The Feeding Ecology of *Aneides flavipunctatus* and Sympatric Plethodontid Salamanders in Northwestern California

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ABSTRACT.—Seasonal and ontogenetic variation in the diets of *Aneides flavipunctatus* and three sympatric plethodontids (*A. lugubris, Batrachoseps attenatus,* and *Ensatina eschscholtzii*) were studied at three localities in northwestern California. A wide variety of prey was eaten by the four species, but 75–95% of the total food volume at any one season and location was contributed by Diplopoda, Coleoptera, Isoptera, Hymenoptera, Diptera, and Collembola. In *A. flavipunctatus,* total food volume per stomach increased with standard length to about 50 mm, then leveled off. The mean number of prey per salamander stomach declined with increasing body size and with the progression of the winter rainy season, but there was no seasonal change in total food volume. Sympatric plethodontid species exhibited considerable dietary overlap, but differed in their mean and maximum prey size. Analysis of stomach contents suggests that these species do not feed indiscriminately: larger salamanders appear to select larger prey, and to ignore most small prey. Interspecific, ontogenetic, and seasonal differences in feeding are discussed in the light of predictions derived from an existing theoretical model of optimal foraging by a "Sit-and-Wait" predator.

Although a number of published analyses of the feeding habits of terrestrial salamanders have considered ontogenetic, interspecific, seasonal, or geographic differences in feeding (Burton, 1976; Bury and Martin, 1973; Fraser, 1976*a, b*; Jaeger, 1972, 1980; Keen, 1979; Maiorana, 1974, 1978*a, b*; Sites, 1978), no previous study has simultaneously considered all of these modes of variation.

I examined the feeding habits of a guild of terrestrial plethodontid salamanders as a function of body size, species identity, season, and geographic location. This research began as part of an intensive study of *Aneides flavipunctatus* (Lynch 1974*a, b*, 1981), and I have accumulated more data on the diet of this species than any other. However, the diets of three broadly sympatric species *A. lugubris, Ensatina eschscholtzii,* and *Batrachoseps attenuatus* were also examined. In this report, I describe the

prey taken by these four species at three localities in northwestern California and then consider the relevance of the results to a theoretical model of predation, and to the question of competition for food in salamanders.

MATERIALS AND METHODS

Study Sites.—Field work was conducted between 1968 and 1972 at three sites in northwestern California, a region that features a Mediterranean-type climate, characterized by mild, wet winters and warm, dry summers. Surface activity by terrestrial salamanders in the study area is normally restricted to the October–April rainy season. In coastal areas, seasonality in temperature is reduced and the effects of the summer drought are somewhat ameliorated by lower temperature and frequent fogs. At Skaggs Springs, an inland site, *A. flavipunctatus* was the most abundant of seven sympatric salamander species found under rocks and logs on an east-facing slope that supported fairly open oak woodland. Conifers were absent from the collecting site, but *Pinus sabiniana*, an indicator of sub-humid conditions, oc-

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curred on exposed slopes within a few hundred meters. The second study site was located near Navarro, approximately 70 km (air line) NW Skaggs Springs, within the Redwood-Douglas Fir vegetation association, in a zone influenced by coastal fog. The Usal site was located on a rolling plateau overlooking the Pacific coast some 150 km (air line) NNW Skaggs Springs. Here, the Redwood-Douglas Fir forest was similar in composition to that at Navarro, but was more extensive. The number of sympatric salamander species at this site (10) equals or surpasses that at any other locality in western North America.

Samples of salamanders were collected during the rainy seasons of 1970–71 and 1971–72. Collections were made in November, January, and April at the Skaggs Springs and Navarro sites, and in November and April in Usal. An additional collection made at Skaggs Springs in November 1968 was available for analysis. Samples were collected at the three sites within the same 24 h period, except in two instances when 2–3 days separated the collections.

Stomach Analysis. —Animals were killed within 3 h of capture by immersion in a dilute solution of chloretone. Specimens were then fixed in dilute formalin and stored in 70% ethyl alcohol. Stomachs were later removed, and their contents were examined under a 15× dissecting microscope equipped with an ocular micrometer. Prey items were identified at least to order, and more abundant taxa were keyed to family or subfamily where possible. Food items were counted and individually measured. Prey volume was approximated as a rectangular solid:

Volume = prey length × average width × average depth.

A total of 690 salamander stomachs were dissected for this study (Table 1). Salamanders were grouped into five size classes according to their standard length (SL), the distance from the snout

TABLE 1. Number of stomachs examined from the three main study sites.

| Species | Locality | | | |
	Skaggs	Na-varro	Usal	Total
A. flavipunctatus	141	104	39	284
A. lugubris	19	110	28	157
B. attenuatus	17	69	72	158
E. eschscholtzii	0	0	53	53
Other species	5	4	30	39
Totals	182	287	221	690

to the posterior angle of the vent: Class I (20–34 mm), Class II (35–49 mm), Class III (50–64 mm), Class IV (65–79 mm), Class V (80–94 mm).

In the following discussion, a "sample" is a collection of salamanders taken at a particular place and time; a "subsample" is a size-specific subset of such a sample.

Feeding Experiments. —Many theories concerning the causes and limits of morphological similarity and divergence (e.g., MacArthur and Levins, 1964; MacArthur, 1965; Levins, 1968; Schoener, 1969, 1971; Roughgarden, 1972; Wilson, 1975) assume a continuous functional relationship between phenotype and ecological performance, but experimental verification of this crucial assumption has often been lacking. A morphological character that serves to predict the position of a predator along some resource dimension (for example, the prey size axis) is termed an "indicator trait" (Roughgarden, 1972). For salamanders, body size, head width, and tooth morphology all are potential indicator traits for predicting prey size. Predator-prey size relationships were examined experimentally to see whether or not stomach analyses provided a realistic picture of intrinsic prey-size limitations for salamanders having different phenotypes.

Using *Aneides flavipunctatus* and *A. lugubris* as predators and living crickets (*Achaeta domestica*) as prey, I asked three

questions: (1) Within a salamander species, is there a consistent relationship between quantifiable aspects of predator morphology and the size of the largest acceptable prey? (2) At a given body size, do salamanders of the two species differ in the size of prey they will accept? (3) Do laboratory feeding trials give an accurate indication of feeding performance under field conditions?

Salamanders were collected at ecologically similar localities in the Coastal Redwood-Douglas Fir belt in Mendocino County, California, and were maintained individually in clear plastic terraria (20 × 10 × 6.5 cm) provided with a layer of moist paper toweling. Temperature was held constant at 15°C, and the experimental animals were exposed to a 12L-12D light cycle. Head width and body weight were measured at the beginning of the experiment. Standard length was estimated from a previously established head width-standard length regression for *Aneides* (Lynch, 1974a).

Crickets were obtained from a commercial dealer and were maintained at room temperature on a diet of chicken mash and water. The size of crickets was determined by measurement of thorax width under a binocular microscope equipped with an ocular micrometer.

Aneides were allowed to feed ad libitum upon crickets of assorted sizes for at least 1 wk before an experiment began. Forty-eight hours prior to the experimental period all crickets were removed, and the toweling was changed.

Experiments were conducted under the same conditions of light and temperature to which the salamanders had become acclimated. A trial began with the introduction of a single large cricket (mean thoracic width = 5.5 mm; SE = 0.2 mm) into the terrarium housing a salamander. After 24 h, the containers were checked for presence or absence of the cricket. If the salamander had eaten the cricket, maximum acceptable prey size (MAPS) could not be specified. If the cricket remained uneaten af-

ter 24 h, it was replaced by one having a width of 5.0 mm. The procedure was repeated every 24 h with crickets of successively smaller sizes (0.5 mm increments) until the salamander either (1) accepted a cricket, the size of which was defined as the maximum acceptable prey size (MAPS), or (2) refused all crickets down to the smallest size available (1.0 mm), in which case maximum prey size remained unspecified. Each salamander was tested only once.

This experimental design did not control for predator hunger level after the first day of the feeding trials. Thus, juvenile *Aneides* that were incapable of ingesting the larger size classes of crickets may have had to wait 6 or more days before sufficiently small crickets were offered. However, the effect (if any) of this increased hunger level on MAPS should have been to increase the maximum size of acceptable prey for small salamanders, i.e., to make MAPS for small salamanders more similar to that for large salamanders. Since the null hypothesis is that no consistent correlation exists between MAPS and predator morphology, the experiment is biased toward non-rejection of the null hypothesis, and is therefore conservative.

RESULTS AND DISCUSSION

General Diet of A. flavipunctatus.—All but 24 of 284 field-collected *A. flavipunctatus* contained food in their stomachs, and several of the 24 individuals were observed to disgorge prey items in the chloretone killing solution. At least 25 invertebrate orders occurred in the diet of *A. flavipunctatus*, but many prey taxa were too small or scarce (or both) to contribute appreciably to the diet. Six arthropod orders (Diplopoda, Coleoptera, Hymenoptera, Isoptera, Diptera, and Collembola) accounted for about 78% of the combined volume of prey in the pooled samples of *A. flavipunctatus*, and for 76–95% of the food volume in any individual sample (Appendices I, II). Most of the diet of post-

juvenile *A. flavipunctatus* (size classes III–V) from all three sites was contributed by four prey orders: Diplopoda (almost entirely cambalid millipedes); Coleoptera (mainly adult carabids, curculionids, and staphylinids); Hymenoptera (almost entirely ants, Formicidae, of the subfamilies Formicinae and Myrmicinae); and Isoptera (mainly termite workers of the family Kalotermitidae). These same prey groups also predominated in the diet of juvenile (Class I and II) *A. flavipunctatus*, but dipterans (mainly Mycetophilidae, Bibionidae, and Anisopodidae) and collembolans (Entomobryidae, Poduridae, and Sminthuridae) also made substantial contributions to the juvenile diet.

Seasonal and Ontogenetic Patterns in the Diet of A. flavipunctatus at Skaggs Springs. —In the fall samples from Skaggs Springs, millipedes were volumetrically the most important prey for salamanders of all sizes (Appendix I). Coleoptera were second in importance in three of the four adult subsamples, but contributed less to the diet of juveniles. Conversely, Collembola contributed a sizeable proportion of the diet of Class I and Class II juveniles at Skaggs Springs, but were of trivial importance in larger salamanders. Termites were patchily distributed among the subsamples; Hymenoptera and Diptera were of minor volumetric importance.

The January diet (Appendix II) was similar to the November diet except that dipteran larvae were a major prey class in winter, particularly for juveniles.

Only three *A. flavipunctatus* could be found in April 1970, so just the April 1971 sample is analyzed here (Appendix III). The major seasonal trend in the spring diet was a marked reduction in the volumetric importance of millipedes, Diptera, and Collembola, and a corresponding increase in the importance of ants and beetles. As in the fall sample, Isoptera were patchily distributed, but were volumetrically significant components of the diet when they did occur.

Seasonal and Ontogenetic Patterns in the Diet of A. flavipunctatus at Navarro and Usal. —The similarity of these two localities to each other in climate and vegetation, and their distinctness from Skaggs Springs in both regards, were reflected in the diet of *A. flavipunctatus* (Appendix IV; Lynch, 1974*a*). Diplopoda, a major component of the diet at Skaggs Springs, were virtually absent from the fall diet at the two Mendocino County localities. Conversely, ants, which were of minor importance in the fall diet at Skaggs Springs, were the dominant prey in four of the five November subsamples from Navarro and Usal. The major difference between the diet of juvenile *A. flavipunctatus* at the Sonoma County vs. Mendocino County localities was the much lower importance of Collembola in the latter.

A single winter sample from Navarro was analyzed (Appendix V). Relative to their occurrence in fall, millipedes increased and ants decreased in the winter diet. Diptera, which showed a distinct winter "bloom" at Skaggs Springs, were only of minor importance at Navarro.

The three adequate April samples are summarized in Appendix VI. The spring diet of the two Mendocino County populations of *A. flavipunctatus* was dominated by ants, which occurred in every subsample, and constituted 11–91% of the total food volume in individual subsamples (Lynch, 1974*a*). Millipedes were of slight volumetric importance. Termites were present in important amounts in all eight subsamples from Navarro, but were absent from the Usal subsamples. Diptera and Collembola were relatively unimportant in the spring diet of *A. flavipunctatus* at the two Mendocino County sites.

Summarizing, the major seasonal and ontogenetic trends in the diet of *A. flavipunctatus* were (1) a sharp ontogenetic decrease in the numbers of Collembola and Acarina, (2) a winter peak in the abundance of Diptera, (3) a spring decline in Collembola and Diplopoda with
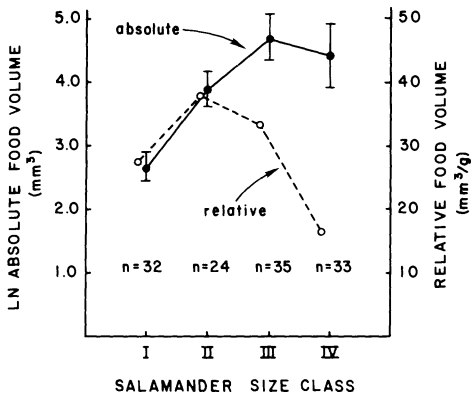
FIG. 1. Estimate of absolute and relative intake of food by *A. flavipunctatus*, based on stomach contents of animals from Skaggs Springs. Symbols are mean values (±2 SE for absolute volumes).

a corresponding increase in the importance of ants. The main geographic trend was a relatively greater importance of social insects (ants and termites) and a lesser importance of millipedes and beetles, at the two coastal localities.

Volumetric vs. Numerical Importance of Prey Taxa.—Because the prey taken by *A. flavipunctatus* varied in volume over several orders of magnitude, correlations between numerical importance (I) and volumetric importance (V) of individual prey taxa were poor. Large prey tended to be infrequent in the diet, whereas minute taxa (e.g., Collembola, Acarina) were abundant. Species of vastly different sizes are included within some major prey taxa (e.g., Coleoptera); other prey groups (e.g., Diplopoda) contain relatively few species, but encompass a great size range of ontogenetic stages.

The existence of complex size variation within and among major prey taxa means that the statistical significance of between-sample differences in volumetric percentages of prey taxa cannot be tested directly using prey abundance data. This follows from the fact that the magnitude of V bears no direct relationship to the number of prey items independently "sampled" by the salamanders. Conversely, a simple comparison of the number of a given general prey taxon in two subsamples may be misleading because of the wide size range of included species. To circumvent these problems, I repeated the dietary analysis considering only the size and abundance of prey items, without regard to their taxonomic identity.

Ontogenetic Trends in Total Prey Volume.—Preliminary analysis revealed no consistent seasonal or geographic trends in the total mean volume of food taken by size-specific subsamples of *A. flavipunctatus* at the three localities (Lynch, 1974a). Accordingly, data were pooled over seasons and localities for analysis of ontogenetic trends, giving a total of 12 subsamples (4 size classes, 3 seasonal intervals).

When empty stomachs and those containing only traces of food were omitted, the distribution of total food volume per stomach was approximately log-normal for salamanders of a given body size, but the mean, variance, and coefficient of variation in the log-transformed volume of food per stomach all increased ($P < 0.01$, t-tests for log-transformed means; $P < 0.05$, F-tests for homogeneity of variance in food volume) with increasing salamander size through Class III (Lynch, 1974a).

The total volume of prey in the stomach of an individual *A. flavipunctatus* was as much as 900 mm³, but typical values ranged from 10–20 mm³ in small juveniles to 75–200 mm³ in large adults. The mean volume of food per stomach increased significantly with body size up to Class III, then leveled off (Fig. 1; Table 2). Mean food volume per stomach ranged from 15 mm³ in Class III juveniles to 100 mm³ in Class III and Class IV adults. *F*-tests for homogeneity of variance in food volume indicated no significant differences among size classes within a given season, but this may be a reflection of relatively small sample sizes. When samples were pooled across seasons, a highly significant ($P < 0.01$) increase in variability of

TABLE 2. Mean total food volume/stomach in *A. flavipunctatus* from Skaggs Springs. Vertical lines indicate size classes that did not differ significantly ($P > 0.05$) in the mean amount of food per stomach.

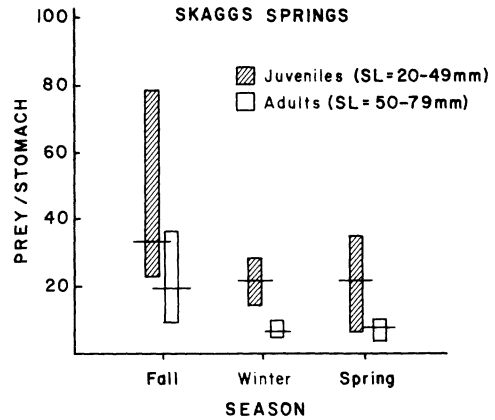| Season	Size class	N	Mean log food volume (mm³)
Fall	I	4	1.00
	II	6	1.64
	III	19	2.06
	IV	17	1.86
Winter	I	24	1.14
	II	14	1.72
	III	15	2.03
	IV	16	2.04
Spring	I	5	1.25
	II	5	1.69
	III	4	1.99
	IV	3	2.23
All seasons combined	I	33	1.14
	II	25	1.69
	III	38	2.04
	IV	36	1.97

FIG. 2. Median prey number vs. body size and season for *A. flavipunctatus* at Skaggs Springs. "Juveniles" (small symbols) are size Classes I and II; "adults" are size Classes III and IV. Vertical bars indicate spread of two middle quartiles.

food volume with salamander size was found for all size class comparisons except Class III vs. Class IV (Table 2).

There were no statistically significant seasonal differences in the volume of food per stomach in any size class (Table 2). Assuming that digestive rates are similar in large and small salamanders (cf. Merchant, 1970) and that the stomach contents of both juvenile and adult salamanders contain prey obtained during the same foraging interval, the relative rate of food intake can be estimated for salamanders of different body sizes (Fig. 2). Relative food intake appeared to decline markedly with salamander body size, especially between Class III and Class IV. This last result reflects an approximately constant absolute food intake for salamanders in Classes III and IV, despite a substantial difference in body size.

The Number of Prey Consumed.—As many as 500 prey were found in a single *Aneides* stomach, but most stomachs contained 5–50 prey. The observed ontogenetic increase in total food volume

per stomach could be achieved by one or a combination of the following general tactics: (1) adults eat a larger number of the same kinds of prey taken by juveniles, (2) adults and juveniles take similar numbers of prey, but mean prey size is larger in adults, or (3) adults take fewer prey than juveniles, but these prey are of disproportionately large size.

To test these alternatives, Spearman rank correlation coefficients were computed for body size vs. number of prey items in the three largest seasonal samples of *A. flavipunctatus* from Skaggs Springs. All three correlation coefficients are significant ($P < 0.05$) and are negative (-0.40, -0.52, -0.85). Thus adult *A. flavipunctatus* tend to take fewer prey than juveniles.

Seasonal trends in prey number taken were examined by combining the four original size classes of salamanders into "juvenile" (Classes I and II) and "adult" (Classes III and IV) groups. Seasonal differences in the number of prey items per stomach were tested for significance using the Wilcoxon Two-Sample Test (Sokal and Rohlf, 1969). Between-year differences in prey number were not significant for a given season ($P > 0.1$ for both the November and

January samples), so samples from different years were combined for seasonal comparisons. Adult salamanders took fewer prey than juveniles at any given season, and salamanders of all sizes tended to take substantially fewer prey as the wet season progressed (Fig. 2). At Skaggs Springs, the median number of prey per stomach in both juveniles and adults declined by nearly 50% between November and January. The spring sample was too small to permit firm conclusions, but prey consumption appeared to level off at this season. A similar seasonal pattern held for salamanders from Navarro (Lynch, 1974a).

Prey Size. —Terrestrial salamanders live in microhabitats that contain potential prey of a wide size range, and it has been suggested that salamanders indiscriminately ingest whatever prey they encounter, limited only by general anatomical constraints (e.g., Hairston, 1949, 1980b, 1981; MacNamara, 1977). The co-occurrence of different species or ontogenetic stages of predators constitutes a kind of internal control in the interpretation of their feeding patterns. Thus, if two microsympatric predators are observed to feed on different prey, there is some basis for inferring differential prey selectivity (Maiorana, 1978a). A crucial question is whether or not the predators being compared are in fact exposed to, and are able to perceive, the same prey universe. To maximize the likelihood of satisfying this key requirement, collecting was restricted to microhabitats where the species and ontogenetic stages co-occured (i.e., beneath medium- to large-sized cover objects). All possible combinations of two and three species under single cover objects were repeatedly observed, and there was no evidence for thermal differentiation among the species (Lynch, 1974a; Feder and Lynch, 1982). Nevertheless, the possibility cannot be completely dismissed that subtle differences in temperature, humidity, or size of refugia may have partially segregated the species and size classes, even

where they appeared to be microsympatric. If these same factors also influenced the size and abundance of available prey, observed dietary differences might in part reflect differential availability of prey.

Prey taken by *A. flavipunctatus* ranged in size from 0.01 mm³ (oribatid mites, small collembolans) to more than 500 mm³ (adult beetles, millipedes, isopods, lepidopteran larvae). Prey volumes were converted to a $\log_2$ scale for analysis. Sixteen such "octaval" intervals were sufficient to include all prey taken by *A. flavipunctatus.*

In Table 3, the 16 logarithmic prey-size categories are condensed into "small" (classes 0–5; volume ≤ 0.2 mm³), "medium" (classes 6–11; volume 0.3–19.1 mm³), and "large" (classes 12–16; volume ≥ 19.2 mm³) groups. "Small" prey constituted the majority of items taken by Class I and II juveniles in the fall and winter samples and were common in the diets of Class III salamanders at those seasons. However, "small" prey were scarce in the juvenile diet in the spring, and were uncommon at all times in the stomachs of large (Class IV) adults. Prey of "medium" size were abundant in the diets of salamanders of all sizes and at all seasons, but were most important late in the season and in larger salamanders. "Large" prey were virtually absent from the diet of juvenile salamanders; they were increasingly numerous in the diets of larger size classes of salamanders, but they contributed a sizeable proportion (>8%) of the total number of prey only in a few subsamples of Class III and IV animals.

The overall importance of prey of different sizes to the diet of *A. flavipunctatus* was clarified by plotting cumulative prey volume against prey size (Fig. 3). Large prey items were strikingly more significant in the total volumetric makeup of the adult diet than their relatively low abundance might suggest. The opposite was true for "small" prey, which contributed 53% of the bulk of the fall diet in Class I juveniles, but less

TABLE 3. Volumetric and numerical (in parentheses) importance of small, medium, and large prey in the diet of *A. flavipunctatus* at Skaggs Springs.

Season	Salamander size class	N	Prey size class			Total prey items
			Small	Medium	Large	
Fall	I	4	.532 (.921)	.468 (.079)	.000 (.000)	177
	II	6	.262 (.919)	.272 (.076)	.466 (.005)	936
	III	19	.027 (.710)	.163 (.229)	.811 (.061)	1185
	IV	17	.005 (.327)	.396 (.591)	.599 (.082)	401
Winter	I	24	.129 (.744)	.871 (.248)	.000 (.000)	618
	II	14	.019 (.528)	.269 (.395)	.712 (.078)	271
	III	13	.001 (.296)	.062 (.426)	.0937 (.306)	116
	IV	12	.001 (.151)	.083 (.622)	.916 (.227)	119
Spring	I	5	.002 (.022)	.811 (.956)	.187 (.022)	91
	II	5	.005 (.100)	.904 (.885)	.090 (.015)	120
	III	4	.001 (.011)	.278 (.971)	.722 (.018)	280
	IV	5	.000 (.046)	.081 (.674)	.919 (.279)	43

than 1% for adults of size Classes III and IV. Large prey (>19 mm³) were absent from the diet of small juveniles, but accounted for 60–81% of the total food volume in adults. Mean prey size increased between November and January for all size classes of salamanders at Skaggs Springs. A resurgence in the relative importance of medium-sized prey in April reflects the influx of ants in the diet at that time (Appendix III).

A final statistic that emphasizes the overriding importance of large, but relatively uncommon, prey in the diet of *A. flavipunctatus* is the mean proportion of the total food volume contributed by the single largest prey item in each stomach. In the Skaggs Springs population, this value increased monotonically with salamander body size, from 37% in Class I juveniles to 64% in Class IV adults (Lynch, 1974a). Thus, although the stomach of an average adult *A. flavipunctatus* contained 7–14 prey, nearly two-thirds of the total food volume was contributed by the single largest prey.

Seasonal and ontogenetic trends in prey size at the other two localities were generally similar to those at Skaggs Springs, except that "medium," rather than "large," prey were the mainstay of the diet for adult *A. flavipunctatus* at the two Mendocino County sites (Lynch, 1974a). This reflects the predominance of ants and termites in salamander diets at these two localities (Appendices IV–VI).

Morphometrics of Species Sympatric with A. flavipunctatus.—In order of increasing SL, the four commonest sympatric plethodontids in the study area were *Batrachoseps attenuatus, Ensatina eschscholtzii, Aneides flavipunctatus,* and *A. lugubris,* the greatest size difference being
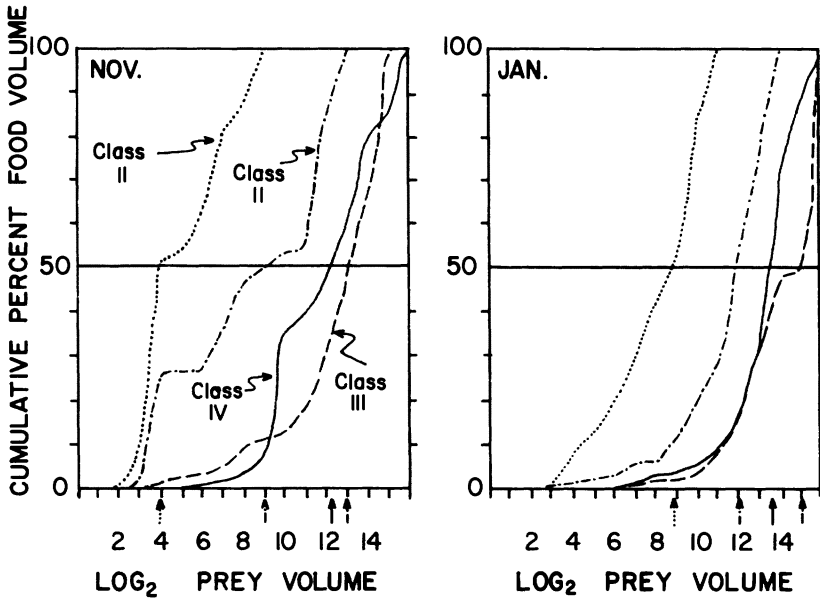
FIG. 3. Cumulative percent of total food volume contributed by prey of increasing size in the diet of *A. flavipunctatus* at Skaggs Springs. Vertical arrows along the abscissa indicate the center of gravity of the prey distributions for each size class of salamanders. Class IV adults are closely similar to Class III adults in relying upon large prey (volume > 11) for more than half of their total food volume. Class II and Class I juveniles rely on progressively smaller prey for the bulk of their diets. Note the seasonal shift to larger prey between November and January.

that separating *B. attenuatus* and *E. eschscholtzii* (Fig. 4). The species fall in the same order if they are ranked by body weight, but the size differential between *E. eschscholtzii* and *B. attenuatus* increases due to the relatively slender habitus of the latter species. Juvenile and subadult stages of all species overlap considerably in body size.

Because these species use their jaws to grasp large prey, which are then swallowed whole, the morphology of the head might limit the size of prey ingested. The degree of skull ossification increases with body size, both within and among species (Wake, 1963, 1966), and there are marked interspecific differences in relative, as well as absolute, head size (Fig. 5). At small body sizes, *Ensatina* has by far the widest head, followed by *A. lugubris, A. flavipunctatus,* and *B. attenuatus.* At larger body sizes, all species except *B. attenu-*

atus tend to converge on a common head shape.

There are substantial interspecific differences in dentition. Evolutionarily specialized features include decreased numbers of teeth, increased size and morphological complexity of individual teeth, and increased sexual dimorphism in both morphology and transition from the primitive bicuspid to the derived unicuspid tooth form (Wake, 1963, 1966; Lynch, 1974a). The four species can be ranked in order of increasing dentitional specialization: *E. eschscholtzii, B. attenuatus, A. flavipunctatus, A. lugubris.*

Ensatina emerges as the most generalized of the four species in morphology (Wake, 1966), and this salamander also has the broadest geographical and elevational distribution of any western plethodontid (Stebbins, 1951, 1966). In contrast, *Batrachoseps* is highly adapted
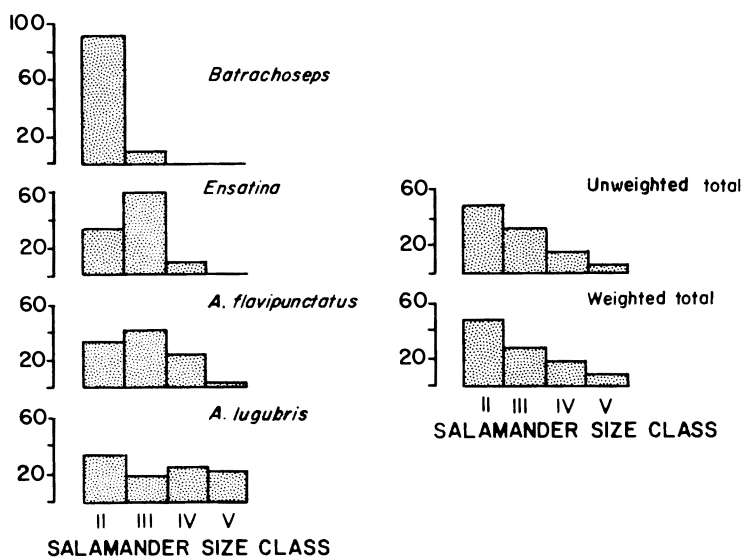
FIG. 4. (SL) standard lengths of four sympatric plethodontids, based on collections from Navarro and Usal. Histograms show the proportion of individuals that fall into each 15 mm size class. Class I juveniles (20–34 mm SL) are omitted due to insufficient samples. The unweighted total histogram shows the overall size distribution of salamanders, assuming that the four species are equally abundant. The weighted total histogram shows the distribution of sizes that result if each species is weighted according to its observed abundance in collections.

for a partly fossorial way of life, as evidenced by its exceptionally small size, greatly reduced limbs, and wormlike habitus. *Batrachoseps* possesses a projectile tongue, also a derived feature (Wake, 1966). *Aneides lugubris*, the largest western plethodontid, is a highly specialized species that has evolved into a different adaptive zone from that occupied by *Batrachoseps*. Although *A. lugubris* appears to be more frequently associated with terrestrial than with arboreal microhabitats (Stebbins, 1951, 1966), it does possess distinctive adaptations for climbing (Wake, 1963). Previous workers have suggested that the formidable dentition of *A. lugubris* may be an adaptation for taking large prey (Storer, 1925; Wake, 1963, 1966; Larson et al., 1981), but no empirical evidence on this point has been presented. An alternative explanation for the enlarged teeth of *Aneides* is that they are used in intraspecific or interspecific aggressive encounters (Cupp, 1980). These two views are not, of course, mutually exclusive.

The fourth species, *Aneides flavipunctatus*, is fairly generalized in ecology, size, and proportions (Lynch, 1974a), and falls between *Ensatina* and *A. lugubris* in dentitional specialization.

If prey size is a simple function of predator size, the average prey size taken by adults of the four species should fall in the same rank order as do the sizes of salamanders themselves. Relative head size might be an important trait for predicting prey size differences between heterospecifics of the same overall body size. Trophic morphology would be expected to play a more important functional role in adults than in juveniles because dentitional specializations and skull ossification are most fully expressed in adults.

The Diet of Species Sympatric with A. flavipunctatus. —Of the terrestrial salaman-
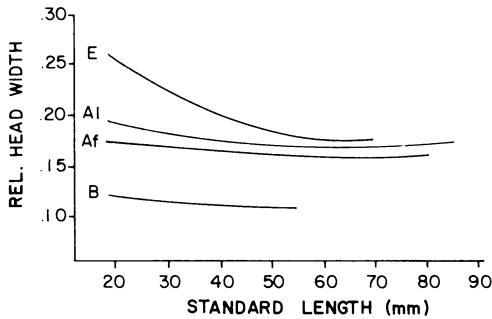
FIG. 5. Interspecific and ontogenetic differences in relative head width (head width/SL) in four sympatric plethodontid species. E = *Ensatina eschscholtzii*, Al = *Aneides lugubris*, Af = *A. flavipunctatus*, B = *Batrachoseps attenuatus*.
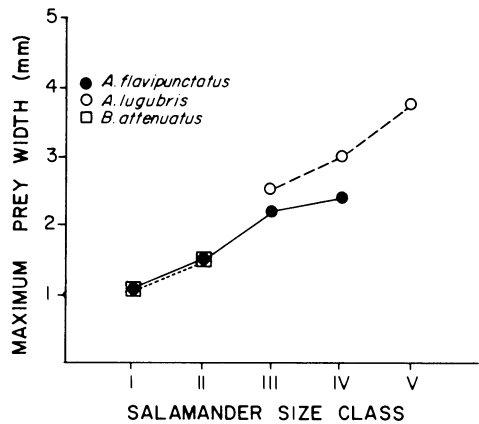

FIG. 6. Maximum prey width vs. SL in three sympatric plethodontids at Skaggs Springs, based on the analysis of stomach contents of 132 *A. flavipunctatus*, 19 *A. lugubris*, and 15 *B. attenuatus*. Differences between *A. flavipunctatus* and *A. lugubris* are significant at $P < 0.05$ for size Classes III and IV.

der species that co-occur with *A. flavipunctatus* at Skaggs Springs, only *B. attenuatus* and *A. lugubris* were sufficiently abundant to permit interspecific comparisons of pooled seasonal collections. As would be predicted from their close morphological resemblance, *A. lugubris* and *A. flavipunctatus* had similar diets (Fig. 6, Table 4). Both species took their prey from the same general taxonomic groups, and showed similar ontogenetic shifts in the relative importance of "small," "medium," and "large" prey items. As predicted, the mean size of the largest prey taken by the largest (i.e., Class V) *A. lugubris* was significantly greater than the maximum prey size of the largest (i.e., Class IV) *A. flavipunctatus*. However, even if the two species are compared at equivalent body sizes, *A. lugubris* tends to take larger prey ($P < 0.05$; Wilcoxon Two-Sample Test). Most *Batrachoseps* at Skaggs Springs fell into size Class II and took smaller prey than did adults of either *Aneides* species (Fig. 6, Table 4). Although juvenile *A. flavipunctatus* exceed adult *Batrachoseps* in relative head size at a common SL, the two species did not differ significantly in prey size at a constant SL ($P > 0.1$; Wilcoxon Two-Sample Test).

The same three species were studied at Navarro (Fig. 7, Table 5). There, *Ba-trachoseps* took significantly smaller prey than *A. lugubris* of the same SL, as predicted on the basis of differences in relative head width. Wilcoxon Two-Sample Tests revealed statistically significant ($P < 0.05$) interspecific differences in the predicted direction at all sizes, except for Class I juveniles of the two *Aneides* species. However, juvenile *Aneides* took significantly larger prey ($P < 0.05$) than did *Batrachoseps* of equivalent SL.

The largest prey taken by adult *A. lugubris* averaged more than four times the volume of those taken by adult *A. flavipunctatus* ($112 mm^3$ vs. $27 mm^3$). In all three species, the largest single prey item in an individual salamander's stomach contributed a relatively high proportion (40-70%) of the total food volume.

The same three species analyzed at Skaggs Springs and Navarro, plus *Ensatina eschscholtzii*, were analyzed at Usal (Table 6). At this locality, as at Skaggs Springs and Navarro, *A. lugubris* derived most of its food volume from "large" prey, while *A. flavipunctatus* de-

TABLE 4. Volumetric and numerical (in parentheses) importance of small, medium, and large prey in the diets of sympatric plethodontids at Skaggs Springs, Sonoma Co. Seasonal samples pooled.

Species	Salamander size class	Prey size class			Total prey items
		Small	Medium	Large	
A. flavipunctatus	I	.117 (.708)	.833 (.290)	.052 (.002)	886
	II	.069 (.765)	.389 (.214)	.542 (.021)	1327
	III	.014 (.555)	.142 (.374)	.845 (.072)	1581
	IV	.003 (.268)	.256 (.604)	.741 (.128)	563
A. lugubris	I	(Insufficient sample)			
	II	(Insufficient sample)			
	III	.000 (.048)	.202 (.667)	.798 (.286)	42
	IV	.000 (.000)	.089 (.623)	.910 (.377)	53
	V	.000 (.022)	.052 (.440)	.949 (.539)	91
B. attenuatus	I	(Insufficient sample)			
	II	.044 (.775)	.349 (.212)	.606 (.010)	376

pended on a mixture of "large" and "medium" prey. Of the four species examined, only *Batrachoseps* obtained a sizeable proportion (12% by volume) of its adult diet from "small" prey. *Ensatina* was the most generalized species with respect to prey size. Even small juvenile *Ensatina* commonly utilized prey from all three size categories, and the proportion of "large" prey in the juvenile diet was higher in *Ensatina* than in any of the other three species. This pattern suggests that the unusually broad head of juvenile *Ensatina* (Fig. 5) is indeed a valid indicator trait for prey size. The relative importance of "large" and "medium" prey in the diet of adult *Ensatina* (Class III) was intermediate between similarly sized *A. lugubris* and *A. flavipunctatus*. This ontogenetic change in ranking of the species according to prey size corresponds to the observed ontogenetic shift in relative head size (Fig. 5).

In summary, despite considerable in-terspecific and ontogenetic overlap in feeding, the available prey spectrum appears to be partitioned by these four sympatric plethodontid species. Again, this conclusion assumes that co-occurring salamanders are exposed to essentially the same prey universe. Both mean and maximum prey size are correlated with salamander body size. The absolute lower size limit of acceptable prey changes relatively little with increasing body size (cf. Wilson, 1975), but the relative and absolute number of small prey that are eaten both decline with increasing salamander size. Because the four species differ in mean body size, adults of each species tend to take prey of different sizes. Additional interspecific differentiation in prey-size is correlated with differences in trophic morphology. The smallest species in the series (*B. attenuatus*) also has the narrowest relative head width and has small teeth, while the largest species (*A. lugubris*) has the largest relative (as well
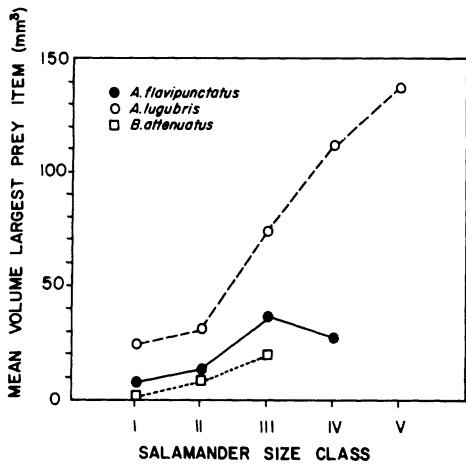
FIG. 7. Maximum prey volume size vs. SL in three sympatric plethodontids at Navarro, based on the analysis of stomach contents of 109 *A. flavipunctatus*, 110 *A. lugubris*, and 69 *B. attenuatus*. All interspecific differences in maximum prey volume are significant at *P* < 0.05, except for Class I individuals of the two *Aneides* species.

as absolute) head and tooth size. As a result, the four species are more different in their feeding habits than would be predicted from body size differences alone.

Experimental Feeding Trials. —Maximum acceptable prey size (MAPS) could not be specified for *Aneides* larger than about 70 mm SL because salamanders of this size were able to consume even the largest available crickets. In addition, a few of the experimental salamanders refused to feed during the experimental period. Usable data were obtained for a total of 28 *A. flavipunctatus* and 15 *A. lugubris*.

The feeding experiments revealed strong correlations between MAPS and all three indices of predator size (SL, head width, body weight) for both species of *Aneides*. Within species, head width and SL (Fig. 8) were equally efficient predictors of MAPS ($r = 0.9$ in both instances); body weight showed a somewhat lower correlation ($r = 0.8$), although this difference was not statistically significant ($P > 0.05$) given the limited sample sizes. In any event, a

cube root transformation of body weight increased the correlation to 0.9.

As had been predicted on the basis of interspecific differences in relative head size and tooth size, and from analysis of the stomach contents of field samples, *A. lugubris* took larger prey in the laboratory tests than did *A. flavipunctatus* of the same SL. When animals of equivalent head size were compared, *A. lugubris* still slightly exceeded *A. flavipunctatus* in MAPS. This small residual interspecific difference could reflect the effects on feeding of the greatly hypertrophied dentition of *A. lugubris*, but larger samples would be required to verify this relationship.

The experimental regression lines of MAPS vs. SL closely correspond to the upper limit of prey actually observed in the stomachs of each of more than 200 *A. flavipunctatus* and *A. lugubris* taken in local sympatry at Navarro (Fig. 9). However, large prey are relatively scarce: at any given time, few salamanders contain prey items as large as their morphology would permit them to attack and subdue.

Morphological Similarity and Interspecific Dietary Overlap in Aneides. —Roughgarden (1972) used a geometric function to relate head-size to prey-size in *Anolis*. I slightly modified Roughgarden's approach to examine dietary overlap as a function of similarity in size between ontogenetic stages of *Aneides flavipunctatus* and *A. lugubris*. For each 15 mm SL interval, a histogram was plotted showing the relative frequency of prey falling into 10 size categories. To reflect the higher food intake by larger salamanders, relative prey-size frequencies were multiplied by a factor proportional to the mean total volume of food contained in the stomach of an average salamander of a given size class. The potential feeding overlap of a salamander of size X on an individual of size Y was then computed using a nonsymmetrical overlap formula (Roughgarden, 1972):

TABLE 5. Volumetric and numerical (in parentheses) importance of small, medium, and large prey in the diets of sympatric plethodontids at Navarro, Mendocino Co. Note that Class II *B. attenuatus* have been divided into 2 subclasses.

Species	Salamander size class	Prey size			Total prey items
		Small	Medium	Large	
A. flavipunctatus	I	(Insufficient sample)			
	II	.067 (.622)	.933 (.378)	.000 (.000)	66
	III	.001 (.038)	.784 (.949)	.215 (.013)	159
	IV	.010 (.191)	.659 (.794)	.331 (.045)	68
A. lugubris	I	.230 (.827)	.770 (.173)	.000 (.000)	230
	II	.004 (.224)	.278 (.740)	.721 (.036)	62
	III	(Insufficient sample)			
	IV	.000 (.020)	.070 (.878)	.930 (.102)	49
	V	.000 (.034)	.044 (.556)	.956 (.414)	29
B. attenuatus	IIA*	.134 (.784)	.866 (.216)	.000 (.000)	88
	IIB**	.102 (.830)	.453 (.165)	.445 (.005)	366

* SL = 20–26.5 mm.
** SL = 27–34 mm.

$$A_{Y,X} = \frac{I_{Y,X}}{A_Y} = 1 - \frac{\sum_i (y_i - x_i)}{\sum iy_i}$$

where $I_{Y,X}$ = area of overlap between prey-frequency histograms of morphs Y and X, A_Y = total area under the prey-frequency histogram for morph Y, x_i and y_i = amount of prey of size class i taken by an average individual predator of size X and size Y, respectively, and $(y_i - x_i) = 0$ for all $y_i < x_i$ (i.e., inter-morph feeding overlap cannot exceed 1.0). Maximum overlap of X and Y is attained if they take the same kinds of food in the same quantities, or if Y's feeding niche is completely included within that of X.

Roughgarden estimated size-specific total food intake from a generalized size-metabolic rate function, and smoothed the prey-frequency data into a unimodal distribution before computing alphas. I assumed that the mean volume of food contained in the stomach is proportional to food intake, and calculated overlap from the original (i.e., unsmoothed) feeding data.

Figs. 10 and 11 and Table 7 summarize the overlap data for different size classes of *A. flavipunctatus* and *A. lugubris*. Fig. 10 illustrates the almost complete overlap of larger morphs on smaller ones, despite the considerable difference in the shape of their respective utilization curves. This relationship, which is reflected in the non-symmetry of the matrix of alpha values (Table 7), might suggest a potential competitive advantage of large predators over smaller ones. However, this conclusion presupposes a sufficiently

TABLE 6. Volumetric and numerical (in parentheses) importance of small, medium, and large prey in the diets of sympatric plethodontids at Usal, Mendocino Co. Based on spring 1970 sample.

Species	Salamander size class	Prey size			Total prey items
		Small	Medium	Large	
A. flavipunctatus	I	.023 (.309)	.977 (.690)	.000 (.000)	97
	II	.002 (.045)	.876 (.940)	.122 (.015)	133
	III	.001 (.078)	.441 (.833)	.558 (.088)	102
	IV	(Insufficient sample)			
A. lugubris	I	(Insufficient sample)			
	II	.005 (.377)	.162 (.531)	.833 (.094)	53
	III	.001 (.056)	.269 (.800)	.730 (.142)	35
	IV	.000 (.037)	.044 (.750)	.956 (.212)	108
B. attenuatus	II	.120 (.724)	.880 (.275)	.000 (.000)	276
E. eschscholtzii	I	.079 (.538)	.734 (.456)	.187 (.006)	160
	II	.028 (.446)	.501 (.553)	.471 (.015)	65
	III	.005 (.197)	.352 (.709)	.643 (.093)	86

high total resource abundance to support large predators (Wilson, 1975).

A logarithmic transformation of standard length yielded a smooth functional relationship between body size separation and alpha (Fig. 11). This is equivalent to comparing size ratios, rather than linear differences in body size. The potential dietary overlap (A) of a smaller morph (s) on a larger one (l) can be expressed in exponential form: $A_{l,s} = C^{-d}$, where d = difference in the logarithms of the standard lengths of the two morphs, and C is a constant.

Calculated average dietary overlap between ontogenetic stages was lower for A. lugubris than for A. flavipunctatus at equivalent body sizes (Table 7, Fig. 11). However, any tendency toward reduced intraspecific competition in A. lugubris due to low dietary overlap might be negated by the presence of numerous very large (Class V) individuals

whose diets almost completely encompass those of smaller individuals. This suggests that juveniles could suffer severe competition for food if they live in close proximity with adults, and if small prey are in short supply. Maiorana (1978b) suggested that just this sort of ontogenetic competitive interaction exists in a population of A. lugubris that she studied on an island in San Francisco Bay.

Predation Models and Salamander Feeding Patterns.—Prey size is a key variable in optimal predation models which assume that a predator ranks prey items according to their relative food value (for a review, see Pyke et al., 1977). Such a model was constructed by Schoener (1969) to represent the feeding behavior of small terrestrial insectivores with sit-and-wait foraging tactics similar to those employed by many plethodontid salamanders. A sit-and-wait predator
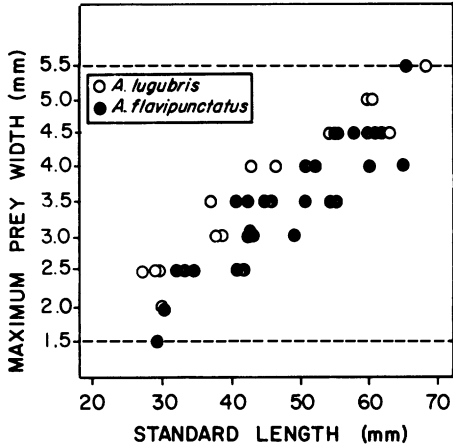
FIG. 8. Maximum accepted prey size (MAPS) for *A. flavipunctatus* and *A. lugubris*, based on experimental feeding of crickets to captive salamanders. Dashed lines indicate the maximum and minimum size of available prey.
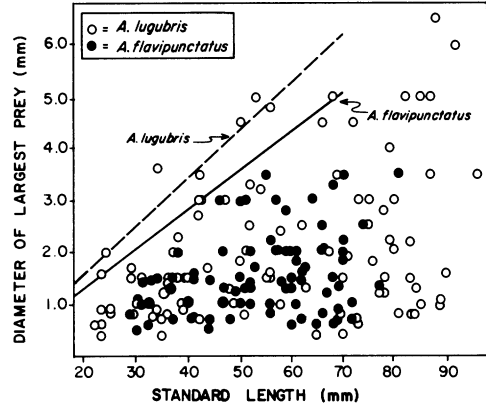
FIG. 9. Diameter of largest prey items found in the stomachs of *A. flavipunctatus* and *A. lugubris* collected at Navarro. The lines are computed regressions for the experimentally determined maximum accepted prey size (MAPS) for *A. flavipunctatus* (solid line) and *A. lugubris* (dashed line).

(Schoener's Type I) is envisioned as waiting passively at a vantage point until a suitable prey organism is sighted. The ideal Type I predator expends little or no energy specifically searching for prey, beyond that which is normally necessary for maintenance, territorial defense, etc. Extensive nocturnal observations of *A. flavipunctatus* and *A. lugubris* indicate that both species spend most of their time sitting motionless on the substrate, often partially concealed by a surface object or burrow. While above-ground movements certainly occur, and may include foraging activity, the normal pattern of surface activity by these salamanders appears closer to a sit-and-wait predator than to an actively searching one.

According to Schoener's model, an optimal predator should attain its necessary caloric intake in the fewest possible feeding acts, i.e., should specialize on prey that have the highest available *r*-values. When a single prey item satisfies the entire energetic requirement of the predator for a given time period, Schoener's (1969) optimization function (*r*) is maximized at a value of 1.0.

The reduced values of *r* that are actually observed in nature will reflect differences among prey items in handling time, pursuit time, size, and distance, as well as the overall abundance of prey and their size distribution.

Schoener used a log-normal distribution of prey sizes based on empirical data from sweep samples (Schoener and Janzen, 1968) to compute R as a function of prey size for sit-and-wait predators of a given size and distance from their prey. He found that R-functions for Type I predators are generally unimodal (Fig. 12), i.e., that an optimal prey size exists for a predator of any given size. The extent to which an actual predator specializes on optimal prey should depend on the ratio between its energetic requirements and the total availability of prey. According to Schoener's formulation and most similar models (cf. Pyke et al., 1977), a predator can "afford" to be highly selective only when food is relatively abundant.

Schoener's model entails some obvious oversimplification (e.g., fixed energetic requirements of predators, minimization of the number of feeding acts as the optimality criterion), some of which are considered in a later paper
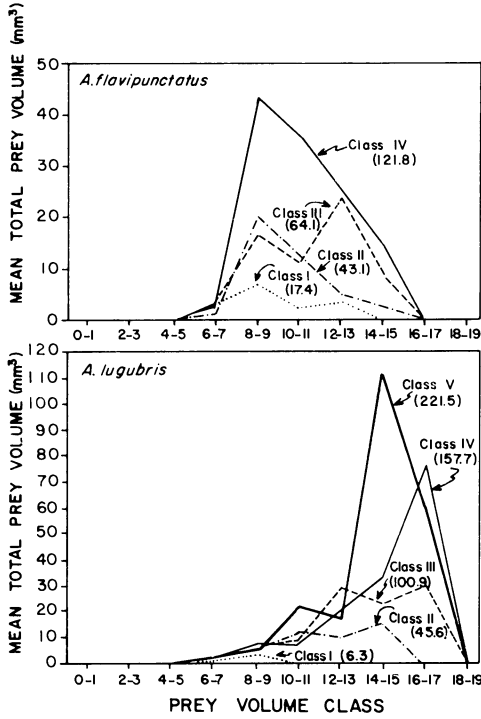
FIG. 10. Mean absolute volumetric contribution of prey items of different sizes to the diet of *A. flavipunctatus* (above) and *A. lugubris* (below) from Navarro. The prey utilization curves of larger size classes tend to enclose those of smaller size classes, despite major differences in the shapes of the functions. *A. lugubris* is seen to specialize on larger prey than *A. flavipunctatus*.
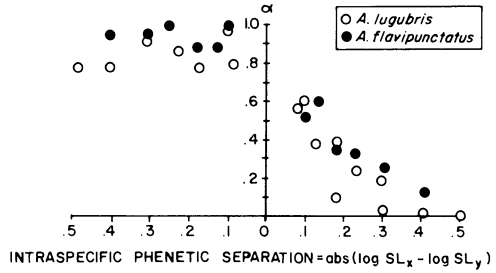

FIG. 11. Intraspecific prey-size overlap coefficients ("alpha's") in *A. flavipunctatus* and *A. lugubris* as a function of predator size. Right side of figure plots potential interference of larger individuals upon smaller ones; left side plots effect of smaller individuals on larger ones. Data from specimens collected at Navarro. For a given difference in body size, *A. lugubris* shows less dietary overlap than *A. flavipunctatus*.

(Schoener, 1971). Realistically modeling the feeding behavior of a predator through its entire life cycle is a complex problem in dynamic programming (e.g., Katz, 1974). Nevertheless, Schoener's original model suggests plausible adaptive bases for some of the ontogenetic and interspecific differences that are observed in the feeding tactics of terrestrial salamanders.

Predictions from Schoener's Model. — Schoener's model generates a number of testable predictions, several of which are non-obvious. As an example, the model predicts that the relative contribution to the diet of a single large prey item should increase with body size for Type I predators (Fig. 12B). That is, large

insectivores are predicted to satisfy their total energy requirements with fewer prey than are small ones. The feeding data for *Ensatina, Batrachoseps,* and both species of *Aneides* are consistent with this prediction, both at the inter- and intraspecific levels: adults of all four species consistently take fewer prey than sympatric juveniles, and larger species take fewer prey than smaller species. A similar ontogenetic pattern was observed in *Plethodon cinereus* (Burton, 1976).

A second prediction is that large Type I predators should utilize a wider range of prey sizes than should smaller predators (Fig. 12B). Such a pattern has been observed in studies of *Anolis* lizards (Schoener, 1968; Schoener and Gorman, 1968), birds (Ashmole, 1968; Storer, 1966; Wilson, 1975), ant-lions (Wilson, 1974), copepods (Wilson, 1973), larval flies (Sprules, 1972), and in at least two previous studies of plethodontid salamanders (Maiorana, 1978a; Sites, 1978). In *Aneides flavipunctatus,* both the range and variance in prey size increased with increasing salamander size, because adult *A. flavipunctatus* continue to ingest at least a few of the small prey that are eaten more frequently by juveniles. Wilson (1975) demonstrated that this pattern is widespread among predators.

TABLE 7. Intraspecific dietary overlap coefficients ("alpha's") for size classes of *A. flavipunctatus* and *A. lugubris* from Navarro, Mendocino Co. Entries indicate the potential effect of an individual of size X on an individual of size Y.

		Size class (X)				
		I	II	III	IV	V
A. *A. flavipunctatus*						
Size	I	1.00	.87	.94	.94	
Class	II	.35	1.00	.88	.99	
(Y)	III	.26	.60	1.00	1.00	
	IV	.13	.34	.52	1.00	
B. *A. lugubris*						
Size	I	1.00	.78	.91	.78	.78
Class	II	.11	1.00	.89	.87	.96
(Y)	III	.05	.40	1.00	.98	.88
	IV	.03	.25	.63	1.00	.81
	V	.02	.20	.40	.58	1.00

A non-trivial evolutionary consequence of Schoener's model is that large sit-and-wait predators should show the most evidence of trophic specialization. This follows from the increasingly leftward skewness of the R-function with increasing predator size (Fig. 12B). Although a relatively large insectivore (80–100 mm in length) may derive a slight net energetic gain from eating very small prey, the optimal prey size for such a predator will be very close to the maximum that it can handle. This is indicated by the steep drop in the R-function to the right of the maximum (Fig. 12B). It follows that natural selection should strongly favor morphological adaptations that allow efficient ingestion of "extra-limital" (i.e., oversize) prey by large insectivorous predators. The R-curves for small predators have lower maxima (implying that there is relatively little to gain by specializing on one particular prey size), and the optimal prey size for small predators is far below the upper size limit of acceptable prey. Consequently, evolutionary adaptations for taking somewhat larger prey should be less advantageous for small insectivores than for larger ones. Similar reasoning led Wilson (1975) to predict that character
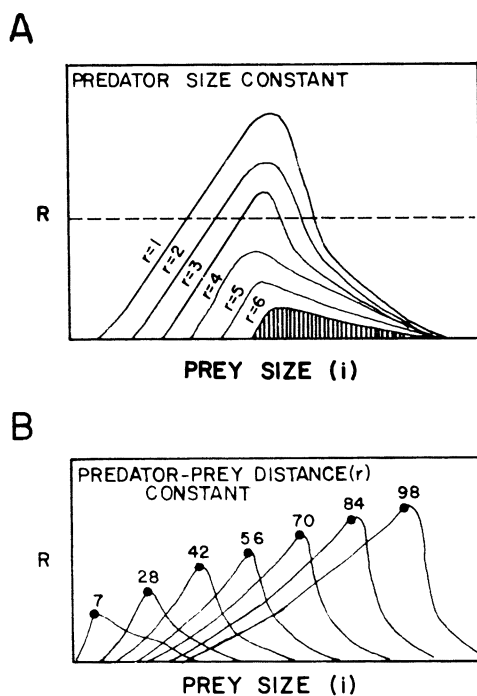

FIG. 12. Schoener's (1969) representation of r-functions for small "sit-and-wait" predators feeding on a log-normally distributed population of insects. The value of r reflects the contribution of a single prey of size (i) to the total dietary needs of the predator, so the maximum in the r-function corresponds to the size of "optimal" prey. The upper figure (A) shows the effect of varying the distance (r) between prey and predator, with predator size held constant. The dashed demarcation line will move up or down as overall abundance of prey increases or decreases. The lower figure (B) shows the effect of predator size (indicated as length in mm at the mode of each r-function) on the size and relative value of optimal prey items, with r held constant.

displacement in trophic morphology should be rare in small predators.

Like most other models of optimal predation (e.g., Emlen, 1966; Holling, 1966; MacArthur and Pianka, 1966; Pulliam, 1974), Schoener's model predicts that predator selectivity will increase as food becomes more abundant. A plausible explanation for the increase in mean prey size over the course of the wet season in the present study is that total prey abundance (or availability)

also increased seasonally, thereby enabling predators to specialize on optimal (i.e., larger) prey. This hypothetical seasonal prey increase should be tested, although the design of a realistic sampling scheme presents problems (Maiorana, 1978b).

It is perhaps worth emphasizing that seasonal feeding patterns differ markedly between eastern North America and California. In the latter area, salamanders are active during the mild, wet winters, but surface activity ceases during the hot and rainless summer months. The reverse pattern of seasonal activity is observed in eastern species.

Circumstantial evidence such as that obtained from stomach analysis cannot, of course, be interpreted as "proof" of the validity of any particular predation model. However, data on food habits may constitute evidence for or against particular conceptualizations of salamander feeding dynamics. The fact that observed ontogenetic, interspecific, and (perhaps) seasonal patterns in feeding ecology are all in qualitative accord with a number of non-trivial predictions of Schoener's (1969) model should provide an impetus for closer examination both of the model and of the animals whose feeding behavior it aims to encapsulate. In particular, it is encouraging that variation in several seemingly disparate dimensions of salamander feeding ecology appear to be explicable within a very general and relatively simple theoretical framework.

Feeding Ecology and Competition. — Controlled field experiments have confirmed the existence of interspecific competition in plethodontid communities (Fraser, 1976b; Hairston, 1980a, 1981; Jaeger, 1970, 1971; Keen, 1982), but there is little agreement as to the ultimate or proximate object(s) of competition. One view holds that salamander populations are food-limited (e.g., Jaeger, 1972, 1980), in which case the results of the present study of food partitioning may be directly relevant to the question of how salamander species co-

exist. An opposing view claims that any observed diet differences among species or morphs of salamanders are mere "epiphenomena," i.e., inconsequential correlates of competition for refugia, nest sites, or other non-food resources that in fact limit salamander populations (e.g., Hairston, 1980a, 1981; Maiorana, 1978b). Part of this controversy appears to revolve around a semantic distinction between "limiting" vs. "limited" resources (Jaeger, 1980; Maiorana, 1978b). In addition, it is not always recognized that intense competition for one resource (e.g., food) can occur even though population size is limited by another resource (e.g., available refugia). That is, food competition could determine *which* (rather than how many) individuals survive or breed successfully (Murray, 1982).

Some objections to the idea that food could be an object of competition for salamanders are based on the assumption that salamanders are unselective predators, and that they enjoy a superabundant food supply. However, laboratory and field studies agree in indicating that plethodontids operate on a restrictive energy budget (Feder, 1983; Fitzpatrick, 1973; Fraser, 1976b; Jaeger, 1972, 1978, 1980; Merchant, 1970). In addition, the present dietary analysis suggests, and laboratory studies strongly confirm, that salamanders are indeed capable of making reasonably subtle distinctions among prey types (Jaeger and Barnard, 1981; Jaeger et al., 1981; Jaeger and Rubin, 1982; Roth, 1976, 1978). These findings do not constitute proof that competition for food exists, but they do refute some of the conventional wisdom that would dismiss such competition as being implausible.

Recent years have witnessed the discovery of an unexpectedly complex array of territorial and other defensive behavior patterns in plethodontids (Arnold, 1982; Cupp, 1980; Jaeger, 1974, 1981; Jaeger and Gergits, 1979; Thurow, 1976; Tristram, 1977). There has been a concomitant shift away from emphasis

on exploitation, and toward interference (cf. Miller, 1969) as the most likely competitive mode for interacting salamander populations (Jaeger, 1974, 1980). Because aggressive behavior often is expressed as defense of a burrow, crevice, or cover object, it is tempting to conclude that these refugia are themselves the ultimate object of competition and therefore the source of population limitation. However, aggressive behavior only evolves to reinforce exploitative competition for a critical resource (MacArthur, 1972). Mere defense of cover objects does not necessarily mean that hiding places are in short supply. Instead, salamanders may be guaranteeing their access to mates (Arnold, 1976), or to localized prey concentrations that serve as food reservoirs when unfavorable weather conditions depress the general level of prey availability (Jaeger 1972, 1978, 1980). Nesting requirements for a few species may indeed be so specialized that selection favors defense of nest sites, as appears to be the case for the crevice-dwelling *Aneides aeneus* (Cupp, 1980). However, there is no good evidence that more typical terrestrial species are limited by availability of nest sites (Hairston, 1981), nor is local salamander density normally restricted by the number of individuals that can physically fit under available cover objects or into burrows and crevices. Salamanders are sometimes observed to be overdispersed (Maiorana, 1978b; Wells, 1980), but this probably reflects aggressive spacing of individuals, not a literal shortage of places to hide.

Summarizing, direct or indirect competition for food among coexisting salamanders appears to be a reasonable possibility, and trophic adaptations for taking large prey could serve to cushion somewhat the impact of any such interaction in the community studied. However, not all salamander species in a local community necessarily compete (Hairston, 1981) and from what Charnov (1976) calls the "viewpoint" of op-timal predation, it also could be argued that inter- and intraspecific feeding differences reflect adaptations for increased individual feeding efficiency, independent of competitive ability. Yet another complication arises from the fact that morphological specializations that are correlated with an increased ability to take "optimal" (i.e., relatively large) prey also tend to increase defensive or aggressive capabilities vis-a-vis competitors or predators (Arnold, 1982; Thurow, 1976). Whether feeding or fighting provided the initial selective basis for the evolution of increased body size and modifications of the jaws and teeth in *Aneides*, both functions appear to be important in contemporary salamander communities. It will be difficult to choose among the many possible evolutionary and ecological scenarios that might have produced the mixture of species distribution patterns and morphologies we observe today, even if a full array of laboratory experiments and field manipulations are brought to bear on the problem. Data from detailed analyses of the feeding habits of natural populations will continue to provide a valuable adjunct in the effort to place salamander ecology on the strongest possible theoretical and empirical footing.

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APPENDIX I.   Contributions of major prey taxa to the fall diet of *A. flavipunctatus* at an inland locality (Skaggs Springs). Tabled entries are percentages of total prey individuals and (in parentheses) total prey volume. Data for November 1968 and November 1970 are combined.

	Salamander size (SL)			
	Class I (20–34 mm)	Class II (35–49 mm)	Class III (50–64 mm)	Class IV (65–79 mm)
No. stomachs	4	5	19	17
Total prey	178	910	882	405
Prey taxon				
Diplopoda	1.1 (64.8)	0.3 (77.8)	2.0 (42.8)	2.5 (26.7)
Coleoptera		0.3 (5.3)	2.9 (20.5)	2.2 (26.0)
Hymenoptera		2.7 (3.5)	10.0 (6.4)	10.7 (4.5)
Isoptera			0.2 (0.1)	39.5 (24.0)
Diptera	5.0 (4.2)	0.7 (0.8)	0.9 (0.3)	1.0 (0.1)
Collembola	75.3 (21.6)	94.1 (8.9)	72.1 (3.4)	31.0 (1.1)
Subtotal	82.4 (90.6)	98.1 (96.3)	88.1 (73.5)	87.8 (82.4)
Chilopoda		0.2 (0.6)	1.1 (4.3)	2.0 (8.2)
Isopoda			0.8 (7.0)	0.2 (1.9)
Acarina	15.2 (1.8)	0.6 (0.1)	2.9 (0.3)	4.2 (0.3)
Orthoptera		0.1 (2.4)	2.5 (12.6)	
Other*	3.4 (7.6)	0.9 (0.5)	4.2 (2.5)	5.7 (7.7)

* Pulmonata, Araneida, Pseudoscorpionidae, Opiliones, Thysanura, Dermaptera, Homoptera, Lepidoptera.

APPENDIX II.   Contributions of major prey taxa to the winter diet of *A. flavipunctatus* at an inland locality (Skaggs Springs). Tabled entries are percentages of total prey individuals and (in parentheses) total prey volume. Data for January 1970 and January 1971 are combined.

	Salamander size (SL)			
	Class I (20–34 mm)	Class II (35–49 mm)	Class III (50–64 mm)	Class IV (65–79 mm)
No. stomachs	24	14	15	16
No. prey	629	277	112	123
Prey taxon				
Diplopoda	0.6 (9.3)	2.1 (19.7)	5.4 (26.9)	10.6 (42.2)
Coleoptera	4.9 (7.3)	8.1 (19.6)	19.6 (35.3)	18.7 (36.6)
Hymenoptera	0.7 (1.9)	1.4 (0.1)	7.1 (0.3)	17.9 (2.6)
Isoptera			1.0 (0.3)	
Diptera	12.7 (43.3)	13.4 (17.2)	24.1 (15.0)	14.6 (3.4)
Collembola	67.4 (20.0)	46.9 (3.2)	25.0 (1.2)	24.4 (1.5)
Subtotal	86.3 (81.8)	71.9 (59.8)	82.2 (79.0)	86.2 (86.3)
Chilopoda			1.8 (2.0)	1.6 (2.9)
Isopoda				0.8 (6.2)
Acarina	4.8 (1.4)	3.2 (0.1)	3.6 (0.0)	4.0 (0.2)
Orthoptera		0.4 (3.0)		
Other	9.0 (17.6)	1.6 (36.8)	11.6 (18.8)	7.2 (5.0)

APPENDIX III. Contributions of major prey taxa to the spring diet of an inland population of *A. flavipunctatus* (Skaggs Springs). Tabled entries are percentages of total prey individuals and (in parentheses) total prey volume. Data for April 1971 collection.

	Salamander size (SL)			
	Class I (20–34 mm)	Class II (35–49 mm)	Class III (50–64 mm)	Class IV (65–79 mm)
No. stomachs	5	5	4	3
Total prey	92	129	254	27
Prey taxon				
Diplopoda		0.8 (8.7)		
Coleoptera	3.3 (9.3)		0.8 (46.3)	18.5 (66.0)
Hymenoptera	73.9 (33.2)	44.2 (30.3)	97.6 (27.7)	44.4 (4.2)
Isoptera	8.7 (18.5)	36.4 (47.3)		
Diptera		0.8 (8.6)		3.7 (4.6)
Collembola		5.4 (0.7)		
Subtotal	85.9 (61.0)	87.6 (95.6)	98.4 (74.0)	66.2 (74.8)
Chilopoda	2.2 (24.3)	0.8 (0.7)		7.4 (20.2)
Acarina	2.2 (0.9)	5.4 (0.4)		
Other	9.8 (13.8)	6.2 (3.3)	1.6 (25.9)	26.5 (5.0)

APPENDIX IV. Contributions of major prey taxa to the fall diet of two coastal populations of *A. flavipunctatus* (data pooled for Navarro and Usal). Tabled entries are percentages of total prey individuals and (in parentheses) total prey volume. No Class I juveniles were found. Data combined for 13–14 November 1970.

	Salamander size (SL)		
	Class II (35–49 mm)	Class III (50–64 mm)	Class IV (65–79 mm)
No. stomachs	8	8	4
Total prey	267	230	67
Prey taxon			
Diplopoda	1.1 (1.6)	0.4 (6.9)	
Coleoptera	7.2 (14.4)	6.6 (28.6)	9.0 (7.2)
Hymenoptera	29.6 (49.1)	65.2 (49.1)	22.0 (36.4)
Isoptera	1.5 (6.1)	1.7 (2.3)	28.4 (26.7)
Diptera	3.0 (1.0)	2.2 (3.1)	3.0 (1.2)
Collembola	27.0 (3.6)	9.2 (0.9)	17.9 (0.1)
Subtotal	69.4 (75.8)	85.3 (90.9)	80.6 (71.6)
Chilopoda	1.1 (1.6)	1.3 (3.2)	1.5 (2.4)
Acarina	19.5 (3.6)	7.4 (0.4)	
Other	9.4 (19.1)	6.4 (6.1)	19.4 (25.7)

APPENDIX V. Contributions of major prey taxa to the winter diet of *A. flavipunctatus* at a coastal locality (Navarro). Tabled entries are percentages of total prey individuals and (in parentheses) total prey volume. Data for 26 February 1971.

	Salamander size (SL)			
	Class I (20–34 mm)	Class II (35–49 mm)	Class III (50–64 mm)	Class IV (65–79 mm)
No. stomachs	5	7	8	2
Total prey	43	53	112	116
Prey taxon				
Diplopoda	9.3 (75.5)	5.7 (43.5)	5.4 (70.0)	0.8 (5.2)
Coleoptera	11.6 (8.7)	1.9 (7.8)	0.9 (0.1)	1.7 (19.8)
Hymenoptera	4.6 (4.5)	7.5 (3.2)	45.5 (22.8)	1.7 (0.1)
Isoptera		15.1 (17.1)		94.0 (73.2)
Diptera		5.7 (0.3)		1.7 (1.7)
Collembola	26.4 (6.4)	45.3 (7.0)	39.3 (3.3)	
Subtotal	51.9 (95.1)	81.2 (79.5)	91.1 (96.2)	100.0 (100.0)
Chilopoda		5.7 (19.9)	1.8 (2.1)	
Acarina	32.0 (1.9)	11.3 (0.4)	3.6 (0.1)	
Orthoptera			0.9 (0.7)	
Other	2.3 (3.0)	1.9 (0.1)	2.7 (0.9)	

APPENDIX VI. Contributions of major prey taxa to the spring diet of two coastal populations of *A. flavipunctatus*. Tabled entries are percentages of total prey individuals and (in parentheses) total prey volume. Data combined for 18 April 1970 and 18 April 1971.

	Salamander size (SL)			
	Class I (20–34 mm)	Class II (35–49 mm)	Class III (50–64 mm)	Class IV (65–79 mm)
No. stomachs	16	24	29	16
Total prey	208	454	391	407
Prey taxon				
Diplopoda	1.9 (4.0)	1.5 (3.2)	2.6 (16.7)	0.5 (2.4)
Coleoptera	12.5 (38.8)	4.2 (6.3)	7.4 (18.8)	2.7 (9.3)
Hymenoptera	38.0 (25.9)	45.4 (34.1)	59.1 (40.6)	75.2 (73.8)
Isoptera	4.8 (11.5)	25.1 (30.7)	6.2 (3.9)	15.9 (8.5)
Diptera	4.3 (7.3)	2.6 (2.3)	1.6 (0.4)	0.7 (0.1)
Collembola	13.4 (1.9)	10.8 (1.9)	12.9 (0.5)	2.5 (0.4)
Subtotal	74.86(89.4)	89.6 (78.5)	89.9 (80.9)	97.5 (94.5)
Chilopoda		0.4 (6.7)	1.0 (2.9)	1.0 (1.6)
Isopoda		0.6 (0.3)	0.3 (2.7)	
Acarina	17.8 (1.8)	3.8 (0.2)	1.8 (0.0)	0.7 (0.0)
Other	7.0 (8.7)	6.1 (14.6)	6.5 (12.8)	0.7 (4.0)