Patterns of Ontogenetic and Geographic Variation in the Black Salamander, *Aneides flavipunctatus* (Caudata: Plethodontidae)

JAMES F. LYNCH

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ABSTRACT

Lynch, James F.   Patterns of Ontogenetic and Geographic Variation in the Black Salamander, *Aneides flavipunctatus* (Caudata: Plethodontidae). *Smithsonian Contributions to Zoology*, number 324, 53 pages, 19 figures, 14 tables, frontispiece, 1981.—*Aneides flavipunctatus*, a terrestrial plethodontid salamander, is virtually restricted to humid, thermally equable areas of northwestern California. The limits of distribution mainly reflect the extent of climatically favorable habitat and the presence of longstanding barriers to dispersal, but competition with other species of salamanders may play a role in excluding *A. flavipunctatus* from mesic, equable areas in the vicinity of the California-Oregon border.

Aneides flavipunctatus exhibits marked ontogenetic and geographic variation in color pattern and external proportions. Within the contiguous portion of the range, variation in individual characters tends to be clinal and correlated with latitude, distance inland, elevation, or other geographic parameters. However, isolated populations at the southern and northeastern limits of distribution exhibit discordant variation relative to their nearest neighbors within the contiguous range.

Northern populations of *A. flavipunctatus* retain a suite of juvenile-like characteristics throughout adulthood, and paedomorphism appears to be an important mechanism by which evolutionary changes have occurred in this species. A Prim Network analysis indicates that phenetic and geographic proximity are highly correlated within the contiguous range of *A. flavipunctatus*, but that peripheral isolates most clearly resemble central "core" populations in morphology.

Contents

FRONTISPIECE.—The Black Salamander, *Aneides flavipunctatus*. (Illustration by the author.)

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Introduction

In recent years, evolutionary biology has witnessed a renewed emphasis on the overriding importance of speciational events in the generation of evolutionary change. Following the publication of Mayr's (1963) classic book, "Animal Species and Evolution," many biologists considered the speciation problem conceptually "solved" for bisexual animal species, although controversy concerning such topics as sympatric speciation has continued. A series of papers by N. Eldredge and S.J. Gould (Eldredge, 1971; Eldredge and Gould, 1972; Gould and Eldredge, 1977) has challenged this complacency. These authors present fossil evidence that by far the greatest proportion of evolutionary diversification occurs in rapid bursts associated with speciation. This "punctuated equilibrium" model of evolution holds that morphological changes within species over time are generally insignificant, a position strongly in opposition to the traditional gradualistic view of evolutionary change.

The present study concerns the relationship between ontogenetic and geographic modes of morphological variation within a single species, *Aneides flavipunctatus*, a terrestrial plethodontid salamander. The goals of the present paper are threefold: (1) to describe quantitatively some intraspecific patterns of ontogenetic and geographic variation, (2) to suggest possible ecological causes and effects of this variation, and (3) to develop the argument that differential development is a plausible evolutionary mechanism whereby substantial geographic variation has been produced in this species.

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Materials and Methods

GEOGRAPHIC DISTRIBUTION

Aneides flavipunctatus was collected throughout its range, and a concerted attempt was made to explore areas outside the known distribution for presence of the species. To aid in understanding the determinants of the distribution, I examined the relationship between the range of *A. flavipunctatus* and patterns of minimum and maximum temperature, thermal equability, annual rainfall, and the distribution of other salamander species.

Temperature data were obtained from isotherm maps for January and July mean temperature (U.S. Department of Agriculture, 1941). Annual rainfall was estimated from the isopleth map published by the California Division of Water Resources (1951). Data for the distribution of other salamander species were obtained from personal collecting, specimen records in the Museum of Vertebrate Zoology, and Stebbins (1966). Thermal equability regimes were delimited using the method of Axelrod and Bailey (1968). Thermal equability is inversely proportional to the deviation of a given climate from the average surface temperature of the earth. At present, this value is 14.2°C (= 57.2°F). The index of equability is influenced not only by annual mean temperature, but also by the magnitude of seasonal fluctuations around that mean. A perfectly equable climate would not deviate from 57.2°F throughout the year. The equability actually observed at a site is expressed as a percentage of the "perfect" equable climate according to the following formula:

$$M = K - 30 \log ([C - T]^2 + [D + 0.366 A]^2)$$

where

M = index of equability (range: 0–100%)

K = constant = 124.3 for degrees F, or 109.0 for degrees C

C = mean temperature central to biotic system of interest; for the earth today this is 57.2°F (=14.2°C)

T = mean temperature of the locality in question

D = constant = 2.62 for degrees F, or 1.46 for degrees C

A = mean annual range of temperatures at the locality in question, approximated as the difference between the mean temperature of the warmest and coldest months

For some organisms (e.g., those adapted to lowland tropical conditions) the mean surface temperature of the earth may not be a particularly meaningful standard for comparison. However, for *A. flavipunctatus* and most other terrestrial salamanders active during the mild winter rainy season of northern California, the ideal equable temperature of 14°C closely approximates the mean surface temperature at which animals are normally active (Lynch, 1974a).

CHARACTER ANALYSIS

Aneides flavipunctatus was collected at 142 localities. Because most morphological traits in salamanders vary with body size or sex, or both, reasonably large sample sizes are necessary for analysis of body proportions and color pattern. In practice, samples of about 15 individuals proved adequate for most purposes, and 37 samples equalled or exceeded this number. The sample localities are listed in Lynch (1974a). All specimens are deposited in The Museum of Vertebrate Zoology, Berkeley, California.

External measurements and observations of color pattern were made on living salamanders that had been anesthetized by immersion in 25% Chloretone solution. The use of live material allowed a greater degree of standardization of proportional measurements than is possible with preserved animals. The latter were used in some instances to augment sample sizes for counts of vertebral number, since trunk segmentation is independent of preservational status. Details con-

cerning the method of measurement of each external character are given in Lynch (1974a).

Salamander systematics traditionally has been constrained by the fact that external characters are few in number, difficult to quantify, and ontogenetically variable. A major advantage of *A. flavipunctatus* for systematic studies is that the color pattern of this species is particularly well-suited to quantitative analysis. To obviate the effects of ontogenetic variation, I used bivariate and multivariate statistical techniques to analyze characters that vary with body size.

Quantitative shifts in the rates of a few developmental processes can produce considerable variation in adult morphology, even in the absence of major genetic reorganization. De Beer (1958), Bonner (1965), Wake (1966), and Gould (1977) all stress the evolutionary importance of paedomorphism, the process whereby traits associated with the juvenile life stage in ancestral forms are maintained into adulthood in descendant lineages. Wake (1966) emphasizes paedomorphosis as an evolutionary mechanism for development of the major groups within the salamander family Plethodontidae. At the outset of the present study, I hypothesized that much of the geographic variation observed in *A. flavipunctatus* is a result of subtle evolutionary shifts in what I perceived to be the probable ancestral pattern of ontogenesis. Much of my analysis, therefore, was aimed at comparing geographic and ontogenetic modes of differentiation.

Color Pattern

Previous workers (Myers and Maslin, 1948; Lowe, 1950; Stebbins, 1951, 1954, 1966; Brown, 1972) have remarked on the striking geographic variation in color pattern exhibited by *A. flavipunctatus* (see also Lynch, 1974b). Throughout most of its range, *A. flavipunctatus* is a black salamander with varying numbers of white spots and greater or lesser amounts of brassy pigmentation concentrated in the dorsal and dorso-lateral regions. The typical color pattern is strikingly similar to that of the eastern plethodontid *Plethodon glutinosus* (see Highton, 1962a).

The most conspicuous markings of *A. flavipunctatus* are discrete, densely pigmented white iridophores. These spots can be accurately counted and measured in specified areas of the body.

The degree of development of brassy and melanic pigmentation is difficult to score on an interval scale, and variation in these traits was quantified with reference to an ordinal scale of standard character states (Lynch, 1974a).

The 10 color characters selected for detailed analysis are as follows: size of white iridophores on the dorsum (DWS), venter (VWS), and chin (CWN); density of brassy iridophores on the dorsum (DBN) and eye (EIR); shape of brassy iridophores on the dorsum (DBS); concentration of brassy iridophore frosting in the ventrolateral region of the trunk (VBC); intensity of melanic pigmentation on the venter (VMD), chin (CMD), and limb-bases (LMD).

Virtually all aspects of the color pattern of *A. flavipunctatus* show ontogenetic variation. Rates of change in character states tend to be most rapid in juveniles and subadults, with little further change once sexual maturity has been attained. I used linear regression techniques to characterize various features of the color pattern for salamanders between 30 and 50 mm in standard length (SL). I computed the regression of each pigmentation character (y_i) to a common x-value ($x_c = 50$ mm).

By this method, it is possible to generate estimated y-values for the same standard SL in all populations, thereby removing the component of variation that is due to size differences. Measurements from animals over a wide size range can be used to compute the regression estimates, so there is no necessity to restrict analysis to individuals of "standard" size.

A related approach, analysis of covariance (ANCOVA), involves direct comparison of the slope and y-intercept of regression lines in different populations, as for example in studies of size-fecundity relationships in *Desmognathus* by Tilley (1968) and in *Gyrinophilus* by Bruce (1972). In the

present context, however, I judged ANCOVA to be less than ideal for two major reasons. First, the standard t-test for difference in the regression coefficient (slope) of the x-y relationship cannot distinguish between parallel distributions, even if there is no overlap in the two data clouds being compared. Second, the attempt to detect differences in elevations of the regression lines being compared is hampered by the fact that the confidence limits around y tend to be relatively wide for x = 0 compared to the narrower confidence limits at x = $\bar{x}$. The hyperboloid shape of the confidence envelope around a regression line is accentuated if there are no actual data points for the entire range of possible x's greater than zero. The latter situation pertains for *A. flavipunctatus*, where observed x's generally exceed 20 mm (Figure 1).

Another reason for comparing regressions at a standard x-value other than x = 0 is that one often is interested to know whether morphometric traits (y's) differ from population to population at a specified body size (x).
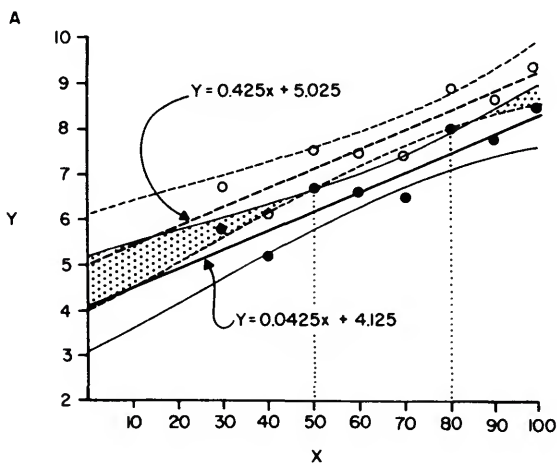
FIGURE 1.—A hypothetical example which illustrates the advantage of comparing regressions at X values near $\bar{x}$, rather than at x = 0. The regression lines have identical slopes (b = 0.0425), but differ in elevation; this difference can only be detected if the lines are compared at x-values between about 50 and 82, due to overlap of the 95% confidence envelopes of the two lines (stippled) at large values of $|\bar{x}-x|$.

In *A. flavipunctatus*, color characters are stabilized in individuals exceeding about 70 mm SL, i.e., there is no significant regression of coloration on body size for larger individuals. For comparisons of salamanders exceeding 70 mm, simple means and standard deviations, rather than projected values, were calculated for each color character.

EXTERNAL PROPORTIONS

The proportional characters examined in *A. flavipunctatus* are mainly those related to feeding and locomotion. The size and shape of "trophic appendages," i.e., anatomical features specifically used in feeding, can be useful predictors of prey size and type, and may thus serve as indices of potential competition within and between species of predators. The presumed relationship between predator morphology and competition (cf. Dunham, et al., 1978) has been most studied in birds (e.g., Hespenheide, 1971, 1973, 1975; Hutchinson, 1959; Karr and James, 1975; Klopfer, 1962; Klopfer and MacArthur, 1961; Lack, 1946, 1947, 1971; Schoener, 1965) and lizards (e.g., Roughgarden, 1972; Schoener, 1966, 1968, 1969a, 1969b). Fraser (1976) and Jaeger (1972) have demonstrated a general relationship between prey size and head size in eastern in plethodontid salamanders of the genus *Plethodon*, and I have documented similar relationships for sympatric plethodontids of the genera *Aneides*, *Ensatina*, and *Batrachoseps* in California (Lynch 1973, 1974a).

Other "indicator traits" (sensu Roughgarden, 1972) may predict locomotor patterns, and hence the kind of microhabitat utilized. An example of such a trait is relative limb length, which has been employed by various investigators as an index to structural microhabitat used by birds (e.g., Grant, 1965, 1966; Lack, 1971) and lizards (Pianka, 1969; Pianka and Parker, 1972).

The external characters I selected for analysis in *A. flavipunctatus* are body length (BL), head length (HDL), head width (HW), forelimb length (FL), hind limb length (HLL), and tail length (TL). The first three of these characters are pre-

dicted to influence the kinds of prey taken; the last three should affect locomotory performance.

Growth in salamanders is more or less continuous, although the growth rate may decline nearly to zero in very large individuals. Virtually all body proportions change with growth, thereby precluding the use of simple summary statistics in describing external form, unless analysis is restricted to animals of a given size. This is a serious drawback in salamander systematics, in view of the scarcity of suitable meristic characters (e.g., scales, warts, tubercles).

A commonly used method for minimizing size-dependent variance in morphology is to divide proportional measurements by some size factor (e.g., SL, body weight) which, it is hoped, will standardize those measurements. However, ratios are inherently more variable and less accurate than the measurements from which they derive (Atchley, 1978; Atchley and Anderson, 1978; Atchley, et al., 1976; Simpson, Roe, and Lewontin, 1960; Sokal and Rohlf, 1969). Even where covariance between a size factor and a proportional character is high, and the regression between the two is strictly linear, the ratio y/x will vary with x unless the regression line happens to pass through the origin. If the y-intercept is greater than zero, as for many external characters in *A. flavipunctatus*, y/x decreases asymptotically with increasing x (Figure 2). Thus, apparent interpopulational differences in character ratios may reflect nothing more than differences in mean body size. This kind of misinterpretation appears to have occurred in Myers and Maslin's (1948) diagnosis of *A. f. niger* as a distinct subspecies. These authors claim that the relative limb length of *A. f. niger* is significantly shorter than that of the nominate race. Reanalysis of the data presented by Myers and Maslin shows that their sample of *A. f. niger* had a considerably larger mean SL than their *A. f. flavipunctatus* sample (75 vs. 65 mm), and that the purported racial differentiation in relative limb length can be attributed plausibly to ontogenetic variation in body proportions.

I decided against the use of ratios in the statis-
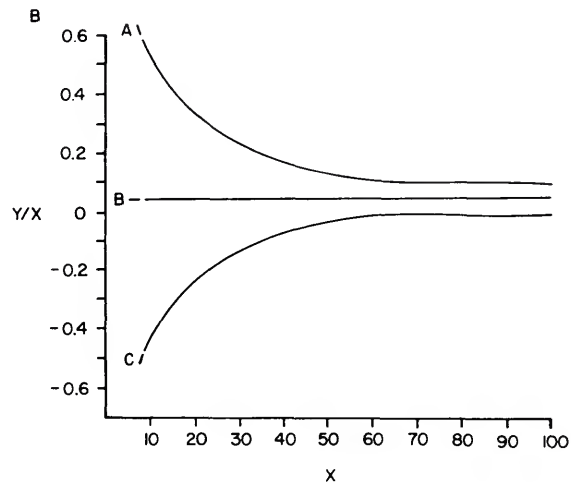
FIGURE 2.—The effect of the location of the y-intercept (a) on the relative magnitude of y (i.e., y/x) (all three plots based on x-y regressions with the same slope (b = 0.0425); curve A, a = 5.0; curve B, a = 0; curve C, a = −5.0; the lack of constancy of y/x when the y-intercept is not zero means that taking ratios of characters is not an effective means of eliminating the effect of size-related variation).

tical analysis of external form, and instead employed regression analysis of origin measurements. Each sample of salamanders was divided into three subsamples which were treated separately in all statistical analyses: (1) juveniles and subadults (20–39 mm SL); (2) adult males (50–79 mm SL); and (3) adult females (50–79 mm SL). Individuals larger than 79 mm SL were not included in the regression analysis, but such animals were generally so uncommon that little information was lost by this omission.

I projected measurements of body proportions to a common body size for inter-population comparisons. For adult salamanders, the standard was a body length (= SL − head length) of 50 mm; for juveniles, standard body length was 20 mm. Body length was used instead of SL because the latter incorporates head length, itself a proportional character of interest.

Model I linear regression was used in all computations. Although Sokal and Rohlf (1969, chapter 14) caution that this model may be in-

appropriate where both x and y vary in uncontrolled fashion, other authorities (e.g., Draper and Smith, 1966) routinely employ Model I regression for data analogous to those here analyzed. The Bartlett Three-group method, the alternative regression model recommended by Sokal and Rohlf, was used to reanalyze several data sets, but no substantial differences from the results of Model I regression analysis resulted. It is doubtful, therefore, that serious errors have been introduced by using the simpler and more familiar of the two possible regression models.

BODY SIZE

In salamanders, as in many tetrapods, body length is closely correlated with body weight and has been used as an index of overall size in the present study. Given a suitable index of individual size (e.g., SL, total length, body weight), there remains the problem of characterizing a population. The distribution of body sizes in collections of salamanders tends to be skewed, polymodal, truncated, and otherwise non-Gaussian. If one wishes to characterize populations with respect to the average size of adult salamanders, the differential abundance of juveniles in various collections is an additional confounding factor (Dunham, et al., 1978). Williams (1972) used maximum observed body size to characterize size patterns in *Anolis* lizards, as did Lindsey (1966a) in a study of latitudinal trends in body size of vertebrates. Schoener (1969c) used the mean SL of the largest third of each sample as an indicator of body size in *Anolis*, while Case (1976) used the mean of the largest decile in his analysis of size in populations of *Sauromalus*. These alternatives all were rejected for the present study because of their dependence on sample size, or presence of juveniles, or both.

To avoid these problems, I excluded juveniles and most subadults from calculations of mean body size by choosing an arbitrary lower limit of 55 mm SL for *A. flavipunctatus* included in mean size computations. This is substantially below the SL at first reproduction for females in all popu-

lations and below the male minimum in most. One might consider this computed mean value as indicative of the average size of what might be termed "ecological adults," rather than reproductively mature individuals, assuming that salamanders of a given body size share ecologically important traits (e.g., average prey size taken, probability of predation, kinds of retreats utilized) that are independent of reproductive maturity.

I tested for sexual dimorphism in SL, using data for twelve samples where n exceeded 25 individuals. The non-parametric Wilcoxon two-sample test was used to compare SL in males vs. females (see Sokal and Rohlf, 1969, section 16). The mean SL of ecological adults was computed for 38 samples where the number of adults exceeded 10.

VERTEBRAL NUMBER

Following Francis (1934) and later workers, I have referred to all presacral vertebrae except the atlas as *trunk vertebrae*. Plethodontid salamanders exhibit varying degrees of intraspecific variation in trunk segmentation. At one extreme are the approximately 75 species of the neotropical genus *Bolitoglossa*, all individuals of which have 14 trunk vertebrae (Wake, 1966; Wake and Lynch, 1976). In contrast to this pattern of complete uniformity, Highton (1957, 1962a) has documented considerable intraspecific variation in species of the North American genus *Plethodon*, with modal vertebral counts ranging from 15–22 among populations of some species. Similar variation is observed in the western North American genus *Batrachoseps* (Brame and Murray, 1968; K. Yanev, unpublished data), where local species populations may show a range of variation of up to four vertebrae.

I examined vertebral variation in *A. flavipunctatus* as a function of latitude, mean temperature, elevation, and annual precipitation. Vertebral number received special attention because Myers and Maslin (1948) used the number of costal grooves as a diagnostic character in their descrip-

tion of *A. f. niger*. Although these authors acknowledged that intrapopulational variation in costal groove counts exists, they believed that high counts characterize *A. f. niger*.

Highton (1957) documented a high correlation between the number of costal grooves and the number of trunk vertebrae in salamanders of the genus *Plethodon*. Based on examination of small series from other salamander genera, Highton suggested that the same correlation observed in *Plethodon* probably characterizes plethodontids, generally.

To verify this relationship for *A. flavipunctatus*, I used X-radiographs and cleared-and-stained preparations of 59 specimens to compare costal groove counts and vertebral number. Costal groove counts were then performed on 1212 *A. flavipunctatus* from 41 localities. For each sample, I calculated the mean and modal vertebral count, and the percentage of the sample with non-modal vertebral counts.

RELATIONSHIP BETWEEN MORPHOLOGICAL AND CLIMATIC VARIATION

Due to their relative inability to regulate body temperature or rate of water loss, terrestrial salamanders are strongly influenced by their physical environment. Although statistical association between physical-climatological variables and morphological variables is not proof of a cause-effect relationship, correlation does focus attention on plausible causal hypotheses.

I employed multiple regression-correlation techniques to study the relationship of mean temperature, latitude, elevation, and rainfall to variation in specified morphological traits. These variables are admittedly "blunt" (sensu Soulé, 1972), but more refined climatic data are not available. This analysis mainly concerns those populations within the continuous range of the species. Isolated populations inhabiting the Santa Cruz Mountains and the Shasta County area exhibit discordant variation in many traits, and are treated separately.

The following predictor variables were employed in the analysis:

1. Latitude: measured in airline miles south of the California-Oregon border.
2. Distance inland: measured in airline miles to the closest coastal point.
3. Annual rainfall: measured in cm per year (data derived from isopleth map prepared by the California State Water Resources Board, 1951).
4. Mean January temperature: measured in degrees Farenheit. Data from U.S. Department of Agriculture (1941).
5. Mean July temperature: measurement and data same as in 4.

The nine morphological characters analyzed, together with their highly correlated "sister" characters, are listed below. All simple correlation coefficients (r's) are significant at the 0.05 level or above, unless otherwise specified (see Table 1).

1. Dorsal white iridophore size (DWS): expresses the general size of discrete white spots. Very highly correlated with size of white iridophores on venter (r = .96) and size of white iridophores on the chin (r = .92).
2. Dorsal white iridophore abundance (DWN): index to overall abundance of discrete white spots. Highly correlated with ventral white iridophore abundance (r = .82), less highly with number of white iridophores on the chin (r = .54).
3. Dorsal brassy pigment development (DBN): highly correlated with presence of lateral "frosting" (see below under results of pigment analysis).
4. Density of melanin network on the chin (CMD): indicator of the general intensity of the dark background pigmentation of *flavipunctatus*. Correlated with the development of melanin in the limb base region (r = .53).
5. Projected forelimb length (FL): indicates general limb length. Very highly correlated with projected hind limb length (r = .92). Forelimb measurement preferred due to lower variance.
6. Projected tail length (TL): poorly correlated with any other variables (maximum r = .44).
7. Projected head width (HW): indicates general head size. Correlated with relative head length (r = .67).
8. Mean snout-vent length of all individuals larger than 55 mm snout-vent (SL): indicates general body size.
9. Mean vertebral number (MVN).

The stepwise linear regression procedure employed in the analysis is well described by Draper and Smith (1966). Programs for the regression and correlation analyses were provided by the

ARIEL statistical library at the University of California, Berkeley, Computer Center. All computations were performed on the CAL 6400 system.

Prim Network Analysis

I summarized the overall phenetic resemblance among 30 reference populations by constructing a Prim Network linking them. The Prim algorithm results in each operational taxonomic unit (OTU) being joined by an internode to the OTU which it most closely resembles phenetically. In this context, resemblance is defined on the basis of the overall degree of differentiation in a specified set of morphological traits. The Prim algorithm was described by Prim (1957), first applied to evolutionary biology by Edwards and Cavalli-Svorza (1963), and has been discussed and compared with similar algorithms in a useful paper by Farris (1970). Although the Prim Network is constructed on strictly phenetic grounds, it can be interpreted as an evolutionary branching sequence if it is assumed that closest phenetic neighbors are also closest cladistic neighbors. Because no OTU is designated a priori as ancestral when the network is constructed, the latter is said to be "rootless" (Farris 1970), i.e., undirected. However, all possible directed ("rooted") evolutionary trees that conform to the Prim algorithm are contained in the Prim Network. This means that if extrinsic information allows one to designate an ancestral OTU, the Prim Network is converted into an evolutionary branching sequence.

To construct the Prim Network, I first tabulated the projected and simple mean values for 17 morphometric characters, using data for standard adult males (Table 2). Ten color characters, six proportional characters, and vertebral number comprise the character set. Samples from the 30 largest population samples were clustered.

Character states were standardized to zero mean and unit standard deviation. Between-population phenetic differences were obtained by dividing the overall phenetic difference by the number of characters examined. This has the

dual advantage of expressing mean divergence on a per-character basis, and in being expressed in standard deviation units.

I constructed the network such that the length of internodal links are proportional to the degree of phenetic separation between OTU's. As a result of evolutionary convergences and reversals, phenetic resemblance among all nonadjacent OTU's cannot be expressed by a two-dimensional network. Nevertheless, by manipulating the angular relationships between branches of the network, it is possible to preserve considerable information concerning similarity of nonadjacent OTU's. Finally, I superimposed the Prim Network over a distribution map of *A. flavipunctatus* to compare geographic proximity vs. phenetic similarity. This technique was used by Edwards and Cavalli-Svorza (1963) in a study of the geographic distribution of human blood types, and is useful in the attempt to assess the impact of possible geographic barriers and climatic transitions on morphology.

Results

Distribution

The Black Salamander inhabits at least two, and probably three, disjunct regions in northwestern California (Figure 3). The smaller of these encompasses the humid, heavily forested Santa Cruz Mountains, south of the mouth of San Francisco Bay. The second isolate is much more extensive—it extends from about 70 km N of the mount of San Francisco Bay northward some 400 km to the vicinity of the California-Oregon border, and is bounded on the east by the Great Central Valley and the rugged Trinity-Siskiyou Mountains. A third, possibly disjunct area consists of the mesic forested country south of Mount Shasta and east of the Trinity Mountains.

Myers and Maslin (1948) described the southern group of populations as a distinct race, *A. f. niger*, tentatively lumping all of the northern populations under the nominate subspecies. The geo-

graphic range of *A. f. niger* was well described by these authors, and my own collecting has added little to our knowledge of the distribution of this form.

The present study has, however, yielded considerable new data concerning the range of *A. flavipunctatus* north of San Francisco Bay. It now appears that the southern distributional limit of the northern populations is in the Russian River drainage, in western Sonoma Co. (Figure 3). The boundary extends eastward from the Pacific coast into Colusa and Yolo counties, on the western flank of the Sacramento Valley. To the north, most of Sonoma, Napa, Mendocino, and Humboldt counties are occupied, as are limited portions of Yolo, Colusa, Tehama, Glenn, Lake, Shasta, Del Norte, and Siskiyou counties. The only Oregon records are from the headwaters of the Applegate River drainage, Jackson Co., within 10 km of the California border (Edmund Brodie, pers. comm.).

In general, *A. flavipunctatus* is found within 80 km of the Pacific coast. Two exceptions are the isolated populations in Shasta Co., which are as much as 160 km inland, and the disjunct chain of populations restricted to moist canyons along the xeric eastern flank of the Inner Coast Range in Colusa, Glenn, and Tehama counties. The latter populations are approximately 100 km (air line) from the coast.

Aneides flavipunctatus is patchily distributed within the limits of its overall range, particularly in the drier inland areas. Almost all known localities are at elevations less than 600 m (Figure 3), and only 3 of 175 stations are above 900 m. Elevations exceeding 1200 m evidently are avoided altogether. Most of the major distributional gaps within the range of *A. flavipunctatus* can reasonably be attributed to this avoidance of high elevations.

INFLUENCE OF PHYSICAL FACTORS ON DISTRIBUTION.—Most of northwestern California has a Mediterranean-type climate. Significant precipitation generally is restricted to the October-April rainy season, although occasional showers and frequent fogs may mitigate summertime drying
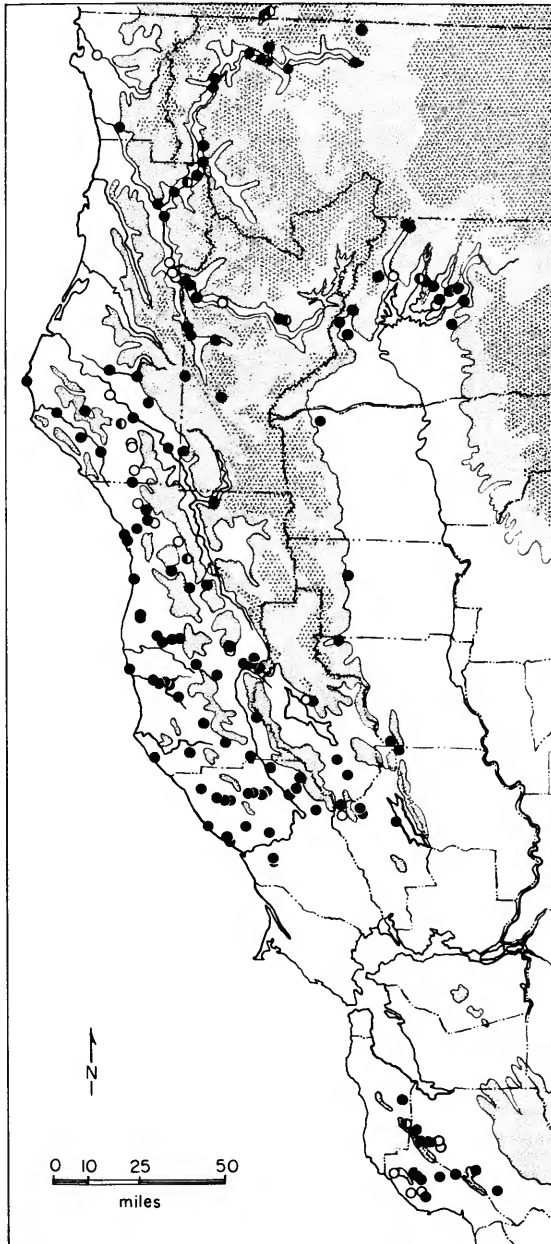

FIGURE 3.—Distribution of *Aneides flavipunctatus* (solid symbols = localities where specimens were collected by the author; open symbols = localities represented by museum specimens collected by others; split symbols = records from literature and other sources; light stippling = areas between 600–1200 m elevation; dark stippling = areas above 1200 m elevation).

conditions, particularly in the coastal region. Because surface activity of *A. flavipunctatus* and other terrestrial salamanders in California is virtually restricted to the winter rainy season, thermal conditions during this period are potentially important determinants of distribution. This situation is markedly different from that in the eastern United States, where a fairly even seasonal distribution of precipitation permits significant warm-season activity by many plethodontids, and where very low winter temperatures suppress cold-season activity.

Comparison of topographic and climatic maps reveals an approximate correspondence between the upper elevational limit of *A. flavipunctatus* and the 2°C mean January isotherm, which in northwestern California tends to occur at approximately 750 m elevation. Areas with January isotherms below 2°C regularly experience sub-freezing temperatures during the winter months, particularly at night when almost all surface activity by plethodontids occurs. Even temperatures somewhat above freezing can be highly detrimental, for normal feeding, growth, and reproductive activity may not be possible under very cold conditions. As an example, Merchant (1970) found that although the eastern plethodontid *Plethodon cinereus* can temporarily tolerate a wide range of temperatures, growth is possible only within a relatively narrow interval (10°–15°C).

The suitability of an area for habitation by *A. flavipunctatus* may be determined partly by the number of days that exceed some lower threshold of favorability for surface activity, rather than by any specific temperature barrier. The length of the "growing season" for a given population of salamanders will also reflect the availability of buffered microhabitats (e.g., springs and streams), so local occurrences will not be wholly explicable by gross climatic features. Nevertheless, the restriction of *A. flavipunctatus* to areas with mild wintertime temperatures is noteworthy.

The possible influence of excessively high temperatures on the distribution of the Black Salamander is more difficult to evaluate, because warm sections of California tend also to be xeric,

thus confounding the effects of high temperature and lack of moisture. Moreover, the highest temperatures are encountered during the summer drought period, when salamanders are protected in subterranean refugia. Salamanders that retreat more than a meter or so beneath the surface experience far less extreme diurnal temperature cycles and a lower mean temperature than do animals at the surface (Geiger, 1966). Rosenthal (1957) documented the dramatic ameliorating effect of even a shallow soil cover in his study of *Aneides lugubris*, a congener that is broadly sympatric with *A. flavipunctatus* through much of northern California.

It would appear, then, that summer temperature is less important than winter temperature as a distributional influence in *A. flavipunctatus*. Even where the disappearance of the species from the surface coincides with rising temperatures in late spring, the proximate cue influencing this movement is likely to be reduced availability of moisture. Evidence for this comes from the observation that salamanders associated with permanently wet microhabitats (seeps, springs, small streams) are active throughout the summer at temperatures substantially above those at which surface activity ceases in populations associated with drier terrestrial microhabitats (Lynch, 1974a).

RAINFALL AND THERMAL EQUABILITY.—Although the humidity of microclimates utilized by terrestrial amphibians will be influenced by vegetation, slope, exposure, soil type, and other local factors, it is reasonable to seek a correlation between the occurrence of species and regional indicators of moisture. Examination of the isohyetal map for California (California State Water Resources Board, 1951) reveals a general correspondence between the range of *A. flavipunctatus* and areas that receive at least 75 cm of annual rainfall, with only about four of 175 localities for the species receiving somewhat less than this amount. Without placing undue emphasis on the precise lower limit of rainfall tolerated by *A. flavipunctatus*, it is clear that the species is adapted to relatively mesic surface conditions.

Certain other plethodontids found in Califor-

nia are not so limited. *Ensatina eschscholtzii, Batrachoseps* (seven species), and *Aneides lugubris* all occur commonly in areas receiving less than 50 cm annual rainfall. *Batrachoseps aridus* (Brame, 1970) and the recently discovered *B. campi* (Marlow, et al., 1979) are associated with springs in desert habitats that receive less than 25 cm of annual rainfall.

No upper limit of rainfall is evident for *A. flavipunctatus.* The species is common in portions of Humboldt, Del Norte, Shasta, and Santa Cruz counties that receive 150–200 cm of rain annually. These are among the wettest areas in California.

The proximate mechanism whereby salamander distribution is affected by rainfall is unknown, but, as with winter temperature, it is likely that rainfall influences the effective length of the salamander "growing season." A direct effect, via desiccation of salamanders (particularly juveniles) trapped by drying conditions, could play a role in excluding *A. flavipunctatus* from drier areas. In this connection, Maiorana's (1977) field observations of mortality of *Batrachoseps attenuatus* due to desiccation may be relevant.

Figure 4 combines a plot of thermal equability with an isohyetal map. The section of northwestern California that combines high thermal equability (M > 50%) and abundant precipitation (annual precipitation > 75 cm) corresponds remarkably well with the observed distribution of *A. flavipunctatus.* Absence of the species from most other sections of the state may be related to unfavorable temperature, insufficient rainfall, or both (Figure 5).

ABSENCE OF *A. flavipunctatus* FROM CLIMATICALLY SUITABLE AREAS.—Perhaps the most puzzling hiatus in the distribution of *A. flavipunctatus* occurs in the seemingly favorable Redwood-Douglas Fir forest of Marin Co., just north of the mouth of San Francisco Bay. The species is abundant immediately to the north and south in areas that appear to be closely similar in climate and vegetation. Myers and Maslin (1948) were aware of this anomalous gap and expressed the opinion that *A. flavipunctatus* eventually would be collected

in Marin Co. Thirty years later, there are still no specimens from the area, and the occurrence of the species there seems highly unlikely.

A somewhat less favorable area that may nevertheless be potentially habitable by *A. flavipunctatus* is the Santa Lucia Mts. of Monterey Co., south of the limit of distribution of *A. f. niger.* Whether or not the species may have occurred in this section of the Coast Range in the past, perhaps during the Pliocene when humid Redwood forest extended far down the coast of California to Santa Barbara Co. (Axelrod, 1959), is a moot question in the absence of relevant fossils. The southern limit of *A. f. niger* in the humid, forested hills of Santa Clara and Santa Cruz counties is marked by the hot, xeric Salinas Valley, a longstanding topographic depression. In the Pliocene, the region presently occupied by the Salinas trough was an embayment of the Pacific Ocean (Oakeshott, 1971; Howard, 1972), and even after the area emerged above sea level in the latest Pliocene, it remained topographically and, probably, climatically distinct from the rugged Coast Ranges to the north and south. The ranges of several other amphibian species also terminate at the Salinas Valley (Table 1).

A third notable absence of *A. flavipunctatus* from apparently suitable regions of California involves the west-facing foothills of the Sierra Nevada range. This extensive, nearly continuous belt of mesic forest is bounded on the west by the hot, xeric Central Valley of California, and on the east by the alpine crest of the high Sierra. To the north, the relatively old granitic rocks of the Sierras are abutted by younger basaltic volcanic rocks of the southern Cascade Range. The latter area receives considerably less rainfall than do the Sierran foothills. This climatic shift, combined with the unfavorable edaphic properties of the lava beds has produced a major distributional hiatus between the mesic, equable Sierra foothills and the even more humid forests flanking Mt. Shasta to the north. Within this "Cascade Bottleneck," the mid-elevation, closed-canopy mixed hardwood-conifer forest of the Sierra Nevada gives way to a more open, xeric-adapted pine-oak
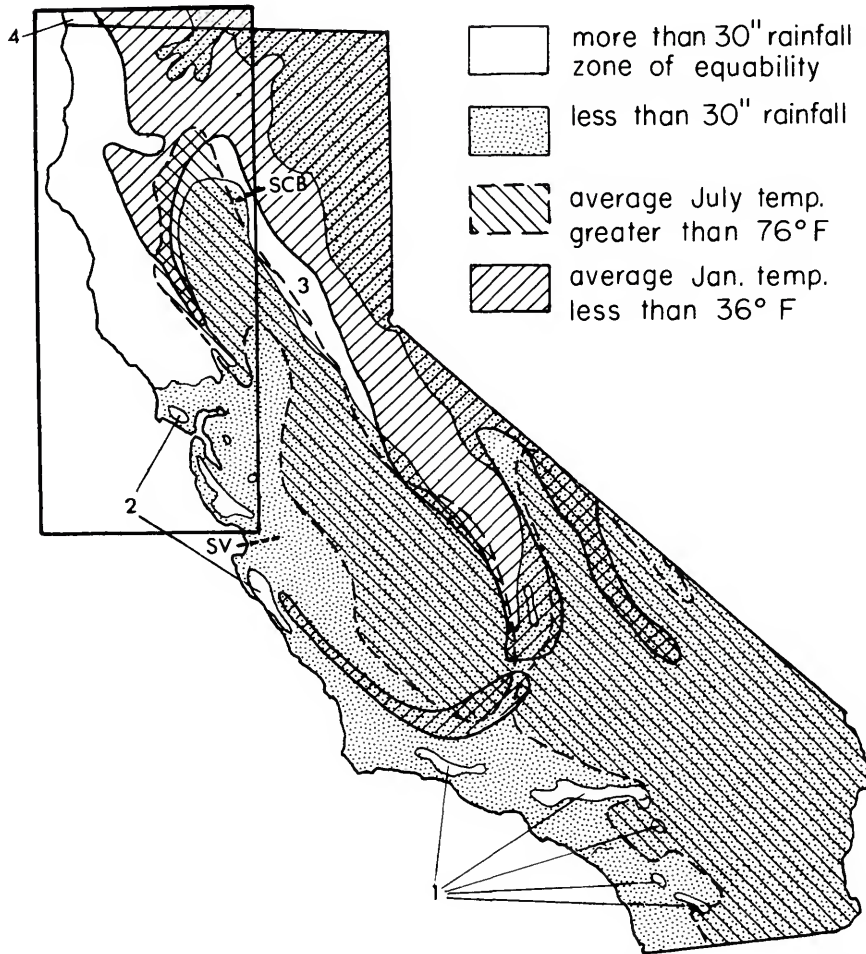
FIGURE 4.—California, snowing regions of high vs. low thermal equability and sparse vs. abundant rainfall (areas without cross-hatching or stippling are most favorable for organisms adapted to mesic, thermally equable conditions; rectangle delimits the area shown in Figure 3; mesic, thermally equable areas uninhabited by *A. flavipunctatus* indicated by numerals: 1 = southern montane isolates, 2 = central Coast Ranges isolates, 3 = Sierran foothills, 4 = north coastal region; heavy dashes are important zoogeographic barriers discussed in the text; SV = Salinas Valley, SCB = southern Cascades bottleneck).

woodland. The only plethodontid known to inhabit this area is the virtually ubiquitous *Ensatina eschscholtzii*, and museum records indicate that this species has been collected only at elevations higher than those normally inhabited by *A. flavipunctatus*.

The possibility that *A. flavipunctatus* previously ranged through the area, but has been extirpated as a result of relatively recent climatic deterioration, seems unlikely given the geologic history of the southern Cascade region. According to MacDonald (1966:66), the "Lassen Strait," a Cretaceous marine embayment that occupied the area presently covered by lava beds in southern Cascades, " . . . persisted as a structural depression—though above sea level and disrupted by
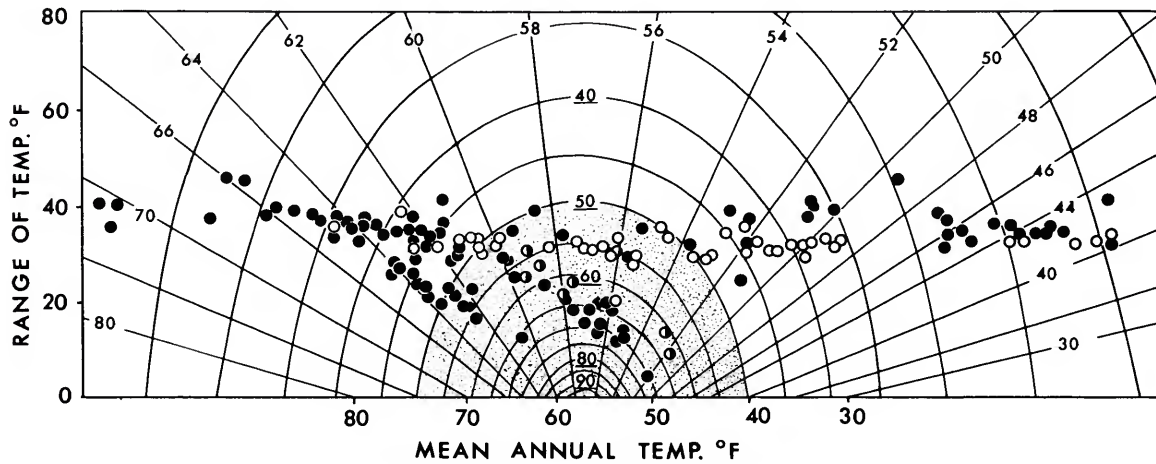
FIGURE 5.—Climates of 146 stations in California, plotted to show annual mean temperature (along radii) and thermal equability (along circumferences) (original data from U.S. Dept. of Agriculture (1941); the stippled region represents climate with an equability value of more than 50%; solid symbols = stations which receive less than 30 inches of precipitation annually; open symbols = stations which receive more than 30 inches of precipitation annually; split symbols = stations within the geographic range of *A. flavipunctatus*, all of which receive at least 30 inches of precipitation annually).

volcanism and faulting—through much of Tertiary time." Thus, it is possible that the area in question has been climatically unsuitable for most terrestrial salamanders for a very long period.

Six salamander species (Table 3) occur at low to moderate elevations immediately to the north or south of the Southern Cascade hiatus, but only two are found in both sides of it. Both exceptional forms (*Ensatina eschscholtzii* and *Taricha torosa*) are found also at high elevations, where the effects of the barrier are ameliorated by higher rainfall and more continuous growth of forest.

The separate or combined effects of dispersal barriers and presently unfavorable climate do not explain the northern terminus of the range of *A. flavipunctatus* in the mesic coastal forests in the vicinity of the California-Oregon border. Possibly a subtle climatic gradient in combination with "diffuse" competition (MacArthur, 1972) with other plethodontids may limit the distribution of the Black Salamander in this area. In northern California, the species is mainly confined to rock rubble (Lynch, 1974a), a habitat also favored by *Plethodon dunni* and *P. elongatus*. Even such unlikely

species as *Aneides ferreus* and *Batrachoseps attenuatus* are encountered regularly in rock rubble along the north coast, though elsewhere they prefer other microhabitats. To the extent that these species compete for food or space with *Aneides flavipunctatus*, they may contribute to the observed absence of the species from southern Oregon. Studies of interspecific distributional relationships in the genus *Plethodon* (e.g., Dumas, 1956; Fraser, 1976; Highton, 1972; Jaeger, 1970, 1971, 1972, 1974) agree in indicating that subtle differences in tolerance to desiccation and unfavorable temperatures may be important determinants of local distributional patterns, and that competition can play a role in limiting the occurrence of salamander species.

COLOR PATTERN

GENERAL COLOR PATTERN.—Terminology used in discussions of pigment cells follows Bagnara (1966). No red pigment cells (erythrophores) are present in *A. flavipunctatus*, so only three kinds of pigment cells need be considered: melanophores

(densely pigmented, dark brown to black cells which form the basic black background coloration), iridophores (bright, silvery reflecting pigment cells), and xanthophores (transparent yellow pigment cells).

The white- to cream-colored spots that conspicuously mark most *A. flavipunctatus* are iridophores. These white spots are the most superficial of the pigment cells and overlie melanophores and the "brassy" pigment network. In juveniles, iridophores have a blue-white appearance under high magnification. In adults, the color generally shifts to white or yellow white.

"Brassy" pigmentation is due to the presence of more deeply seated, less densely aggregated iridophores overlain by clear yellow xanthophores. Xanthophores also are responsible for the transparent yellow color at the limb bases of juveniles. All juvenile *A. flavipunctatus*, as well as adults from northern populations, are heavily frosted with a conspicuous network or suffusion of "brassy" pigment. In most cases, the compact white iridophores that form spots are quite distinct in color and shape from the more diffuse pigmentation forming the brassy network.

JUVENILE PIGMENTATION.—The smallest *A. flavipunctatus* I have collected are 19–20 mm SL. Small juveniles generally appear at the surface shortly after the onset of the fall rains in October or November. By the time warming and drying conditions curtail surface activity in mid-spring, such juveniles have attained a snout-vent length of approximately 32 mm. Second-year individuals are generally between 35 and 50 mm SL. In the following discussion, "small juvenile" refers to first-year salamanders, whereas "large juvenile" refers to second-year individuals; the general term "juvenile" includes both first- and second-year individuals.

Small juveniles are similar morphologically throughout most of the range of *A. flavipunctatus*. All possess abundant brassy iridophores that form a virtually continuous network over the melanic pigmentation of the dorsum. Scattered across the dorsal surface are small (approx. diameter = 0.2 mm) white to blue-white iridophores which form

clearly defined spots that overlie the diffuse brassy pigment. In the region of the dorsum between the axilla and groin, these white spots number from about 50 to 130, the average being about 110.

There is invariably a reduction in the density of the melanic pigment at the limb bases relative to the dorsum or distal limb segments; in many cases melanophores are completely absent from the limb bases. Some clear yellow coloration is generally present at the limb bases in small juveniles.

Juvenile *A. flavipunctatus* have very small white iridophores scattered over the venter. In many instances, the melanophore network is reduced in intensity or broken apart in the gular and midventral region.

ADULT PIGMENTATION.—Adult *A. flavipunctatus* are highly variable in color pattern. The most constant feature is the presence of a heavy melanic network on the dorsum. Typically, the black pigmentation is sufficiently dense that underlying tissue is not visible. Ventral melanic pigmentation is less intense and has the appearance of a net, rather than a solid wash of dark color. Melanism is most reduced in the region of the chin, tail tip, and limb bases, where only scattered melanophores may be present.

White iridophores, which are invariably small (diameter = 0.2 mm) and abundant in juveniles, may be absent in adults. If present, iridophores in adults are almost always considerably enlarged (up to nearly 3.0 mm in diameter).

The brassy pigmentation characteristic of juveniles is typically absent in adults, but the ontogenetic rate of loss varies geographically. Adults from the northern portion of the range tend to retain brassy pigmentation.

The clear yellow xanthophores present at the limb bases of juveniles are lost or greatly reduced in adults throughout the range.

ANALYSIS OF SELECTED INDIVIDUAL CHARACTERS.—The R-matrix (Table 1) reveals a complex pattern of correlation among characters. For example, in adult males the size of white iridophores on the dorsum is highly correlated with the size of white ventral iridophores ($r = 0.965$) and with

the size of white iridophores on the chin (r = 0.917). The abundance of the white iridophores in the same three regions of the body is highly correlated as well. Clearly, the individual characters in these complexes are not independent measures of variation. In contrast, certain other pairs of characters (e.g., spot size vs. spot abundance in the dorsal region) which one might expect to show parallel variation, in fact vary independently (r = 0.08; p > 0.1). For the following analysis, I have chosen several characters which, based on the pattern of correlations, appear to be useful indices to major independent modes of variation in pigmentation. These characters are dorsal white iridophore size, dorsal white iridophore number, dorsal brassy pigmentation, and development of the melanin net in the chin area. Other color characters will be touched upon briefly.

1. Dorsal White Iridophore Diameter: As indicated above, this character is highly correlated with spot size on the belly and chin, and provides a useful index to iridophore size. Coded values for this character range from 1 (0.1 mm) to 9 (2.7 mm).

Very small juveniles (20-25 mm SL) from all parts of the range of *A. flavipunctatus* have dorsal white iridophores which are about 0.2 mm in diameter. As growth proceeds, regional differences in spot-size becomes evident (Table 4). By the time juveniles attain a standard length of 40 mm, the size of dorsal white iridophores is significantly correlated with the size that ultimately will be attained by adults (Figure 6). Figures 7 and 8 illustrate ontogenetic trends in dorsal white iridophore size for several representative populations of *A. flavipunctatus.* Ontogenetic variability in this character levels off in adult salamanders.

Projected mean values (coded) for this character, calculated at a common SL = 40 mm vary from 1.0 to 2.4 units (mean = 1.4 units = 0.30 mm).

For adults, 60-79 mm SL, the sample means range from 0.5 to 8.6 units, with a grand mean of 2.9 units (0.77 mm). As can be seen in Table 4 and Figure 6, spot size generally increases with
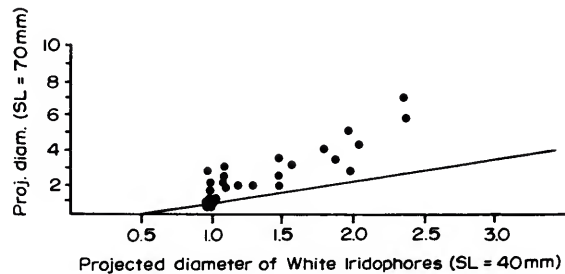
FIGURE 6.—Diameter of white dorsal iridophores (DWS) in 27 populations of *A. flavipunctatus* compared at SL = 40 mm and SL = 70 mm (each symbol represents projected mean values from a single locality; the sloping line represents no ontogenetic changes in iridophore size).
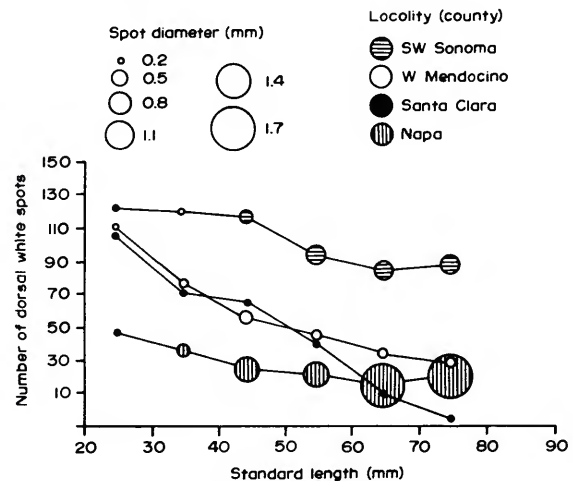
FIGURE 7.—Ontogenetic changes in the size and abundance of white dorsal iridophores in *A. flavipunctatus* compared for four regions (data from several closely spaced localities combined for each regional plot; the Santa Clara Co. populations are *A. f. niger;* the remaining populations are from the southern half of the range of *A. f. flavipunctatus*).

body size. Four of the five apparent exceptions to this generalization are populations of *A. f. niger,* adults of which often lack spots. The slight apparent reduction in mean spot diameter for these populations is due to inclusion in the calculations of some individuals which lack spots. Any iridophores present in adult *A. f. niger* are about the same size as in juveniles.

In general, spot size is larger in inland popu-

DIAMETER OF DORSAL WHITE IRIDOPHORES

☐ 0.0-1.4
▨ 1.5-2.9
▨ 3.0-4.4
▨ 4.5-5.9
▨ 6.0-7.4
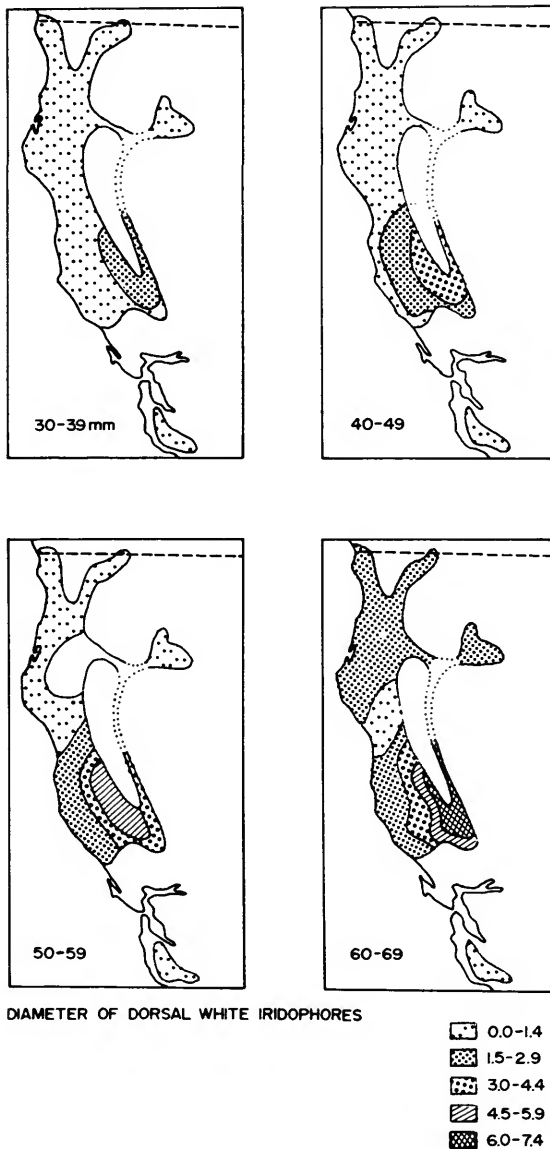
FIGURE 8.—Geographic and ontogenetic differentiation in the diameter of dorsal white iridophores (standard length indicated at lower left of each map).

lations than near the coast. However, the isolated inland group of populations in Shasta County do not follow this trend. These animals have smaller iridophores than would be predicted on the basis of their distance inland.

2. Abundance of Dorsal White Iridophores: Hatchling *A. flavipunctatus* are invariably dusted with numerous white iridophores. Very small individuals are not sufficiently abundant in my collections to allow a precise evaluation of the initial abundance of white iridophores, but there is clearly more variation in this character than in white iridophore size. Based on projections to SL = 20 mm, the mean spot number in hatchlings ranges from about 50 (some populations in the inner coast range of Lake, Napa, and Glenn counties), to about 125–150 (coastal Sonoma and Mendocino counties.

In most populations, ontogeny entails a decrease in the number of white iridophores (Table 5). In two exceptional populations (Salmon Pt. and Nosoni Creek), the apparent ontogenetic increase in spot number is due to fragmentation of pre-existing iridophores, rather than to de novo development of iridophores. The apparent increase in spot number in the other two apparently exceptional populations is within the limit of statistical error for the sample sizes available. Figures 7, 9, and 10 illustrate ontogenetic changes in white iridophore abundance in representative populations. There is a highly significant correlation (r = 0.59, P < 0.01) between iridophore abundance in 40 mm juveniles and 70 mm adults; if the isolated populations of *A. f. niger* and Shasta Co. *A. f. flavipunctatus* are omitted, this correlation increases to 0.72.

In general, animals with low numbers of dorsal iridophores occur near the coast, along the inner coast ranges, and south of San Francisco (*A. f. niger*). Abundantly spotted animals occur in the south-central portion of the range (Mendocino and Sonoma counties), and in the Shasta County populations (Figure 10).

3. Brassy Dorsal Pigmentation: The development of brassy pigmentation was measured on a scale from 0 (absent) to 7 (heavy network essentially covering the whole dorsum).

All small juvenile *A. flavipunctatus* possess abundant brassy pigmentation. Mean coded values are 5–7 in most samples. Populations inhabiting the inner coast range have the fewest brassy irido-
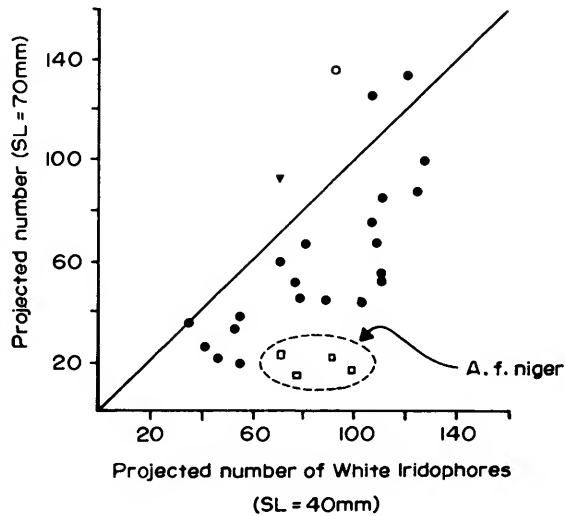
FIGURE 9.—Number of white dorsal iridophores (DWN) compared in 27 populations of *A. flavipunctatus* at SL = 40 mm and SL = 70 mm (the diagonal line indicates no ontogenetic change; the only two populations which appear to show a marked increase in iridophore abundance are Salmon Point, Mendocino Co. (triangle) and Nosoni Creek, Shasta Co. (open circle); these anomalies probably reflect decomposition of pre-existing iridophore patches; populations of *A. f. niger* (open squares) show the most dramatic reduction in DWN).

FIGURE 10.—Geographic and ontogenetic differentiation in the number of dorsal white iridophores in *A. flavipunctatus* (standard length indicated at lower left of each map).

phores, but even here the pigmentation is conspicuously present in small juveniles.

Adults in northern populations tend to maintain this juvenile pattern, but elsewhere it is lost as ontogeny proceeds. Where juvenile brassy coloration is maintained in adults, the morphology of the pigment masses is somewhat changed. In adults, the reflecting iridophores tend to be more deeply imbedded below the epidermis, giving a darker, more coppery color as compared to the clear golden yellow typical of juveniles. A similar ontogenetic change was described for *Aneides ferreus* by McKenzie and Storm (1971).

Outside the northern area, the juvenile brassy network tends to break up as growth proceeds. As the network disintegrates, individual dendritic pigment masses become discernable. As salamanders attain larger size, these iridophores gradually contract to a spiculate, then a punctate morphol-

ogy before finally disappearing. The rate of this ontogenetic change varies between populations (Figure 11, Table 6); juveniles from southern inland populations of *A. f. flavipunctatus* tend to lose their brassy pigmentation at a smaller body size than do those from northerly, coastal localities.

DENSITY OF BRASSY IRIDOPHORES

▨	100 - 91 (heavy)
▦	90 - 51
▢	50 - 31
▨	30 - 0 (few or none)
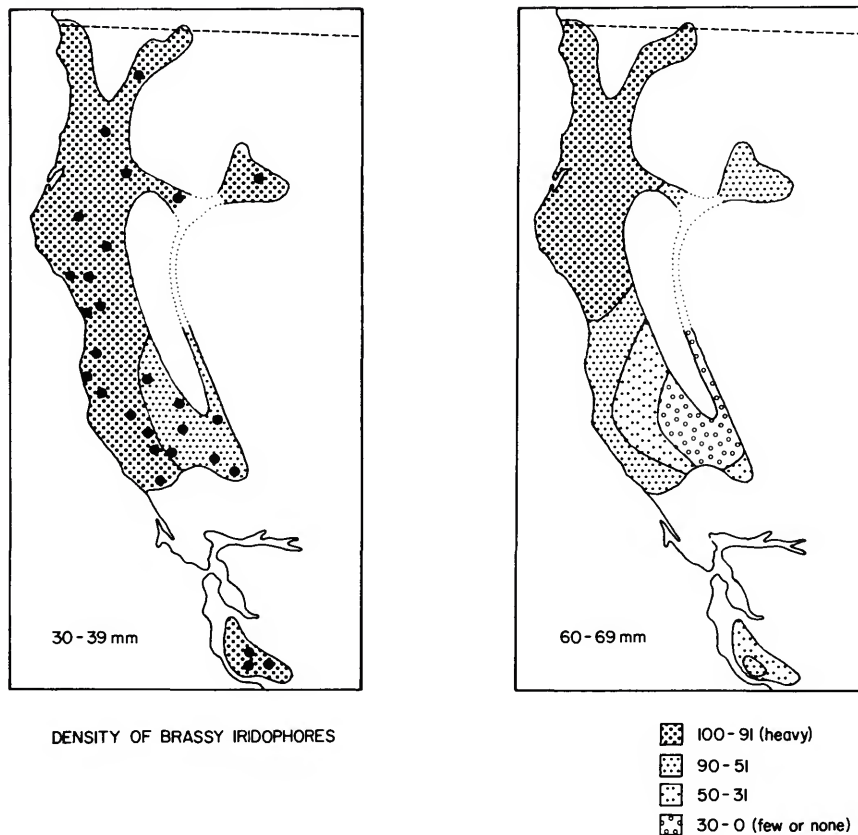
FIGURE 11.—Geographic and ontogenetic differentiation in the number of dorsal brassy iridophores in *A. flavipunctatus* (standard length indicated at lower left of each map; circles are main localities on which contour maps are based).

Again, the development of this character in populations *A. flavipunctatus* in Shasta Co. is discordant to what is found in the nearest populations to the northwest and west in Siskiyou and Trinity counties (Figure 11).

4. Development of Melanophore Network on the Chin: Variation in the density of melanic pigmentation is most easily observed on the extremities of *A. flavipunctatus*. As noted earlier, chin melanism is significantly correlated with limb melanism (Table 1), and was the indicator of melanism chosen for analysis. The density of melanophores was expressed on a scale ranging from 1 (extremely dense, solid mass of black pigment) to 6 (melanophores essentially absent). Mean indices were calculated for large juveniles (40 mm projected SL) and adults (60–79 mm).

As can be seen in Table 7, there is a strong tendency for ontogenetic increase in the relative density of the melanin net in the gular region. Adults with the highest indices (i.e., the most juvenile-like pattern) occur along the inner coast ranges north to Trinity and Siskiyou counties. Coastal populations are somewhat darker. Shasta County populations of *A. f. flavipunctatus* and populations of *A. f. niger* have the heaviest melanin network. As in most other characteristics, these two isolates are morphologically distinct from their nearest neighbors within the range of *A. f. flavipunctatus*.

5. Variation in Other Aspects of Color Pattern: A heavy lateral concentration ("frosting") of silvery iridophores occurs in adults of some populations of *A. flavipunctatus*; this feature is analogous to what is seen in certain populations of the superficially similar eastern plethodontid *Plethodon glutinosus* (Highton, 1962a). The lateral concentration of white or brassy pigment appears relatively late in ontogeny, and juveniles invariably lack lateral frosting. There is a very close association between the development of lateral frosting and the retention of the juvenile dorsal brassy pigmentation (Table 8). Heavy lateral frosting occurs in 13 of 14 populations whose adults retain heavy brassy pigmentation (the remaining population shows a less intense development of frosting). The probability of this association being due to chance is less than 0.001 ($X^2 = 32.9$; df = 2). None of the 23 populations which show little or no retention of juvenile brassy pigmentation exhibit any development of lateral frosting.

A second trait that is apparently linked with retention of juvenile brassiness is the tendency for ventral iridophores to form irregular patches and a diffuse network, rather than the typical discrete, compact pigment masses. The geographic distribution and ontogeny of this character is virtually identical to that of the lateral frosting character, and most populations from northern Mendocino and Trinity Counties to the northern distributional limit of the species have both features well developed. An exception is the Shasta County group of populations which lacks both traits.

In summary, several complexes of intercorrelated pigmentation features can be distinguished:

1. Spot size group: size of dorsal white iridophores, size of ventral white iridophores, and size of white iridophores on chin.
2. Spot abundance group: number of dorsal white iridophores, number of ventral white iridophores, and number of white iridophores on chin.
3. Melanism group: chin melanism and limb melanism (also melanism of tail tip and belly).
4. Brassy pigment group: dorsal brassy pigmentation, lateral frosting, and ventral suffusion of iridophores.

PROPORTIONAL MEASUREMENTS

HEAD SIZE.—In *A. flavipunctatus* the size and shape of the head shows sexual, ontogenetic, and geographic variation. Juveniles have relatively longer and wider heads than do adults of either sex (Table 2). Sexual differences are subtle (usually < 2%), making it difficult to demonstrate statistically significant dimorphism in any given sample, but in 27 of 29 populations for which at least five adults of each sex were available for analysis, the projected mean head length is greater for males than for females. The two apparent exceptions are based on small samples, and the slight reversal in dimorphism (0.1% and 0.3% respectively) is almost certainly due to sampling error. The likelihood of the observed preponderence of populations with large-headed males being due to chance is very small (P < 0.001).

A similar dimorphic pattern exists for head width, with the projected mean for males being greater than that for females in 26 of 29 population samples. The three apparent exceptions are best viewed as resulting from sampling errors.

There is significant variation in relative head size among populations, but no consistent geographic pattern is evident. The possible correlation between relative head size and geographic-climatic factors is examined below in the multiple regression analysis.

LIMB LENGTH.—Juvenile *A. flavipunctatus* invariably exceed adults in relative limb length (Table 2). Projected mean forelimb and hind limb lengths for juveniles body length = 20 mm average 34.6% and 38.6% (respectively) of body length; for 50 mm females the figures are 27.8% and 32.5% of body length, and for 50 mm males the values are 28.9% and 33.8%. The overall pattern of sexual dimorphism is consistent—in 27 of 29 samples, the projected mean forelimb length is longer for males than for females; in 30 of 31 samples, males have longer projected mean hind limb lengths than females. Thus, ontogeny involves a decrease in *relative* limb length, and

females show a greater relative reduction than males.

TAIL LENGTH.—Evaluation of ontogenetic, sexual, and geographic variation in relative tail length is difficult for this character because of high variance, much of which is attributable to inclusion of individuals with regenerated tails in the samples analyzed. Individuals with obviously regenerating tails were not included, but fully regenerated tails can be distinguished from intact (i.e., "original") tails only by the presence of a notochord in the latter. This subtle distinction requires histological preparation of a tail slice, and was not attempted. An unknown number of regenerated tails are therefore included in the data set.

Tail length is approximately equal to body length in adult *A. flavipunctatus*, and there appears to be a little or no sexual dimorphism in relative tail length. In three of the four largest samples (McGuire Hill and Salmon Point, Mendocino Co.; Skaggs Springs, Sonoma Co.), there is no dimorphism (to the nearest mm) in the predicted mean tail length for adults at 50 mm body length. In the fourth sample (Brookdale, Santa Cruz Co.), males appear to have slightly longer tails than females (49.1 mm vs. 47.1 mm), but the difference is not statistically significant (t = 1.689; P > 0.1; df = 43). The remaining samples are too small to allow meaningful individual tests of sexual dimorphism.

The ontogenetic pattern of variation in relative tail length is consistent. In 17 of 20 samples which include at least eight juveniles for comparison with adults, juveniles (projected body length = 20 mm) have shorter relative tail lengths. In two of the three apparent exceptions, there is no difference in relative tail length (to the nearest 2%) between adults and juveniles. In the third sample, the juveniles appear to have slightly longer relative tail lengths than adults, but the difference is not statistically significant.

Again, a sign test rejects the null hypothesis that there is no tendency for juveniles to have shorter relative tail length than adults in the 20 largest samples (P < 0.01). Considering only the twenty samples with at least eight juveniles, unweighted mean relative tail length is 0.88 for juveniles vs. 0.98 for adults (both sexes combined). On the average, then, relative tail length increases by about 10% as salamanders increase in body length from 20 mm to 50 mm.

Within the contiguous range of *A. f. flavipunctatus* there is no obvious regional differentiation in relative tail length. Animals from the Santa Cruz and Shasta isolates appear to have somewhat shorter tails than do those from other populations, but the difference is not significant according to the Wilcoxon two-sample test (U = 81; P > 0.2).

BODY SIZE

Table 9 summarizes the results of the tests for significant sexual dimorphism in standard length (SL). Of the twelve largest samples tested, males average larger in six, females in two, and there is no difference (to the nearest mm) in the remaining four. The apparent sexual differences in body size are statistically significant in only two samples: in one of these, males are significantly larger, while in the other, females are significantly larger. I conclude that there is not evidence for consistent dimorphism in body size, and that the few seemingly exceptional populations probably reflect sampling errors rather than important sexual dimorphism. For the remaining analysis, I have combined data for males and females and computed only the unweighted mean SL for individuals of both sexes which exceed 55 mm.

Calculated in this way, mean SL ranges from 63 to 75 mm in the populations sampled. I calculated the expected body weights of *A. flavipunctatus* having these SL's from the SL-body weight regression equation obtained for a series of 51 *A. flavipunctatus* from Salmon Point, Mendocino County (Figure 12). The expected weight of a 63 mm individual is 3.3 grams, while that for a 75 mm individual is 6.4 grams. Thus, the average "ecological adult" from some populations is nearly twice as heavy as in others. Since reproductive maturity is reached at a larger size in
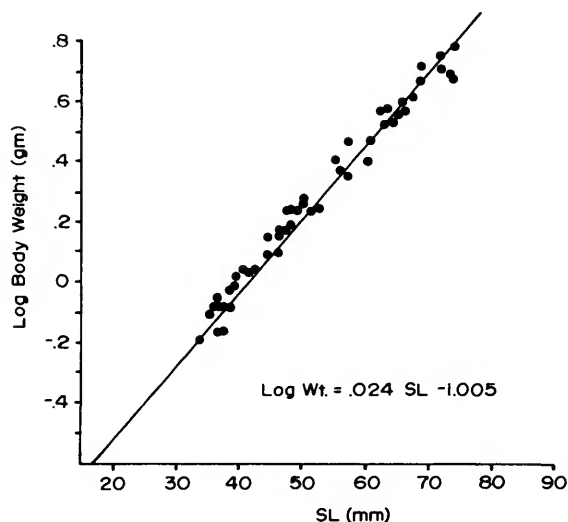
FIGURE 12.—Semilog regression of body weight on standard length in *A. flavipunctatus* (based on 51 individuals collected at Salmon Point, Mendocino Co., California).

FIGURE 13.—Correlation between mean body size and latitude in 31 samples of *A. f. flavipunctatus* (only individuals with SL > 55 mm considered in computing mean SL; correlation is significant at $p < 0.01$).

populations with large mean body size, the difference in mean body size of reproductively mature individuals is even greater than indicated by the difference in "ecological adult" body size.

Populations with larger mean SL are concentrated in the northern part of the range (Figure 13). There also is a tendency for animals from inland populations to be larger than those from coastal localities.

VERTEBRAL NUMBER

GENERAL.—The relationship between the number of trunk vertebrae and the number of costal grooves is the same in *A. flavipunctatus* as in *Plethodon*, as Highton (1957) suggested. In 56 of 59 specimens (95%), the number of trunk vertebrae counted from X-radiograms or cleared-and-stained animals, was found to be one more than the number of costal grooves (providing the latter counts are made in the manner Highton specified).

Samples of *A. flavipunctatus* have a modal number of either 16 or 17 trunk vertebrae, but occasional individuals with 15 or 18 vertebrae are

encountered (Table 10). Both 16- and 17-vertebrae animals are present in most large samples, but the mean vertebral number is usually close to one or the other value. In 37 of the 41 samples of *A. flavipunctatus*, more than two-thirds of the individuals fall into the modal class. Highton (1962a) found a similar tendency toward dominance by the modal class in eastern *Plethodon*.

GEOGRAPHIC VARIATION.—Several distinct areas of differentiation in trunk segmentation are evident (Figure 14). From south to north, the first such area is the isolated range of *A. f. niger* in the Santa Cruz Mountains. Individuals of this subspecies tend toward high vertebral counts, the modal number being 17 in all populations examined. Variation around the mode is slight: 95% of the individuals examined have the modal number of vertebrae.

North of San Francisco Bay, the variational pattern is more complex, and several foci of differentiation are evident. The southern part of this area, from coastal Sonoma County inland to eastern Napa County and northwest to central Mendocino County, is occupied by populations with modal counts of 16 vertebrae. Myers and Maslin (1948) probably examined salamanders
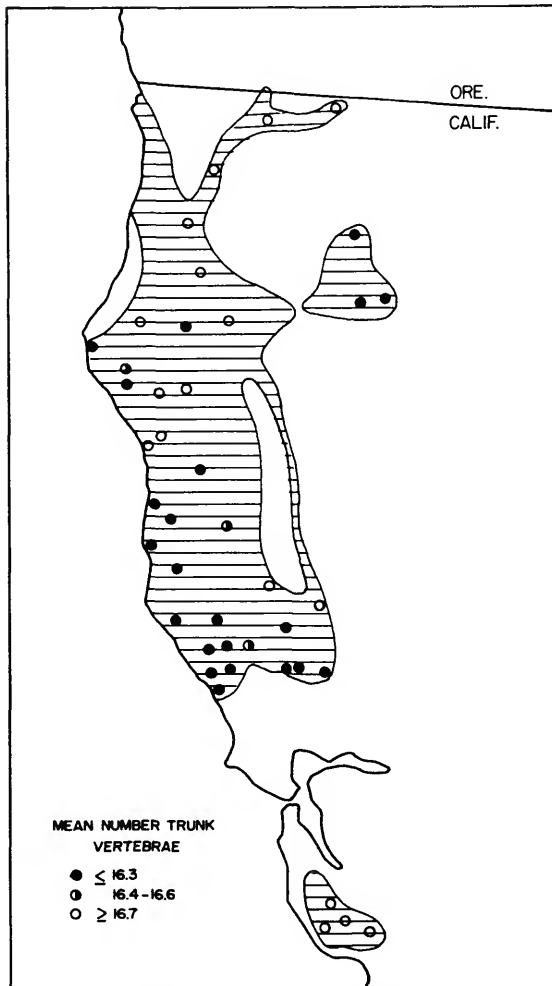
Figure 14.—Geographic variation in mean number of trunk vertebrae in *A. flavipunctatus*.

from this general region when they compared vertebral numbers in *A. f. niger* to the nominate subspecies. Variability within populations tends to be low; the mean vertebral number generally falls between 16.0 and 16.2.

North of central Mendocino County, the modal number of vertebrae increases from 16 to 17. This higher value is maintained to the northern limit of the range in Del Norte and Siskiyou counties. In the vicinity of the Pacific Coast, the transition from predominantly 16- to predominantly 17-

vertebrae populations appears to occur in Mendocino County, between Fort Bragg ($\bar{x}$ = 16.2) and Usal ($\bar{x}$ = 16.8), a distance of 40 km. This same area also is a zone of transition in the pigmentation of *A. flavipunctatus* (see "Discussion" below).

Populations with 17 vertebrae occur from the Rockport area near the coast of northern Mendocino Co., eastward to the flanks of the Inner Coast Ranges, and then south in a narrow, possibly discontinuous band through eastern Mendocino and northern Lake counties. Populations at the southern end of the Inner Coast Range in Colusa and Yolo counties also show modal counts of 17 vertebrae, as do the few small samples on the SE flanks of the range in western Colusa and Glenn counties. The overall pattern, then, is long U-shaped band of 17-vertebrae populations around the southern end of the Inner Coast Range. To the west and south are populations of *A. flavipunctatus* with a modal vertebral number of 16. The transition from 17- to 16-vertebrae populations appears to be relatively abrupt. A sample from the vicinity of Middletown, in central Lake County, shows a strong mode of 16-vertebrae, while samples from Colusa and Yolo Counties, less than 25 km NE of the Middletown population, show equally strong modes at 17-vertebrae. No populations with a fairly even distribution of 16- and 17-vertebrae individuals have been discovered in this area.

Two local areas of low vertebral counts exist in the northern part of the range of *A. f. flavipunctatus*. The smaller of these is in western Humboldt County, between Cape Mendocino and U.S. Hwy. 101, and is evidently centered in the vicinity of Ettersberg, where all animals examined have 16-vertebrae (n = 12). Between Ettersberg and Dyerville, approximately 18 km to the east, mean vertebral number increases to 17.0. North and east of Dyerville, populations show strong modalities at 17-vertebrae, with the exception of a series of nine 16-vertebrae animals from the upper Mad River and South Fork of the Trinity River in Trinity County. Using a binomial test, the probability that 16, rather than 17, is the modal

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number here (i.e., that the proportion of animals with 16 vertebrae exceeds 50%) is greater than 95%. The population in question inhabits what is evidently a narrow cul-de-sac of suitable habitat and may be geographically isolated.

The last area of differentiation is the Shasta County isolate. All samples from this area show strong modalities at 16-vertebrae. The nearest large samples outside this area, from the vicinity of Salyer and Burnt Ranch in Trinity County, some 80 km west of the nearest Shasta County locality, have modal counts strongly centered at 17. Whether there is a gradual shift in vertebral number between these localities is not known, as few specimens have been found in the relatively xeric Digger Pine woodland and chapparral which characterize the intervening region. Four *A. flavipunctatus* taken near Junction City, in east-central Trinity County approximately 35 km west of the Shasta population, all have 17-vertebrae, but without larger samples it is not possible to tell whether individuals with 16 vertebrae comprise an important component in the population.

Relationship of Morphological Variation to Geographic and Climatic Features

Results of the Regression Analysis.—Table II summarizes some pertinent aspects of the regression-correlation analysis of the effect of geographic and climatic variables upon selected morphological traits. For each morphological character (y_i), I have listed the predictor variables $(x_i, x_j, \ldots, x_n)$ which make statistically significant contributions to the stepwise regression, and have indicated the coefficient of multiple determination (R^2).

1. Dorsal White Iridophore Size (DWS): This character is positively correlated with distance inland and negatively correlated with latitude, such that *A. flavipunctatus* from southern, inland localities tend to have the largest spots. The multiple correlation coefficient is very high (R = 0.926, P < 0.001), and the effects of latitude and distance inland alone are sufficient to ac-

count for 86% of the observed variance in spot size of standard adults.

2. Dorsal White Iridophore Number (DWN): This character and DWS are not significantly correlated (r = 0.085), so one would expect a different pattern of correlation with environmental variables. In fact, none of the five predictor variables has any significant relationship with DWN. The highest simple correlation (r = 0.294) is an insignificant (P > 0.1) association with latitude.

3. Dorsal Brassy Iridophore Development (DBN): The retention of the juvenile "brassy" pigmentation is positively correlated with latitude and negatively correlated with distance inland (R = 0.914). Thus, the maximum brassiness is observed in northern populations close to the coast.

4. Density of Melanic Network on the Chin (CMD): The same two predictors are important for this variable as for DBN, but here both partial coefficients are positive. Thus, animals with the greatest reduction in intensity of the melanin network occur at northern and inland stations.

5. Forelimb Length (FL): The best predictor of forelimb length is latitude; distance inland has a small, but significant additional effect. The R-value for these two variables vs. forelimb length is 0.689, so slightly less than 50% of the total variation in forelimb length is accounted for by the regression. Both partial correlation coefficients are positive, indicating that long-legged populations tend to occur farther north and farther inland.

6. Tail Length (TL): Relative tail length does not follow the same pattern of geographic variation as relative limb length. The only significant partial correlation is between tail length and elevation. The correlation is positive, so animals from localities at high elevations tend to have relatively long tails. The observed relationship is not strong (r = 0.506), but this is not surprising in view of the high variance associated with tail length measurements.

7. Head Width (HW): Relative head width is significantly associated with distance inland and mean January temperature (R = 0.428). Both

partial regression coefficients are positive, which means that animals with wider heads tend to come from cool, inland sites.

8. *Mean Standard Length of Ecological Adults (SL):* The analysis confirms the impression that larger body size is associated with higher latitude in *A. flavipunctatus*. Latitude shows a significant positive correlation with size (r = 0.593); January temperature shows a negative correlation, but its influence is only of marginal significance (P < 0.1). Salamanders living at more northerly latitudes (and in places with cooler mean January temperatures) tend to have large mean body size. Figure 13 summarizes the correlation between SL and latitude.

9. *Vertebral Number:* Both latitude and distance inland are correlated significantly with variation in mean vertebral number; *A. flavipunctatus* from northerly, inland stations tend to have more vertebrae than those from southerly, coastal localities.

Figure 15 is a Prim Network that connects 30 reference populations (Figure 16) on the basis of
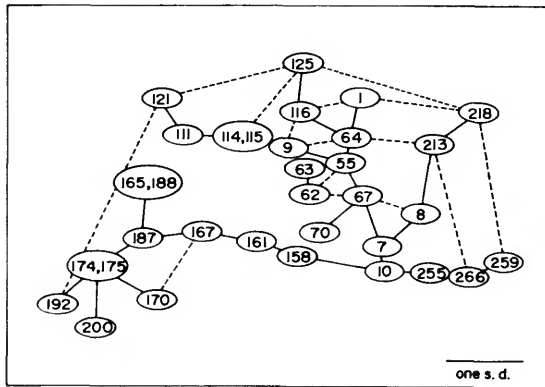
Figure 15.—Prim Network linking 30 samples (OTU's) of *A. flavipunctatus.* The internodes (heavy solid lines) are drawn with their length proportional to the phenetic separation of the OTU's they join (scale at lower right of figure indicates one standard deviation unit of average character difference); the dashed lines reflect accurately the phenetic separation of non-adjacent OTU's on the network; two dimensional distances between other non-adjacent OTU's (e.g., 200 and 259) are not necessarily represented accurately in this diagram.
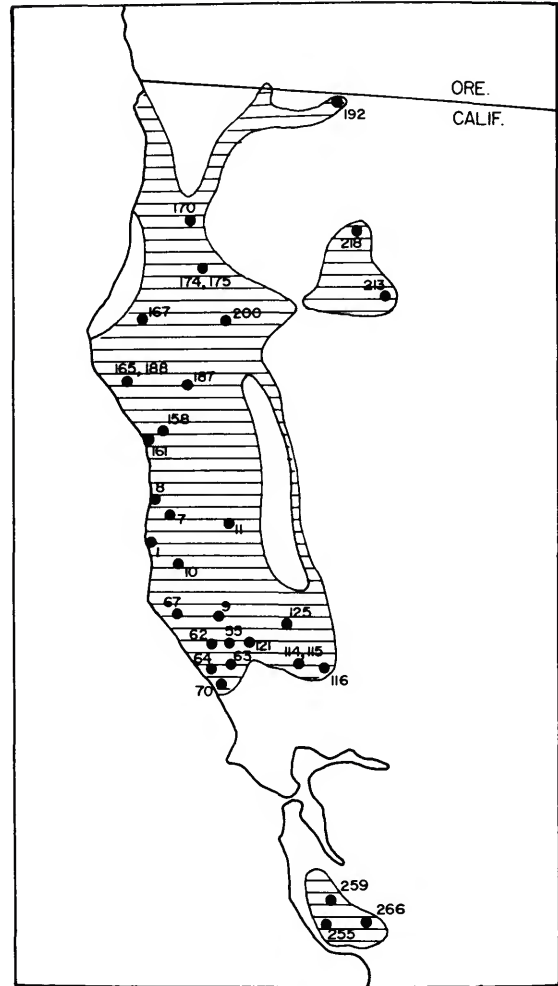
Figure 16.—Location and code numbers of the 30 samples of *A. flavipunctatus* considered in the Prim Network analysis.

overall phenetic similarity of adults. The branching sequence is derived from the data matrix of standardized phenetic distances (Table 12). I have drawn the network so that the length of the internodal connections are proportional to the *square* of the mean phenetic distance between connected populations, thus emphasizing interpopulation differences in phenetic distance.

Several features of the Prim Network are noteworthy. First, it is clear that the phenetically-based groupings of populations in the Prim Net-

work make geographic sense, i.e., neighboring populations tend to show a high level of phenetic resemblance. For example, the three samples of *A. f. niger* from the Santa Cruz Mountains form a distinct cluster, as do the two populations from the Shasta County isolate. Although the overall concordance of the phenetic and geographic groupings is quite good, as can be seen when the Prim Network is laid over the distribution map (Figure 17), closest geographic neighbors are not invariably closest phenetic neighbors. Some discrepancies are minor, and can be attributed to statistical error in the clustering process, or to insignifcant differences in phenetic distances among closely similar population. For example, the Prim Network connects the Skaggs Springs sample (055) to sample from the Sonoma Queen Mine (063), some 25 airline km away, rather than to the Stewart's Point sample (062), which is only 8 km from Skaggs Springs. However, animals from all three localities are so similar to one another (the difference in mean phenetic distance among them is only 0.03 standard deviation units), that the minor difference between geographic and phenetic distance is trivial.

Of more interest are the phenetic resemblances the two geographically isolated groups of populations show to each other and to other populations. On the basis of geographic proximity, one would predict that the phenetic affinities of populations from the Shasta County isolate would be with populations from adjacent Trinity and Siskiyou counties, and that populations of *A. f. niger* isolated south of San Francisco Bay should most closely resemble the nearest populations of the nominate race in Southern Sonoma County. In fact, animals from both isolates are most similar phenetically to *A. f. flavipunctatus* from West-Central Mendocino County (Samples 008 and 010). The Nosoni Creek population (213) in Shasta County, for example, is 200 km from the Fort Bragg population (008) in coastal Mendocino County and shows a mean phenetic distance of 0.80 standard deviations, whereas the Nosoni Creek-Salyer difference is 2.04, despite the fact that the Nosoni-Salyer distance is only about 110

FIGURE 17.—The Prim linkage depicted in Figure 15 superimposed on a locality map for the 30 OTU's. Here the linkage pattern is preserved, but the lengths of the internodes no longer reflect inter-OTU phenetic separation: note the phenetic linkage of populations in the northeast (Shasta Co.) and south (Santa Cruz Mts.) with central coastal populations of *A. f. flavipunctatus*.

airline km. Even more unexpected is the relatively strong phenetic resemblance between the two isolated populations. The phenetic difference between the Nosoni Creek population and the Clear Creek population of *A. f. niger* (255) over 400 km to the south is only 1.08 units, indicating that the

Shasta County animals are more similar in morphology to those in the distant Santa Cruz Mts. than they are to nearby populations in Trinity County. Examination of the distance matrix indicates that the morphological gap between Shasta and Trinity County populations of *A. flavipunctatus* is very nearly the maximum difference found between any two populations within the entire species range.

ONTOGENETIC VARIATION AND PAEDOMORPHISM

Relative to adults, juvenile *A. flavipunctatus* have relatively larger heads, longer limbs, shorter tails, smaller, but more abundant white iridophores, more extensive brassy pigmentation, and a less intense development of melanin pigmentation (Table 13). If a paedomorphic mode of evolution has been important in *A. flavipunctatus*, one might predict that adults in some populations should retain an entire suite of "juvenile" characteristics in addition to the juvenile brassy pigmentation (DBN). An examination of the character correlation matrices reveals that possession of relatively long limbs, retention of small (but abundant) white iridophores, and lack of heavy melanin pigmentation all are significantly correlated with the retention of juvenile brassy pigmentation in adults. I conclude that there is indeed a tendency for an entire complex of "juvenile" characters to be retained in certain populations.

To quantify this variation, I calculated a paedomorphic index for each population. To do this, I first selected morphological traits whose expression can be considered to vary from less to more paedomorphic. For example, the morphological analysis showed that juveniles always have relatively larger heads than adults, but that adults from some populations show less deviation from the juvenile head proportions than do those from others. With respect to this character, then, large-headed populations can be considered more paedormorphic than small-headed ones.

Six external characters were deemed appropriate for this analysis: head length (HL), forelimb length (FL), abundance of dorsal white irido-

phores (DWN), size of dorsal white iridophores (DWS), extent of dorsal brassy pigmentation (DBN), and intensity of melanic pigment in the chin area (CMD).

Each character was recoded and standardized such that the most "adult" state was equal to zero, while the most paedomorphic (i.e., "juvenile") state was unity. Thus, for any value (x) of character (i)

$$x_i' = \frac{x_i - x_{min}}{x_{max} - x_{min}}$$

where x_i' = standardized valued of x_i.

x_{min} = minimum untransformed value of x_i among all samples examined

x_{max} = maximum untransformed value of x_i among all samples examined

The paedomorphic index (PI) for any population is simply the sum of the x_i values over n characters, divided by n:

$$PI = \left(\sum_i x_i' \right) \Big/ n$$

PI can vary between zero and unity, with high values indicating a strong tendency to retain juvenile characteristics. Table 14 gives PI values for 30 populations of *A. flavipunctatus*. Values range from 0.22 to 0.68, with a mean of 0.43. Geographic trends are evident (Figure 18), with the greatest degree of paedomorphism found in the northern part of the contiguous range of *A. f. flavipunctatus*. All populations north of the Leggett-Usal area in northern Mendocino Co. have PI's greater than 0.50. Intermediate values (0.35–0.50) occur in southern and eastern Mendocino Co. and in the Shasta Co. isolate. The lowest PI's (< 0.35) occur in the southeastern portion of the range of *A. f. flavipunctatus* and in the populations of *A. f. niger* isolated south of San Francisco.

Thus, the northern part of the range of *A. flavipunctatus* is inhabited by populations with paedomorphic tendencies in both pigmentation and external proportions. The least paedomorphic populations are found in peripheral localities at the southern and eastern extremities of the range.
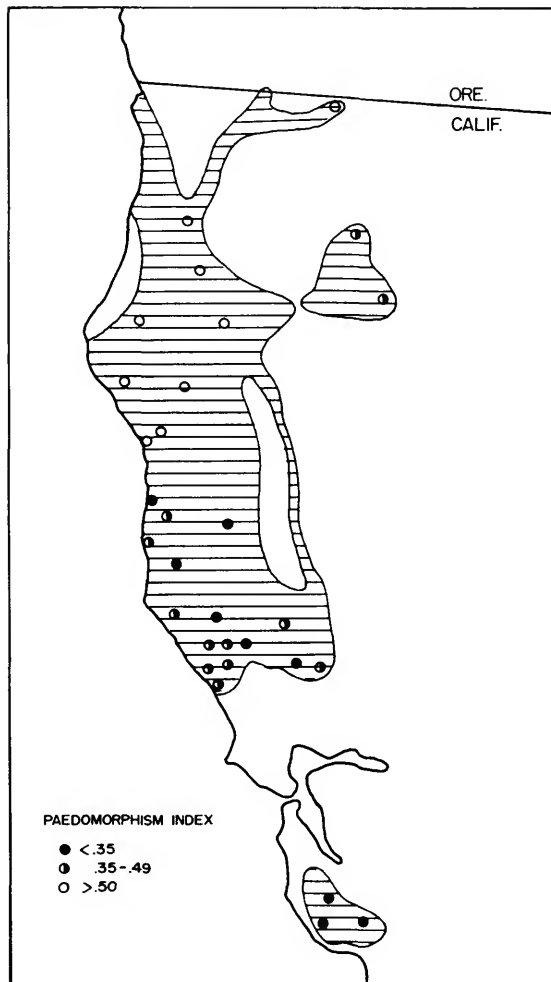
FIGURE 18.—Geographic variation in the paedormorphism index (PI). High values (open symbols) indicate marked tendency toward retention of juvenile characteristics.

It seems likely that an intermediate rate of ontogenetic change, rather than either of these extremes, is primitive. Juveniles of all species of *Aneides*, as well as some species of *Plethodon*, possess abundant metallic iridophore pigmentation, but this pigmentation is lost or greatly reduced in adults. There is a concurrent tendency toward loss of white or yellow iridophores and a darkening of the melanin network as ontogeny progresses. This general pattern is typical of *A. flavi-*

punctatus with intermediate PI's (e.g., the Sonoma-Mendocino populations), which show not only ontogenetic loss of juvenile brassy pigment and intensification of melanin, but also a reduction in the number of white iridophores with growth. Some large adults from this area are completely unspotted and virtually indistinguishable from individuals of the isolated race *A. f. niger.*

Populations of *A. f. niger* are characterized by a relative acceleration of ontogenetic changes in morphology. Melanin is heavily deposited even in relatively small individuals. White iridophores are abundant in juveniles but are soon resorbed, so that most adult *A. f. niger* are unspotted.

An alternate interpretation is that *A. f. niger* itself preserves the primitive ontogenetic pattern of change, and that all populations of *A. f. flavipunctatus* show a slight degree of paedomorphism imposed upon the primitive pattern. However, in view of the more generalized overall morphology of the Sonoma-Mendocino *A. flavipunctatus* (see below), it is more likely that these latter populations, rather than *A. f. niger*, are most similar to the ancestral stock.

Populations of *A. flavipunctatus* which inhabit the dry Inner Coast Ranges north of San Francisco Bay also possess adult morphologies suggestive of accelerated or exaggerated ontogenetic development, but here the characters involved are the increased rate of loss of juvenile brassiness and the increased rate of growth in the size of white iridophores. In contrast, populations *A. flavipunctatus* north and northeast of the Inner Coast Range (except those in the Shasta isolate) have morphologies which appear to be the result of slowing down of the "primitive" ontogenetic differentiation, such that a number of juvenile traits either are preserved throughout adulthood, or are lost at a relatively slow rate. Despite their large body size, adult northern *A. flavipunctatus* generally possess abundant brassy pigmentation, fairly small white iridophores, a lightly developed melanin network, and somewhat juvenile-like body proportions.

The functional significance of the adult color patterns which result from the retention of se-

lected juvenile characteristics is not certain. Part of the observed variation could reflect phenotypic response to differing environmental conditions, but a strong genetic component must be involved as well. Modification of the "normal" ontogenetic rate of character chance may be the evolutionary mechanism by which selectively beneficial adult color patterns are produced. Lowe (1950) suggested that the white-spotted *A. flavipunctatus* of inland regions are protectively colored, since they tend to inhabit rather open and well-illuminated habitats; in such areas, a relatively light overall body color would be advantageous in matching the background. The generally darker coastal forms are said by Lowe to inhabit shaded forest habitats where uniform dark coloration is advantageous. Stebbins (1949) and Brown (1970) suggested a similar explanation for the distribution of blotched and unblotched races of *Ensatina eschscholtzii* in California.

I have noted local situations where *A. flavipunctatus* appears especially well camouflaged, but the match appeared to be with very localized substrates beneath the surface objects where the salamanders were encountered, rather than with the floor of the surrounding forest or woodland. One such situation occurs in western Sonoma and Mendocino Counties, an area inhabited by very dark *A. flavipunctatus* marked with scattered white flecks. The substrate on which I have most commonly found these salamanders is dark, rocky soil beneath rocks or logs in relatively well-illuminated situations (often with no tree cover of any kind). Small bits of white fungi are frequently present on the bare soil, which is usually confined to the area beneath the cover object. Against this background, *A. flavipunctatus* is cryptic, but the substrate away from cover objects provides sharp contrast to the color of the salamanders. Brown (1970) noted that the colors of the various geographic races of *Ensatina eschscholtzii* correspond remarkably well with those of the fungi in the microhabitats where the salamanders occur.

The matching of salamander and substratum also seems especially effective in the Humboldt-Trinity-Del Norte-Siskiyou County region. Here

the paedomorphic green-gray color of adult *A. flavipunctatus* corresponds closely to the color of the metamorphics of the Franciscan, Galice, and other local formations (Irwin, 1960) which form the talus slides inhabited by the species in this area. The rock fragments and inorganic grit, particularly when wet, show a striking resemblance in color and tone to *A. flavipunctatus*. As in the previous example, the salamanders appear to be protectively colored with respect to the substrate associated with their refugia, rather than the surrounding forest floor.

Although these examples are anecdotal, they do provide a possible selective interpretation for geographic differentiation in gross body coloration and pattern. The individual components of color pattern may not all be exposed to consistent directional selective pressure; for example, there may be several morphogenetic pathways leading to a lightening of the overall body color (e.g., through proliferation of small spots or increase in the size of a few large spots). Whether paedomorphic tendencies in body proportions have an adaptive basis or are simply "carried along" as pleiotropic expressions of a general retardation in ontogenetic differentation is unclear.

Discussion

CAUSES AND SIGNIFICANCE OF GEOGRAPHIC VARIATION IN BODY SIZE

Given a statistically significant correlation between indicators of cooler climate and large body size in *A. flavipunctatus*, the question arises: Is there a cause-and-effect relationship between temperature and body size, or is there some unanalyzed factor, itself correlated with temperature, which accounts for the geographic relationships observed?

Ray (1960) demonstrated a consistent phenotypic response to varying thermal regimes in growth and development of a variety of poikilotherms, including anuran amphibians. For most of the diverse taxa investigated by Ray, lower environmental temperatures caused slower devel-

opment and delayed reproduction, but resulted in larger mean adult body size. These results suggest that the direction of phenotypic responses to some environmental signals is not independent of the nature of the signal itself. If Ray's results apply to ectotherms generally, one would predict that, other things being equal, *A. flavipunctatus* exposed to lower environmental temperatures should attain a larger adult body size. In the absence of significant counteracting selective pressure against larger body size, the observed latitudinal pattern of variation in body size could be a direct effect of temperature. Any selective advantage to larger body size in cooler regions could augment this purely phenotypic response, a phenomenon Levins (1968) has called "cogradient geographic variation." Selective pressure *against* larger size in cooler regions (e.g., shortage of food, presence of large competitors) could partially or wholly negate any purely phenotypic response through genetic re-organization of developmental patterns. This would result in what Levins calls "contragradient geographic variation."

It is difficult to determine whether temperature-related intraspecific variation in size is widespread in salamanders, for there have been few detailed studies. Highton (1962b) showed that *Plethodon glutinosus* grows at a faster rate in the southern part of its range than in the north, and that southern animals are smaller in adult size. Subsequently, however, Highton (pers. comm.) has determined that two species are involved, and that no clinal variation in size exists within either one. Hairston (1949) found a negative correlation between body size and environmental temperature in an altitudinal study of *Desmognathus ochrophaeus* in the Appalachian region of eastern North America. This finding is consistent with the pattern observed in *A. flavipunctatus*.

A contrary example is provided by Stebbins (1949) in his classic study of geographic variation in *Ensatina eschscholtzii* in California and Oregon. Northern races (*E. e. picta* and *E. e. oregonensis*) are *smaller* than the southern races (*E. e. eschscholtzii*), and two montane subspecies (*E. e. klauberi* and *E.

e. platensis) do not differ in size from their lowland counterparts at the same latitude.

There are obvious possible ecological (as opposed to purely physiological) functions of large vs. small size in *Aneides flavipunctatus*. Mortality schedules may be changed if large and small animals suffer differential predation pressure. As an example, the probability of predation by small salamander-eating snakes such as *Thamnophis* and *Diadophis* should be lower for large *Aneides flavipunctatus* than smaller ones. Laboratory observations by S. J. Arnold and myself of the feeding behavior of captive *Thamnophis elegans* support this hypothesis. Small salamanders generally are attacked and eaten quickly, but adult *Aneides flavipunctatus* (and *A. lugubris*) frequently escape even large garter snakes by aggressively biting when seized. In a few instances snakes were badly mauled by the salamander, and one large adult *Thamnophis elegans* actually died of injuries sustained in an unsuccessful attack on an adult *Aneides lugubris*. Brodie (1978) has described similar antipredator behavior in plethodontids of the genus *Desmognathus*.

A more subtle, yet highly effective, anti-predation tactic of *A. flavipunctatus* is the production of copious amounts of dermal mucous. The secretion resembles rubber cement, and appears to act mainly as a mechanical deterrent. In several instances, we noted that *Thamnophis* were unable to separate their jaws following contact with this sticky skin secretion. The point is not merely that salamanders possess defensive adaptations, but that the effectiveness of these deterrents is quantitative—large salamanders produce more secretion than smaller ones, and, at least under laboratory conditions, are more successful in avoiding capture. Thus, one would predict that the large adults typical of northern populations of *A. flavipunctatus* should be less subject to predation than smaller adults typical of southern populations.

A second major ecological effect of geographic variation in body size involves changes in natality. Salthe (1969) showed that fecundity is correlated with body size for salamanders of a given reproductive mode. Tilley (1968) documented a

similar correlation both within and between species of the plethodontid genus *Desmognathus*.

Following Blanchard (1936), Tilley (1968), Houck (1977), and other workers, I counted enlarged ovarian follicles (> 1.5 mm diameter) in female *A. flavipunctatus*, and plotted body size vs. fecundity for 112 reproductively mature females collected throughout the range. As illustrated in Figure 18, there is a highly significant correlation between clutch size (x_1) and body size (x_2), with $r_{12} = 0.606$ (P < 0.01). I attempted to reduce the unexplained variation by adding latitude (x_3) as a variable, but the multiple correlation coefficient is not significantly greater than the simple correlation $(R_{1.23} = 0.621)$. The partial correlation coefficient relating latitude to fecundity, with the effect of body size held constant, is insignificant $(r_{13.2} = 0.173$, P > 0.1), indicating a lack of important latitudinal effects on the size-fecundity relationship.

The size-fecundity regression can be used to estimate clutch size for average females in populations with small vs. large mean body size (Figure 19). A 63 mm female *A. flavipunctatus* (mean SL for southern populations) produces an average of about nine eggs per clutch, while a 75 mm female (typical of northern populations) has a mean clutch size of approximately 13. Thus, geographic differences in mean adult body size are potentially important to the demography of local populations. However, evaluation of the reproductive impact of variation in size would require presently unavailable data on size and age at first reproduction, periodicity of reproduction, and survivorship.

A third possible effect of variation in mean adult body size is through size-specific feeding patterns. Data presented elsewhere (Lynch, 1973, 1974a, and in preparation) show that adult salamanders tend to take larger prey than juveniles, but that both mean prey size and total prey volume level off in animals larger than about 50 mm SL. This means that interpopulational differences in adult body size are unlikely to have an important direct effect on the basic pattern of food utilization by local populations.
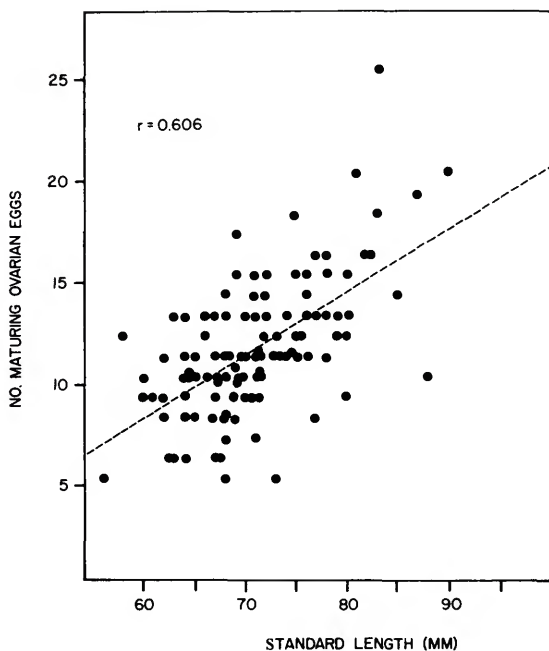
FIGURE 19.—Correlation between the standard length of female *A. flavipunctatus* and the number of maturing ovarian eggs (the correlation is significant at p < 0.01).

CAUSES AND SIGNIFICANCE OF VARIATION IN NUMBER OF TRUNK VERTEBRAE

The validity of vertebral number as a taxonomic character for distinguishing the two subspecies of *A. flavipunctatus* is challenged by the occurrence of populations with modal counts of 17 as well as 16 vertebrae within the range of the nominate subspecies. The overall pattern of geographic and intrapopulational variation in morphology is not unlike that found by Highton (1962a) in his study of *Plethodon cinereus*. In both species, regional trends are evident, but these cannot be completely explained by a simple clinal relationship or physical influence. Thus, although there is a general tendency for increasing vertebral number in northern populations of *Aneides flavipunctatus flavipunctatus*, the isolated Shasta County populations are low in vertebral number despite their northerly location, and populations of *A. f. niger* have consistently high vertebral

counts despite their extreme southerly location. A further parallel between *A. flavipunctatus* and *Plethodon cinereus* is the tendency for local populations to be strongly dominated by the modal vertebral number. Intermediate situations, where less than two-thirds of the individuals in a population fall into the modal class, are rare (4 of 41 samples = 9.7%). The large-scale geographic pattern, then, is a mosaic of 16- and 17-vertebrae regions, although evidence has been presented for local clinal changes over part of the species range.

Abrupt transitions in modal vertebral number tend to occur in the same regions where other morphological characters, notably pigmentation features, also show marked changes. Thus, populations of *A. f. niger* are different from the nearest populations of *A. f. flavipunctatus* to the north in vertebral number as well as pigmentation. In coastal Mendocino County, the transition from white-spotted black animals to brassy-greenish animals with strong concentrations of lateral frosting is accompanied by a shift from 16 to 17 vertebrae. Finally, the Shasta County populations, which are separated from the Trinity County populations by the rugged Trinity Mountains, are distinctive with respect to trunk segmentation as well as pigmentation.

In areas where changes in coloration are more gradual, as between southern Sonoma and central Mendocino Counties, changes in vertebral number also tend to be gradual, although most local populations are nevertheless dominated by one or the other vertebral morph.

Finally, as with body size, there is the question of the relative importance of environmental vs. genetic factors in the determination of vertebral number. For fishes, the geographic and laboratory evidence are complementary: fishes living at northern latitudes tend to have more vertebrae than their low-latitude counterparts, and fishes which undergo development in cold water tend to develop more vertebrae than siblings which develop in warm water. Peabody and Brodie (1975) documented a similar negative correlation between developmental temperature and vertebral number in the salamander *Ambystoma macu-*

latum. However, Lindsey (1966b) found that a cooler developmental environment resulted in differentiation of fewer vertebrae in the salamander *Ambystoma gracile*, and Fox and co-workers (1948, 1961) reported similar results for experimentally incubated snakes (*Thamnophis*). The significance of the findings of Lindsey and Fox is difficult to assess, since neither experiment was designed to detect the V-shaped or inverted V-shaped response curves characteristic of some fishes and snakes (Taning, 1952; Barlow, 1961; Fowler, 1970; Osgood, 1978). Nevertheless, it is clear that temperature often influences trunk segmentation in ectothermal vertebrates.

On the other hand, genetically based variation in vertebrae number definitely occurs in salamanders. Highton (1960) demonstrated that vertebral number has a significant genetic component in *Plethodon cinereus*, the estimated heritability being about 0.6. Highton suggests that this figure is an underestimate of the true genetic component. Similar genetic input has been demonstrated experimentally for fishes (Barlow, 1961).

Without data on parent-offspring phenotypes, one can only speculate on the relative importance of environmental vs. genetic factors in the determination of vertebral number in *Aneides flavipunctatus*. If the geographic isolates in the Santa Cruz Mountains and in Shasta County are omitted from consideration, there is an increase in the mean number of vertebrae from 16 to 17 from south to north. If no adaptive advantage accrues to salamanders with either 16 or 17 vertebrae, environmental influences (e.g., thermal conditions during embryonic development) might be free to modify the genetic determination of trunk segmentation within these rather narrow variational limits. In geographically isolated populations (e.g., Shasta County and the Santa Cruz Mountains) local genetic differentiation may have resulted in an anomalous shift in vertebrae number. This hypothesis is consistent with the low degree of variability in vertebrae number observed in the Shasta and Santa Cruz Mountains isolates, since a tendency toward fixation is expected where genetic drift has occurred.

An alternative, adaptive explanation of variation in vertebral number would be that body shape per se is of ecological significance, i.e., that relatively short-bodied forms (those with fewer vertebrae) might be better adapted for a scansorial existence near the surface, while long-bodied forms (those with more vertebrae) might be better adapted for burrowing through rock talus. Rock talus is in fact the favored microhabitat in the norther part of the range of *A. f. flavipunctatus*, but the transition from 16 to 17 vertebrae occurs far to the south of the transition from woodland to rock talus habitats. Furthermore, *A. flavipunctatus* inhabiting the Shasta County and Santa Cruz Mountains isolates are at opposite ends of the variational range of vertebral number, yet are extremely similar with regard to microhabitat and activity patterns; salamanders in both areas favor a *Desmognathus*-like streamside microhabitat, and show extensive summertime activity (Lynch, 1974a).

Thus, the least unsatisfactory explanation for the observed pattern of variation in trunk segmentation in *Aneides flavipunctatus* is that vertebral number is determined by an interplay of genetic and environmental influences within a narrow, possibly selectively neutral, range of variation.

Multiple Regression Analysis

The stepwise multiple regression analysis suggests that the patterns of morphological variation exhibited by *A. flavipunctatus* can be attributed to genetic and/or phenotypic responses of individual characters to geographic and climatic variables. Of the five predictor variables, latitude shows the most consistent correlation with aspects of morphological variation, with distance inland also being important in several cases. Elevation and mean January temperature each contribute significantly to variation in one morphological trait; the importance of the latter variable probably would be greater if more precise local thermal data were available. One predictor, mean annual precipitation (MAP), had no significant effect on any of the morphological traits examined. A pos-

sible explanation for the latter finding is that rainfall mainly determines the length of the season of activity, rather than the humidity of the microhabitat during activity periods. Because plethodontids lack effective physiological means of avoiding water loss (Brown, 1972) surface activity is generally confined to periods when atmospheric humidity is close to 100%.

An exception to this generality is seen in the Shasta and Santa Cruz Mountains isolates, where salamanders are associated with very wet streamside microhabitats, and are active even during the summer dry season. These animals are frequently found in contact with standing water, and Brown (1972) has suggested that Santa Cruz *A. flavipunctatus* possess special physiological adaptations for semiaquatic life. The Prim Network analysis showed that the Santa Cruz Mountains and Shasta Co. populations are more similar to one another morphologically than would be predicted on the basis of their wide geographic separation. The unexpectedly close phenetic similarity between the Shasta and Santa Cruz populations is almost certainly the result of convergent evolutionary adaptation to a semi-aquatic way of life, rather than an indication of close genetic similarity.

While the micro-humidity experienced by *A. flavipunctatus* probably is fairly similar throughout the range, with the exceptions just noted, this is not the case for temperature. The species has been found active at the surface at substrate temperatures betwen 2° C and 19° C (Lynch, 1974a). Populations which inhabit the equable southern coastal portion of the range, where prolonged intervals of subfreezing temperatures are rare, experience a substantially different thermal regime from populations at the northern end of the distribution, where snowfall is common and subfreezing temperatures are a normal part of the wet season environment. It is understandable, therefore, that morphological differentiation is more strongly correlated with indicators of thermal conditions (e.g., latitude) than with indicators of humidity (e.g., mean annual precipitation).

PRIM NETWORK ANALYSIS

The Prim analysis provides information which may bear upon questions regarding the past and present distribution of *A. flavipunctatus*.

It was suggested in an earlier section that the ancestral *A. flavipunctatus* was probably associated with Arcto-Tertiary geoflora (sensu Axelrod, 1948) which covered northern California until the Pliocene. The Coast Redwood (*Sequoia sempervirens*), which presently is restricted to the humid coastal region of northwestern California and extreme southwest Oregon, is a relict of this ancient floral association. Paleobotanical evidence (Axelrod 1948, 1950, 1976) indicates the former existence of Redwoods and other Arcto-Tertiary derivatives far to the north, south, and east of their present distributions. During the early to middle Pliocene, the entire area presently inhabited by *Aneides flavipunctatus* probably supported humid forest and had an equable climate.

The Prim analysis shows that populations of *A. flavipunctatus* which now inhabit the Redwood Forest region of western Sonoma and Mendocino counties are morphologically generalized (i.e., intermediate). This is also the part of the range where *A. flavipunctatus* appears to be most widely distributed and abundant. It is reasonable to suggest that these populations, which remain associated with relicts of the ancient Arcto-Tertiary geoflora, also retain a morphological resemblance to the ancestral form.

The Prim Network shows that populations of *A. flavipunctatus* which inhabit two widely separated geographic isolates are unexpectedly similar to one another phenetically. Even more surprising is the fact that the closest phenetic relationships of the two isolates are with populations in the Redwood belt of western Sonoma and Mendocino counties. If the two isolates are in fact similarly adapted, somewhat evolved relicts of the previously widespread and morphologically generalized ancestor, whose closest modern analogue occurs in the humid redwood belt, then the pattern of similarities makes zoogeographic and evolutionary sense. Recent electrophoretic analysis

of *A. flavipunctatus* by Larson (1980) has confirmed that *A. flavipunctatus* is highly fragmented genetically as well as phenetically. In addition, Larson presents strong biochemical evidence that the phenetic resemblance between the Shasta County and Santa Cruz Mountains isolates does not reflect close genetic relationship, but instead probably represents in situ adaptations to similar climate and microhabitat.

I concur with Lowe (1950) in interpreting the morphological divergence of populations at the eastern periphery of the range of *A. flavipunctatus* in the inner coast ranges as in situ responses to deteriorating climatic conditions, although a late Pliocene disjunction appears more likely than the Pleistocene date proposed by Lowe. Lowe pointed out that inland populations of *A. flavipunctatus* are associated with ecotonal elements of the xeric Madro-Tertiary geoflora that penetrated California from the south and east as the climate became drier during the latter portion of the Tertiary. The patchy inland distribution of *A. flavipunctatus*, and its restriction to mesic microhabitats (e.g., mine openings, sheltered canyons), are suggestive of a contracting distribution. A similar relictual pattern has been documented for the Tailed Frog (*Ascaphus truei*), another Arcto-Tertiary associate (Metter, 1967). The disjunct distributions of several other western amphibians (*Dicamptodon ensatus*, *Taricha granulosa*, *Plethodon vandykei*) suggest that the relictual pattern is widespread, although repeated cycles of mesic and dry conditions since the mid-Pliocene may have complicated the present distributional picture.

Finally, the Prim Network laid over the distribution map (Figure 15) serves to emphasize potential barriers to gene flow between populations. The Trinity Mts. provide one obvious example. To judge from the low degree of phenetic similarity between Trinity Co. populations west of the Trinity divide and Shasta Co. populations east of it, this rugged ridge is an effective barrier, which has allowed the evolution of substantial differentiation to either side of it.

Within the contiguous range of *A.f. flavipunctatus* phenetic connections tend to parallel the coast,

especially in the Sonoma-Mendocino County area. Since climatic and vegetational zones in this part of California also tend to be oriented parallel to the coast, it appears that climate and habitat are more important determinants of phenetic similarity than simple geographical proximity. Evidently, genetic interchange in an East-West direction has been sufficiently restricted in the Sonoma-Mendocino area that moderate local morphological differentiation has occurred.

PAEDOMORPHISM AND SPECIATION
IN *A. flavipunctatus*

Compared with most eastern salamanders, particularly members of Highton's (1962a) "Eastern Small *Plethodon*" group, *Aneides flavipunctatus* shows extensive geographic variation in morphology. Among some eastern *Plethodon* external morphological variation is so subtle that even the most experienced workers cannot distinguish full species on the basis of color and proportions (Highton and Webster, 1976; Larson and Highton, 1978). One of the few North American plethodontids that exceeds *A. flavipunctatus* in morphological variability is *Ensatina eschscholtzii*, a western species whose extensive distribution completely encompasses that of *A. flavipunctatus* (Stebbins, 1949). *Batrachoseps attenuatus*, another highly variable western plethodontid, recently has been shown to be a composite of several sibling species, based on detailed electrophoretic studies (Yanev, 1978). Larson's (1980) electrophoretic data for *A. flavipunctatus* indicate that the high degree of morphological differentiation documented in the present study is parallel by substantial genetic subdivision, but that genetic differentiation in this species does not exceed that observed in morphologically conservative eastern *Plethodon* (e.g., *P. cinereus, P. dorsalis*).

Paedomorphosis appears to have been a dominant mode of evolutionary change in *A. flavipunctatus*. At present, a formerly widespread taxon, that presumably was morphologically uniform at one time, is differentiating in response to a combination of local isolation and changing environmental conditions. The dramatic topographic-climatic heterogeneity typical of western North America has the dual effect of increasing local isolation of populations, while at the same time presenting a wide variety of environmental "problems" for adaptive evolution to solve. Both of these factors promote the sort of morphological and ecological diversification of which evolutionary radiations are made. In this connection, it can be noted that plethodontid diversity in Middle America is also exceptionally high in areas with high topographic and climatic diversity (Wake and Lynch, 1976).

The selective basis for morphological diffentiation remains conjectural, but is clear that heterochrony, the selective modulation of ontogenetic patterns of character development, is one mechanism by which this differentiation has been achieved. This is most evident with respect to color pattern, but proportional differences also are involved. Populations of *A. flavipunctatus* have evolved dramatically different morphologies as a result of variation in the rate of ontogenetic change in a handful of character complexes. The fact that much of this variation is associated with climatic-topographic gradients is of interest, despite our present inability to disentangle phenotypic, adaptive genetic, and selectively neutral and pleiotropic genetic responses. Experimental rearing of juvenile *A. flavipunctatus* under varying thermal regimes, combined with electrophoretic screening of morphologically distinctive populations (Larson, 1980), could resolve some of these questions.

Finally, the results of the present study may be considered in light of the continuing controversy concerning the primacy of gradual phyletic evolution within lineages, as opposed to long-term morphological stasis within species, "punctuated" by rapid bursts of change associated with speciation (cf. Eldredge and Gould, 1972; Gould and Eldredge, 1977). The morphological and biogeographic data presented here, and the electrophoretic data of Larson (1980), agree in indicating highly variable rates and directions of morphological evolution in different populations of *A.*

flavipunctatus. Moreover, the degree (and presumably the rate) of morphological divergence from the ancestral phenotype in some instances reflects the extent of climatic-vegetational change that occurred in various parts of the present species distribution as the late Tertiary climate deteriorated. As remnants of the formerly widespread Arcto-Tertiary geoflora contracted to their present limited coastal distribution, some (perhaps most) populations of *A. flavipunctatus* undoubtedly underwent extinction. Others, particularly in areas just inland of the humid coastal forests, were exposed to selective forces which, while severe, were not sufficiently extreme to cause regional extinction. Instead, local distributions became limited to highly favorable microhabitats, and morphological divergence proceeded apace. Still other populations, especially in humid coastal areas, probably underwent only minor morphological changes.

Larson's (1980) electrophoretic data show that striking shifts in color pattern, external proportions, trunk segmentation, and body size were not accompanied by unusually extensive genetic reorganization. Indeed, genetic divergence among populations of *A. flavipunctatus* is well within the range observed in plethodontid species with much more conservative phenotypes (e.g., *Plethodon cinereus*, *P. dorsalis*), and is substantially less than the divergence observed between pairs of sibling species (e.g., *P. cinereus-P. serratus*, *P. dorsalis-P. websteri*) that are virtually indistinguishable on morphological grounds (Highton, 1979; Highton and Webster, 1976; Larson, 1980; Larson and Highton, 1978).

In effect, the present distribution of *A. flavipunctatus* constitutes a mosaic of morphologically and genetically diversified populations. Some of these, particularly in the coastal Redwood area, appear to fit the Gould-Eldredge model of morphological stasis over long periods of geologic time, but others have undergone dramatic in situ divergence from the primitive phenotype over a period of perhaps a few million years (Larson, 1980). A stratigraphic sequence of fossils of a species with this pattern of geographic variation would yield very different impressions of the importance of stasis vs. phyletic gradualism, depending on exactly where within the distributional range the sequence of fossils was deposited. That is to say, both the phyletic mode and the punctuated equilibrium mode of evolution may occur side by side within the limits of a single biological species.

Summary

1. The geographic distribution of the Black Salamander, *Aneides flavipunctatus*, has been analyzed. Collections from 142 localities in northwestern California indicate that the species is virtually restricted to low-lying thermally equable areas that receive at least 75 cm of annual precipitation. The broad limits of distribution appear to be determined mainly by climatic factors in combination with dispersal barriers, except in the coastal area near the California-Oregon border. The latter region has a humid, equable climate that seems suitable for *A. flavipunctatus*. In this area, interactions with other species of salamanders, particularly members of the genus *Plethodon* may account for the absence of *A. flavipunctatus*. The apparent absence of the species from coastal Marin Co., north of San Francisco Bay, is unexplained.

2. The basic color pattern of adult *A. flavipunctatus* consists of white iridophores scattered over a dense melanic background. "Brassy" iridophores are abundant in all juveniles, and are retained in adults in some parts of the range. White iridophores typically enlarge, but become fewer in number, as ontogeny proceeds. Melanic pigmentation is usually more dense in larger individuals.

3. The modal number of trunk vertebrae is 16 or 17 in all populations examined, although occasional individuals have as many as 18 or as few as 15 vertebrae. One vertebral count generally predominates in most populations. There is a clinal shift from lower to higher mean vertebral number as one moves northward through the contiguous range of *A. f. flavipunctatus*. Isolated

groups of populations in Shasta Co. and in the Santa Cruz Mountains have modal vertebral counts which differ from those in the nearest populations within the contiguous range.

4. A multiple regression-multiple correlation analysis reveals significant correlations between several geographic predictor variables and individual morphological traits. Latitude is the most consistently important predictor of character shifts, but distance inland, elevation, and mean January temperature each shows a statistically significant association with at least one morphological trait. Compared to populations in the southern part of the range, northern *A. flavipunctatus* average larger in body size, are relatively longer legged, show a greater tendency to retain the juvenile brassy pigmentation throughout adulthood, have smaller white iridophores, are less melanic, and have more vertebrae. All of these traits, except vertebral number, reflect a tendency toward paedomorphism by northern *A. flavipunctatus*.

5. A Prim Network analysis of *A. flavipunctatus* from 30 populations shows that geographic proximity is most often correlated with phenetic similarity. However, isolated populations in Shasta Co. and in the Santa Cruz Mountains are closer phenetically to distant populations in coastal Mendocino and northern Sonoma counties than to their nearest geographic neighbors. The Sonoma-Mendocino populations appear to be the most generalized morphologically, and it is suggested that they retain similarities to the ancestral forerunner of *A. flavipunctatus*.

Appendix

Tables

Table 1.— R-matrix of inter-character correlations in adult males of 37 populations of *A. flavipunctatus* (sixteen characters: MVN = mean vertebral number, HL = head length, HW = head width, FL = forelimb length, HNL = hind limb length, TL = tail length, DBN = number of brassy iridophores on dorsum, DWS = size of white iridophores on dorsum, DWN = number of white iridophores on dorsum, CWS = size of white iridophores on chin, CWN = number of white iridophores, VWS = size of white iridophores on venter, VWN = number of white iridophores on venter, FMD = development of melanin net at base of forelimb, CMD = development of melanin net on chin, EYD = development of iridophores in eye; underlined correlation coefficients are significant at p ≤ 0.05)

Characters	MVN	HL	HW	FL	HNL	TL	DBN	DWS	DWN	CWS	CWN	VWS	VWN	FMD	CMD	EYD
MVN																
HL	.028															
HW	-.195	.670														
FL	.417	.685	.403													
HNL	.312	.744	.442	.920												
TL	0.000	.276	.141	.021	-.005											
DBN	.374	.228	-.005	.425	.489	.373										
DWS	-.279	.439	.523	.199	.174	-.191	.434									
DWN	.460	-.191	-.047	-.161	-.072	-.433	-.120	.085								
CWS	-.217	.743	.706	.417	.344	.129	.405	.917	-.028							
CWN	-.188	-.285	-.207	-.073	.111	-.141	.769	-.373	.541	-.180						
VWS	-.319	.608	.646	.361	.301	-.099	.520	.965	.051	.948	-.185					
VWN	.441	-.394	-.116	-.408	-.170	-.415	.314	-.174	.825	-.228	.755	-.093				
FMD	-.008	.221	.322	.299	.164	-.101	.199	.147	.184	.213	.130	.296	.096			
CMD	.194	.364	.278	.413	.419	.200	.562	.222	-.145	.584	-.020	.642	-.131	.534		
EYD	.272	.157	.164	.189	.147	.379	.303	-.141	-.190	.166	.016	.017	.418	.312	.302	—

TABLE 2.—Sexual and ontogenetic differences in body proportions for *A. flavipunctatus* (each dimension gives a proportion of body length (standard length — head length) for adult males (M) and females (F) at body length = 50 mm, and for juveniles (J) at body length = 30 mm; characters are HDL = head length, HDW = head width, FOREL = forelimb length, HNDL = hind limb length, and TAIL = tail length)

Locality code	HDL			HDW			FOREL			HNDL			TAIL		
	M	F	J	M	F	J	M	F	J	M	F	J	M	F	J
001	.32	.31	.38	.22	.20	.26	.29	.28	.35	.34	.33	.39	.96	.96	.98
007	.32	.31	.36	.21	.20	.26	.28	.27	.32	.33	.33	.36	1.00	1.00	.98
008	.31	.30	.36	.21	.19	.25	.27	.26	.30	.32	.33	.24	1.03	–	.86
009	.33	.32	.40	.22	.20	.26	.28	.27	.34	.33	.30	.39	1.01	.98	.97
010	.32	.31	.40	.20	.20	.26	.28	.27	.35	.33	.31	.38	1.00	1.03	.98
055	.32	.31	.39	.22	.20	.26	.29	.27	.35	.34	.32	.41	1.01	1.02	.98
062	.32	.32	.39	.21	.20	.26	.29	.27	.35	.34	.31	.39	1.00	1.01	.96
063	.32	.32	.38	.22	.20	.26	.29	.28	.37	.34	.32	.40	1.00	1.05	1.00
064	.36	.32	.39	.22	.20	.25	.29	.27	.35	.34	.32	.40	.94	1.00	.96
067	.32	.31	.39	.20	.19	.26	.28	.27	.35	.34	.32	.40	.93	–	.99
070	.31	.30	.38	.21	.19	.26	.28	.26	.34	.31	.31	.38	1.03	1.06	.97
111	.32	.31	.38	.22	.20	.25	.29	.27	.35	.33	.33	.39	.97	.93	.91
114, 115	.32	.31	.36	.22	.20	.25	.28	.27	.36	.33	.32	.38	1.01	.92	–
116	.33	.32	.39	.21	.20	.26	.30	.29	.37	.35	.34	.40	.92	.98	.97
121	.32	.31	.37	.21	.20	.25	.27	.26	.34	.32	.31	.38	.93	.91	–
123	–	.32	–	–	.20	–	–	.30	–	–	.34	–	–	.93	–
125	.34	.32	–	.23	.21	–	.31	.28	–	.36	.33	–	–	.95	–
155, 184	–	.33	–	–	.20	–	–	.28	–	–	.34	–	–	–	–
158	.33	.32	.38	.20	.20	.27	.29	.28	.37	.34	.32	.41	1.03	1.00	1.05
161	.31	.30	.37	.21	.20	.26	.29	.27	.37	.34	.32	.42	1.03	1.02	.88
165, 188	.34	–	.38	.22	–	.26	.30	–	.34	.34	.34	.39	1.07	1.03	.91
167	.32	.31	.37	.21	.20	.25	.29	.27	.36	.34	.32	.40	1.04	1.02	.87
170	.34	.32	.39	.22	.20	.26	.31	.29	.37	.35	.34	.39	.99	.95	.82
174, 175	.33	.33	.40	.22	.20	.25	.31	.30	.36	.35	.34	.40	.98	1.03	.83
181	.33	.31	.37	.22	.20	.26	.29	.29	.37	.35	.34	.40	.94	.92	.78
187	.33	.32	.39	.22	.20	.25	.29	.28	.34	.34	.33	.39	1.05	1.00	.78
189	–	–	.39	–	–	.24	–	–	.34	–	–	.38	–	–	.79
192	.33	.32	–	.22	.20	–	.31	.30	–	.35	.34	–	.95	.86	–
200	.34	.32	.39	.21	.20	.26	.32	.30	.36	.36	.34	–	1.00	.94	.90
205–207[a]	–	.30	.35	–	.20	.24	–	.29	.32	–	.34	.36	.95	1.05	.83
213[a]	.31	–	.35	.22	–	.25	.28	–	.32	.34	–	.36	.92	–	.84
218[a]	.30	.30	–	.20	.20	–	.27	.27	–	.32	.31	.30	.88	.88	–
255[b]	.31	.31	.36	.21	.20	.25	.28	.27	.32	.33	.32	.36	.98	.94	.84
257[b]	–	.30	.35	–	.20	.25	–	.28	.33	.33	.32	.36	–	.91	.85
259[b]	.31	.31	.35	.20	.20	.25	.28	.27	.34	.32	.32	.37	.96	.95	.85
266[b]	.32	.31	.37	.21	.20	.26	.28	.27	.32	.33	.32	.37	.94	.96	.88

[a] *A. f. flavipunctatus* from Shasta Co.
[b] *A. f. niger.*

TABLE 3.—The effect of the Salinas Valley (SV) and the Southern Cascade Bottleneck (CB) on the distribution of species of amphibians

Spp. which range south to the Salinas Valley	Spp. which range both north and south of the Salinas Valley	Spp. which range north to the Salinas Valley
Ambystoma macrodactylum *Aneides flavipunctatus* *Dicamptodon ensatus* *Taricha granulosa*	*Ambystoma tigrinum* *Aneides lugubris* *Batrachoseps attenuatus* *Bufo boreas* *Ensatina eschscholtzii** *Hyla regilla* *Rana boylei* *R. aurora*	*Batrachoseps nigriventris*

Spp. which range south to the Southern Cascades	Spp. which range through the Southern Cascades into the Northern Sierra Nevada	Spp. which range north to the Southern Cascades
Aneides flavipunctatus *Ascaphus truei* *Dicamptodon ensatus* *Hydromantes shastae*	*Ambystoma macrodactylum* *Bufo boreas* *Ensatina eschscholtzii** *Hyla regilla* *Rana boylei* *R. muscosa* *Taricha torosa*	*Batrachoseps attenuatus* *Aneides lugubris?*

* Subspecific break.

TABLE 4.—Ontogenetic changes in the diameter of white dorsal iridophores in *Aneides flavipunctatus* (values in coded units; column A = projected mean iridophore size for SL (40 mm); column B = projected mean iridophore size at SL (70 mm); column C = direction of ontogenetic change, N.C. = no significant change)

Locality	Code	A	B	C
Salmon Point	001	1.0	2.7	+
McGuire Hill	007	1.2	1.8	+
Fort Bragg	008	1.5	1.8	+
Cloverdale	009	2.2	4.1	+
Navarro	010	1.3	1.8	+
Skaggs Springs	055	1.5	3.4	+
Stewart's Point Rd.	062	1.8	3.3	+
Sonoma Queen Mine	063	–	2.9	?
Cazadero	064	–	2.9	?
Signal Ridge	067	1.6	3.0	+
Monte Rio	070	1.5	2.4	+
Potter Valley	111	2.4	5.7	+
Aetna Springs	114, 115	2.4	6.8	+
Berryessa	116	2.0	4.9	+
Geyserville	121	2.0	4.9	+
Middletown	123	–	8.6	?
Slate Rock Canyon	125	–	?	?
Longvale	155, 156, 184	–	4.0	?
Leggett	158	1.0	0.9	N.C.
Usal	161	–	0.5	?
Ettersberg	165, 188	–	1.8	?
Grizzly Cr.	167	1.2	1.9	+
Weitchpec	170	1.1	2.0	+
Salyer	174, 175	1.1	2.5	+
Rogers Cr.	181	1.1	3.0	+
Alderpoint	187	1.0	1.7	+
Davis Cr.	189	1.0	1.0	N.C.
Hilt	192	–	3.6	?
Hyampom	200	1.8	4.0	+
Squaw Cr.[1]	205–207	1.0	1.1	N.C.
Nosoni Cr.[1]	213	1.0	2.0	+
Castle Crags[1]	218	–	2.0	?
Brookdale[2]	255	1.0	0.8	–
Summit Dr.[2]	257	1.0	0.8	–
Saratoga[2]	259	1.0	0.5	–
Uvas Cr.[2]	266	1.0	0.7	–

[1] *A. f. flavipunctatus* from Shasta Co.
[2] *A. f. niger.*

TABLE 5.—Projected mean abundance of white dorsal iridophores (DWN) and standard error of predicted mean (S.E.) in large juvenile (SL = 40 mm) and adult (SL = 70 mm) *A. flavipunctatus* (direction of ontogenetic shift in iridophore abundance indicated in last column; parentheses enclose non-significant shifts, p > 0.05)

Locality	Code	Juveniles			Adults			
		n	DWN	S.E.	n	DWN	S.E.	
Salmon Point	001	50	3.6	.17	57	4.7	.45	(+)
McGuire Hill	007	30	4.0	.32	52	2.3	.53	—
Fort Bragg	008	10	1.8	.33	5	1.8	.09	N.C.
Cloverdale	009	(4)	–	–	8	2.2	.18	?
Navarro	010	25	5.2	.30	18	2.2	.43	—
Skaggs Springs	055	10	6.4	.66	42	5.0	.38	(−)
Stewart's Point Rd.	062	9	6.3	.64	9	4.4	.26	—
Sonoma Queen Mine	063	(2)	–	–	22	4.0	.61	?
Cazadero	064	5	5.6	1.70	13	4.3	.39	—
Signal Ridge	067	7	5.4	.72	7	6.3	1.48	(+)
Monte Rio	070	7	6.1	.68	7	6.7	.84	(+)
Potter Valley	111	10	2.7	.27	19	1.7	.12	—
Aetna Springs	114, 115	9	2.1	.23	9	1.3	.08	—
Berryessa	716	18	3.9	.16	13	3.0	.14	—
Geyserville	121	16	3.9	.29	18	2.6	.06	—
Middletown	123	(1)	–	–	7	2.4	.11	?
Shale Springs Canyon	125	(0)	–	–	9	2.3	.08	?
Longvale	155, 156, 184	(3)	–	–	7	4.0	.38	?
Leggett	158	10	2.4	.77	11	1.1	.39	(−)
Usal	161	(3)	–	–	8	0.6	.20	?
Ettersberg	165, 188	(2)	–	–	5	1.4	.13	?
Grizzly Cr.	167	7	2.8	.42	12	1.9	.60	(−)
Weitchpec	170	12	5.6	.78	8	2.6	.70	—
Salyer	174, 175	16	5.5	.60	12	3.4	1.65	(−)
Rogers Cr.	181	11	4.5	.42	3	2.3	.19	—
Alderpoint	187	9	5.6	.82	22	2.7	.80	—
Davis Cr.	189	6	2.8	.50	5	1.0	.00	—
Hilt	192	(2)	–	–	8	3.5	1.11	?
Hyampon	200	5	5.4	1.07	6	3.8	.88	(−)
Squaw Cr.[1]	205, 207	15	4.1	.44	7	3.4	2.88	(−)
Nosoni Cr.[1]	213	20	4.7	.30	4	6.8	4.12	?
Castle Crags[1]	218	(1)	–	–	9	8.6	1.51	?
Brookdale[2]	255	38	4.6	.29	19	1.1	.12	—
Summit Dr.[2]	257	6	3.6	.56	5	1.2	.31	—
Saratoga[2]	259	19	3.9	.29	13	0.8	.52	—
Uvas Cr.[2]	266	18	5.0	.47	7	0.9	.18	—

[1] *A. f. flavipunctatus* from Shasta Co.

[2] *A. f. niger.*

TABLE 6.—Projected mean abundance of brassy dorsal iridophores (DBN) in large juveniles (SL = 40 mm) and adults (SL = 70 mm) of *A. flavipunctatus* (direction of ontogenetic shift indicated in last column; N.C. = shifts of less than 0.5 units are scored "no change")

Locality	Code	Juveniles		Adults		
		n	DBN	n	DBN	
Salmon Point	001	44	5.1	54	3.2	—
McGuire Hill	007	31	4.4	32	1.4	—
Fort Bragg	008	10	4.9	5	2.8	—
Cloverdale	009	4	4.3	8	0.0	—
Navarro	010	25	4.3	18	0.4	—
Skaggs Springs	055	11	2.4	42	0.1	—
Stewart's Point Rd.	062	9	3.1	9	0.1	—
Sonoma Queen Mine	063	(2)	–	22	0.0	—
Cazadero	064	5	0.5	13	0.2	—
Signal Ridge	067	7	2.9	7	0.3	—
Monte Rio	070	7	3.4	7	1.1	—
Potter Valley	111	9	3.5	19	0.3	—
Aetna	114, 115	9	1.4	9	0.0	—
Berryessa	116	18	1.8	13	0.3	—
Geyserville	121	16	2.1	18	0.0	—
Middletown	123	(1)	–	7	0.0	?
Shale Springs Canyon	125	(2)	–	9	0.0	?
Longvale	155, 156, 184	(3)	–	7	3.8	?
Leggett	158	9	5.2	11	5.5	N.C.
Usal	161	(3)	–	8	5.6	?
Ettersberg	165, 188	(2)	–	5	5.2	?
Grizzly Cr.	167	7	5.7	12	5.2	N.C.
Weitchpec	170	13	5.0	8	5.5	N.C.
Salyer	174, 175	15	5.4	12	5.0	N.C.
Rogers Cr.	181	11	5.6	3	5.7	N.C.
Alderpoint	187	9	5.6	21	5.2	N.C.
Davis Cr.	189	6	5.7	5	5.0	N.C.
Hilt	192	(2)	–	8	4.8	?
Hyampom	200	5	4.6	6	4.3	N.C.
Squaw Cr.[1]	205–207	15	3.8	7	2.1	—
Nosoni Cr.[1]	213	19	4.2	4	2.8	—
Castle Crags[1]	218	(1)	–	9	2.3	?
Brookdale[2]	255	35	4.9	19	1.4	—
Summit Dr.[2]	257	6	4.3	5	0.6	—
Saratoga[2]	259	22	4.5	13	0.1	—
Uvas Creek[2]	266	18	4.7	7	0.7	—

[1] *A. f. flavipunctatus* from Shasta Co.
[2] *A. f. niger.*

TABLE 7.—Ontogenetic changes in melanism of chin region in *A. flavipunctatus* (values in coded units, higher numbers indicate less melanism; column A = projected mean value of chin melanism index (CMD) for large juveniles (SL = 40 mm); column B = projected mean value of chin melanism index for adults (SL = 70 mm); column C = direction of ontogenetic change; N.C. = no change)

Locality	Code	A	B	C
Salmon Point	001	4.1	3.9	N.C.
McGuire Hill	007	4.2	4.2	N.C.
Fort Bragg	008	4.0	3.8	N.C.
Cloverdale	009	5.2	3.7	—
Navarro	010	4.4	3.7	—
Skaggs Springs	055	4.6	3.9	—
Stewart's Point Rd.	062	4.4	4.0	N.C.
Sonoma Queen Mine	063	–	4.1	?
Cazadero	064	4.8	3.8	—
Signal Ridge	067	4.0	4.1	N.C.
Monte Rio	070	4.2	3.6	—
Potter Valley	111	5.0	4.9	N.C.
Aetna Springs	114, 115	4.0	4.4	N.C.
Berryessa	116	4.8	4.3	—
Geyserville	121	4.3	4.6	N.C.
Middletown	123	–	4.1	?
Shale Springs Canyon	125	–	4.4	?
Longvale	155, 156, 184	–	4.7	?
Leggett	158	4.9	4.5	N.C.
Usal	161	–	4.5	?
Ettersberg	165, 188	–	4.8	?
Grizzly Cr.	167	5.2	5.4	N.C.
Weitchpec	170	5.8	4.1	—
Salyer	174, 175	5.3	4.9	N.C.
Rogers Cr.	181	5.9	–	?
Alderpoint	187	5.7	5.0	—
Davis Cr.	189	5.7	4.8	—
Hilt	192	–	5.8	?
Hyampom[1]	200	5.2	4.5	—
Squaw Cr.[1]	205–207	3.9	4.0	N.C.
Nosoni Cr.[1]	213	4.2	4.0	N.C.
Castle Crags[1]	218	–	4.0	?
Brookdale[2]	255	4.0	3.3	—
Summit Dr.[2]	257	4.0	4.0	N.C.
Saratoga[2]	259	4.0	3.4	—
Uvas Cr.[2]	266	4.2	3.6	—

[1] *A. f. flavipunctatus* from Shasta Co.
[2] *A. f. niger.*

TABLE 8.—Association of development of lateral frosting (LFR) with development of brassy dorsal pigmentation (DBN) in 37 populations of *A. flavipunctatus* (data pertain to adults 60–79 mm SL)

LFR	DBN			Totals
	Heavy (≥ 3.0)	Moderate (1.0–2.9)	Light (0–0.9)	
Heavy	13	0	0	13
Absent or trace	1	7	16	24
Totals	14	7	16	37

$$x^2 = 32.9 \qquad df = 2 \qquad (p < 0.001)$$

$$\text{Coefficient of contingency} = \frac{x^2}{N + x^2} = 0.686$$

TABLE 9.—Comparison of mean standard length (SL) of males and females in 12 large samples of adults (only individuals with SL > 55 mm are considered; larger sex is underlined; N.S. = not significant)

Locality	Code	N		SL		Significance	SL (both sexes)
		Male	Female	Male	Female		
Salmon Point	001	21	10	65.0	68.1	N.S.	66.0
McGuire Hill	007	25	25	65.4	69.0	*	67.9
Navarro	008	19	21	69.3	66.7	N.S.	67.9
Skaggs Springs	005	31	23	64.4	63.7	N.S.	64.1
Guereneville	063, 070	12	19	68.5	68.1	N.S.	68.2
Potter Valley	111	23	16	64.1	63.6	N.S.	63.9
Geyserville	121	17	13	71.1	64.5	*	68.3
Leggett	158	9	10	74.7	69.2	N.S.	71.8
Usal	161	14	11	70.9	68.8	N.S.	70.0
Alderpoint	187	14	18	72.8	70.9	N.S.	71.8
Santa Clara Co.	259, 266	13	16	69.2	68.6	N.S.	68.9
Santa Cruz Co.	255, 257	15	17	65.7	60.8	N.S.	63.2
		204	193				

* Difference significant at p < 0.05, using Wilcoxon two-sample test.

TABLE 10.—Numbers of trunk vertebrae in 41 samples of *A. flavipunctatus* based on counts of costal grooves supplemented by x-radiograms and examination of cleared and stained preparations (fractional counts may be result of preservation artifacts, but often reflect fact that some individuals have different numbers of ribs on right and left sides; individuals showing asymmetrical costal groove counts not included in computation of sample means ($\bar{x}$) or percent of individuals falling into modal category)

Locality code	N	15	15.5	16	16.5	17	17.5	18	$\bar{x}$	Percent in modal category
001	106			81	3	22			16.2	79.4
007	58			38	1	19			16.3	66.7
008	15			12		3			16.2	80.0
009	17			16		1			16.0	94.1
010	47			30	3	14			16.3	68.2
055	55			53		2			16.0	96.4
062	31			29		2			16.1	93.5
063	25			20		5			16.2	80.0
064	20			16		4			16.2	80.0
067	21	1		19		1			16.0	90.5
070	22			16		6			16.3	72.7
111	46			17		29			16.6	63.0
114, 115	26			25		1			16.0	96.2
116	35			34		1			16.0	97.1
121	47			23	5	19			16.4	47.8
123	9			1	1	7			16.9	87.5
125	10			10					16.0	100.0
130	25			2		23			16.9	92.0
131	40	2		38					16.0	95.0
145	33			2?		30		1?	17.0	100.0
155, 156, 184	12			10		2			16.2	83.3
158	29			3		26			16.9	89.7
161	24			31	1	20			16.9	87.0
165, 188	14	2?		12					16.0	100.0
166	11			7		4			16.4	63.6
167	20			4		16			16.8	80.0
170	29					27		2	17.1	93.1
174, 175	35			7		27		1	16.8	77.1
181	25			1		24			17.0	96.0
182, 140, 141	20					20			17.0	100.0
187	30					24		6	17.2	80.0
189	11			6		5			16.4	54.5
192	17			1		16			16.9	94.1
200	17					16		1	17.0	94.1
205–207[a]	17			14	1	2			16.2	87.5
213[a]	41			38		3			16.0	92.7
218[a]	12			10	1	1			16.1	90.9
255[b]	77			3		72	2		17.0	96.0
257[b]	11					8	1	2	17.2	80.0
259[b]	39			2		36		1	17.0	92.3
266[b]	34					33		1	17.0	97.1
N = 1212										

[a] *A. f. flavipunctatus* from Shasta Co.

[b] *A. f. niger.*

TABLE 11.—Summary of Multiple Regression–Multiple Correlation Analysis in which the effect of five potential predictor variables (latitude, distance inland, elevation, mean annual precipitation, and mean January temperature) is assessed with regard to the following response variables: mean diameter of white dorsal iridophores (DWS), mean abundance of white dorsal iridophores (DWN), mean abundance of brassy dorsal iridophores (DBN), mean development of melanin network in the chin region (CMD), mean relative length of forelimb (FL), mean relative length of tail (T), mean relative head width (HW), mean standard length (SL), mean number of trunk vertebrae (MV); R is the multiple correlation coefficient; N.S. = not significant

Response variable	Significantly correlated predictor variables (in order of importance)	R
DWS	distance inland (+) latitude (−) mean Jan temp. (+)[a]	.926[d]
DWN	latitude (+)[a]	.294 N.S.
DBN	latitude (+) distance inland (−)	.914[d]
CMD	latitude (+) distance inland (+)	.706[d]
FL	latitude (+) distance inland (+)	.689[d]
TL	elevation (+)	.506[c]
HDW	distance inland (+) mean Jan temp. (+)	.477[b]
SL	latitude (+) mean Jan temp. (+)[a]	.593[c]
MVN	latitude (+) distance inland (+)	.645[c]

[a] Significance level = $P < .1$.
[b] Significance level = .05.
[c] Significance level = .01.
[d] Significance level = .001.

TABLE 12.—Standardized distance matrix used to construct Prim Network for adult males (see text for explanation)

Localities	001	007	008	009	010	055	062	063	064	067	070	125	111	114, 115	116	121	158	161	165, 188	167	170	174, 175	187	192	200	213	218	255	259	266
001																														
007	.66																													
008	.94	.52																												
009	1.03	.64	.89																											
010	.83	.25	.54	.72																										
055	.59	.53	.78	.55	.56																									
062	.66	.52	.89	.62	.64	.37																								
063	.63	.51	.92	.55	.63	.34	.33																							
064	.55	.67	.96	.65	.72	.34	.55	.42																						
067	.70	.67	.72	.80	.70	.41	.53	.49	.60																					
070	.76	.71	.58	1.01	.75	.66	.66	.53	.77	.52																				
125	1.46	1.35	1.69	.82	1.45	1.54	1.22	.81	1.18	1.40	1.81																			
111	.93	.68	1.12	.62	.81	.70	.64	.71	.80	.92	1.62	1.07																		
114, 115	1.18	.65	.95	.50	.70	.66	.80	.76	.99	.97	1.22	.95	.55																	
116	.84	.82	1.12	.62	.95	.65	.69	.75	.63	.82	1.13	.72	.67	.81																
121	1.16	.84	1.10	.66	.93	.74	.93	1.06	.93	1.06	.99	1.16	.52	.74	.77															
158	1.01	.88	1.14	1.27	.86	1.17	1.17	1.13	1.33	1.15	1.44	2.50	1.18	1.20	1.44	1.56														
161	.91	.89	.92	1.40	1.00	1.21	1.18	1.18	1.40	1.09	1.14	2.12	1.18	1.42	1.46	1.45	.36													
165, 188	1.08	1.19	1.26	1.18	1.47	1.32	1.38	1.08	1.32	1.27	1.60	1.53	1.28	1.40	1.40	1.72	.96	1.00												
167	.98	.92	1.06	1.30	1.08	1.20	1.12	1.28	1.33	1.10	1.31	1.87	.94	1.31	1.32	1.31	1.27	.57	.85											
170	1.01	1.22	1.58	1.29	1.39	1.33	1.43	1.20	1.27	1.60	1.76	1.17	1.40	1.58	1.24	1.77	.99	1.08	1.30	1.04										
174, 175	.92	1.26	1.61	1.43	1.35	1.35	1.30	1.25	1.19	1.49	1.62	1.61	1.11	1.58	1.18	1.48	1.01	1.05	.94	.73	.72									
187	.97	1.07	1.33	1.33	1.32	1.23	1.20	1.09	1.41	1.31	1.48	1.90	1.10	1.42	1.46	1.50	.70	.75	.70	.58	.91	.61								
192	1.24	1.94	2.04	1.76	1.94	1.70	1.56	1.22	1.32	1.88	2.04	1.96	1.42	1.92	2.16	1.71	1.50	1.29	1.34	.97	1.16	.58	.83							
200	1.14	1.32	1.58	1.35	1.52	1.36	1.37	1.48	1.47	1.36	1.73	1.38	1.33	1.45	1.67	.94	1.11	1.16	1.34	1.04	.76	.74	.98	1.16						
213	.80	.92	.80	1.28	.99	.85	1.08	1.04	.87	.83	.82	1.72	1.36	1.29	1.12	1.32	1.15	1.26	1.67	1.54	1.61	1.63	1.58	1.94	1.63					
218	1.10	1.12	.80	1.47	1.09	1.19	1.41	1.35	1.23	.96	.88	2.07	1.65	1.58	1.40	1.41	1.52	1.47	2.12	1.79	2.09	2.04	2.00	2.35	1.93	.55				
255	.97	.48	.68	1.08	.45	.84	.89	1.06	1.06	1.08	.92	1.74	.95	.96	1.18	1.14	.81	.96	1.60	1.26	1.32	1.48	1.28	1.88	1.54	1.08	1.28			
259	1.30	.80	.82	1.18	.57	1.10	1.17	1.22	1.22	1.19	1.17	1.84	1.28	.95	1.32	1.21	.97	1.20	1.98	1.46	1.69	1.84	1.44	2.16	1.76	1.27	1.24	.40		
266	1.06	.64	.83	1.28	.50	1.05	.95	1.05	1.03	1.20	1.10	1.74	.99	1.00	1.20	1.15	.82	1.04	1.68	1.28	1.42	1.48	1.38	1.75	1.55	1.28	1.31	1.28	.32	—

TABLE 13.—Comparison of typical juvenile and adult conditions in major features of the color pattern of *A. flavipunctatus*

Character	Typical juvenile condition	Typical adult condition
Melanophore network	network fine, some gaps ventrally and at limb bases	network heavy, few or no gaps ventrally and at limb bases
Size of white iridophores	always small (0.2 mm)	generally larger
Abundance of white iridophores	always abundant	generally less abundant or absent
Density of dorsal brassy iridophores	always conspicuously present and forming network	generally absent (except in far north)

TABLE 14.—Paedomorphism Index for each of six characters in 30 populations of *A. flavipunctatus* (the sum of the individual indices ($\bar{x}_i$) divided by the number of characters (six) = overall Paedomorphism Index (PI); abbreviations as in Table 2; localities coded as in Table 6)

Locality	Characters						x_i	PI
	HDL	FOREL	DBN	DWS	DWN	CHNW		
001	.454	.462	.561	.728	.500	.240	2.945	.491
007	.318	.308	.246	.840	.192	.360	2.264	.377
008	.227	.038	.491	.840	.128	.200	1.924	.321
009	.682	.154	.000	.656	.179	.360	2.031	.338
010	.318	.231	.070	.840	.179	.160	1.798	.300
055	.500	.346	.018	.742	.538	.240	2.384	.397
062	.409	.346	.018	.655	.462	.280	2.170	.362
063	.409	.346	.000	.704	.410	.320	2.189	.365
064	.636	.423	.035	.704	.449	.200	2.447	.408
067	.454	.308	.053	.692	.705	.320	2.032	.422
070	.227	.154	.193	.766	.756	.120	2.216	.369
111	.454	.346	.053	.359	.115	.740	1.967	.328
114, 115	.409	.231	.000	.222	.064	.440	1.366	.223
116	.636	.615	.053	.457	.282	.400	2.443	.407
121	.318	.038	.000	.321	.231	.520	1.428	.238
125	1.000	.769	.000	.000	.205	.320	2.294	.382
158	.591	.346	.965	.951	.038	.480	3.371	.562
161	.182	.385	.982	1.000	.000	.480	3.029	.505
165, 188	.773	.500	.912	.840	.077	.600	3.702	.617
167	.500	.500	.912	.827	.141	.840	3.720	.620
170	.909	.808	.965	.815	.231	.320	4.048	.675
174, 175	.682	.769	.877	.754	.333	.640	4.055	.676
187	.545	.346	.912	.852	.244	.680	3.579	.596
192	.545	.769	.842	.617	.346	1.000	4.119	.686
200	.773	1.000	.754	.668	.384	.480	4.059	.676
213[a]	.277	.154	.491	.825	.769	.280	2.736	.456
218[a]	.000	.000	.404	.815	1.000	.280	2.499	.416
255[b]	.273	.308	.246	.963	.038	.000	1.866	.311
259[b]	.136	.231	.018	1.000	.000	.040	1.425	.238
266[b]	.273	.154	.123	.975	.000	.120	1.645	.274

[a] *A. f. flavipunctatus* from Shasta Co.
[b] *A. f. niger.*

Literature Cited

Atchley, W. R.
  1978. Ratios, Regression Intercepts, and the Scaling of Data. *Systematic Zoology*, 27:78-83.
Atchley, W. R., and D. Anderson
  1978. Ratios and the Statistical Analysis of Biological Data. *Systematic Zoology*, 27:71-78.
Atchley, W. R., C. T. Gaskins, and D. Anderson
  1976. Statistical Properties of Ratios, I: Empirical Results. *Systematic Zoology*, 25:137-148.
Axelrod, D. I.
  1948. Climate and Evolution in Western North America during Middle Pliocene Time. *Evolution*, 2:127-144.
  1950. Evolution of Desert Vegetation in Western North America. *Carnegie Institute of Washington Publication*, 590:215-306.
  1959. Geological History. *In* P. A. Munz, editor, *A California Flora*, pages 5-9. Berkeley and Los Angeles: University of California Press.
  1976. History of the Coniferous Forests, California and Nevada. *University of California Publications, Botany*, 20:1-62.
Axelrod, D. I., and H. P. Bailey
  1968. Cretaceous Dinosaur Extinction. *Evolution*, 22:595-611.
Bagnara, J. T.
  1966. Cytology and Cytophysiology of Non-Melanophore Pigment Cells. *International Review of Cytology*, 20:173-205.
Barlow, G. W.
  1961. Causes and Significance of Morphological Variation in Fishes. *Systematic Zoology*, 10:105-117.
Blanchard, F. N.
  1936. The Number of Eggs Produced and Laid by the Four-toed Salamander, *Hemidactylium scutatum* (Schlegel) in Southern Michigan. *Papers of the Michigan Academy of Sciences, Arts, and Letters*, 21:567-573.
Bonner, J. T.
  1965. *Size and Cycle, an Essay on the Structure of Biology.* Princeton: Princeton University Press.
Brame, A. H.
  1970. A New Species of *Batrachoseps* (Slender Salamander) from the Desert of Southern California. *Los Angeles County Museum Contributions in Science*, 200:1-11.

Brame, A. H., and K. F. Murray
  1968. Three New Slender Salamanders (*Batrachoseps*) with a Discussion of Relationships and Speciation within the Genus. *Bulletin of the Los Angeles County Museum*, 4:1-35.
Brodie, E. D., Jr.
  1978. Biting and Vocalization as Antipredator Mechanisms in Terrestrial Salamanders. *Copeia*, 1978:122-129.
Brown, A. G.
  1972. Responses to Problems of Water and Electrolyte Balance by Salamanders (Genus *Aneides*) from Different Habitats. Unpublished Ph.D. dissertation, University of California, Berkeley.
Brown, C. W.
  1970. Hybridization among the Subspecies of the Plethodontid Salamander *Ensatina eschscholtzii*. Unpublished Ph.D. dissertation, University of California, Berkeley.
Bruce, R. C.
  1972. Variation in the Life Cycle of the Salamander *Gyrinophilus porphyriticus*. *Herpetologica*, 28:230-245.
California State Water Resources Board
  1951. Water Resources of California. *California State Water Resources Board Bulletin*, No. 1.
Case, T. J.
  1976. Body Size Differences between Populations of the Chuckwalla, *Sauromalus obesus*. *Ecology*, 57:313-323.
de Beer, G.
  1958. *Embryos and Ancestors.* Third edition. Oxford: Clarendon Press.
Draper, N. R., and H. Smith.
  1966. *Applied Regression Analysis.* New York: John Wiley and Sons, Inc.
Dumas, P. C.
  1956. The Ecological Relations of Sympatry in *Plethodon dunni* and *Plethodon vehiculum*. *Ecology*, 37:484-495.
Dunham, A. E., D. W. Tinkle, and J. W. Gibbons
  1978. Body Size in Island Lizards: A Cautionary Tale. *Ecology*, 59:1230-1238.
Edwards, A. W. F., and L. L. Cavalli-Sforza
  1963. Reconstruction of Evolutionary Trees. *In* Phenetic and Phylogenetic Classification. *Systematics Association Publication*, 6:67-76.
Eldredge, N.
  1971. The Allopatric Model and Phylogeny in Paleozoic Invertebrates. *Evolution*, 25:156-167.

Eldredge, N., and S. J. Gould
1972. Punctuated Equilbria: An Alternative to Phyletic Gradualism. *In* T. J. M. Schopf, editor, *Models in Paleobiology*, pages 82–115. San Francisco: Freeman, Cooper, and Company.

Farris, J. S.
1970. Methods for Computing Wagner Trees. *Systematic Zoology*, 19:83–92.

Fowler, J. A.
1970. Control of Vertebral Number in Teleosts: An Embryological Problem. *Quarterly Review of Biology*, 45:148–167.

Fox, W.
1948. Effect of Temperature on Development of Scutellation in the Garter Snake, *Thamnophis elegans atratus*. *Copeia*, 1948:252–262.

Fox, W., C. Gordan, and M. H. Fox.
1961. Morphological Effects of Low Temperatures during the Embryonic Development of the Garter Snake. *Zoologica*, 46:57–71.

Francis, E. T. B.
1934. *The Anatomy of the Salamander.* Oxford: Oxford University Press.

Fraser, D. H.
1976. Coexistence of Salamanders in the Genus *Plethodon:* A Variation of the Santa Rosalia Theme. *Ecology*, 57:238–251.

Geiger, R.
1966. *The Climate near the Ground.* Cambridge: Harvard University Press.

Gould, S. J.
1977. *Ontogeny and Phylogeny.* Cambridge: Belknap Press.

Gould, S. J., and N. Eldredge
1977. Punctuated Equilibria: The Tempo and Mode of Evolution Reconsidered. *Paleobiology*, 3:115–151.

Grant, P. R.
1965. A Systematic Study of the Terrestrial Birds of the Tres Marias Island, Mexico. *Postilla*, 90:1–106.
1966. Further Information on the Relative Length of the Tarsus in Land Birds. *Postilla*, 98:1–13.

Hairston, N. G.
1949. The Local Distribution and Ecology of the Plethodontid Salamanders of the Southern Appalachians. *Ecological Monographs*, 19:47–73.

Hespenheide, H. A.
1971. Food Preference and the Extent of Overlap in Some Insectivorous Birds, with Special Reference to the Tyrannidae. *Ibis*, 113:59–72.
1973. Ecological Inferences from Morphological Data. *Annual Review of Ecology and Systematics*, 4:213–229.
1975. Prey Characteristics and Predator Niche Width. *In* M. L. Cody and J. M. Diamond, editors, *Ecology and Evolution of Communities*. Cambridge: Belknap Press.

Highton, R.
1957. Correlating Costal Grooves with Trunk Vertebrae in Salamanders. *Copeia*, 1957:107–109.
1960. Heritability of Geographic Variation in Trunk Segmentation in the Red-backed Samalander, *Plethodon cinereus. Evolution*, 14:351–360.
1962a. Revision of North American Salamanders of the Genus *Plethodon. Bulletin of the Florida State Museum of Biological Sciences*, 6:235–367.
1962b. Geographic Variation in the Life History of the Slimy Salamander. *Copeia*, 1962:597–613.
1972. Distributional Interactions among Eastern North American Salamanders of the Genus *Plethodon. In* P. C. Holt, editor, The Distributional History of the Biota of the Southern Appalachians, Part III: Vertebrates. *Research Division Monograph* (Virginia Polytechnic Institute and State University), 4:139–188.
1979. A New Cryptic Species of Salamander of the Genus *Plethodon* from the Southeastern United States (Amphibia: Plethodontidae). *Brimleyana*, 1:31–36.

Highton, R., and T. P. Webster
1976. Geographic Protein Variation and Divergence in Populations of the Salamander *Plethodon cinereus. Evolution*, 30:33–45.

Houck, L. D.
1977. Reproductive Biology of a Neotropical Salamander, *Bolitoglossa rostrata. Copeia*, 1977:70–83.

Howard, A. D.
1972. *Evolution of the Landscape of the San Francisco Bay Region.* Berkeley and Los Angeles: University of California Press.

Hutchinson, G. E.
1959. Homage to Santa Rosalia, or Why Are There So Many Different Kinds of Animals? *American Naturalist*, 93:145–159.

Irwin, W. P.
1960. Geological Reconnaissance of the Northern Coast Ranges and Klamath Mountains, California, with a Summary of the Mineral Resources. *California Division of Mines Bulletin*, 179:1–80.

Jaeger, R. G.
1970. Potential Extinction through Competition between Two Species of Terrestrial Salamanders. *Evolution*, 24:632–642.
1971. Moisture as a Factor Influencing the Distributions of Two Terrestrial Salamanders. *Oecologia* (Berlin), 6:191–207.
1972. Food as a Limited Resource in Competition between Two Species of Terrestrial Salamanders. *Ecology*, 53:535–546.
1974. Competitive Exclusion: Comments on Survival and Extinction of Species. *Bioscience*, 24:33–39.

Karr, J. R., and F. C. James
    1975. Ecomorphological Configurations and Convergent Evolution. *In* M. L. Cody and J. M. Diamond, editors, *Ecology and Evolution of Communities.* Cambridge: Belknap Press.
Klopfer, P. H.
    1962. *Behavioral Aspects of Ecology.* Englewood Cliffs: Prentice-Hall.
Klopfer, P. H., and R. H. MacArthur
    1961. On the Causes of Tropical Species Diversity and Niche Overlap. *American Naturalist,* 95:223–226.
Lack, D.
    1946. Competition for Food by Birds of Prey. *Journal of Animal Ecology,* 15:123–129.
    1947. *Darwin's Finches.* Cambridge: Cambridge University Press.
    1971. *Ecological Isolation in Birds.* Cambridge: Harvard University Press.
Larson, A.
    1980. Paedomorphosis in Relation to Rates of Morphological and Molecular Evolution in the Salamander *Aneides flavipunctatus* (Amphibia, Plethodontidae). *Evolution,* 34:1–17.
Larson, A., and R. Highton
    1978. Geographic Protein Variation and Divergence in the Salamanders of the *Plethodon welleri* Group (Amphibia, Plethodontidae). *Systematic Zoology,* 27: 431–438.
Levins, R.
    1968. *Evolution in Changing Environments.* Princeton: Princeton University Press.
Lindsey, C. C.
    1966a. Body Sizes of Poikilotherm Vertebrates at Different Latitudes. *Evolution,* 20:456–465.
    1966b. Temperature-controlled Meristic Variation in the Salamander *Ambystoma gracile. Nature,* 209:1152–1153.
Lowe, C. H., Jr.
    1950. Speciation and Ecology in Salamanders of the Genus *Aneides.* Ph.D. dissertation, Los Angeles: University of California.
Lynch, J. F.
    1973. The Feeding Ecology of Some Sympatric Western Plethodontids: Implications for Competitive Interactions. *HISS News Journal,* 1:60–61.
    1974a. Ontogenetic and Geographic Varation in the Morphology and Ecology of the Black Salamander *(Aneides flavipunctatus).* Ph.D. dissertation, Berkeley: University of California.
    1974b. *Aneides flavipunctatus. Catalogue of American Amphibians and Reptiles,* 1974:158.1–158.2.
MacArthur, R. H.
    1972. *Geographical Ecology: Patterns in the Distribution of Species.* New York: Harper and Row.

MacDonald, G. A.
    1966. Geology of the Cascade Range and Modoc Plateau. *In* E. H. Bailey, editor, Geology of Northern California. *California Division of Mines and Geology Bulletin,* 190:63–96.
Maiorana, V. C.
    1977. Observations of Salamanders (Amphibia, Urodela, Plethodontidae) Dying in the Field. *Journal of Herpetology,* 11:1–5.
Marlow, R. W., J. M. Brode, and D. B. Wake
    1979. A New Salamander, Genus *Batrachoseps,* from the Inyo Mountains of California, with a Discussion of Relationships in the Genus. *Natural History Museum of Los Angeles County Contributions in Science,* 308:1–17.
Mayr, E.
    1963. *Animals Species and Evolution.* Cambridge: Belknap Press.
McKenzie, D. S., and R. M. Storm
    1971. Ontogenetic Color Patterns of the Clouded Salamander, *Aneides ferreus* (Cope). *Herpetologica,* 27: 142–147.
Merchant, H.
    1970. Estimated Energy Budget of the Red-backed Salamander, *Plethodon cinereus.* Ph.D. dissertation, New Jersey: Rutgers University.
Metter, D. E.
    1967. Variation in the Ribbed Frog *Ascaphus truei,* Stejneger. *Copeia,* 1967:634–649.
Myers, G. S., and T. P. Maslin
    1948. The California Plethodont Salamander *Aneides flavipunctatus* (Strauch), with Description of a New Subspecies and Notes on Other Western *Aneides. Proceedings of the Biological Society of Washington,* 61: 127–138.
Oakeshott, G. B.
    1971. *California's Changing Landscapes.* New York: McGraw Hill.
Osgood, D. W.
    1978. Effects of Temperature on the Development of Meristic Characters in *Natrix fasciata. Copeia,* 1978: 33–47.
Peabody, R. B., and E. D. Brodie
    1975. Effect of Temperature, Salinity, and Photoperiod on the Number of Trunk Vertebrae in *Ambystoma maculatum. Copeia,* 1975:741–746.
Pianka, E. R.
    1969. Sympatry of Desert Lizards *(Ctenotus)* in Western Australia. *Ecology,* 50:1012–1030.
Pianka, E. R., and W. S. Parker
    1972. Ecology of the Iguanid Lizard *Callisaurus draconoides. Copeia,* 1972:493–508.
Prim, R. C.
    1957. Shortest Connection Networks and Some Gener-

alizations. *Bell System Technical Journal*, 36:1389–1401.

Ray, C.
  1960. The Application of Bergmann's and Allen's Rules of the Poikilotherms. *Journal of Morphology*, 106:85–108.

Rosenthal, G. S.
  1957. The Role of Moisture and Temperature in the Local Distribution of the Plethodontid Salamander *Aneides lugubris*. *University of California Publications in Zoology*, 54:371–420.

Roughgarden, J.
  1972. Evolution of Niche Width. *American Naturalist*, 106:683–718.

Salthe, S. N.
  1969. Reproductive Modes and the Number of Sizes of Ova in the Urodeles. *American Midland Naturalist*, 81:467–490.

Schoener, T. W.
  1965. The Evolution of Bill Size Differences among Sympatric Congeneric Species of Birds. *Evolution*, 19:189–213.
  1966. The Ecological Significance of Dimorphism in Size in the Lizard *Anolis conspersus*. *Science*, 155:474–476.
  1968. The *Anolis* Lizards of Bimini: Resource Partitioning in a Complex Fauna. *Ecology*, 49:704–726.
  1969a. Models of Optimal Size for Solitary Predators. *American Naturalist*, 103:277–313.
  1969b. Optimal Size and Specialization in Constant and Fluctuating Environments. *Brookhaven Symposium in Biology*, 22:103–114.
  1969c. Size Patterns in West Indian *Anolis* Lizards, I: Size and Species Diversity. *Systematic Zoology*, 18:386–401.

Simpson, G. G., A. Roe, and R. C. Lewontin
  1960. *Quantitative Zoology*. Revised edition. New York: Harcourt, Brace, and Company.

Sokal, R. R., and F. J. Rohlf
  1969. *Biometry*. San Francisco: W. H. Freeman and Company.

Soulé, M.
  1972. On the Methodology of Geographic Variation Analysis. *Systematic Zoology*, 21:443–445.

Stebbins, R. C.
  1949. Speciation in Salamanders of the Genus *Ensatina*. *University of California Publications in Zoology*, 48:377–526.
  1951. *Amphibians of Western North America*. Berkeley and Los Angeles: University of California Press.
  1954. *Amphibians and Reptiles of Western North America*. New York: McGraw-Hill Book Company, Inc.
  1966. *A Field Guide to Western Reptiles and Amphibians*. Boston: Houghton Mifflin.

Tåning, A. V.
  1952. Experimental Study of Meristic Characters in Fishes. *Biology Review of the Cambridge Philosophical Society*, 27:169–193.

Tilley, S. G.
  1968. Size-Fecundity Relationships and Their Evolutionary Implications in Five Desmognathine Salamanders. *Evolution*, 22:806–816.

United States Department of Agriculture
  1941. Climate and Man. In *Yearbook of Agriculture*. Washington: U.S. Government Printing Office.

Van Denburgh, J.
  1895. Notes on the Habits and Distribution of *Autodax iecanus*. *Proceedings of the California Academy of Science*, 5:776–778.

Wake, D. B.
  1966. Comparative Osteology and Evolution of the Lungless Salamanders, Family Plethodontidae. *Memoirs of the Southern California Academy of Science*, 4:1–111.

Wake, D. B., and J. F. Lynch
  1976. The Distribution, Ecology, and Evolutionary History of Plethodontid Salamanders in Tropical America. *Natural History Museum of Los Angeles County Science Bulletin*, 25:1–65.

Williams, E. E.
  1972. The Origin of Faunas: Evolution of Lizard Congeners in a Complex Island Fauna: A Trial Analysis. *In* T. Dobzhansky, M. K. Hecht, and W. C. Steere, editors, *Evolutionary Biology*, 6:47–89.

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