Thamnophis elegans* on slugs, fish, and small mammals. *Thamnophis sirtalis* and *T. ordinoides*, which are more widely distributed on Vancouver Island than is *T. elegans*, have not been shown to modify their diets in the absence of *T. elegans*, but it is suggested that this lack of niche shift may be due to variations in prey availability. Neither innate differences in food preferences among the species nor interspecific competition for food have been shown to explain the observed differences in diet among the three species. Certain types of prey appear more likely than others to turn up in large numbers in stomach samples and it is suggested that this may be due to variations in ease of capture and (or) abundance. Possible explanations of the observed diets are discussed.

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On observe souvent que les espèces sympatriques et très apparentées partagent les ressources de l'environnement entre elles. Cette étude est une recherche des différences entre les habitudes alimentaires naturelles de trois espèces de couleuvres (*Thamnophis*) sur l'île de Vancouver. *Thamnophis sirtalis* se nourrit d'amphibiens et de vers de terre, *Thamnophis ordinoides* de vers de terre et de limaces, et *Thamnophis elegans* de limaces, de poissons, et de petits mammifères. *T. sirtalis* et *T. ordinoides* se rencontrent sur toute l'île de Vancouver tandis que *T. elegans* est limité à la partie sud-est; cependant *T. sirtalis* et *T. ordinoides* ne modifient pas leur diète en l'absence de *T. elegans*. On suggère que ce manque de déplacement des niches résulte des variations dans la disponibilité des proies. Apparemment, les différences entre les régimes des trois espèces ne sont pas entièrement attribuables aux préférences alimentaires ni à la compétition interspécifique. Quelques types de proies se retrouvent plus souvent que d'autres en grand nombre dans l'estomac de ces couleuvres; ces proies sont peut-être plus faciles à attraper ou plus abondantes que les autres. On discute de quelques explications possibles des différences alimentaires observées.

Introduction

The garter snakes (*Thamnophis*) represent one of the most widespread groups of snakes in North America, often occurring in communities of three or four species. As is frequently the case in groups of closely related, sympatric species, coexisting garter snake species have often been found to show resource partitioning, particularly in terms of diet (Hebard 1950; Carpenter 1952; Fouquette 1954; Fleharty 1967; White and Kolb 1974). In most studies, however, it has not been clear whether the resource partitioning was due to interspecific competition or to some other cause. Other authors (Jordan 1967; Hart 1975) have not found significant differences in diets of coexisting garter snakes. It has been suggested that competition for food is not important in influencing diets of garter snakes and that food habits are dictated more by factors such as food availability (White and Kolb 1974; Hart 1975), especially in northern areas where density-independent factors are more important than density-dependent factors in affecting snake population levels (Hart 1975).

Three species of garter snake occur on Vancouver Island. The Puget Sound red-sided garter snake (*Thamnophis sirtalis pickeringi*) and the northwestern garter snake (*Thamnophis ordinoides*) are found throughout the island, while the wandering garter snake (*Thamnophis elegans vagrans*) is restricted to the southeastern portion of the island. All three are locally sympatric on southern Vancouver Island. Elsewhere, both *T. sirtalis* and *T. elegans* are wide-ranging species and the observations of many authors indicate that both species eat a wide variety of prey over their geographic ranges, although diets at particular localities may be more restricted. *Thamnophis ordinoides* occupies a smaller total geographic range and has a more restricted diet. To my knowledge, however, little attempt has been made to examine the diets of these three snake species where they occur in sympatry. An earlier study (Carr and Gregory 1976) of the responses (in terms of tongue flicks) of young of the three species to surface odors of various possible prey suggested that potential food niche breadths and overlaps are very great. The objectives of this paper therefore are to describe the actual diets of the three species in the field on Vancouver Island and discuss possible causes of any patterns of resource use observed.

Methods

Snakes of all three species were collected from various locations on Vancouver Island during the summers of 1974, 1975, and 1976. No particular sampling plan was followed with respect to these locations, and sampling intensity varied from site to site. The number of snake species found at various locations varied from one to three, although there were usually at least two. Each individual snake was palpated to force regurgitation of stomach contents, which were preserved in 10% formalin for later examination in the laboratory. Prey were then grouped into broad taxonomic categories and the data recorded as numbers of snakes containing a particular food type. Repeated observations on the same individual snakes were assumed to be independent since they were generally quite separated in time. In the analysis of these data no distinction was made between snakes containing a single individual of a particular prey type and those containing several individuals since the number eaten might depend simply on the number encountered at any one time rather than the active selection of several individual items by the snake. Also, it was often difficult to determine exactly how many prey items were present. No attempt was made to determine the volume or mass of each prey type since stages of digestion varied considerably. Snakes encountered in the process of eating a prey item were recorded as containing that prey item.

The data from all localities were pooled to yield an overall picture of diet in the three species. This might be criticized on the grounds that it would be more reasonable to consider the diet of each species separately in the presence and absence of the other species in order to detect any niche shifts. Comparisons of this type, however, depend on conditions being similar in all environments (except for the presence and absence of the potential competitors). In fact, if the availabilities of various kinds of food differ substantially among environments, niche shifts may not occur.

The null hypothesis of no differences in diet was tested by means of a contingency table (χ^2). Niche breadth along the food-type dimension was measured for each species using a measure of diversity given by MacArthur (1972, p. 197). This diversity index is calculated as $B = 1/\sum^{n} p_i^2$ (where n = number of different resources, p_i = proportion of all resources actually used, which is made up of resource i); the value of B varies from 1 to n. Niche overlap for each pair of species was measured using a symmetrical measurement given by Pianka (1973). Using this measurement, overlap is calculated as $O_{jk} = \sum^{n} p_{ij}p_{ik} / \sqrt{\sum p_{ij}^2 \sum p_{ik}^2}$ (where p_{ij} and p_{ik} are p_i values for species j and k respectively); O_{jk} varies from 0 (no overlap) to 1 (total overlap) in value. The niche overlap measurements for each pair of species were averaged to estimate mean niche overlap.

Using those stomach samples in which numbers of individual prey eaten could be easily estimated, frequencies of occurrence of different numbers of individual items were recorded for each prey type and each snake species. Instances of snakes containing more than one food type were also noted. Finally, since snakes were individually marked, repeated stomach samples were obtained for a few snakes. Temporal variations in diet were not analyzed.

Results

In all, 179 stomach examinations of *T. sirtalis*, 387 of *T. ordinoides*, and 499 of *T. elegans* were made; of these 78, 149, and 154 yielded food for the three species respectively. Table 1 summarizes the data on stomach contents. *Thamnophis sirtalis* was found to feed primarily on amphibians and earthworms. Eight species of amphibians were eaten (six salamanders, two anurans) at three stages of the life cycle (larvae, metamorphosing individuals, adults); the western toad (*Bufo boreas*) was the only native amphibian not recorded. Earthworms were not identified to species nor were the bird and leech. *Thamnophis ordinoides* fed exclusively on slugs (various species) and earthworms (not identified). *Thamnophis elegans* had the most varied diet, but fed mainly on slugs (various species), fish (including unidentified intertidal sculpins and blennies, three-spined sticklebacks, *Gasterosteus aculeatus*, and introduced freshwater fish such as pumpkinseed sunfish, *Lepomis gibbosus*), and small mammals (all Townsend's vole, *Microtus townsendi*, except for one wandering shrew, *Sorex vagrans*). Other items eaten by *T. elegans* represented a very small proportion of its total diet. Of these minor items, only the reptiles were identified to species: all were individuals of *T. ordinoides*. In both instances where amphibians were recorded, larval anurans had been eaten. In *T. sirtalis* and *T. elegans*, the occasional miscellaneous invertebrates obtained from stomachs were mostly small arthropods and it was not clear whether they had actually been eaten by the snake or been contained within some other prey eaten by the snake. In two cases, the miscellaneous invertebrates obtained

TABLE 1. Numbers of stomach examinations yielding various food types. Categories of prey types are ordered in such a way as to show most clearly diet differences and overlaps

Food type	*T. sirtalis*	*T. ordinoides*	*T. elegans*
Empty stomachs	101	345	238
Amphibians	41		2
Earthworms	24	67	5
Slugs		63	60
Fish			41
Mammals			17
Birds	1		2
Leeches	1		
Reptiles			4
Vertebrate remains	1		
Miscellaneous invertebrates	4		4
Unidentified remains	13	39	32

TABLE 2. Summary of niche breadth and niche overlap calculations; symbols as in text

	T. sirtalis		*T. ordinoides*		*T. elegans*	
Food type	f_i*	p_i	f_i	p_i	f_i	p_i
Amphibians	41	0.612			2	0.015
Earthworms	24	0.358	67	0.515	5	0.038
Slugs			63	0.485	60	0.458
Fish					41	0.313
Mammals					17	0.130
Birds	1	0.015			2	0.015
Leeches	1	0.015				
Reptiles					4	0.031
Σ	67	1.000	130	1.000	131	1.000
B	1.987		1.998		3.054	
O_{jk}		0.367				
			0.057			
					0.597	

NOTE: Mean O = 0.340.
*f, absolute frequency.

from *T. sirtalis* were tapeworms (order Proteocephalidae). These probably originated in frogs eaten by the snakes (Mace, personal communication). In comparing the diets of the three species, only prey types which comprised 10% or more of the diet of at least one of the three species were considered. These prey types were amphibians, earthworms, slugs, fish, and mammals. The χ^2 obtained from the resulting 3 × 5 contingency table was 320.97 with 8 df ($P < 0.001$), indicating significant differences among the diets of the three species.

There was no obvious relationship between the number of snake species present and diet in any particular species among locations. No new prey types were taken by any species in any location, although the proportions of various prey taken differed somewhat from location to location. Sample sizes were small for several localities, however, so that variation among sites was not analyzed.

Table 2 summarizes the calculations of niche breadths and niche overlaps; the categories of vertebrate remains, miscellaneous invertebrates, and unidentified remains were not used in these calculations. *Thamnophis elegans* had the broadest food type niche and *T. sirtalis* the narrowest. While *T. sirtalis* and *T. elegans* barely overlapped in diet, *T. ordinoides* overlapped extensively with both of them; its combined overlap with the other two species was nearly total since it had no exclusive food resources.

In cases where the number of individual prey in a stomach sample could be estimated, most stomachs contained one prey item only. Slugs were often consumed in large numbers, averaging 1.50/stomach in *T. ordinoides* and 2.84/stomach in *T. elegans* (one *T. elegans* contained 20 slugs). *Thamnophis elegans* also tended to contain fairly large numbers of fish (average of 1.36/stomach). Otherwise, the average number of items (of a given prey type) per stomach ranged from 1 to 1.17 (except for the two instances of *T. elegans* feeding on amphibians, in which four larval anurans were taken in each case). These averages are all based only on stomach samples containing the prey type in question. They are also conservative figures in that the number of individual items present may have been underestimated in some cases, especially where many prey items were present and (or) fragmented. Combinations of two different prey types were found infrequently in stomach samples, but in 20 of 23 cases, slugs were one of the prey types. Earthworms were present in 16 of these samples and the combination of slug–earthworm was represented by 14 observations (13 *T. ordinoides* and 1 *T. elegans*). Only 11 individual snakes were caught more than once (average of 2.1 captures) with food in their stomachs; of these, 9 had eaten the same food type (either earthworms or slugs) on two occasions, although 2 of the 9 also consumed other prey.

Discussion

Thamnophis sirtalis is the most widespread member of its genus in North America. The voluminous literature on food habits of this species has been summarized by Fitch (1965); his summary suggests that while *T. sirtalis* is a generalized feeder, amphibians and earthworms form the principal part of its diet. Evidently, however, there is some geographic variation in diet: earthworms tend to be more important in eastern North American

TABLE 3. Summary of feeding habits of *T. sirtalis*, *T. ordinoides*, and *T. elegans vagrans* based on literature survey for western North America

Species	Locality	Dietary items	Reference
T. sirtalis	Powell River, B.C.	Intertidal fish	I. Thornton (personal communication)
	Near Comox, B.C.	Robin nestlings	K. Martin (personal communication)
	Washington	"Aquatic animals" (especially salamanders), young bird	Hebard (1951)
	Friday Harbor, Washington	Various species of intertidal fish	Batts (1961)
	Oregon	Amphibians, fish	Stewart (1968)
	California	Fish, amphibians, slugs, earthworms, leeches	Fitch (1941)
	Sagehen Creek, California	Amphibians, fish, meadow mice, leeches	White and Kolb (1974)
	Montana	Leeches, amphibians, earthworms, slugs, small mammal, bird	Anderson (1977)
T. elegans vagrans	Qualicum Beach, B.C.	Small mammals (chiefly voles), fish, earthworms, slugs	N. Dawe (personal communication)
	Mittlenatch Is., B.C.	Snails (intertidal and terrestrial), polychaetes, crabs, grasshoppers, various species of intertidal fish, comorant nestlings (plus embryo remains and yolks of broken eggs), gull nestlings, guillemot nestlings, crow eggs and young, white-footed mice, regurgitated gull foods, camper refuse	Campbell (1969)
	Washington	"Aquatic animals", small rodents (chiefly voles)	Hebard (1951)
	California	Fish, amphibians, slugs, rodents, lizards	Fox (1952)
	California	Sparrows, lizards, amphibians, slugs, fish, worms, mice, leeches, snails	Fitch (1941)
	San Bernardino Mtns., California	Beetles, toads, frogs, lizards, ants, spiders, bird	Cunningham (1955)
	Montana	Leeches, slugs, fish, amphibians, small mammal, bird	Anderson (1977)
	Utah	Lizards	Knowlton (1946)
	Utah	Fish, amphibians, lizards, small rodents, insects	Tanner (1949)
	New Mexico	Earthworms, fish, amphibians	Fleharty (1967)
T. ordinoides	Qualicum Beach, B.C.	Slugs, earthworms	N. Dawe (personal communication)
	Washington	Mainly slugs	Hebard (1951)
	Oregon	Mainly slugs	Stewart (1968)
	California	Slugs, earthworms, plethodontid salamanders, red-legged frog	Fitch (1941)

populations while amphibians are more commonly eaten in the west. The studies of Carpenter (1952) and Gregory and Stewart (1975) support this conclusion, as does this study. Items in the diet of western populations of *T. sirtalis* have been recorded by several authors and are summarized in Table 3. No distinction has been made in Table 3 among the various subspecies of *T. sirtalis* as it is not apparent to me either from the literature or from personal observation that ecological differences are correlated with subspecific designations.

In the case of *T. elegans*, however, different subspecies are often ecologically quite different. This western species is comprised of a complex of different types whose taxonomic relationships are not clear (Fitch 1948; Fox 1948). Consequently, only the reported food habits for *T. elegans vagrans* are considered here (Table 3). (*Thamnophis elegans vagrans* is an extremely versatile feeder, perhaps the best example of its generalized food habits being provided by Campbell (1969). Campbell based his study mainly on actual observations of feeding on Mittlenatch Island off the east coast of Vancouver Island; *T. elegans vagrans* is the only snake on Mittlenatch Island and feeds on a very large variety of prey there (Table 3). Most other authors, however, have also reported a fair variety of food types in the diet of this subspecies (Table 3). If other subspecies of *T. elegans* were included, the observed diet would be expanded even further.

In contrast with the first two species, *T. ordinoides* is almost invariable in its diet (Table 3). Except for Fitch's (1941) study, only slugs and earthworms have been reported as dietary items; Fitch recorded the red-legged frog as a prey only once.

Little work has been done on resource partitioning among these three snake species. Stewart (1968) examined coexisting *T. sirtalis* and *T. ordinoides* in Oregon, while Dawe (personal communication) studied coexisting *T. ordinoides* and *T. elegans* on Vancouver Island. Both obtained generally similar results to those reported here. Hebard (1951) found all three species coexisting in close proximity at his study site in Washington and concluded that *T. sirtalis* fed mainly on aquatic animals in a marsh and *T. elegans* preyed on mice while *T. ordinoides* fed on slugs. Batts (1961) found that only *T. sirtalis* fed on intertidal fish at Friday Harbor, Washington, although both other snake species were found above the intertidal zone. Batts did not report on the food habits of *T. elegans* and *T. ordinoides* at this locality. The reason for the difference between Batts' observations and mine regarding *T. sirtalis* is not clear, but I am planning to investigate diets of all three species at Friday Harbor. Anderson (1977) examined the diets of sympatric *T. sirtalis* and *T. elegans* at several localities in Montana. Although considerable variation was noted among localities and diets of the two species often overlapped, *T. sirtalis* fed mainly on leeches and amphibians, while *T. elegans* generally ate leeches, slugs, amphibians, and fish. In this study, the pattern of resource use by the three species on Vancouver Island is quite clear: *T. sirtalis* feed mainly on amphibians and earthworms, *T. ordinoides* on earthworms and slugs, and *T. elegans* on slugs, small mammals, and fish. Although the proportions of these various prey types taken apparently vary from locality to locality, I have found no sites where other major prey types are consumed by any of the three species.

Arnold (1972) observed that sympatric snake species tend to eat different types of prey but stated that this could be due to any or a combination of habitat differences, temporal differences in foraging activity, differences in prey size eaten, and innate differences in prey preferences. Any or all of these could contribute to the explanation of the pattern of resource partitioning observed in this study. It is probably worthwhile to consider the possibility of innate differences in prey preferences first. Casual observation of captive adult specimens of Vancouver Island species suggests that prey types commonly eaten in nature are preferred, but since early experience and imprinting may considerably influence later food preferences (Fuchs and Burghardt 1971), this observation does not provide evidence of innate differences in feeding habits. Possibly more to the point is the observation from the literature (Table 3) of the wide spectrum of food items recorded in natural diets of *T. sirtalis* and *T. elegans* at various localities and the fact that most records of food habits for coexisting pairs of these species suggest some degree of resource partitioning. Arnold's (1977) study, however, indicates that geographic variation in propensities to eat certain kinds of prey may sometimes exist.

One of the most profitable approaches to investigating innate food preferences of snakes has been to score tongue flick – attack responses of newborn snakes to chemical extracts of various prey types. Frequently, good correlations have been found between response scores and real diets in the field (Burghardt 1968, 1969, 1970). In an earlier study, Carr and Gregory (1976) tested the responses of young garter snakes (in terms of tongue flicks only) to surface chemical stimuli of various prey types and found that the relative responses of the three species from the Vancouver Island area to the various stimuli were quite different from the actual diets observed in the field. If it is assumed (perhaps incorrectly) that the tongue flick data are simple indicators of relative food preferences and that food preference is an important determinant of diet in these snakes, then the potential niche breadth of each species is great and all potential niche overlaps are nearly maximum. There are a number of objections to regarding the spectrum of such responses as a measure of the potential diet of a species (Carr and Gregory 1976), but it is at least a first approximation. Presumably then, the potential diets of the three species as indicated in the laboratory may be modified by other factors in the field and differences in actual food habits are not attributable solely to innate differences in food preferences. A more definitive study of innate food preferences, however, might alter this conclusion.

Schoener (1974), in surveying the literature on niche partitioning (mainly for terrestrial vertebrates), concluded that separation is most common along habitat dimensions, with food-type and temporal dimensions being the next most important dimensions respectively. Obviously, it is difficult to estimate the relative importance of these various dimensions in causing niche differentiation. At present, I have no data suggesting niche separation of the three species in my study area along temporal dimensions. On the other hand, some differences in habitat use are apparent. Although *T. sirtalis* occupies a wide variety of habitats, it tends to be most abundant near bodies of water (Fitch 1941; Stewart 1968; personal observation). *Thamnophis elegans vagrans* also tends to occur near bodies of water (Fitch 1941; personal observation) but may also occur in open, terrestrial habitats (Campbell 1969). *Thamnophis ordinoides* is a strictly terrestrial snake, occurring most commonly in cleared areas but also occasionally in wooded areas (Fitch 1941; Stewart 1968; personal observation). In general, *T. ordinoides* and *T. elegans* seem to prefer open habitats; only *T. sirtalis* appears to inhabit heavily forested situations to any degree. Coexistence of the three is not uncommon, however, so that habitat separation alone may not adequately explain the diet differences observed. At the same time, the significance of habitat heterogeneity is worthy of further investigation. In other studies, habitat differences have apparently been more important. White and Kolb (1974) concluded that differences between food habits of *T. sirtalis* and *T. elegans elegans* in their study area were based mainly on differential habitat use.

Some authors (White and Kolb 1974; Hart 1975) have felt that prey availability is an important factor in determining diets of garter snakes. Although most prey types recorded in this study are widespread on Vancouver Island, variations in their availability may explain differences in the proportions of various food types taken by each snake species at different localities. The among-sites variation in food habits observed by Anderson (1977) may also be related to variations in food availability. Certainly, prey species within any prey category may be taken according to their availability (Fitch 1941; Gregory and Stewart 1975). Variations in the availability of certain food types may also explain why *T. sirtalis* and *T. ordinoides* do not exploit prey normally eaten by *T. elegans* where these snakes occur outside the range of *T. elegans* on Vancouver Island. It is not yet known what factor(s) limit the range of *T. elegans* on Vancouver Island, but its range does apparently coincide with the area of greatest availability of its two exclusive food types, nonsalmonid fish and small mammals (specifically *Microtus*). Fish consumption appears to be heaviest in warm, intertidal waters and where freshwater fish such as pumpkinseed sunfish (*Lepomis gibbosus*) have been introduced in southern Vancouver Island; sculpins and sticklebacks are also frequently taken from streams near salt water. Otherwise, throughout most of the interior of the island, only salmonid fish occur and these seem to be rarely (if ever) eaten by snakes. Fitch (1941) found no evidence of either *T. sirtalis* or *T. elegans vagrans* feeding on salmonids in California, even though both ate other species of fish. Perhaps salmonids are too difficult to catch because of their behavior and habitat preferences. Other authors, however, have reported salmonids in the diet of *T. elegans vagrans* (Tanner 1949; Anderson 1977) and captive snakes will consume almost any type of fish offered to them, so that this question has yet to be resolved. Other species of garter snakes are also known to eat salmonids (Fitch 1941; Fleharty 1967). In any case, it does not appear that salmonids are normally taken by snakes on Vancouver Island, so that there appears to be little in the way of fish resource for snakes to exploit over much of the island. Nevertheless, local naturalists have occasionally seen snakes in tide-pool areas outside the range of *T. elegans*. Since Batts (1961) reported *T. sirtalis* feeding on intertidal fishes at Friday Harbor, Washington, *T. sirtalis* is probably involved in such sightings; Thornton, (personal communication) has confirmed seeing *T. sirtalis* in intertidal waters at Powell River, B.C. Even in the more sheltered areas of southeastern Vancouver Island, however, intertidal feeding by *T. elegans* is relatively rare so that it seems unlikely that the colder and (or) wave-pounded shores around the rest of the island would often provide attractive foraging areas for snakes. This point probably merits further study as it may provide an actual example of niche shift.

As for small mammals, *T. elegans* in my study area seems to feed almost exclusively on *Microtus townsendi*. Although *Microtus* occurs all over Vancouver Island, it is not abundant in the heavily forested areas outside the range of *T. elegans*, even after these areas have been logged over (Campbell, personal communication). The white-footed mouse (*Peromyscus maniculatus*) is abundant throughout the island, but I have no evidence that *T. elegans* takes this species as prey in the wild. Campbell (1969) found that *T. elegans* ate *Peromyscus* on Mittlenatch Island, off the east coast of Vancouver Island, and captive *T. elegans* will readily eat this mouse. *Peromyscus* is a faster, more active animal than is *Microtus* and may be difficult for snakes to capture in most situations. Dawe (personal communication) has found two instances of *T. elegans* eating shrews (*Sorex*) at Qualicum Beach, Vancouver Island, but there is no evidence that shrews figure importantly in the diet of this snake species anywhere.

Finally, it is possible that the diet differences observed are partly the result of interspecific competition for food. If this competition is ongoing, diet differences should be phenotypic and it should be possible to observe diet shifts under appropriate circumstances. As noted above, the lack of diet shift by *T. sirtalis* and *T. ordinoides* in the absence of *T. elegans* on Vancouver Island does not provide evidence against competition because the availability of different prey types is not constant in all parts of the island. Consequently, only inferential evidence is available at this time. At first glance, garter snakes would appear unlikely to compete for food, mainly because of their low annual food requirements (Porter and Tracy 1973), suggesting that they should rarely be expected to encounter absolute shortages of food. Nevertheless, changes in sizes of snake populations have sometimes been correlated with variations in food supply (Fitch 1965; Parker and Brown 1973; Platt, personal communication). Stewart (1968) felt that there was probably a shortage of food for large *T. sirtalis* in late summer in one of his study sites.

If snakes do compete for food, it is probably through an exploitative interaction based on differential abilities to capture various kinds of prey. In particular, active prey (frogs, mice, fish, etc.) may not be exploited efficiently even by species which regularly feed on them. In another study (Gregory, unpublished data), I showed that red-legged frogs (*Rana aurora*) exhibit effective predator avoidance behavior in the presence of moving snakes (*T. sirtalis*) and are generally difficult for snakes to catch. Casual observation of snakes in general leads me to believe that snakes are often not very efficient at capturing active prey; captive snakes frequently seem to catch active prey only because of the restrictive confines of the cage. If so, slight differences in capturing abilities of coexisting snake species for various prey types could lead to food partitioning, especially if food is not very abundant to begin with.

Prey types which are less capable of escape behavior are probably more easily caught by snakes when encountered and may sometimes be eaten in large numbers (e.g. slugs). I have also observed *T. sirtalis* consuming large numbers of earthworms which had emerged in abundance in a field in southern Ontario following a heavy rain. Although my data are few, slugs and earthworms may be relatively likely to appear with other prey in stomach samples and to be repeatedly eaten by individual snakes. This seems to be true even if the data for *T. ordinoides* are ignored and may reflect the ease of capture and (or) abundance of such prey, although other explanations are possible. In addition, prey which are normally difficult to catch may sometimes be taken in greater quantities because of very high abundance and (or) unusual ease of capture. Intertidal fish, for example, are often found in tide pools and other confined areas and are probably more easily caught than are fish in other situations. Also, in this study, two *T. elegans* containing several fish each were found foraging in a stagnant pond full of dead and dying sticklebacks. Similarly, three mammals found in one *T. elegans* were all young *Microtus* and had probably been obtained from a nest.

Obviously, several unanswered questions remain concerning the feeding ecology of garter snakes on Vancouver Island. Two of the more interesting ones are (*a*) how do prey abundance and 'catchability' affect diet composition, and (*b*) are differences in diets of coexisting snakes related to differences in prey sizes taken? These and other questions will be addressed in future studies.

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