Ecology, 63(5), 1982, pp. 1232–1236

GARTER SNAKE DIETS IN A FLUCTUATING ENVIRONMENT: A SEVEN-YEAR STUDY[1]

DONALD G. KEPHART AND STEVAN J. ARNOLD
Department of Biology, The University of Chicago, Chicago, Illinois 60637 USA

Abstract. Diets of the terrestrial garter snake (*Thamnophis elegans*) and the common garter snake (*T. sirtalis*) were studied during seven consecutive summers at a lake in northern California, USA. The snakes were opportunistic feeders; their diets varied dramatically from year to year, parallel with the abundance of prey. Snakes foraged more successfully, judging from the incidence of stomachs containing prey, in years when metamorphic toads (*Bufo boreas*) were available. Breeding failure in toads was associated with lowering lake level.

Key words: Bufo; *competition; diet; Eagle Lake; environmental fluctuation; fish; niche overlap; optimal foraging; pluvial lake; postpluvial aridity; temporal variation;* Thamnophis.

INTRODUCTION

During the Pleistocene epoch in the Great Basin of western North America, cool pluvial periods alternated with warmer interpluvial periods. During pluvial periods glaciers marched in the mountains, and lakes filled the lowland basins, but during interpluvial periods, the glaciers retreated and pluvial lakes evaporated. The general climatic trend since the last pluvial period, ≈10 000 yr ago, has been a steady increase in aridity. Although lake levels have fluctuated during the current postpluvial period, the general climatic trend has been towards evaporation and extinction of pluvial lakes (Antevs 1948, Morrison 1965).

Eagle Lake is an isolated basin on the western edge of the Great Basin in Lassen County, California. Its fish fauna clearly indicates its former close proximity to pluvial Lake Lahotan, which once covered much of western Nevada (Snyder 1915, Hubbs and Miller 1948). The water level of Eagle Lake has fluctuated during the postpluvial period as revealed by the presence of wave-cut terraces far above the present lake, analysis of submerged trees, and historical records (Grinnell et al. 1930, Harding 1935). Since we began fieldwork at Eagle Lake in 1974, the water level has dramatically fluctuated, with a net lowering of 2 m.

This paper reports the diet of the garter snake *Thamnophis elegans* over a 7-yr period at Eagle Lake. The period of study is far too short to reveal how this species reacted to the complex environmental changes of the postpluvial period. However, our study does show how diet changed during a period of fluctuating lake level. Since *T. elegans* is distributed throughout the Great Basin, the events we observed at Eagle Lake may have occurred on numerous postpluvial lake shores.

Year-to-year variation in snake diet has not previously been addressed. Garter snake diets, for example, have been recorded for many individual species (e.g., Lagler and Salyer 1945, Hamilton 1951, Asplund 1963, Fitch 1965, Clark 1974, Gregory and Stewart 1975, Arnold 1981*a*). In several cases, two or more coexisting species have been studied with respect to diet overlap and competition (e.g., Carpenter 1952, Fouquette 1954, Fleharty 1967, Stewart 1968, White and Kolb 1974, Gregory 1978). Either these studies were performed during a single season, or records were pooled across years. Arnold and Wassersug (1978) reported shifts in foraging behavior in response to the metamorphosis of toads, but quantitative data were not presented. Microgeographic variation in garter snake diets in the Eagle Lake region is reported by Kephart (1982).

STUDY AREA AND METHODS

Eagle Lake (elevation 1555 m) straddles an ecotone between the Transition and Upper Sonoran Life Zones (Grinnell et al. 1930). Our study site at Pikes Point (40°33′24″N, 120°47′5″W; "locality 3" of Arnold and Wassersug 1978), at the southeastern end of the lake, lies in a yellow pine forest characteristic of the Transition Life Zone. Pikes Point consists of a series of basaltic ridges that extend into the lake and interdigitate with small meadows (Fig. 1). These meadows were innundated during years of high lake level (1974–1975) and became marshes with stands of emergent bulrushes (*Scirpus* sp.). The marshes disappeared as the lake level lowered, leaving relatively dry, grassy meadows between the rocky ridges.

The site was visited each summer from 1974 to 1978 for periods of 2–4 wk and for much longer periods in 1979 and 1980. For consistency of comparison across years, only the June and July records will be reported here.

Snakes were collected by hand every several days and then returned to their site of capture the following

[1] Manuscript received 19 February 1981; accepted 25 June 1981; final version received 14 January 1982.

FIG. 1. Pikes Point, the study site at Eagle Lake, California, in July 1976. One of several adjacent, basaltic ridges that protrude into the lake is shown at the center of the figure. One of the small meadows between these ridges is also visible just below the rocky point. Sagebrush (*Artemisia* sp.) is visible in the foreground, and yellow pine forest (*Pinus jeffreyi* and *P. ponderosa*) is in the background.

day. Each animal was forced to regurgitate (Carpenter 1952), and (beginning in 1978) was given an individually coded ventral scale clip for future identification, using a technique similar to that of Brown and Parker (1976). Recovered prey items were identified and counted on the spot. The snakes did not appear to be injured by this procedure, and many of them were recaptured over successive years of this study.

RESULTS

We obtained 688 prey items from 493 *Thamnophis elegans* and 36 *T. sirtalis* during this study. The yearly tallies are presented in Table 1. The diet of *T. elegans* will be discussed in greater detail than that of *T. sirtalis* because the sample sizes are much larger. For simplicity of presentation, prey items will be grouped into three categories: fish (speckled dace [*Rhinichthys*

TABLE 1. Summer diets of *Thamnophis elegans* and *T. sirtalis* at Eagle Lake, California, 1974–1980. N = the total number of snakes captured and examined for stomach contents. "Number of stomachs" refers to the number of stomachs containing prey of a particular kind. Since some stomachs contained more than one kind of prey, the "total number of stomachs" (second to last column) sometimes sums to more than the total number of stomachs containing prey.

				Stomachs containing prey							
				Anurans		Fish		Leeches		Total	
Year	Species	N	Number of stomachs empty	Number of stomachs	Number of items	Number of stomachs	Number of items	Number of stomachs	Number of items	Number of stomachs	Number of items
1974	*T. elegans*	14	5	5	24	3	4	1	1	9	29
	T. sirtalis	1	0	1	9	0	0	0	0	1	9
1975	*T. elegans*	41	10	27	92	3	3	2	3	32	98
	T. sirtalis	4	2	2	30	0	0	0	0	2	30
1976	*T. elegans*	69	40	2	2	23	28	5	12	30	42
	T. sirtalis	4	3	0	0	1	1	0	0	1	1
1977	*T. elegans*	73	39	0	0	28	115	7	9	35	124
	T. sirtalis	8	5	0	0	0	0	3	5	3	5
1978	*T. elegans*	123	62	40	187	10	10	15	25	65	222
	T. sirtalis	16	7	9	60	1	1	1	4	11	65
1979	*T. elegans*	102	86	0	0	15	22	1	1	16	23
	T. sirtalis	3	3	0	0	0	0	0	0	0	0
1980	*T. elegans*	71	49	0	0	11	13	12	27	23	40
	T. sirtalis	0	0	0	0	0	0	0	0	0	0
Total	*T. elegans*	493	291	74	305	93	195	43	78	210	578
	T. sirtalis	36	20	12	99	2	2	4	9	18	110

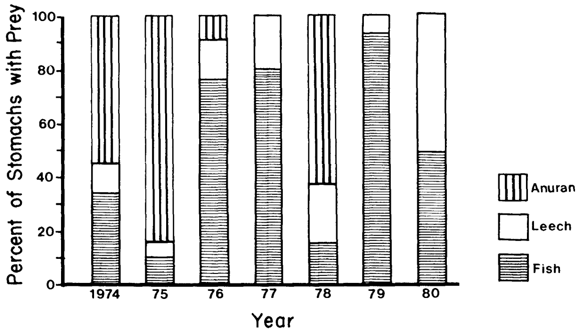

FIG. 2. Summer diets of *T. elegans* at Eagle Lake. The histograms show the proportion of stomachs containing prey in each of the three indicated categories.

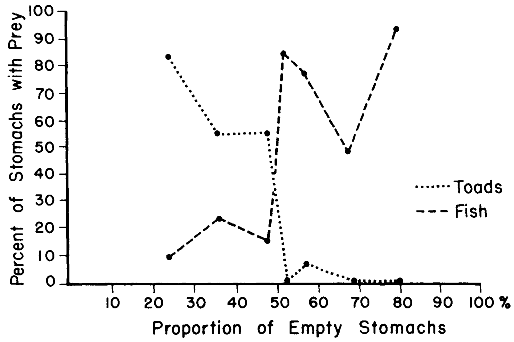

FIG. 3. Dietary shift in *T. elegans* at Eagle Lake as a function of overall prey availability (as indicated by the incidence of empty stomachs). The proportions of stomachs containing toads (*Bufo boreas*) or fish are shown as functions of the proportion of stomachs in the same sample that were empty. Each sample point represents a different year.

osculus], Lahontan redside [*Richardsonius egregius*], Tui chub [*Gila bicolor*], and, rarely, small Tahoe sucker [*Catostomus tahoensis*]), anurans (western toads [*Bufo boreas*], and, rarely, Pacific tree frogs [*Hyla regilla*]), and leeches (*Erpobdella punctata*).

Diets of *T. elegans* varied tremendously among years ($\chi^2 = 211.0$, 18 df, $P < .0001$, based on number of stomachs, including "empty;" $\chi^2 = 558.6$, 12 df, $P < .0001$, based on number of items; Fig. 2).

Snakes appeared to shift their foraging site in response to availability of different prey, as indicated by Arnold and Wassersug (1978). Metamorphic *Bufo boreas* were abundant in the meadows in 1974, 1975, and 1978, and garter snakes were correspondingly common there. In years when metamorphic toads were absent or rare (1976, 1977, 1979, 1980), garter snakes were found primarily on the rocky ridges, where they foraged along the lake shore for fish and leeches. In these years snakes were rare in the meadows. Toads bred successfully only in years when the lake flooded the low-lying meadows and created extensive areas of suitable habitat. Thus, fluctuations in the availability of toads were related to lake levels during the years of our study (correlation between June water level and incidence of toads in the diet, $r = .80$, 5 df, $P < .05$).

The shift in foraging site and diet may be explained by the fact that toads are apparently the most profitable prey at Eagle Lake (i.e., easiest to capture). A greater proportion of the *T. elegans* population had prey in their stomachs in years when toads predominated in the diet ($r = .85$, 5 df, $P < .05$; Fig. 3). Direct behavioral observations of foraging snakes also indicate that toads are particularly easy prey. Predation of *Bufo* was associated with synchronous metamorphosis that produced localized aggregations of metamorphic toads at extraordinary densities (Arnold and Wassersug 1978). At Colman Lake (7.5 km southwest of Eagle Lake), garter snakes foraging in such aggregations captured >1 metamorphic toad/min. In contrast, at another site near Eagle Lake, garter snakes foraging midwater in dense schools of fish captured ≈1 fish/h. Both *T. elegans* and *T. sirtalis* appear inept at capturing fish unless the fish are stranded, as in a drying pool (Drummond 1980, D. G. Kephart and S. J. Arnold, *personal observation*). However, such favorable situations do not occur at Eagle Lake. Instead, snakes typically captured fish by ambushing them among rocks or by swimming through fish schools.

Diet specialization by individual snakes in the field is an issue of some interest. Twenty-one marked *T. elegans* were caught with prey in their stomachs on more than one occasion during this study. The kinds of prey taken on the first and second captures were not associated, based on a 3 × 3 contingency table with the prey categories: anurans, fish, and leeches ($\chi^2 = 3.04$, 4 df, $.75 > P > .50$). This is apparently the first test for individual diet specialization in a free-ranging population of reptiles.

The diets of *T. sirtalis* and *T. elegans* included the same prey, but *T. sirtalis* mainly preyed on anurans (Table 1). *T. sirtalis* relied heavily upon toads in the same years as *T. elegans*, but seemed less able to switch to fish as an alternative prey ($\chi^2 = 4.30$, 1 df, $P < .05$). No *T. sirtalis* were found in the study area after the last two toadless years.

DISCUSSION

A diet shift in the garter snake *Thamnophis elegans* was associated with a net lowering of water level at Eagle Lake over a 7-yr period. As the lake level receded, toads (*Bufo boreas*) stopped breeding, and metamorphic toads disappeared from the diet. Breeding failure in the toads may have been due to changing vegetation, alkalinity, or other factors. The lowering lake level drained shallow marshes containing bulrushes (*Scirpus* sp.). A recently exposed shoreline that lacks emergent vegetation may not be satisfactory for toad breeding. On the other hand, the alkalinity of the lake may have increased to a critical level. Eagle Lake is usually sufficiently alkaline to prevent establishment of non-native trout (Busack et al. 1980).

These observations of breeding curtailment in a toad, and diet shift in a snake, indicate that significant ecological events are associated with even geologically brief periods of lowering lake level. Since fluctuating lake levels have characterized the Great Basin during the entire postpluvial period, studies of contemporary ecological concomitants may be useful for reconstruction of changing paleoenvironments.

The diet shift observed in *T. elegans* is consistent with models of optimal foraging (cf. Pyke et al. 1977). That is, the diets of the snakes seem to be determined by the prey with more favorable search and capture costs (toads), despite the availability of alternative prey in all years (fish). Snakes are long lived relative to the time scale of these changes (e.g., of the 40 *T. elegans* marked in 1978 that were ever recaptured, 75% were seen more than a year later). Consequently the observed diet shift reflects foraging choices by individual snakes and not a population turnover.

Although the absence of diet specialization by individual *T. elegans* in the field may seem surprising in light of laboratory diagnoses of feeding polymorphism in newborn snakes from this same population (Arnold 1977, 1981*a, b, c*), these two results are actually compatible. The laboratory studies demonstrated discrete, heritable polymorphisms for refusal of specific prey types, not snakes specialized to feed on only one class of prey. The simple contingency table analysis performed on the field records would have been quite sensitive to specialists, but much less so to generalists who simply failed to consume one prey type.

Environmental fluctuations of the kind observed in this study may constitute fluctuations in selection and promote random drift in gene frequencies (Wright 1931, 1948, 1969, 1977). Drift may enable a population perched on a suboptimal adaptive peak to cross a saddle and then advance towards a higher peak under the force of mass selection (selection at the level of individuals). Unlike drift due to sampling accidents, drift due to fluctuations in selection is promoted by large population size (Wright 1977). In other words, environmental fluctuations might represent temporal flux in the adaptive surface, and this in conjunction with mass selection could help shuffle a large population towards the highest peak on the surface. The population of *T. elegans* at Eagle Lake may be experiencing such a process. Year-to-year fluctuation in the availability of toads may very well constitute temporal flux in selection for behaviors and morphologies that enhance toad predation. Heritable variation in predatory responses to toads are reported for this population by Arnold (1981*a*), so there is genetic variation for drift and selection to act on. Thus an interaction between selection and random drift imposed by environmental flux may be responsible for the present behavioral composition of this population. The possible role of migration from surrounding populations will be discussed in a later report.

The pattern of extreme year-to-year variation revealed here should serve as a cautionary note for studies of diet and niche, particularly for comparisons of two or more species based on data from a single year. A single-year study at Eagle Lake could have shown either that *T. sirtalis* has virtually complete diet overlap with *T. elegans*, or that *T. sirtalis* was completely absent. The actual picture is more complex than either of these extremes.

A growing series of long-term ecological studies documents striking temporal fluctuation in resources and demography (e.g., Ballinger 1977, Dunham 1980, Rotenberry 1980). These studies and the present report suggest that environmental fluctuations may frequently drive populations away from demographic and genetic equilibria. Such results challenge the domain of equilibrium models of niche spacing and competition, and strengthen the view of Tinkle (1979) and Wiens (1977) that certain important insights can only be gained from long-term ecological studies.

Acknowledgments

We thank L. Arnold, H. Arnold, H. Drummond, and especially L. Houck for help with fieldwork. D. Cahoon of the California Department of Water Resources supplied the data on lake levels. R. Barnett and L. and D. Pope of the Eagle Lake Biological Field Station of Chico State University provided logistical support during the 1980 field season. R. Huey and K. Kephart made helpful comments on an earlier draft of this manuscript. This work was partially supported by the Bache Fund of the National Academy of Sciences, the Gaige Fund of the American Society of Ichthyologists and Herpetologists, the Hinds Fund of the University of Chicago, the Andrew W. Mellon Foundation, a National Science Foundation Graduate Fellowship, National Science Foundation grants BNS 76-00619 and DEB 78-12560 (to S. J. Arnold), the Searle Foundation, and the Spencer Foundation.

Literature Cited

Antevs, E. 1948. The Great Basin with emphasis on glacial and postglacial times. III. Climatic changes and pre-white man. Bulletin of the University of Utah **38**:168–191.

Arnold, S. J. 1977. Polymorphism and geographic variation in the feeding behavior of the garter snake *Thamnophis elegans*. Science **197**:676–678.

———. 1981*a*. The microevolution of feeding behavior. Pages 409–453 *in* A. Kamil and T. Sargent, editors. Feeding behavior: ecological, ethological, and psychological approaches. Garland Press, New York, New York, USA.

———. 1981*b*. Behavioral variation in natural populations. I. Phenotypic, genetic, and environmental correlations between chemoreceptive responses to prey in the garter snake, *Thamnophis elegans*. Evolution **35**:489–509.

———. 1981*c*. Behavioral variation in natural populations. II. The inheritance of a feeding response in crosses between geographic races of the garter snake, *Thamnophis elegans*. Evolution **35**:510–515.

Arnold, S. J., and R. J. Wassersug. 1978. Differential predation on metamorphic anurans by garter snakes (*Thamnophis*): social behavior as a possible defense. Ecology **59**:1014–1022.

Asplund, K. K. 1963. Ecological factors in the distribution of *Thamnophis brachystoma* (Cope). Herpetologica **19**:128–132.

Ballinger, R. E. 1977. Reproductive strategies: food availability as a source of proximal variation in a lizard. Ecology **58**:628–635.

Brown, W. S., and W. S. Parker. 1976. A ventral scale clipping system for permanently marking snakes. (Reptilia, Serpentes). Journal of Herpetology **10**:247–249.

Busack, C. A., G. H. Thorgaard, M. P. Bannon, and G. A. E. Gall. 1980. An electrophoretic, karyotypic and meristic characterization of the Eagle Lake trout, *Salmo gairdneri aquilarium*. Copeia 1980:418–424.

Carpenter, C. C. 1952. Comparative ecology of the common garter snake (*Thamnophis s. sirtalis*) the ribbon snake (*Thamnophis s. sauritus*) and Butler's garter snake (*Thamnophis butleri*). Ecological Monographs **22**:235–258.

Clark, D. R. 1974. The western ribbon snake (*Thamnophis proximus*): ecology of a Texas population. Herpetologica **30**:372–379.

Drummond, H. 1980. Aquatic foraging in some New World Natricine snakes: generalists and specialists and their behavioral evolution. Dissertation. University of Tennessee, Knoxville, Tennessee, USA.

Dunham, A. E. 1980. An experimental study of interspecific competition between the iguanid lizards *Sceloporus merriami* and *Urosaurus ornatus*. Ecological Monographs **50**:309–330.

Fitch, H. S. 1965. An ecological study of the garter snake, *Thamnophis sirtalis*. University of Kansas Publication of the Museum of Natural History **15**:493–564.

Fleharty, E. D. 1967. Comparative ecology of *Thamnophis elegans*, *T. cyrtopsis*, and *T. rufipunctatus* in New Mexico. Southwestern Naturalist **12**:207–230.

Fouquette, M. J. JR. 1954. Food competition among four sympatric species of garter snakes. Texas Journal of Science **6**:172–188.

Gregory, P. T. 1978. Feeding habits and diet overlap of three species of garter snakes (*Thamnophis*) on Vancouver Island. Canadian Journal of Zoology **56**:1967–1974.

Gregory, P. T., and K. W. Stewart. 1975. Long-distance dispersal and feeding strategy of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in the Interlake of Manitoba. Canadian Journal of Zoology **53**:238–245.

Grinnell, J., J. Dixon, and J. M. Linsdale. 1930. Vertebrate natural history of a section of northern California through the Lassen Peak region. University of California Publications in Zoology 35, Berkeley, California, USA.

Hamilton, W. J., Jr. 1951. The food and feeding behavior of the garter snake in New York. American Midland Naturalist **46**:385–390.

Harding, S. T. 1935. Changes in lake levels in Great Basin area. Civil Engineering **5**:87–90.

Hubbs, C. L., and R. R. Miller. 1948. The Great Basin, with emphasis on glacial and postglacial times. II. The zoological evidence: correlation between fish distribution and hydrographic history in the desert basins of western United States. Bulletin of the University of Utah **38**:18–166.

Kephart, D. G. 1982. Microgeographic variation in the diets of garter snakes. Oecologia (Berlin) **52**:287–291.

Lagler, K. F., and J. C. Salyer II. 1945. Influence of availability on the feeding habits of the common garter snake. Copeia 1945:159–162.

Morrison, R. B. 1965. Quaternary geology of the Great Basin. Pages 265–285 *in* H. E. Wright, Jr. and D. G. Frey, editors. The Quaternary of the United States. Princeton University Press, Princeton, New Jersey, USA.

Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quarterly Review of Biology **52**:137–154.

Rotenberry, J. R. 1980. Dietary relationships among shrubsteppe passerine birds: competition or opportunism in a variable environment? Ecological Monographs **50**:93–110.

Snyder, J. O. 1915. The fishes of the Lahontan system of Nevada and northeastern California. United States National Marine Fisheries Service Fishery Bulletin **35**:31–86.

Stewart, F. R. 1968. Some observations on the natural history of two Oregon garter snakes (genus *Thamnophis*). Journal of Herpetology **2**:71–86.

Tinkle, D. W. 1957. Ecology, maturation and reproduction of *Thamnophis sauritus proximus*. Ecology **38**:69–77.

———. 1979. Long-term field studies. Bioscience **29**:717.

White, M., and J. A. Kolb. 1974. A preliminary study of *Thamnophis* near Sagehen Creek, California. Copeia 1974:126–136.

Wiens, J. A. 1977. On competition and variable environments. American Scientist **65**:590–597.

Wright, S. 1931. Evolution in Mendelian populations. Genetics **16**:97–159.

———. 1948. On the roles of directed and random changes in gene frequency in the genetics of populations. Evolution **2**:279–294.

———. 1969. The theory of gene frequencies. Volume 2. Evolution and the genetics of populations. University of Chicago Press, Chicago, Illinois, USA.

———. 1977. Experimental results and evolutionary deductions. Volume 3. Evolution and the genetics of populations. University of Chicago Press, Chicago, Illinois, USA.