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

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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 alternat-
ed with warmer interpluvial periods. During pluvial periods glaciers marched in the mountains, and lakes
filled the lowland basins, but during interpluvial peri-
ods, the glaciers retreated and pluvial lakes evapor-
rated. 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 prox-
mity to pluvial Lake Lahotan, which once covered
much of western Nevada (Snyder 1915, Hubbs and
Miller 1948). The water level of Eagle Lake has fluc-
tuated during the postpluvial period as revealed by the
presence of wave-cut terraces far above the present
lake, analysis of submerged trees, and historical rec-
ords (Grinnell et al. 1930, Harding 1935). Since we be-
gan 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
hores.

Year-to-year variation in snake diet has not previ-
ously been addressed. Garter snake diets, for exam-
ple, 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 1981a). In several cases, two or more co-
exising species have been studied with respect to diet
overlap and competition (e.g., Carpenter 1952, Fou-
quette 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 Tran-
sition Life Zone. Pikes Point consists of a series of
basaltic ridges that extend into the lake and interdig-
itate with small meadows (Fig. 1). These meadows
were inundated during years of high lake level
(1974–1975) and became marshes with stands of emer-
gent 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.
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.

### 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.

<table>
<thead>
<tr>
<th>Year</th>
<th>Species</th>
<th>N</th>
<th>Number of stomachs empty</th>
<th>Number of Anurans</th>
<th>Number of Fish</th>
<th>Number of Leeches</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Number of items</td>
<td>Number of items</td>
<td>Number of items</td>
<td></td>
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<tr>
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<td>4</td>
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<td>29</td>
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<tr>
<td></td>
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<td>1</td>
<td>0</td>
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<td>0</td>
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<td>10</td>
<td>27</td>
<td>3</td>
<td>2</td>
<td>32</td>
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<tr>
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<td>2</td>
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<tr>
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<td>0</td>
<td>11</td>
<td>12</td>
<td>23</td>
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<tr>
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<td>T. sirtalis</td>
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<td>0</td>
<td>0</td>
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<td>0</td>
</tr>
<tr>
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<td>291</td>
<td>74</td>
<td>93</td>
<td>43</td>
<td>210</td>
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<tr>
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<td>T. sirtalis</td>
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<td>20</td>
<td>12</td>
<td>2</td>
<td>4</td>
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</tr>
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</table>

### 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

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**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.
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 ($\chi^2 = 211.0, 18 \text{ df}, P < .0001$, based on number of stomachs, including “empty”; $\chi^2 = 558.6, 12 \text{ df}, P < .0001$, 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, $r = .80, 5 \text{ df}, P < .05$).

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 ($r = .85, 5 \text{ df}, P < .05$; 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 incept 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 $3 \times 3$ contingency table with the prey categories: anurans, fish, and leeches ($\chi^2 = 3.04, 4 \text{ df}, .75 \geq P > .50$). 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 ($\chi^2 = 4.30, 1 \text{ df}, P < .05$). 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, 1981a, 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 perchéd 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 (1981a), 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**

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