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garter snake *Thamnophis atratus*, with a synopsis of the *Thamnophis*
couchii complex**

Boundy, John Jeffrey, M.A.

San Jose State University, 1990

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BIOGEOGRAPHY AND VARIATION IN SOUTHERN POPULATIONS OF THE GARTER SNAKE
***THAMNOPHIS ATRATUS*, WITH A SYNOPSIS OF THE *T. COUCHII* COMPLEX**

A Thesis

Presented to

The Faculty of the Department of Biological Sciences

San Jose State University

In Partial Fulfillment

of the Requirements for the Degree

Master of Arts

By

Jeffrey Boundy

May, 1990

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ABSTRACT

BIOGEOGRAPHY AND VARIATION IN SOUTHERN POPULATIONS OF THE GARTER SNAKE *THAMNOPHIS ATRATUS*, WITH A SYNOPSIS OF THE *T. COUCHII* COMPLEX

by Jeffrey Boundy

Variation in southern populations of the garter snake, *Thamnophis atratus*, is examined. Eighteen morphological characters are compared among eight geographically separate populations of California. Males and females are significantly different in half of the characters and are compared separately. Variation in head morphology, scalation, and color pattern suggest the presence of three subspecies. A new subspecies, *T. a. zaxanthus*, is described for the Diablo and Santa Lucia Range populations. *T. a. atratus* is restricted to the Santa Cruz Mountains, and *T. a. aquaticus* to the North Bay region. A biogeographical model is proposed for the derivation of the three subspecies. Ecological factors and geological events are believed responsible for subspecific differentiation. Evidence is presented for retention of *T. atratus* as a species separate from *T. couchii*, and for recognition of subspecies. A summary of characteristics and distribution of the members of the *T. couchii* complex is provided.

ACKNOWLEDGEMENTS

The systematic problems discussed here were first noticed by me in garter snakes gathered afield in my youth. My parents are outdoor enthusiasts, and happily took my brothers and me to the hills around the Santa Clara Valley to hunt snakes. They encouraged me to pursue my interest in snakes, and to continue my formal education.

Unfortunately, my undergraduate grades prohibited furtherance of my scholastic career. At this point Dr. Tom Balgooyen "strong-armed" my way into the Graduate Program at San Jose State University. To increase my knowledge of these snakes, the doors were opened at the Museum of Vertebrate Zoology at Berkeley, where Dr. Dave Wake, Dr. Harry Greene, Dr. Robert Stebbins, Dr. Dave Good, Bob Macey, and Dr. Bill Rainey extended courtesies and advice. This was also the case at the California Academy of Sciences, where I was assisted by Dr. Alan Leviton, Dr. Bob Drewes, Jens Vindum, and Jim O'Brian, and, at San Luis Obispo, where Dr. Fred Andoli allowed me to borrow the collection's garter snakes.

The snakes used in this thesis were the product of hours of field work and forced marches encumbered upon Owen, Steve, Tony, Darrel, Tom, Blair, Bill, Chuck, Billy, Android, and my brothers, all of them extraordinary field collectors.

"Unexpected" deadlines were a nuisance to all, and Dr. Hassur, Dr. Balgooyen, Dr. Kenk, and Dr. Shellhammer responded to all to see my Masters Program to completion.

Anyone who has dealt with computers and biostatistics will know my appreciation for my "backstage" statistics advisors, Dr. Charles Bell and Dr. Bill Bros.

Thamnophis atratus zaxanthus, holotype

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INTRODUCTION

Garter snakes, *Thamnophis*, are a Nearctic genus of 28 species occurring from central Canada to Costa Rica. They are conspicuous by their abundance and variety, over 70 subspecies having been described. The entire genus was last reviewed by Ruthven (1908). Although he found the relationships of some species unclear, others were assigned to definite species groups. One of these, the *T. ordinoides* group, exhibits broad variation in morphology and ecology. It contains the largest, most aquatic species in the genus, *T. gigas*, as well as one of the smallest terrestrial species, *T. ordinoides*. As late as 1940 these two and intermediate forms were considered conspecific (Fitch, 1940). At that time, *T. ordinoides* contained nine subspecies, ranging over most of western North America. Sympatry of two or more of these subspecies, convergence of characters, and intrasubspecific variation have made systematic analysis of the group vexing.

The *ordinoides* group has a complex taxonomic history. Garter snakes were first collected in the western United States for the Smithsonian Institution during the 1840's. From these, Baird and Girard (1852, 1853) described as new *Tropidonotus ordinoides*, *Eutainia* [= *Thamnophis*] *leptocephala*, *E. elegans*, and *Eutaenia vagrans*, and, Hallowell (1853) named *Tropidonotus trivittatus*. From subsequent collections, Kennicott (1859, 1860) named *Eutaenia couchii*, *Eutainia cooperi*, *E. atrata*, and *E. Hammondii*. In 1883, Yarrow described *Eutaenia Henshawi* and *E. vagrans plutonia*. Cope (1883, 1891) described *Eutaenia biscutata*, *E. elegans brunnea*, *E. e. lineolata*, and *E. infernalis vidua*. In 1891, he reviewed United States *Thamnophis* and synonymised *cooperi* and *atrata* with *E. ordinoides leptocephala*. All others were considered subspecies of *Eutaenia elegans*: *Henshawi* was synonymised with *plutonia*, *Hammondii* with *couchi*, and *trivittata* with the subspecies *elegans*. The Chicago Field Museum made collections in the Pacific Northwest and in 1899, Meek named *Thamnophis rubristriata* and *T. leptocephala olympia*. That year, Mocquard named *Tropidonotus Digueti* from a collection of Baja California animals received by the Paris Museum. Brown (1903) reviewed

Pacific Coast *Thamnophis* and showed that Cope's *vidua* was based on the cotypes of Kennicott's *atrata*.

The variation exhibited by western *Thamnophis* had prompted the naming of each variety. As more specimens reached collections, it was found that there was tremendous overlap of distributions and many intermediate varieties, (VanDenburgh 1897, Brown 1903, Thompson 1915). It became clear that the variations did not always reflect true relationships and the naming of new forms ceased for nearly 30 years.

Ruthven (1908) reviewed the genus and concluded that the 18 named varieties of the *T. ordinoides* group could be allocated to three polymorphic, yet monotypic, species: *T. ordinoides* of the Pacific Northwest, *T. elegans* of California and the Intermountain West, and *T. hammondi* of Southern California.

VanDenburgh and Slevin were the first reviewers with field experience with western garter snakes and had acquired a large collection of them at the California Academy of Sciences. From these they (1918) revised the *ordinoides* group because Cope (1891) had left taxonomy of the group in "most puzzling confusion" and Ruthven examined too few western specimens. Their conclusions have provided the basis for the current taxonomic arrangement. Although all forms except *digueti* were considered conspecific, the delineation of subspecies showed foresight. The aquatic, unstriped, spotted forms of Central California and the Sierra Nevada were allocated to the subspecies *couchii*. The highly variable striped populations of the Pacific Coast were allocated to the subspecies *atratus* (including *vidua*). The subspecies *ordinoides* (including *leptocephala*, *cooperi*, *rubistriata*, and *olympia* as synonyms), *elegans* (including *trivittata*, *brunnea*, and *lineolata*), *biscutatus*, *hammondi* and *vagrans* (including *plutonia* and *Henshawi*) were defined as presently understood. In 1923 they described the subspecies *hueyi* from Baja California populations of *elegans*.

Fitch (1936) found spotted aquatic snakes in southwest Oregon and named them *T. o. hydrophila*. He later (1940) revised the *ordinoides* group, naming the giant San Joaquin Valley snakes *T. o. gigas*. He was the first reviewer (1940, 1941) to integrate garter snake ecology and systematics. He

defined an aquatic group (*couchii*, *gigas*, *hydrophilus*, *hammondii*, and *digueti*) and two terrestrial groups (*ordinoides* and *atratus*, and, *elegans*, *hueyi*, *vagrans*, and *biscutatus*) recognizable on both ecological and morphological grounds. The terrestrial group included snakes that were boldly striped, had broad, flat heads, enlarged posterior supralabials (due to enlarged salivary glands), large eyes and pupils, and dark irises. The aquatic morph included drab-colored, spotted snakes, with narrow heads, pointed snouts, slightly enlarged posterior supralabials, smaller eyes and pupils, and pale irises. Each group was composed of intergrading subspecies, sympatric with the other groups. The three groups were linked by pairs of subspecies: *hydrophilus* and *biscutatus*, *atratus* and *ordinoides*, and, *atratus* and *elegans* appeared to intergrade in parts of northern California. However, all forms besides *hammondii* and *digueti* remained conspecific.

Mayr (1941, 1942) argued that sympatry between two or three subspecies was untenable based on the classic species concept of reproductive isolation through ecological and morphological differences. He suggested that Fitch adhered too strictly to principles of intergradation, and that each group represented biological species. Johnson (1947) described *T. elegans nigrescens* from western Washington, and also suggested elevating the ecological groups to specific status. Fitch (1948) countered with evidence based on the intergroup "links", arguing that Mayr and Johnson had ignored these. However, Fox (1948a) found that the subspecies *ordinoides* and *atratus* did not interbreed in their contact zone along the California-Oregon border. Fitch agreed with Fox's findings and both concluded that *T. ordinoides* was monotypic while the remaining subspecies were retained with *T. elegans*. Fitch also found intergrades between *T. e. couchii* and *T. hammondii*, reducing the latter to subspecific status.

Smith (1942) described *T. ordinoides errans* from Mexico. Fitch (1948) suggested that its remoteness from the other members of the group and discrete differences between *errans* and *vagrans*, the nearest subspecies, warranted specific status for *errans*. He also suggested that characters used by Johnson to distinguish *nigrescens* from *vagrans* were not restricted to western Washington populations, but were within parameters for *vagrans* throughout its range. However, he has since recognized

nigrescens as a subspecies of *T. elegans* without explanation (Fitch, 1983). Webb (1976) examined additional specimens of *errans* from the geographical hiatus between it and *vagrans*. He discovered characters intermediate between the two forms suggesting intergradation and subspecific status for *errans*. Fitch (1980) proposed that such characters were the result of previous genetic continuity and that geographic separation has allowed *errans* to become a specific isolate.

Fox (1951) examined hundreds of *T. e. atratus* and found it to comprise three subspecies. Typical *atratus* occurred south of San Francisco Bay which separated it from his new subspecies *T. e. aquaticus*. Differences were based on coloration and pattern, *aquaticus* being intermediate between *atratus* and *hydrophilus*. Because these three subspecies were linked by intergrades, *atratus* was transferred to Fitch's aquatic group. Fox also described *T. e. terrestris*, a form broadly sympatric with *atratus*, *aquaticus*, and *hydrophilus* but intergrading only with *T. e. elegans*. He showed that the aquatic group formed a Rassenkreis in the mountains surrounding the Central Valley, terminating in broad overlap of *hammondii* and *atratus* on the central coast. In the Klamath River system, he found snakes intermediate between the subspecies *hydrophilus* and *biscutatus*. Supposing these to be intergrades, he felt that the aquatic and terrestrial groups should remain conspecific.

Savage (1960) elevated the aquatic group to specific status without explanation. In 1963 collections were made in the Klamath region by Louisiana State University to re-investigate relationships between the two groups. Rossman (1964, 1979) found two morphotypes and no intermediates in Fox's contact zone. *Hydrophilus* exhibited certain pattern variations, convergent with *biscutatus*, which Fox had considered intergrades between the two. Fox and Dessauer (1964) found that blood proteins represented two discrete groups, each corresponding to Rossman's two morphotypic species. These studies served to eliminate supposed intergradation between the aquatic and terrestrial groups.

Lawson and Dessauer (1979) analyzed biochemical and genetic variation in the *ordinoides* group (except *T. digueti*) which further demonstrated that *T. elegans* and *T. couchii* are genetically distinct species. They found *T. couchii* to comprise two divergent subgroups: *couchii* - *hammondii*, and,

gigas - *hydrophilus* - *atratus* - *aquaticus* - *ordinoides*. The subgroups were separated by a relatively large Nei genetic distance (0.19). *T. ordinoides* showed close relationship with *T. couchii atratus* but remained specifically distinct, although it and other members of its subgroup were separable by genetic distances of similar magnitude. Further studies by Lawson (pers. comm.) have shown *ordinoides* to be allied with the *elegans* group.

Relationships were clarified through morphological studies by Rossman and Stewart (1987). They analyzed adjacent subspecies in their respective contact zones and found "marked morphological differences, and minimal or no gene flow". They elevated *T. couchii*, *T. gigas*, *T. hammondii*, and *T. atratus* (including *hydrophilus*, *aquaticus*, and *atratus* as subspecies) to specific status. Intraspecific variation was not analyzed and *T. digueti* was not discussed. Stebbins (1985) considered *digueti* to be conspecific with *T. hammondii* without explanation.

The *Thamnophis ordinoides* group currently consists of eight species: *T. ordinoides*, *T. elegans*, *T. errans*, *T. couchii*, *T. gigas*, *T. hammondii*, *T. digueti*, and *T. atratus*. The last five species comprise Fitch's aquatic group (*couchii* complex). All species except *T. digueti* exhibit intraspecific variation (Fitch, 1940, Fox, 1951, Rossman, 1979, Rossman and Stewart, 1987). The greatest variation is found in *T. atratus*. Northern specimens represent Fitch's aquatic group. Southern snakes resemble, morphologically and ecologically, the terrestrial group. In the southern subspecies (*atratus*), Fox (1951) found inland specimens to be three-striped while those from the San Francisco Peninsula were "blue-black" with only the dorsal stripe present. He found the intraspecific variation "difficult to explain" and did not define the two color morphs as subspecies.

During the 1970's the author observed these two color morphs to exist on either side of the Santa Clara Valley, with intermediates occurring on the southeast slope of the Santa Cruz Mountains. This prompted an analysis of variation in the subspecies *atratus*, the results of which are presented herein. The hypothesis presented is that overall variation in southern *T. atratus* reflects a partial shift towards the terrestrial morph, due to ecological selective pressures. Bellemin and Stewart (1977) have already suggested pattern convergence between southern *T. atratus* and *T. elegans*. For the present

analysis, characters were selected which would determine the extent to which the former have varied from Fitch's aquatic morph.

Because the *couchii* complex has not been reviewed as a whole since Fitch (1940), and because of the diffuse nature of subsequent literature on the complex, a synopsis of the group is included. This includes a summary of intraspecific variation, distinguishing characters, and distribution.

MATERIALS AND METHODS

A total of 785 snakes, live and preserved, were examined from the southern half of the distribution of *Thamnophis atratus*. All specimens in the collections of the California Academy of Sciences, Museum of Vertebrate Zoology, California Polytechnic Institute, and San Jose State University were examined (see List of Specimens Examined). From 1969 through 1987, 417 *T. atratus* were observed in the field. Coloration, pattern, and ecological notes were recorded for each, and all but 63 snakes were released. Four gravid females, from both sides of the Santa Clara Valley, were kept alive until parturition. These, their offspring, and the rest of the 63 retained snakes were preserved for the SJSU collection.

Preserved, mature snakes were sexed by dissection, or by examining shape of the tail base: tails of females begin a gradual taper immediately posterior to the vent while males exhibit a parallel-sided base along the hemipenial distance (fig. 1). Many juvenile snakes were not sexed since sexual dimorphism is not evident until maturity. Snout to vent (SVL) and total length (TTL) were measured to the nearest millimeter. Only snakes over 350 mm SVL, the approximate minimum adult SVL (Rossman, 1979), were used for the multivariate analysis, to assure that the proportions of cephalic features had stabilized. Gape length (GL) was measured to the nearest tenth mm. (fig. 2). Counts were made of ventrals (V), subcaudals (S), preoculars (PrO), postoculars (PtO), supralabials (SL), infralabials (IL), and temporals. Anterior scale rows (ASR) were counted at the tenth ventral scale posterior to the chin shields. Midbody scale rows (MSR) were counted halfway between snout and vent. Posterior scale rows (PSR) were counted at the third ventral anterior to the vent. Scale rows were counted in an alternating, rather than diagonal, fashion so that counts were made coplanar with their respective reference ventral.

Dorsal stripe width was measured, in number of scale rows covered, at the widest part in the nuchal area (ADSW), and at a point about 1/3 the distance to the vent (MDSW). A ranked value

Fig. 1. Underside of tails showing sexual dimorphism.

Fig. 2. Cephalic measurements.

(STR) was derived from relative visible intensity of the lateral stripe, if present, pigmentation of supralabials, and intensity of ventral dark pigment. Dark snakes with only a dorsal stripe were given the lowest value of 1 (fig. 3b), while three-striped snakes with pale labials and venter received the highest value, 5 (fig. 3d and 4d). Values given to the patterns in fig. 3a and 3c were 2 and 3, respectively.

Clinal trends in cephalic proportions were compared through the following six ratios (fig. 2): R1: antepenultimate supralabial width / height (to eliminate contour curvature of the SL, the outer scale covering was removed and measured on a flat surface); R2: internasal length / internasal width; R3: length of internasal-rostral contact / length of nasal-rostral contact; R4: anterior chin shield length / posterior chin shield length; R6: eye diameter (ED) / gape length; R7: interocular width (IOW) / gape length. Measurements were made with dial calipers. A seventh ratio, R5, compares tail length (TL) to total length. The use of ratios in multivariate analyses has been discouraged (Atchley, Gaskins, and Anderson, 1976). However, Berry (in Iverson, 1981), and Heyer (1978), found results from the use of ratios to parallel those obtained using linear measurements. I have chosen to use Ratios 1-4 in the multivariate analysis because 1) values for each were normally distributed, and 2) many data elements for linear components of the ratios were lost prior to data input for the analysis.

Southern *T. atratus* was divided into seven geographic areas for biogeographic analysis (fig. 5). Five of these represent geographically isolated population groups. The other two (Areas C and E) represent annectant populations selected to determine intergradation between Areas. Area A includes all of Marin Co., and Sonoma Co. west of the Russian R. and Sonoma Valley. Area B includes all of Napa and Solano Counties. Area C includes the San Francisco Peninsula north of Half Moon Bay and San Andreas Res. Area D includes southern and central San Mateo Co. and the Santa Cruz Mtns. south to the San Lorenzo R. and Guadalupe Creek watersheds. Area E includes the southeast flank of the Santa Cruz Mtns. north to Alamitos Cr. and east of the summit. Area F includes the Diablo Range from Contra Costa Co. south to Tres Pinos Cr. Area G includes the outer coast from Monterey to Santa Barbara Counties.

To test for adequacy of classification of specimens, a multivariate analysis was performed with

Fig. 3. Dorsal patterns of *Thamnophis atratus*. A. *T. a. atratus* X *aquaticus* MVZ 47923, San Mateo Co.; B. *T. a. atratus* SJSU 5680, San Mateo Co.; C. *T. a. atratus* X *zaxanthus* SJSU 5693, Santa Cruz Co.; D. *T. a. zaxanthus* (holotype) MVZ 207940, Santa Clara Co.

Fig. 4. Dorsal patterns of *Thamnophis atratus*. A. *T. a. hydrophilus* MVZ 17425, Jackson Co., OR; B. *T. a. hydrophilus* SJSU 3002, Colusa Co.; C. *T. a. hydrophilus* MVZ 42527, Trinity Co.; D. *T. a. aquaticus* SJSU 3035, Napa Co.

Fig. 5. Population samples (Areas A-G).

the SYSTAT Discriminant Function program. This program predicted group membership of specimens by Area, and determined which variables discriminated between Areas. It determined basic statistics (mean, range, and standard deviation), character correlations through the Pearson Correlation Matrix (to avoid repetition of characters), overall significance between Areas (Wilks' lambda test), significance of each variable by a Univariate F test, relative weight of each variable by squared multiple correlations, significance of canonical factors through a test of residual roots, canonical plots by sex and Area, and canonical loadings per variable, to indicate relative value of each variable in separating Areas. One hundred eighteen adult males and 115 adult females were utilized. BIOSTAT TTest application was used to determine significance of sexual dimorphism for each character by comparing value pairs for each sex.

Museum acronyms: CAS California Academy of Sciences, San Francisco. CAS-SU Stanford University collection housed at CAS. CPS California Polytechnic Institute, San Luis Obispo. MNHN Museum National d'Histoire Naturelle, Paris. MVZ Museum of Vertebrate Zoology, Berkeley. SJSU San Jose State University, San Jose. USNM National Museum of Natural History, Washington D. C.

RESULTS

SEXUAL DIMORPHISM. Prior to an analysis of variance, sexual dimorphism was examined to insure statistical homogeneity. Sixteen characters were analyzed using Student's t-test (table 1). Male SVL is significantly ($p < .001$) shorter than that of females. This is true of all *Thamnophis* studied by Fitch (1981). Males possess proportionately longer tails (R5), a condition typical of most snakes (Klauber, 1943). They have significantly higher V and S counts, consistent with other members of the *T. ordinoides* group (Fitch, 1940). Adult female *Thamnophis* are chunk-headed as a result of enlarged salivary glands, reflected in significantly taller posterior SL (R1). ED and IOW are proportionately smaller than in males (R6 and R7). However, ED from Area D snakes was not sexually dimorphic. R2 and R4 are not sexually dimorphic, although means for males are higher for both. Color pattern did not vary between sexes. Rossman and Stewart (1987) found higher ASR counts in female *T. gigas*, but no significant difference was noted in southern *T. atratus*. Thirteen non-correlated characters were examined by discriminant function analysis. Predicted vs. actual assignment resulted in 112 (97.4%) of 115 correct female assignments, and 115 (97.5%) of 118 correct male assignments. Wilks' lambda test provided an F-statistic = 63.506. Significant sexual dimorphism in half of the characters tested necessitates separate multivariate analyses for males and females.

BASIC STATISTICS. Nineteen characters were initially analyzed by MANOVA: SVL, V, S, ASR, MSR, PSR, G, ED, IOW, ADSW, MDSW, STR, and R1-7. R6 and R7 were dropped from the discriminant function analysis, since the linear components of each were included separately. Means, range, and standard deviation are illustrative of clinal trends within the species, and among the seven Areas analyzed (tables 2 and 3). For the correlated linear measurements (SVL, ED, GL, IOW) there is an increase in length to the south and inland. Relative TL (R5) increases northward and coastally. Scute counts (V and S) increase to the north and inland. Scale rows increase north and inland, except

Character	mean, SD, N		(p)
	♂	♀	
SVL	420.0 ± 4.56, 25	468.9 ± 7.45, 25	0.001
V	158.4 ± 0.53, 25	152.4 ± 0.57, 25	0.001
S	80.4 ± 0.51, 25	72.9 ± 0.43, 25	0.001
ASR	19.5 ± 0.09, 25	19.2 ± 0.06, 25	n.s.
MSR	18.4 ± 0.08, 25	18.5 ± 0.07, 25	n.s.
PSR	15.5 ± 0.07, 25	15.2 ± 0.06, 25	n.s.
ADS	3.6 ± 0.07, 20	3.5 ± 0.07, 20	n.s.
MDS	2.3 ± 0.03, 20	2.2 ± 0.04, 20	n.s.
STR	1.7 ± 0.11, 20	1.7 ± 0.09, 20	n.s.
R1 (Area F)	82.6 ± 0.65, 28	78.5 ± 0.65, 41	0.05
R1 (Area D)	85.9 ± 0.65, 35	79.1 ± 0.70, 35	0.001
R2	109.2 ± 1.10, 19	108.3 ± 1.30, 19	n.s.
R3	91.0 ± 1.30, 25	80.5 ± 1.75, 25	0.001
R4	79.3 ± 0.90, 19	78.7 ± 0.80, 19	n.s.
R5	26.0 ± 0.15, 18	24.5 ± 0.20, 18	0.001
R6 (Area F)	18.8 ± 0.15, 20	17.5 ± 0.15, 20	0.001
R7	39.9 ± 0.30, 16	36.5 ± 0.30, 16	0.001

Table 1. Students T-test results showing sexual dimorphism.

AREA	N	BVL	V	B	ABR	NSR	PSR	G	ED	ICW	ADSV
A	16	380.25 ± 27.46 (350-430)	157.13 ± 3.96 (149-166)	83.75 ± 4.09 (70-93)	19.00 ± 0.00 (19)	19.00 ± 0.00 (19)	15.38 ± 0.81 (15-17)	14.80 ± 1.05 (13.0-16.8)	2.69 ± 0.22 (2.17-3.05)	5.92 ± 0.22 (5.48-6.44)	3.19 ± 0.60 (2.1-4.3)
B	14	407.36 ± 25.33 (355-462)	161.14 ± 3.84 (156-168)	82.71 ± 3.56 (75-88)	19.57 ± 0.94 (19-21)	19.00 ± 0.00 (19)	16.16 ± 1.03 (15-17)	15.79 ± 1.23 (13.9-18.7)	3.02 ± 0.22 (2.57-3.41)	6.12 ± 0.41 (5.49-7.00)	2.85 ± 0.43 (1.9-3.3)
C	15	406.73 ± 25.05 (365-450)	150.87 ± 4.03 (144-158)	77.20 ± 4.02 (71-84)	19.27 ± 0.70 (19-21)	18.47 ± 0.92 (17-19)	15.00 ± 0.00 (15)	15.92 ± 1.22 (13.8-17.8)	2.92 ± 0.22 (2.48-3.36)	6.26 ± 0.44 (5.41-6.72)	3.74 ± 0.89 (2.8-6.4)
D	12	397.72 ± 30.20 (350-457)	153.41 ± 2.91 (146-159)	79.41 ± 5.02 (67-89)	19.16 ± 0.52 (19-21)	18.13 ± 1.01 (17-19)	14.94 ± 0.35 (13-15)	15.56 ± 1.30 (12.8-18.0)	2.92 ± 0.21 (2.40-3.50)	6.13 ± 0.40 (5.50-7.00)	3.76 ± 0.79 (2.9-6.5)
E	8	412.63 ± 27.60 (370-457)	157.38 ± 3.20 (153-162)	79.00 ± 4.24 (73-88)	19.50 ± 0.93 (19-21)	18.00 ± 1.07 (17-19)	15.00 ± 0.00 (15)	16.56 ± 1.14 (15.0-18.0)	3.22 ± 0.33 (2.70-3.55)	6.50 ± 0.53 (5.60-7.00)	3.81 ± 0.86 (3.0-5.0)
F	21	415.39 ± 41.66 (354-514)	159.52 ± 4.93 (149-168)	80.62 ± 4.87 (69-89)	19.38 ± 0.81 (19-21)	18.52 ± 0.87 (17-19)	15.38 ± 0.81 (15-17)	15.99 ± 1.19 (13.9-18.7)	3.03 ± 0.31 (2.51-3.83)	6.18 ± 0.58 (5.14-7.21)	3.60 ± 0.56 (2.8-5.0)
G	12	400.00 ± 31.96 (350-461)	153.33 ± 3.55 (149-161)	75.50 ± 4.60 (65-82)	19.17 ± 0.81 (19-21)	18.83 ± 0.57 (17-19)	15.50 ± 0.91 (15-17)	16.52 ± 1.08 (14.8-18.5)	3.08 ± 0.15 (2.82-3.44)	6.59 ± 0.44 (6.05-7.61)	2.78 ± 0.55 (1.5-3.5)
A	1.92 ± 0.49 (1.2-2.9)	3.94 ± 1.37 (1.0-5.0)	1.10 ± 0.10 (0.94-1.32)	0.94 ± 0.21 (0.66-1.45)	0.93 ± 0.10 (0.81-1.16)	0.79 ± 0.08 (0.66-0.98)	0.267 ± 0.007 (0.256-0.281)	0.184 (0.15-0.21)	0.399 (0.36-0.44)		
B	1.91 ± 0.32 (1.3-2.6)	5.00 ± 0.00 (5.0)	1.04 ± 0.06 (0.93-1.17)	0.93 ± 0.17 (0.66-1.30)	0.93 ± 0.07 (0.82-1.07)	0.80 ± 0.09 (0.66-1.00)	0.267 ± 0.011 (0.251-0.289)	0.189 (0.15-0.20)	0.390 (0.35-0.42)		
C	2.45 ± 0.24 (2.2-3.0)	2.77 ± 1.16 (1.0-5.0)	1.10 ± 0.08 (0.98-1.23)	0.95 ± 0.20 (0.61-1.31)	0.85 ± 0.10 (0.68-1.00)	0.77 ± 0.07 (0.65-0.90)	0.265 ± 0.009 (0.253-0.288)	0.183 (0.17-0.21)	0.393 (0.35-0.45)		
D	2.43 ± 0.57 (1.6-4.0)	1.31 ± 0.70 (1.0-4.0)	1.04 ± 0.09 (0.76-1.26)	0.85 ± 0.17 (0.45-1.09)	0.86 ± 0.08 (0.75-1.00)	0.76 ± 0.06 (0.53-0.96)	0.263 ± 0.014 (0.221-0.280)	0.188 (0.16-0.22)	0.397 (0.35-0.45)		
E	2.25 ± 0.20 (2.1-2.7)	3.13 ± 1.03 (1.0-4.5)	1.09 ± 0.06 (0.98-1.18)	0.99 ± 0.10 (0.86-1.12)	0.83 ± 0.04 (0.78-0.89)	0.81 ± 0.07 (0.71-0.91)	0.255 ± 0.004 (0.247-0.263)	0.191 (0.18-0.20)	0.393 (0.36-0.63)		
F	2.20 ± 0.21 (1.8-2.5)	5.00 ± 0.00 (5.0)	1.11 ± 0.07 (0.99-1.21)	0.92 ± 0.16 (0.59-1.25)	0.83 ± 0.07 (0.67-0.96)	0.80 ± 0.09 (0.56-0.99)	0.260 ± 0.010 (0.235-0.280)	0.190 (0.16-0.22)	0.390 (0.33-0.44)		
G	2.00 ± 0.23 (1.5-2.4)	4.96 ± 0.14 (4.5-5.0)	1.08 ± 0.10 (0.91-1.26)	0.92 ± 0.17 (0.66-1.26)	0.83 ± 0.08 (0.62-0.95)	0.78 ± 0.06 (0.67-0.89)	0.257 ± 0.006 (0.246-0.268)	0.187 (0.17-0.21)	0.400 (0.36-0.44)		

Table 2. Basic statistics for males.

AREA	IT	SVL	V	g	ASR	MSR	PSR	g	ED	ICW	ADSV	WDSV
A	12	394.50 ± 38.97 (336-459)	148.75 ± 3.93 (144-156)	74.67 ± 1.97 (71-78)	19.33 ± 0.78 (19-21)	18.83 ± 0.58 (17-19)	15.83 ± 1.03 (15-17)	14.40 ± 1.31 (14.0-19.0)	2.80 ± 0.26 (2.52-3.42)	6.15 ± 0.32 (5.16-7.08)	3.53 ± 0.71 (2.2-6.7)	1.74 ± 0.59 (1.2-2.8)
B	10	493.90 ± 75.23 (383-609)	154.60 ± 2.27 (152-159)	76.10 ± 2.18 (74-79)	19.40 ± 0.84 (19-21)	19.00 ± 0.80 (19)	16.00 ± 1.05 (15-17)	20.15 ± 3.21 (15.2-25.0)	3.48 ± 0.38 (3.04-4.26)	7.10 ± 0.45 (5.87-8.48)	3.11 ± 0.67 (2.1-4.6)	1.98 ± 0.43 (1.2-2.6)
C	15	442.33 ± 41.69 (366-525)	147.13 ± 3.56 (141-151)	70.07 ± 3.11 (65-75)	19.13 ± 0.52 (19-21)	18.33 ± 0.96 (17-19)	15.33 ± 0.92 (15-17)	18.47 ± 1.79 (15.1-21.5)	3.07 ± 0.34 (2.59-3.78)	6.83 ± 0.43 (6.09-7.87)	3.43 ± 0.77 (2.0-4.6)	2.40 ± 0.26 (2.1-2.9)
D	37	445.88 ± 69.14 (331-582)	147.09 ± 3.22 (141-155)	70.78 ± 3.11 (64-79)	19.22 ± 0.71 (18-21)	18.19 ± 1.00 (17-19)	15.13 ± 0.49 (15-17)	18.12 ± 2.56 (14.2-23.3)	3.31 ± 0.39 (2.60-4.16)	6.73 ± 0.79 (5.08-8.15)	4.11 ± 1.01 (2.1-6.3)	2.86 ± 0.85 (1.8-4.6)
E	9	483.47 ± 61.85 (417-557)	147.00 ± 1.73 (146-149)	70.33 ± 3.79 (66-71)	21.00 ± 0.80 (21)	17.67 ± 1.16 (17-19)	15.00 ± 0.80 (15)	18.90 ± 1.73 (16.9-19.9)	3.32 ± 0.38 (2.94-3.70)	7.78 ± 0.74 (6.45-7.83)	3.67 ± 0.55 (3.1-4.2)	2.20 ± 0.70 (1.5-2.9)
F	31	471.45 ± 80.20 (339-701)	154.26 ± 3.34 (142-167)	73.55 ± 4.05 (66-83)	19.52 ± 0.89 (19-21)	18.61 ± 0.80 (17-19)	15.37 ± 0.75 (15-17)	18.68 ± 2.65 (15.0-24.4)	3.77 ± 0.41 (2.49-4.08)	6.86 ± 0.83 (5.45-8.65)	3.43 ± 0.53 (2.9-4.9)	2.23 ± 0.36 (1.0-2.8)
G	12	463.30 ± 69.67 (388-627)	147.58 ± 4.06 (140-156)	69.75 ± 2.99 (63-74)	19.23 ± 0.78 (19-21)	18.47 ± 0.78 (17-19)	15.83 ± 1.03 (15-17)	19.39 ± 2.30 (15.8-23.0)	3.33 ± 0.32 (2.78-3.75)	7.36 ± 0.80 (5.98-8.53)	2.95 ± 0.36 (2.3-3.6)	2.00 ± 0.20 (1.6-2.4)
A		3.75 ± 1.01 (2.0-5.0)	0.88 ± 0.11 (0.75-1.20)	1.08 ± 0.14 (0.91-1.46)	0.83 ± 0.16 (0.56-1.15)	0.79 ± 0.08 (0.67-0.95)	0.232 ± 0.009 (0.240-0.266)	0.174 (0.15-0.21)	0.383 (0.35-0.42)			
B		4.45 ± 0.44 (4.0-5.0)	0.86 ± 0.07 (0.72-0.95)	1.05 ± 0.09 (0.93-1.18)	0.80 ± 0.17 (0.57-1.09)	0.74 ± 0.06 (0.66-0.83)	0.249 ± 0.005 (0.237-0.255)	0.177 (0.15-0.20)	0.355 (0.32-0.40)			
C		2.53 ± 0.61 (1.5-4.0)	0.82 ± 0.06 (0.70-0.90)	1.13 ± 0.07 (0.99-1.23)	0.86 ± 0.14 (0.66-1.07)	0.77 ± 0.07 (0.65-0.88)	0.244 ± 0.009 (0.238-0.261)	0.169 (0.15-0.18)	0.345 (0.34-0.42)			
D		1.19 ± 0.48 (1.0-3.0)	0.79 ± 0.09 (0.60-0.97)	1.04 ± 0.07 (0.88-1.16)	0.83 ± 0.13 (0.58-1.07)	0.74 ± 0.07 (0.59-0.88)	0.241 ± 0.009 (0.231-0.261)	0.182 (0.15-0.20)	0.371 (0.32-0.42)			
E		2.67 ± 1.53 (1.0-4.0)	0.79 ± 0.05 (0.74-0.84)	1.15 ± 0.11 (1.05-1.27)	0.77 ± 0.11 (0.69-0.90)	0.73 ± 0.04 (0.73-0.81)	0.240 ± 0.009 (0.232-0.249)	0.187 (0.17-0.22)	0.383 (0.38-0.39)			
F		4.87 ± 0.45 (3.0-5.0)	0.79 ± 0.08 (0.59-0.94)	1.05 ± 0.10 (0.89-1.27)	0.86 ± 0.18 (0.67-1.03)	0.78 ± 0.08 (0.67-1.03)	0.244 ± 0.014 (0.223-0.274)	0.175 (0.15-0.21)	0.371 (0.33-0.41)			
G		4.88 ± 0.31 (4.0-5.0)	0.82 ± 0.08 (0.69-0.96)	1.09 ± 0.09 (0.94-1.23)	0.85 ± 0.15 (0.57-1.10)	0.76 ± 0.06 (0.69-0.84)	0.239 ± 0.009 (0.224-0.255)	0.172 (0.15-0.18)	0.379 (0.34-0.42)			

Table 3. Basic statistics for females.

ASR, which increase southward. Stripe width increases towards Area D from north, south, and inland. A similar pattern exists for STR value: there is a decrease as Area D is approached from all directions. Values for R1 and R2 showed no clinal variation. Values for R3 are bimodal, separated at the San Francisco Bay. Values for R4 show more uniformity of chin shield lengths to the north, south, and inland from Area D. R6 indicates that relative eye size increases southward and inland. R7 indicates that IOW increases coastally, but north-south values are non-clinal. These trends are diagrammed in fig. 6.

CORRELATION. Correlation of characters was determined through Pearson correlation matrix (table 4). SVL, G, IOW, and ED were highly correlated (>0.608). ED was expected to be affected by the aquatic-terrestrial morph shift, and was retained. R5 was highly correlated with S (>0.571), and dropped from further analysis, to favor the non-ratio measurement.

DISCRIMINANT FUNCTION ANALYSIS. The remaining thirteen characters were subjected to multivariate analysis for each sex. For MALES, Wilks' lambda test resulted in $F = 6.245$, and $p > .0001$, between Areas A-G. Univariate F tests showed ten variables to be significant ($p < .05$), eliminating ASR, R2, and R4. Squared multiple correlations found the ten variables to be weighted in the following order: STR (0.794), V (0.457), ED (0.258), PSR (0.255), ADSW (0.247), MDSW (0.241), S (0.240), R3 (0.201), MSR (0.179), and R1 (0.111). The test of residual roots indicates that only Factors 1-3 were significant ($p < .0001$), with canonical correlations $> .500$. The canonical plots (figs. 7 and 8) indicate that Factor 1 shows separation of Area D from Areas A-B and F-G. Areas C and E are believed to represent intergrade populations (see below). Canonical loadings for each variable (table 5) show that STR (0.838), V (0.286), PSR (0.219), and MDSW (0.214) affect this separation. Factor 2 separates Areas A-B from F-G by ED (0.445), R3 (0.427), S (0.408), and STR (0.306). Factor 3 separates Area A from B, and F from G, based on V (0.728).

For FEMALES, Wilks' lambda test also resulted with $p < .0001$ (F statistic = 6.407).

Fig. 6. Clinal trends in variation from north (top) to south (bottom), and inland (right).

	SVL	V	S	ASR	MSR	PSR	GL	ED	IOW	ADSW	HDSH	STR	R1	R2	R3	R4	R5
SVL	1.000																
V	0.208	1.000															
S	0.059	0.395	1.000														
ASR	0.115	0.115	0.036	1.000													
MSR	0.107	0.155	0.108	0.159	1.000												
PSR	0.101	0.245	0.012	0.119	0.268	1.000											
GL	0.793	-0.030	-0.021	0.161	0.077	0.034	1.000										
ED	0.611	0.036	0.011	0.146	0.021	0.096	0.668	1.000									
IOW	0.608	-0.104	-0.032	0.077	0.090	0.023	0.744	0.651	1.000								
ADSW	0.001	-0.057	0.136	0.086	-0.039	-0.293	-0.047	-0.058	-0.071	1.000							
HDSH	-0.087	-0.177	-0.054	0.070	-0.057	-0.357	-0.126	-0.064	-0.026	0.578	1.000						
STR	0.131	0.492	0.100	0.137	0.304	0.394	0.057	0.090	0.029	-0.273	-0.354	1.000					
R1	-0.061	0.052	0.021	0.062	-0.026	-0.071	0.018	0.041	-0.066	0.046	0.080	0.101	1.000				
R2	0.113	0.175	0.071	-0.017	0.036	0.107	0.030	-0.087	0.017	0.047	-0.037	0.216	-0.019	1.000			
R3	-0.270	0.098	0.182	-0.120	0.083	0.115	-0.238	-0.212	-0.239	-0.078	-0.090	-0.040	0.095	0.025	1.000		
R4	-0.143	0.151	0.083	0.091	0.152	0.228	-0.086	0.049	-0.019	-0.077	-0.142	0.204	0.048	-0.060	0.056	1.000	
R5	-0.159	-0.008	0.571	0.039	0.073	-0.061	-0.099	-0.186	-0.141	0.104	-0.095	-0.040	-0.081	-0.110	0.090	0.022	1.000

PEARSON CORRELATION
MATRIX

Table 4. Pearson Correlation Matrix for males.

Fig. 7. Canonical plot: males factor 1 vs. factor 2.

Fig. 8. Canonical plot: males factor 1 vs. factor 3.

FACTOR		1	2	3	4	5	6
MALES	V	0.268	-0.174	0.728	0.346	-0.034	-0.107
	S	0.084	-0.408	0.265	0.374	0.080	0.153
	ASR	0.044	0.098	0.236	-0.096	0.148	0.503
	MSR	0.171	-0.168	-0.189	-0.140	0.033	0.165
	PSR	0.219	-0.128	0.168	-0.409	-0.025	0.293
	ED	0.038	0.445	0.353	-0.296	0.258	-0.179
	ADSW	-0.191	0.127	0.132	0.564	-0.115	0.520
	MDSW	-0.214	0.181	0.023	0.118	-0.364	0.637
	STR	0.838	0.306	0.004	0.141	-0.130	0.131
	R1	0.075	0.111	-0.179	0.451	0.144	0.118
	R2	0.059	0.063	-0.042	0.112	0.557	0.277
	R3	0.060	-0.427	0.009	-0.121	0.411	0.207
	R4	0.080	0.033	0.060	0.129	0.285	-0.022
FEMALES	V	0.235	-0.563	0.263	-0.030	-0.037	0.540
	S	0.150	-0.165	0.677	0.057	0.070	-0.004
	ASR	0.048	-0.052	-0.095	0.675	0.034	-0.001
	MSR	0.102	0.080	0.188	-0.259	0.124	-0.123
	PSR	0.080	0.315	0.121	-0.216	0.339	0.073
	ED	0.005	-0.408	-0.253	0.003	0.771	-0.004
	ADSW	-0.156	-0.312	0.111	0.128	-0.210	-0.261
	MDSW	-0.199	-0.437	-0.156	-0.094	0.004	0.074
	STR	0.770	0.040	-0.435	-0.247	-0.244	-0.235
	R1	0.043	0.344	0.309	-0.044	0.201	-0.023
	R2	0.004	0.359	-0.163	0.148	-0.103	0.726
	R3	-0.001	0.018	-0.096	-0.150	-0.147	0.078
	R4	0.064	0.060	0.079	0.059	-0.275	0.211

Table 5. Canonical factor loadings.

The univariate F-test found 11 variables to be significant ($p < .05$), eliminating R3 and R4. Squared multiple correlations weighted the eleven characters as follows: STR (0.837), V (0.419), MDSW (0.320), S (0.304), ADSW (0.225), ED (0.199), ASR (0.140), PSR (0.138), R1 (0.128), R2 (0.121), and MSR (0.117). The test of residual roots indicated that Factors 1-4 were significant ($p < .01$), with canonical correlations > 0.482 . Canonical plots of discriminant scores (figs. 9-11) show that Factor 1 discriminates between Area D and Areas A-B, F-G. This is based on coloration (STR = 0.770, MDSW = 0.199) and V (0.235). Factor 1 also separates Area F from G, based on V and MDSW. Factor 2 separates Area A from B, based on V (0.563), MDSW (0.437), and ED (0.408). Factor 3 separates Areas A-B from Areas F-G, based on S (0.677), STR (0.435), and R1 (0.309). Factor 4 again separates Areas A and B, based on ASR (0.675). It also separates Area F from G by the same variable.

Predicted vs. actual assignments based on discriminant scores shows homogeneity (at least 75% correct assignment) for all but Areas C and F (table 6). However, when Areas F and G are combined, predictability increases to 85.5%. For Area C, 70.0% of the snakes are correctly assigned, while an additional 13.3% are assigned to Area D and 3.3% to Area A. This suggests that Area C snakes are intermediate between Area A and D snakes.

Fig. 9. Canonical plot: females factor 1 vs. factor 2.

Fig. 10. Canonical plot: females factor 1 vs. factor 3.

Fig. 11. Canonical plot: females factor 1 vs. factor 4.

ACTUAL	PREDICTED								
	AREA	A	B	C	D	E	F	G	TOTAL
A	21	2	3				2		28
B		20					4		24
C				21	4	2		2	30
D				7	57				64
E					1	10			11
F	2	8				1	34	7	52
G							3	21	24
TOTAL	23	30		31	62	13	43	30	

Table 6. Predicted vs. actual classification.

DISCUSSION

SEXUAL DIFFERENCES: Sexual differentiation may have resulted from ecological-reproductive differences. Overall larger size of females may be based on increased nutritive requirements, and positive size-fecundity correlation. Fitch (1984) points out that males of the *T. couchii* complex average 82% of the female SVL, and 55% of the female weight. *Thamnophis* is ovoviviparous, producing 90 or more young at a time (Stebbins, 1985). The young must be large enough at birth to feed upon specific prey. Female size must correspond to volume requirements of large numbers of specific-sized embryos. In addition, greater female size may be correlated with larger prey size, and increased body musculature. Terrestrial garter snakes, which prey heavily on microtines are known to constrict (Fox, 1951, H. W. Greene, pers. comm.). Captive gravid females were found to have greater nutritive requirements than males (pers. obs.). Fed slightly more than males, the gravid snakes exhibited weight loss, late parturition, and produced underdeveloped, stillborn young. Quantitative studies of nutritive requirements between sexes in *Thamnophis* are lacking. It is suspected that females preferentially prey on highly nutritive prey such as microtines and bird nestlings. Males may favor cold-blooded prey. During mid-summer, when large numbers of *T. atratus* congregate at streams in the Diablo Range, gravid females are rarely encountered. It is believed that they remain concealed in dense vegetation, where warm-blooded prey is more abundant, and chances of predation less frequent.

The differences in cephalic proportions between the sexes are probably correlated with prey differences. The enlarged salivary glands present in females may cause the lesser R1 value. The lower significance of this value in Area F as compared to Area D indicates that females from Area D may be more reliant on terrestrial "dry" prey. Lower R3 values for females indicate a broader snout (terrestrial trait), yet R7 suggests a narrower head. However, it is the salivary glands which broaden the head by forcing the floating jaw components outward. This would increase the gape as required by larger female prey size. Smaller eyes in females is convergent with aquatic snakes, but may be related to some

other aspect of ecology.

Longer tails in males may be related to the presence of hemipenes, and serve as a locomotor adaptation for swimming.

LENGTH: Four correlated characters (SVL, GL, ED, IOW) are a function of linear size, and all have identical clines: length increases to the south and inland. Maximum TTL is greatest in the southern two subspecies (see Synopsis). The Dillon Beach, Marin Co. population (type locality of *aquaticus*) is dwarfed in comparison to other samples. Of 20 adult snakes measured from this locality, only 3 (15%) exceeded the mean SVL for Area A. Fox (1951) discusses this situation in light of the climatic change from cool, fog belt at Dillon Beach, to a warm, sunnier climate in Napa Co. He suggested three explanations: 1) slower growth-rate of cold-climate individuals; 2) selection for a low surface-volume ratio in cool-climate poikilotherms; 3) smaller size at sexual maturity, at which point growth rate decreases rapidly. He suggested that the coastal snakes grew less rapidly than inland snakes, causing them to reach maturity at a smaller size. Maturity was determined by age, rather than size. Fox, Gordon, and Fox (1961) found that gravid *T. elegans* kept at cool temperatures produced smaller young than snakes kept at warmer temperatures. In addition to Fox's proposals, the value of prey differences must be considered (see Ecology: Food). The increased terrestriality in southern snakes provides a different, perhaps more nutritive prey base, than the aquatic, northern snakes. Smith and Patton (1988) determined that size differences, used to define subspecies of a pocket gopher (*Thomomys bottae*) were based on the nutrition availability during years when specimens were collected. They concluded that size was not genetically based in pocket gophers, and probably other organisms as well. Evidence suggests that climate and nutrition effect size of *T. atratus*. Therefore, it is not used in the taxonomy of the species.

SCUTELLATION: Fox (1948b), and Fox, Gordon, and Fox (1961) demonstrated that cold-developed embryos had lower scales counts than high temperature embryos. It is expected that *T. atratus* would

have the highest counts to the south and inland. V, S, ASR, MSR, and PSR all increase inland. It is probable that this is correlated with warmer climate inland. However, each of these characters increase to the north, rather than south. Although ASR average slightly fewer in Areas A and C, snakes from southern Oregon and northern California possess the highest averages for the species. Because primitive members of the *T. couchii* complex have the highest counts, it is believed that the north-south cline reflects a genetic shift from a primitive to advanced state. These values for sympatric *T. elegans* increase from north to south (Fox, 1951). Within the distribution of southern *T. atratus*, values for V and S are nearly identical between the two species, suggesting convergence. However, clines for scale rows are opposed from southern Oregon to central California. Apparently, V and S counts follow a genetic trend in each species, while scale rows may depend on environmental selection. Two of the stoutest forms, *T. gigas* and *T. elegans biscutatus*, possess relatively high scale row counts. Thus, number of scale rows may reflect relative girth, which in turn may depend on prey type and size. A quantitative study of relationships between girth, prey, and fecundity is needed.

RELATIVE TAIL LENGTH: *T. atratus* has the longest relative tail length within the *T. couchii* complex. There is a north to south, coast to inland decrease in R5. Highly aquatic, lentic *Thamnophis* have longer tails than terrestrial forms. However, the highly aquatic, lotic *T. gigas*, is also short-tailed. The long tail may be a locomotor adaptation for running water. R5 values parallel increased terrestriality in southern *T. atratus*. The coastward increase may not be consistent in northern *T. atratus*. The increase from Area F to D is minor, and there is no difference between Area A and B males. For females, there is a coastward increase from Area B to A, and a slight inland increase from Area D to F. These differences negate themselves, and there may be no real coastal-inland difference in relative tail length.

CEPHALIC PROPORTIONS: Within southern *T. atratus*, no identifiable linear clines are found for R1 and R2. However, Fox (1951) shows a north to south convergence in these, towards *T. elegans*

terrestris, from throughout the distribution of *T. atratus*. The terrestrial shift in these characters for *T. atratus* apparently occurs north of Areas A-G. Area D snakes are the most terrestrial of the species (see Ecology), and values for R1 and R2 from this Area are the lowest. R1 is believed to be directly related to feeding, as it corresponds to salivary gland size. Taub (1967) found relatively large numbers of mucous cells associated with Duvernoy's gland in *T. elegans*, but not in *T. sirtalis*. Duvernoy's gland of *T. elegans* possessed the greater storage capacity of *Thamnophis* he examined. No *T. couchii* complex members have been examined for these characters. It is expected that southern *T. atratus*, especially from Area D, would show an increase in glandulosity over northern conspecifics. The R2 values from Area D are the opposite of those expected for terrestrial snakes.

The R4 values approximate 1 for *T. elegans*, and decrease in *T. atratus*. This may be a factor of GL. Fox (1951) shows a marked difference in GL/head length between the two species, *T. elegans* having the shorter gape. Shorter gape may be reflected in short PCS. Area D snakes have the shortest PCS, perhaps shortest relative gape, in southern *T. atratus*, indicating convergence with *T. elegans*. This is probably related to feeding. A shorter gape would allow greater area for posterior cephalic musculature and secretory glands. This would facilitate capture and pre-digestion of large, dry, terrestrial prey such as microtines and bird nestlings. Varkey (1979) compared cephalic musculature in *Thamnophiines*. *T. elegans* has a square-backed parietal, and broad supraoccipital crest. Attachment of the *M. adductor mandibulae externus* is broad on the latter. *T. couchii* has a posteriorly elongate parietal, and shortened, narrow supraoccipital crests. Muscle attachment to the latter is limited, but broad along the posterior parietal. One operation of these muscles is to contract Duvernoy's glands, and probably, serous cells (Cundall, 1987). Sexual variation and relative muscle mass was not noted. An analysis of these, and posterior jaw attachment of musculature, might prove or disprove some of the above mentioned theories.

Values for R3 are dichotomous, separated at San Francisco Bay. *T. atratus aquaticus* possesses the higher value, suggesting broader contact of internasals and rostral. This is the terrestrial trait. Fitch (1940) shows a southward increase of R3 value in the subspecies *hydrophilus*. The data from this study

indicate a follow through of the aquatic-terrestrial cline to Areas A and B. South of San Francisco Bay there is an immediate return to *hydrophilus* values. This may be due to an overlooked factor influencing the two measurements used for R3.

Relative eye diameter and pupil size increase in terrestrial snakes (Bellemin and Stewart, 1977) (fig.12). Aquatic *Thamnophiines* are characterized by relatively small pupils (figs. 13 and 14) and pale irises. The pale irises enhance underwater visibility. Diurnal, terrestrial snakes (*Coluber*, *Masticophis*, *T. elegans*) have dark irises, believed to reduce sun glare. This character follows a north to south cline in *T. atratus*, approaching the terrestrial character. Fox (1951) diagnosed snakes from south of San Francisco Bay as having darker irises than *T. atratus aquaticus*. The increase in R6 to the south follows the expected pattern. The inland increase is discordant, considering the greater use of aquatic habitats by Area F snakes.

The coastward increase in IOW ($R7=0.397$ vs. 0.391) is consistent with increased terrestriality. The north to south increase is not as great (0.395 vs. 0.394), but remains consistent with the expected cline. Increased IOW is probably necessitated by increased prey size encountered by terrestrial snakes.

All cephalic proportions examined appear to vary in response to prey detection-consumption needs. Because the differences noted correspond to anatomical adaptations, they are valued as taxonomic criteria. Smith and Patton (1988) observed that "Cranial shape is... considered to represent underlying genetic influences and to identify more closely historical (phyletic) evolutionary units."

TEETH: No analysis of tooth counts was made for the present study. In Siskiyou Co., Rossman (1979) found *T. a. hydrophilus* to have from 21-27 maxillary teeth and 24-30 dentary teeth per side. Sympatric *T. elegans* had 14-17 and 16-18 teeth, respectively. The lower number in the terrestrial form may correlate with a shorter gape. Rossman believed the differences in tooth numbers was related to prey type. Variation in tooth number in *T. elegans* from various parts of its range corresponded to competition with different arrays of *Thamnophis* species. A skull of *T. atratus* from Area D has 14 maxillary and 22 dentary teeth, suggesting a change towards terrestrial characters from the subspecies

Fig. 12. Heads of *Thamnophis* top: *T. ordinoides*, SJSU 3013 Douglass Co., OR; middle: *T. elegans terrestris*, SJSU 3318 Santa Clara Co.; bottom: *T. atratus atratus*, SJSU 3356 San Mateo Co.

Fig. 13. Heads of *Thamnophis*. top: *T. atratus aquaticus*, SJSU 3035 Napa Co.; middle *T. a. hydrophilus*, SJSU 3002 Colusa Co.; bottom: *T. gigas*, MVZ 63883 Butte Co.

Fig. 14. Heads of *Thamnophis*. top: *T. couchii*, SJSU 5388 Lassen Co.; middle *T. hammondi* ssp, CPS 243 San Luis Obispo Co.; *T. hammondi*, SJSU 5362 San Bernardino Co.

hydrophilus. A clinal analysis of dentition is needed.

COLORATION: The north to south change from spotted to striped snakes in *T. atratus* takes place north of Areas A-G. Thus, all snakes examined are striped. Variations in lateral stripe intensity and ventral color seem to converge in Area D. As one approaches the Santa Cruz Mountains, dorsal stripe width increases, lateral stripe contrast decreases, and darkening of ventral surfaces increases (fig. 3b). Parallels to this color pattern occur in other regions. All three species of *Thamnophis* in western Washington exhibit increased melanism, warranting subspecific distinction in two of these (see Introduction). The photograph of *T. ordinoides* in Griehl (1982) shows color and pattern typical of *T. a. atratus*. This is also seen in two *T. atratus* (MVZ 48013 and 48016) from coastal Sonoma Co. In these, the dorsal stripe is narrow, and cephalic proportions are similar to the subspecies *hydrophilus*. Black sides and ventral melanism appear to be associated with heavily-forested habitats. The broad, bright dorsal stripe of Area D snakes is inconsistent with overall melanism. Sympatric *T. elegans* possess a narrow dorsal stripe (Bellemín and Stewart, 1977), but these favor coastal grassland-scrub. The increased dorsal stripe width of *T. atratus* may allow better visualization of this anti-predator device in poorly-lit habitats (see Ecology).

Aside from iris color, Fox (1951) discussed slight color differences between snakes north and south of San Francisco Bay. Area A and B snakes have a gray ground color, pale yellow dorsal stripe, and salmon midventral suffusion (fig. 4d). Area D-G snakes have abundant black suffusion on the dark fields, bright yellow to yellow-orange dorsal stripe, and yellow or yellow orange midventral suffusion (fig. 3d). The latter two color differences fade in preservative and were not quantified for this study. Area F snakes have more yellow in the pattern than any other *Thamnophis* examined. Two other Diablo Range endemics, the salamander *Ensatina eschscholtzi xanthoptica* and striped racer *Masticophis lateralis euryxanthus*, are diagnosed by increased yellow in their coloration (Stebbins, 1949; Riemer, 1954).

Dubious value has been placed on color differences, since changes can occur within few

generations and over short geographical distances. However, when differences in a variety of characters are correlated within homogeneous populations, taxonomic value can be assumed.

CANONICAL SEPARATION: Specimens from Area D were the most significantly differentiated from other Areas (mean Chi-square statistic=375.6). The most distinguishing character of Area D snakes is the STR value: 1.35 for Area D and 4.66 for Areas A,B,F,and G. V count is nearly identical (for males) between Areas D and G, but Area D mean (153.4) was lower than the mean for Areas A,B, and F (159.2). PSR counts in Area D are lower than all others: 15.0 vs. 15.6. For Area D, MDSW averages over one and two half scale rows (2.65) while the other areas average one and two half rows (2.04). Area D snakes are unique in having darkened SL and venters, lacking lateral stripes, having a broader dorsal stripe, lower V count (not distinct from Area G), and averaging fewer PSR. V count is a variable character, as it is influenced by the embryo incubation temperature (Fox, 1948b). Because V count can be significantly changed in a single generation, it has no value as a subspecific character, but is of value in combination with other characters to aid in diagnoses. PSR count is clinal in the species, but significantly different in Areas D and E from all other Areas, and lowest for the species. Although PSR and V counts may be manipulated by incubation temperature, they also represent a north-south cline opposing temperature limitations. This may reflect genetic influences not overcome by environment. These characters are not discretely different from other populations, and individual snakes cannot be diagnosed based only on scale counts. Coloration, however, is discretely different. The dark ventral and supralabial color, lack of lateral stripes, and broad dorsal stripe, in combination, are unique to Area D snakes (fig. 3b). All young of several broods of Area D snakes possessed this characteristic coloration, indicating that this pattern has been selected for in the past, and is now genetically fixed. The light, three-striped pattern is omnipresent in all broods examined from Areas A, B, and F. In Areas C and E the patterns are mixed. Because of their unique color pattern, and a combination of other character extremes, many of which may be genetically based, taxonomic recognition of Area D snakes is warranted.

Factor 2 for males and Factor 3 for females both separate Areas A-B from F-G. Characters separating the North and South Bay populations are not discrete. Area F-G snakes are longer (mean SVL=409.7 vs. 392.9; mean ED=3.05 vs. 2.84), have shorter tails ($R5=0.259$ vs. 0.267); fewer S (mean=78.8 vs. 83.3), and more pointed internasals ($R3=0.83$ vs. 0.93). All means for the preceding are for males. STR differs (4.92 for Areas F-G, 4.28 for Areas A-B), but it is thought to be caused by intergrade influences in coastal Marin Co. snakes. Females have significantly taller 6th SL in Areas F-G ($R1=0.80$ vs. 0.87). Although these and the aforementioned color differences are subtle, the fact that nine characters (see also Synopsis) distinguish North Bay from South Bay snakes indicates marked selective and isolation factors at work. Due to these differences, and the genetic distinctness of the two Area pairs (Lawson and Dessauer, 1979), taxonomic recognition for both is warranted.

Factor 3 of males and Factor 2 of females separate between Areas A and B. This is based on V (mean=157.1 vs. 161.1 for males), MDSW (mean=1.84 vs. 1.94), SVL (mean=380.3 vs. 407.4 for males), and ASR (mean=19.1 vs. 19.5). The coast vs. inland nature indicate that differences in V and ASR are climate-based and not taxonomically valid. Length is probably also based on climate, and the mean for Area A is biased by the "dwarfed" Dillon Beach sample. Although MDSW may be a valid diagnostic character, the wide overlap in values and minor difference between means prohibits taxonomic distinction between Areas A and B.

These Factors also separate Area F from G (mean V=159.5 vs. 153.3 in males; mean MDSW=2.21 vs. 2.00; mean ASR=19.5 vs. 19.3). The coast-inland nature is similar to the situation for Areas A and B, and the same arguments for taxonomic unity are valid.

INTERGRADES: Within the range of southern *T. atratus* are five areas of intergradation. In northwest Sonoma Co. some of the snakes show characters of *T. a. hydrophilus*. They have high V and S counts, occasionally lack lateral stripes, and have dark spots in the dark fields. Fox (1951) considered intergradation between the subspecies *hydrophilus* and *aquaticus* to be abrupt, both morphologically and geographically, occurring at the Gualala River. This is near the genetic shift point discussed under

Biogeography. A genetic study in this region is needed to determine the nature of contact at all points where the two forms meet.

Area C is composed of snakes intermediate in color and pattern between the subspecies *aquaticus* and the dark form of *atratus* (fig. 3a). The change is gradual from the Marin Peninsula to the San Andreas Rift Lakes. Some snakes from Half Moon Bay to Pescadero have faint stripes. This appears to be clinal intergradation, in which characters have shifted along a geographic gradient from one extreme to another. The ends of these extremes are homogeneous (at least morphologically) groups of populations.

Area E contains a mixture of snakes bearing character extremes, and others which are intermediate. The dark form of *atratus* occurs south to Uvas Canyon, while striped snakes overlap them north to the Los Gatos Creek drainage. At Uvas Canyon and upper Guadalupe Creek both forms have been found sympatrically, in addition to intermediates. Of 26 snakes from Area E and Guadalupe Creek, 38% are dark, 19% are striped, and 43% are intermediate. All snakes in the oak savannah below Uvas Canyon and south of the Santa Teresa Hills are the striped form. These are identical in color and pattern to snakes east of the Santa Clara Valley. The overlap of the two forms, in sympatry with intergrades, suggests recent secondary contact in Area E (see Biogeography).

The southwest side of the Santa Cruz Mountains, from Soquel Creek east, contains populations of nearly identical intergrade snakes. These have faint lateral stripes and slightly darkened venters (fig. 3c). It is probable that these snakes resulted from initial contact when the striped form reached the south end of the Santa Cruz Mountains. The intergrade zone may have broadened, creating a buffer from constant influence from the striped form. Also, the heavily forested summit may prevent the striped form from remaining in contact with most of these populations. There is some gradation, with snakes from the geographical extremes (Soquel Creek and Hecker Pass) increasingly resembling the dark and striped forms respectively.

Fox (1951) stated that "the transition from *aquaticus* to *atratus* [striped form] is gradual,...I have arbitrarily divided the two races at the San Francisco Bay." Fox's concept of the subspecies

aquaticus included the variable snakes occurring north to Trinity Co. He cited the four Solano Co. specimens as being intergrades because of enlarged supralabials and intermediate color. The large size of the supralabials is due to the fact that two were huge females (with enlarged salivary glands). One male has SL in proportion with *aquaticus*, and the other was not measured. All have gray ground color and narrow dorsal stripes as typical of *aquaticus*. These snakes are similar to Napa Co. snakes, and bear little resemblance to Area F snakes. Snakes from Contra Costa Co. are typical of the striped form of *atratus*. Unfortunately the subtle color differences between *aquaticus* and striped *atratus* are not evident in preserved specimens, and no fresh specimens from Contra Costa Co. were available for study. No snakes were seen in the Carquinez Straits region between Suisun Cr. and the Berkeley Hills. Until such snakes are examined, intergradation between the two forms remains theoretical.

Overall variation in southern *T. atratus* is consistent with color convergence with *T. elegans* suggested by Bellemin and Stewart (1977), and the hypothesis presented here is that the convergence is morphological, effected by ecological parameters.

ECOLOGY

At the north end of the range of *Thamnophis atratus*, the subspecies *hydrophilus* is highly aquatic (Fitch, 1940). Snakes from the San Francisco Bay region are semiterrestrial (Fox, 1951; pers. obs.). This ecological shift is thought to be the result of change in habitat, and competition with various combinations of other species of *Thamnophis*. It is further hypothesized that both color pattern and anatomical changes within *T. atratus* are ecologically related.

MACROECOLOGY: Southwest Oregon and northern California have an abundance of large rivers (Rogue, Applegate, Smith, Klamath, Shasta, Trinity, Eel, Mad, Navarro, Russian, etc.). Large numbers of *T. atratus* collected in these drainages by Fitch, Fox, and Rossman indicate their abundance there. The rivers are typically lotic all year, with rock, sand, or gravel beds. Snakes rarely venture far from these or smaller bodies of water (Fitch, 1940). Northern snakes bear the morphological characters ascribed to the aquatic group by Fitch. There are few large rivers or streams in the San Francisco Bay region (San Lorenzo, Coyote) and most are intermittent. Here, *T. atratus* has adapted to a semiterrestrial life style, and acquired some morphological characters of Fitch's terrestrial group. This is believed to result from changed requirements for survival and feeding. South of the Pajaro Gap large rivers are again prevalent (San Benito, Salinas, Carmel, San Antonio, Nacimiento, Cuyama, etc.). However, *T. atratus* has not taken up a highly aquatic life style here. The morphological differences between *T. a. atratus*, *T. a. aquaticus*, and *T. a. hydrophilus* (see Synopsis: *Thamnophis atratus*) may be related to these differences in habitat. Snakes adapted to a semiterrestrial life style would be reproductively isolated from the highly aquatic forms, and thus evolve independently.

Vegetation varies markedly between these habitats. Much of southwest Oregon and northern California is forested. Southward and inland, canopy vegetation is patchy in oak savannah-woodland,

and is often restricted to riparian strips. This is reflected in an increased coastward restriction of *T. atratus* distribution from north to south (fig. 15). In conjunction, color pattern shifts from drab, spotted to boldly-striped. The drab, spotted pattern is a camouflage advantage in gravel-bottomed streams. Snakes moving on the bottom of these are nearly invisible. I have lost sight of snakes, even though in plain view, as their pattern and sinuous movements blended with the gravel and riffles. However, a boldly-striped pattern might be detrimental to survival in such situations. *T. atratus* in Coyote Cr. were readily observed due to their contrasting pattern and bright colors. Striping is advantageous to terrestrial snakes as both camouflage in vegetation, and as an illusionary escape device. The dorsal stripe leaves the observer with a brief after-image posterior to the retreating snake, and I have found this to cause near or total misses in grabbing for snakes. Striping in these snakes, apparently detrimental in the water, is probably offset by its terrestrial advantage when streams dry up in summer (table 7). The intermittency of streams forces the snakes to be terrestrial for at least part of the year, hence the striping. The seasonal return to water is probably opportunistic. It is believed that color pattern has positive survival value, and is related to the marked habitat differences between northern and central California.

MICROECOLOGY: Southern populations of *T. atratus* are not wholly terrestrial due to both feeding and vegetative cover requirements. In the Santa Cruz Mtns. both prey and understory vegetation are widely dispersed. In the Diablo Range, aquatic prey and cover are restricted to riparian strips. Table 7 indicates a significant increase in riparian strip utilization in Diablo Range vs. Santa Cruz Mtns. snakes.

Four habitats in the range of southern *T. atratus* were sampled for garter snakes. These represent exemplary sites to demonstrate ecological interactions between *Thamnophis* species south of San Francisco Bay:

1) Ano Nuevo Pt., San Mateo Co: This is a low, coastal bluff, covered with coastal scrub, grassland, and several marshes. In two visits there, the following *Thamnophis* were observed: *T. elegans* 18 (65.0%); *T. sirtalis* 9 (31.5%); *T. atratus* 1 (3.5%).

Fig. 15. Distribution of aquatic (vertical) and terrestrial (horizontal) morphs of *Thamnophis atratus*. Bold lines enclose dense-canopy forest.

AREA D - Santa Cruz Mountains

months	$\leq 20m$	$> 20m$	total	
Oct.- Apr.	21	15	36	
May- Sept.	10	13	23	G = .718
total	31	28	59	

AREA E - Southeast slope, Santa Cruz Mountains

months	$\leq 20m$	$> 20m$	total	
Oct.- Apr.	30	15	45	
May- Sept.	87	29	116	G = .740
total	117	44	161	

AREA F - Diablo Range

months	$\leq 20m$	$> 20m$	total	
Oct.- Apr.	32	12	44	
May- Sept.	118	8	126	G = 10.352
total	150	20	170	

Table 7. Seasonal use of streams by *Thamnophis atratus*.

2) Upper Guadalupe Cr., east slope of the Santa Cruz Mtns., Santa Clara Co: This is an intermittent stream through dense-canopy, oak-laurel forest. From 1975 to 1986, 68 (89.5%) *T. atratus* and 8 (10.5%) *T. elegans* were found there.

3) Headwaters of Coyote Cr., Diablo Range, Santa Clara Co: This is a mixture of oak woodland-grassland, and chaparral. The stream is intermittent with variable canopy. In eight trips in which garter snakes were found, only 1 (1.2%) *T. elegans* was encountered. The remaining 80 (98.8%) garter snakes seen were *T. atratus*.

4) San Benito Co: Throughout the county, habitat varies from semiarid grassland, to oak-pine savannah, and chaparral. Aquatic habitats include permanent and intermittent streams, cattle tanks, and small reservoirs. Although ecologically similar to the Coyote Cr. sample, this area is distinct biogeographically, lying south of the Pajaro Gap. From 1973 to 1988 I observed 25 (73.6%) *T. sirtalis*, 5 (14.7%) *T. atratus*, and 4 (11.7%) *T. hammondi*.

In coastal California *T. sirtalis* is a lowland, semiterrestrial species, occupying a niche similar to that of *T. atratus*. However, their topographic preferences cause near allopatry. At locations of sympatry, one is markedly more abundant than the other, depending on topography. At Ano Nuevo Pt., Valencia Lagoon in coastal Santa Cruz Co., and streams in the Santa Clara Valley, *T. sirtalis* is the more abundant species. In upland habitats (Loch Lomond Res., Santa Cruz Co., and Arroyo Bayou and Del Puerto Can. in the Diablo Range) *T. atratus* is more abundant. South of the Pajaro Gap *T. sirtalis* is the abundant species irrespective of topography. This is probably a result of reversed arrival time during the Pleistocene. The Pajaro Gap would have prevented *T. atratus* from moving south into San Benito Co., until *T. sirtalis* had become established there via the San Joaquin Valley, prior to closure of the Pajaro Gap (see Biogeography).

Thamnophis elegans is terrestrial, and achieves its greatest abundance in dense understory in coastal lowlands. Because it and *T. sirtalis* are lowland species, occupying terrestrial and aquatic niches respectively, *T. atratus* is nearly excluded. The single specimen observed at Ano Nuevo was in a pond. It was not observed at the marshes along Pescadero Cr., although *T. elegans* and *T. sirtalis* were abundant

there. Immediately backing the coast here are the Santa Cruz Mtns. *T. sirtalis* becomes scarce as elevation increases, and I have seen only one individual in these mountains during 21 years of collecting. Eastward from the coast, the relative abundance of *T. elegans* and *T. atratus* shifts in favor of the latter. This follows a decrease in available canopy from the coast to the inner Diablo Range, producing an abundance gradient. Along the Skyline summit, northwest of Saratoga Gap, Santa Cruz Mountains, the few observations suggest a near equal abundance of the two species. On the eastern slope, the Guadalupe Creek survey shows a decrease in *T. elegans*. The Coyote Creek survey, representing maximal canopy for the Diablo Range, shows further decrease. *T. elegans* has not been found east of that locality.

Thamnophis hammondi, like northern *T. atratus*, is a highly aquatic species. It does not occur north of the Pajaro Gap, although suitable habitat is found there. Its presence south of the Pajaro Gap may prevent *T. atratus* from taking up a highly aquatic life style in the region's larger streams. Here, *T. atratus* is restricted to a semiterrestrial niche terrestrially above *T. hammondi*, and in close competition with *T. sirtalis*, hence its relative rarity.

Between 1969 and 1988, 417 *Thamnophis atratus* were observed in the field, south of San Francisco Bay. These were seen under the following conditions, in decreasing order of frequency:

in a stream or creek:	135 (32.4%)
DOR (dead on road):	75 (18.0%)
in a pond, cattle tank, or reservoir:	73 (17.5%)
abroad in a canopied area, away from water:	52 (12.5%)
under a surface object:	47 (11.3%)
abroad in riparian vegetation:	17 (4.1%)
AOR (alive on road):	11 (2.6%)
abroad in open grassland:	4 (1.0%)
hibernating:	3 (0.6%)

Half of those seen were in water.

SEASON: *Thamnophis atratus* is most common during four months, April through July (76%) (fig. 16). Because of more even temperature range, greater rainfall, and uniform canopy, Area D snakes are less cyclic in yearly activity. Area D snakes were found in more equal abundance during the cool-wet (October-April) and hot-dry (May-September) parts of the year (67% vs. 33%) than Area F snakes (usually encountered during the hot-dry period (76%)). The Diablo Range exhibits rapid drying of vegetation beginning in late April. Large numbers of snakes congregate in streams and riparian strips. Field observations reveal that activity of other reptiles decreases rapidly at the beginning of June. For *T. atratus*, the riparian vegetation provides necessary cover and supports prey. As streams dry, aquatic organisms are more easily located and captured in isolated pools. Many of the snakes seen in the streams were seen foraging on minnows and tadpoles. At Poverty Flat, on upper Coyote Creek, one *T. atratus* was observed on 10 April 1986. On 11 May, 25 snakes were seen, mostly in the water. It is believed that differences in distribution of canopy, water availability, and prey distribution cause the different activity cycle in Area D and F snakes.

FOOD: Quantitative feeding studies are unavailable because Fitch's (1940, 1941) concept of *T. atratus* included *T. elegans terrestris*. Fox (1952) found that *T. elegans* from Area F fed largely on banana slugs (*Ariolimax*), while snakes from Area C fed almost exclusively on microtines. James, Petrinovich, and Petrinovich (1983) found *T. elegans* in San Francisco feeding on *Zonotrichia* nestlings, *Microtus*, *Reithrodontomys*, and very small *Sylvilagus bachmani*. Fitch (1940) found 139 prey items in 96 *T. atratus hydrophilus* from throughout its range. Of these, 131 were fish and tadpoles. The remainder were adults of *Rana boylei*, a highly aquatic species. In the present study, *T. atratus* were not routinely checked for prey. Casual observations revealed only fish and amphibians. The presence of *Ensatina eschscholtzi* in one indicates some terrestrial feeding. Thus, southern *T. atratus* probably occupies a feeding niche different from northern conspecifics.

Mushinsky (1987) summarized the findings of numerous feeding studies of symmetric *Thamnophis*. The conclusion was that garter snakes are opportunistic feeders, exhibiting dietary shifts

Fig. 16. Monthly captures of *Thamnophis atratus*.

in proportion to relative abundance of sympatrics and available prey. Dietary shifts were noted in areas as small as Vancouver Island. Prey-type shifts in southern *T. atratus* could easily occur along the coastal California ecological gradient.

BIOGEOGRAPHY

Geographic distribution and variation patterns exhibited by *Thamnophis atratus* suggest a complex biogeographic history. Based on geological, geographical, fossil, morphological, and electrophoretic data, a hypothetical scenario for the derivation of varieties of *Thamnophis atratus* can be developed. In the following analysis, geographical history is derived from Howard (1962), Peabody and Savage (1958), Morafka and Banta (1972), and Yanev (1980). Ages are determined from geologic and electrophoretic data.

Thamnophis belongs to the tribe Thamnophiini of the Colubrid subfamily Natricinae. Origins and dispersal of the Thamnophiini are problematic. Malnate (1960) and Cadle (1987) agree that Bering Land Bridge dispersal during the Cenozoic was likely. No living or fossil Natricines are reported from South America, further supporting northern origins in the New World. Colubrids appeared simultaneously during the late Oligocene in North America and Europe. The earliest known Natricine, *Neonatrix*, appeared on both continents during the Miocene. Rossman and Eberle (1977) suggested that Old World Natricine karyotypes, scutellation, and cranial and hemipeneal morphology, were primitive, indicating east-to-west dispersal from Asia. It is probable that contact between Old and New World Natricines was broken at the late Miocene, since no genera were common to both land masses by the Pliocene (Holman, 1979). About 8 mya (million years ago) the New World Thamnophiini diverged from Old World Natricines (Mao and Dessauer, 1971; Dessauer, Cadle, and Lawson, 1987).

Fossil Natricines were present in the central U. S. from the middle Miocene (Holman, 1979). Fossil *Thamnophis* were not recorded until the late Pliocene, about 3-4 mya. No fossil *Thamnophis* are known from the western U. S., and no fossils of the *T. ordinoides* group, or possible ancestors have been found (Fitch, 1983, 1984; Kirk, 1979). However, biochemical evidence (Lawson and Dessauer, 1979) suggests that *T. ordinoides* group snakes existed 5.5 mya. The inferred presence of *Nerodia* (= *Thamnophis*) *valida* on the Baja California cape about 10 mya suggests an earlier existence

(Murphy, 1983). Lawson (1987) indicates that this species and *T. couchii* were separate at least 5.6 mya. In spite of lack of fossil evidence, it is probable that primitive *Thamnophis* existed in the western U. S. 6 or more mya. Because the *T. ordinoides* group is endemic to western North America, and other *Thamnophis* species (*T. marcianus*, *T. sirtalis*) appear to have originated on the Great Plains, primitive *Thamnophis* to the west were probably directly ancestral to the *T. ordinoides* group.

At the beginning of the Pliocene, 12 mya, the central California Coast Ranges formed a continuous chain. The Sierra Nevada crest was at about 3000 feet. The Arcto- and Madro-Tertiary geofloras connected to form modern floral assemblages (Axelrod, 1958). Ten mya, much of central California was flooded by inland seas, which had maximal extent at this time. Higher mountains existed as islands, and those west of the San Andreas Fault were located about 200 miles south of the present location. The northern Diablo and Santa Cruz Ranges were not yet uplifted. For the next 10 million years, a series of uplifts, faulting, flooding, and climatic changes in the central Coast Ranges determined the biogeography of the regions herpetofauna.

Eight mya an inland sea extended from near Mt. St. Helena to the north end of the Transverse Ranges (fig. 17). Recently uplifted points of the southern Diablo Range were insular and probably lacked snakes. Through uplift, the Gabilan and Santa Lucia Ranges were reconnected with the Transverse Ranges. The early-derived forms of the *T. couchii* complex (*T. couchii* and *T. hammondi*) are drab, aquatic snakes and this was probably true of the ancestral form of the complex. Such snakes probably occurred throughout the Sierra Nevada and mesic environment to the east. The current presence of drab, aquatic snakes in the Santa Lucia Range suggests that mainland snakes repopulated the Santa Lucia-Gabilan block.

Five mya, northward movement west of the San Andreas fault separated the Santa Lucia-Gabilan block from the Transverse Ranges, opening the Purissima Sea (fig. 18). The Marin Peninsula was uplifted southward enough to include the San Francisco Peninsula. High points in the southern Diablo Ranges uplifted and interconnected. The *T. couchii* complex differentiated from *T. elegans* about 4.6 mya (Lawson and Dessauer, 1979). Fox (1951) believed this took place in the Siskiyou

Fig. 17. Central California 8 million years ago. Shading represents distribution of ancestral *Thamnophis couchii*. SF=San Francisco present location.

Fig. 18. Central California 5 million years ago (see Fig.17).

region.

Four mya a cooling, drying trend possibly halted movement of *T. couchii* into the northern California Coast Ranges from the Sierra Nevada. The Mojave Desert was established, isolating California snakes from genetic flow south and east. Uplift of mountains and northward movement west of the San Andreas fault continued.

At the beginning of the Pleistocene, 2.5 mya, the Purissima Sea was dried by uplift (fig. 19). The Merced Sea was also reduced and its outlet through the Pajaro Gap provided the only break in the Coast Ranges. *T. atratus* evolved from *T. couchii* at the Sierra Nevada-Cascade interface about 2.8 mya. In the following 2 million years cyclical warming-cooling allowed southward dispersal of primitive *T. atratus* to the Pajaro Gap. In what is now the North Bay and San Francisco Peninsula, a striped, semiterrestrial morph developed in response to decreased forestation and reduced stream size. This morph differentiated from *T. atratus hydrophilus* about 0.7 mya, perhaps at a genetic/morphologic shift zone running east-west through the Gualala-Mt. St. Helena region. Species affected at this zone include *Dicamptodon* (D. Good, pers. comm.), *Ensatina* (Wake and Yanev, 1986), *Rana aurora* (Green, 1985), *Elgaria coerulea* (Fitch, 1935), and *Diadophis* (Blanchard, 1942). Several taxa reach their southmost distribution here although suitable habitat occurs farther south: *Taricha rivularis*, *Ambystoma gracile*, *Aneides ferreus*, and *Aneides flavipunctatus flavipunctatus* (Stebbins, 1985). It is also the southmost extent of intergradation between *T. a. hydrophilus* and *T. a. aquaticus* (Fox, 1951).

The striped snakes extended southward on two fronts. Along the forested, outer coast, a dark morph extended through the San Francisco Peninsula and Santa Cruz Range to the Pajaro Gap. Snakes in the inland mountains retained the original, striped pattern. Uplift of the northern Diablo Range within the next million years allowed for dispersal of the striped morph south to the Pajaro Gap (fig. 20).

About 1 to 0.5 mya the Sierra Nevada crest was uplifted to over 10000 ft, causing a shift in drainage patterns. In response, the outlet of the remnant Merced Sea shifted northward (fig. 21). This was facilitated by volcanic uplift in the Pajaro region. The new Golden Gate outlet separated the San

Fig. 19. Central California 2.5 million years ago shading: *T. couchii*; diagonal lines: *T. hammondii*; vertical lines: *T. atratus*

Fig. 20. Distribution of *Thamnophis atratus* 1 million years ago. Shading represents increased darkening or lightening of snakes.

Fig. 21. Distribution of *Thamnophis atratus* 0.5 million years ago. Shading represents increased darkening or lightening of snakes.

Francisco and Marin Peninsulas, and inner Coast Range. This shift separated both the dark and striped morphs at the San Francisco Bay, but allowed the striped morph to extend further south in the Diablo and Gabilan Ranges. *T. hammondii*, which differentiated from *T. couchii* in the southern Sierra Nevada 1.7 mya, had moved northward after the closure of the Purissima Sea. The paucity of large streams in the San Francisco Bay area may have prevented *T. atratus* from returning to a highly aquatic ecotype, similar to *T. a. hydrophilus*. The presence of the aquatic *T. hammondii* in the central Coast Ranges may have prevented *T. atratus* from returning to an aquatic ecotype there, although larger rivers (Salinas, San Antonio, Carmel, Nacimiento) are present south of the Pajaro Gap.

Within the past 0.5 million years, the striped morph has reached the Santa Lucia Range via the Salinas River (fig. 21). *T. atratus* has not been collected in the lower Salinas Valley, and the Santa Lucia and Gabilan populations are presently separated.

Intergradation between the dark and striped morphs on the Marin Peninsula was broken by the opening of the Golden Gate. This explains the presence of intergrades on the north San Francisco Peninsula. At one time the Santa Clara Valley separated the dark and striped morphs. Intergradation at the south end of the Santa Cruz Range suggests secondary contact, resulting from cross-valley invasion by the striped morph (fig. 21). This situation is reflected in several other species. Hjelle (1972) described a new subspecies of the scorpion *Uroctonus mordax* from the Santa Cruz Range. However, the Diablo Range race occurs in the Uvas area. This is also the situation with the Diablo Range subspecies of *Ensatina eschscholtzii*. D. B. Wake (pers. comm.) points out that salamanders from the southeast slope of the Santa Cruz Range resemble those from the Diablo Range rather than the remainder of the Santa Cruz Range. The southeast slope is also the only part of the Santa Cruz Range reached by *Pinus sabiniana* (R. Myatt, pers. comm.). It is suggested here that within the past 0.5 million years, possibly during one of the recent glacial maxima, there was a cross-valley mesic environment. This apparently allowed unidirectional flow of Diablo Range animals to the southeast flank of the Santa Cruz Range.

The Salinas Valley presents a similar problem. Faintly-striped snakes from the southwest side of the Santa Cruz Range suggest genetic flow from the south. Yanev (1980) found a similar situation between *Batrachoseps attenuatus* and *B. pacificus*. Their contact zone was the interface between the Santa Cruz Range and Monterey Bay lowlands. This geographic pattern is also seen in *Taricha torosa* (Hedgecock and Ayala, 1974), *Diadophis* (Blanchard, 1942) and *Pituophis* (pers. obs.). Aside from reasons given under Discussion: Intergrades, *Thamnophis atratus*, within the past 0.5 million years, may have had access across the lower Salinas Valley, allowing the dark and striped morphs to intergrade.

TAXONOMIC CONSIDERATIONS

The multivariate analysis has demonstrated various character weights and combinations between the seven southern population groups of *Thamnophis atratus*. The degrees of differentiation theoretically correspond to different taxonomic levels. Fox's (1951) proposal of two subspecies, separated by San Francisco Bay, is found to be correct in a broad sense. However, geographic variation within these subspecies suggests that a taxonomic reinterpretation is necessary.

Rossman and Stewart (1987) elevated four taxa in the *couchii* complex to species status. This is corroborated by biochemical analysis (Lawson and Dessauer, 1979). However, their proposals have not received full acceptance (H. W. Greene, pers. comm.). To propose nomenclatural changes for any of the *T. atratus* populations, the status of the *couchii* complex taxa must be established.

Mayr's (1941) suggestion that the *ordinoides* group comprised at least three species has been confirmed, as outlined in my introduction. In the following discussion I rely on his concepts of subgeneric classification. His discussions of species definitions (1963, 1976) indicate that several criteria are broadly accepted by systematists: morphological distinctness, genetic distinctness, and reduced hybridization. Rossman and Stewart found significant morphological distinctness at contact zones. These zones correspond to stepped clines defined by Endler (1977). *T. a. atratus* is as different morphologically from *T. a. hydrophilus* as the latter is from *T. couchii* at their contact zone (see Synopsis). Mayr (1976) suggests that such variation would not justify species status in itself, as intraspecific variation may be as great, or greater, than interspecific variation. This is the case with *T. atratus* and *T. couchii*.

Lawson and Dessauer found multiple levels of genetic differentiation in the complex. *T. atratus* and *T. couchii* were separated by Nei distance = .14, and contained paired subclades. These were separated by Nei distance = .07 - .09. Although Arnold (in Lawson and Dessauer) showed that the different taxa hybridize readily in captivity, Rossman and Stewart found relatively few hybrids at any of

the contact zones. This suggests that, under natural conditions, there is a high degree of reproductive isolation. Thus, hybrid zones have become established within the *couchii* complex, but hybridization has diminished through some isolating mechanism(s). Endler proposed that after such isolating mechanisms have evolved, speciation has completed. Based on the cumulative genetic evidence, Dessauer, Cadle, and Lawson (1987) considered all four taxa to be specifically distinct. This, combined with the morphological evidence, affirms that the taxa correspond to multidimensional species as defined by Mayr (1963). Thus, unless further zones of genetic isolation are located, the variation indicated by the multivariate analysis corresponds to infraspecific levels within the species *T. atratus*.

No discussion of the *couchii* complex has failed to mention its clinal nature. Rossman and Stewart believed *T. a. aquaticus* represents a broad zone of intergradation between northern and southern extremes of variation. Mayr (1963) stressed that species consist of genetically interacting populations along a geographic dimension. Endler (1977) expanded on this concept, defining modes of genetic speciation among such populations. Endler supposed that, through genetic drift, most species are polytypic over a geographic area. They are, therefore, composed of subspecific, genetically distinct units, encompassing a given number of their populations.

A number of subspecific categories have been proposed: race, variety, morph, semispecies, deme, subspecies, etc. Only subspecies rank has achieved taxonomic recognition. Mayr (1963) defined a subspecies as "an aggregate of local populations of a species, inhabiting a geographic subdivision of the range of the species, and differing taxonomically from other populations of the same species." He cautioned that each population may differ from each other and, therefore, a subspecies may itself be polytypic. Thus, there may be a continuum of levels of differentiation within a species.

Unequal levels of variation in species have been difficult to categorize taxonomically. Yanev (1980) found different levels of molecular variation in *Batrachoseps*. The *B. pacificus* complex contained six genetic varieties which had diverged at different times. Several were phenotypically identical and genetically similar. Others, having diverged earlier, were morphologically distinct, and separated by greater Nei distance. She considered these latter forms to be semispecies. Wilson and

Meyer (1983) discussed the division of *Lampropeltis triangulum* into 25 subspecies. They believed the species contained three primary pattern types: saddled, cross-banded, and ringed. Each of these had been subdivided into additional subspecies on the basis of head patterns, band widths, and combinations of each. Such combinations are the basis for all seven subspecies of *L. zonata* (Zweifel, 1952). None of these is based on anatomical or confirmed genetic differences. This situation is in contrast to the patternless *Coluber constrictor*, represented in the western United States by a single subspecies. Wilson and Meyer suggest that pattern variation may provide artificial evidence for genetic variation. They, and Blaney (1977), arranged morphotypes on phenograms. The levels at which morphotypes branched were assigned a rank from slightly differentiated local populations to primary species subclades.

A uniting argument in the preceding studies is that a single infraspecific taxonomic unit does not adequately describe the full range of variation within a species. Wilson and Meyer took a conservative approach by refusing taxonomic recognition to weakly differentiated populations. They elected instead to describe in detail the geographic trends in variation within fewer, well-defined subspecies.

The delimitation of subspecies is problematic. Wilson and Brown (1953) outlined four situations which make delimitation difficult: 1) independently diverging characters; 2) recurrence of a character in widely separated populations; 3) microgeographic races; and 4) arbitrariness of character weights. To these I add: 5) phenotypically homogeneous intergrade populations; 6) smooth, non-stepped clines.

On the West Coast, *Thamnophis sirtalis* demonstrates independent divergence. Snakes nearest the coast are red-headed while those inland are black-headed. Overall melanism increases towards the north (pers. obs.). This creates a geographic quad, with dark, red-headed snakes to the northwest, lighter, black-headed snakes to the southeast. In *T. atratus*, the narrow north-south distribution, and biogeographic events have restricted gene flow, chiefly, to a single axis. Most of its variation is restricted, therefore, to a single cline.

Disjunct character recurrence is exemplified in the salamander *Plethodon jordani*. Distinct morphs recur on certain mountaintops while others are scattered in intervening lowlands. Highton (1962) did not recognize any of eight described subspecies, due to the nonsequential nature of the variation. The *T. couchii* complex exhibits a continuous, though punctuated cline, and disjunction is unrecorded.

The pocket gophers, *Thomomys*, exhibit extreme microgeographic variation. Hall and Kelson (1959) assign 300 subspecies to 6 species in western North America. The multivariate analysis, and character means, show that southern *T. atratus* is phenotypically homogeneous in annectant populations, divided among no more than three or four forms.

Counts of ventrals and subcaudals were once given priority in studies of geographic variation (VanDenburgh and Slevin, 1918, 1919). However, Fox, Gordon, and Fox (1961) demonstrated that these characters may not be genetically based, but could be controlled by temperature. A significant change in counts was created in a single generation of offspring. It would be appropriate that characters leading to, or resulting from, reproductive isolation should receive greatest weight in variation studies. In *T. atratus*, the change in cephalic structure, scutellation, and pattern is correlated with the genetic shifts outlined by Lawson and Dessauer (1979).

In any directional cline, differentiation may be so gradual as to be imperceptible from population to population. This results in distinctive subspecies at the geographic extremes, with a broad zone of intergradation between. Most clines, however, are stepped (Endler, 1977), leaving zones of apparently homogeneous intergrade populations. Species often have such phenotypically similar populations sectioned into blocks. These are intermediate between adjacent blocks, but with narrow intergrade zones separating them. The intermediate blocks comprise valid subspecies, as with *Lampropeltis getulus* and *L. triangulum* (Williams, 1978, Blaney, 1977). Some intergrade zones may be so broad as to have received subspecific status. The "Florida kingsnake" and "coastal plain milksnake" are examples. Each represents continuous, non-stepped clines, between homogeneous subspecies, and are true phenotypic intergrades.

Rossman and Stewart (1987) suggest that *T. a. aquaticus* represents a broad, clinal intergrade between *T. a. atratus* and *T. a. hydrophilus*. During my preliminary examination of snakes from north of San Francisco Bay, I found that those from immediately north of the Bay more closely resembled *T. a. atratus* than adjacent populations in Mendocino and Lake Counties. There appears to be a rapid shift in certain characters in this region, so that *T. a. aquaticus* may be dimorphic north to south. This is detailed in the account following *T. atratus* (see synopsis). Lawson and Dessauer found *T. a. aquaticus* to be genetically similar to *T. a. hydrophilus* (Nei distance = .011). They did not specify which population was sampled for that particular analysis. The broad cline suggested by Rossman and Stewart may be stepped within. The snakes from immediately north of the Bay (my Areas A and B), together with *T. a. atratus*, form a closely related subgroup, perhaps a semispecies. The relationship of northern "*aquaticus*" requires further study.

The preceding arguments dealt with the difficulty in categorizing multidimensional, continuous evolutionary processes. At present, southern *T. atratus* is a polymorphic species, containing several recognizable, intergrading population groups. Although these may warrant taxonomic status, there has been a recent deemphasis on subspecies recognition (Frost and Vandevender, 1979, Stebbins, 1985). Any taxonomic proposal must, therefore, be justifiable.

There are several benefits to recognizing subspecies. Many species are widely distributed, occurring in a variety of ecological conditions. Life histories are variable within such species (Fitch, 1985). Because subspecies boundaries are often geographically and ecologically based, certain life histories would be unique to each. Species with such variable life histories are more easily studied when divided into ecotypic subspecies (Jameson, Mackay, and Richmond, 1966).

Formal taxonomic proposal requires careful research and preparation. Modern pre-publication review process eliminates proposals which may have been hastily executed. It also provides an opportunity for constructive insight by other specialists. The casual reference to a species as being polymorphic serves no purpose other than to suggest that further study is needed. Known geographic variation should be defined and diagnosed. Karl Jordan (1896) proposed "...the study of localized

varieties is of the greatest importance in respect to the theory of evolution: the study of geographic races or subspecies or incipient species is a study of the origin of species."

The variation found within southern *T. atratus* warrants that the three recognizable population groups be awarded subspecific status: *T. a. atratus* of the Santa Cruz Mountains, *T. a. aquaticus* of the North Bay region, and an unnamed subspecies in the Diablo and Santa Lucia Ranges. This form is named and diagnosed in the following section.

SYNOPSIS

Data provided in the following accounts are taken from specimens at SJSU, CPS, CAS, and MVZ, and, from published accounts, chiefly, VanDenburgh and Slevin (1918), Fitch (1940), Fox (1951), and Rossman and Stewart (1987). A summary of characters for the *T. couchii* complex is provided in table 8. Distribution of the complex is shown in fig. 22. A key to the taxa is provided at the end of this section.

Thamnophis couchii, Sierra Garter Snake

Eutaenia couchii Kennicott, 1859:10 Type locality: "Bank of Pit river, California" (probably near the mouth of Hat Cr., Shasta Co., according to Fitch, 1940:59) Holotype: USNM 866

Diagnosis: maximum total length: 1062 mm; ventrals, males: 166-187 (mean 174.6, n=68), females: 161-178 (mean 169.4, n=86); subcaudals, males: 84-99 (mean 91.6, n=48), females: 72-88 (mean 79.9, n=67); ASR 21, rarely 23; MSR 21, rarely 19; PSR 17; SL 8, rarely 9; IL 10 (37%) or 11 (63%); preoculars 1 (76%) or 2 (24%); dorsal stripe obscure and narrow, present anteriorly; lateral stripes prominent; dark fields gray to olive, covered by alternating black blotches which overlap at the corners; muzzle relatively pointed (MW/ML mean = 0.89); eye and pupil relatively small (ED/FL mean = 0.66); top of head dark, with paired, dark neck blotches; parietal spot present: pre- and postoculars light; pale crescent at the corner of the mouth extends to the temporals; broad, dark crescents present on SL sutures; suture between SL 6 and 7 nearly vertical, failing to bisect eye when projected; venter dusky-brown, often salmon-tinted; dark markings present on the ventral sutures; tail moderately long, 25.3% TTL in males, 23.6% in females.

	pattern	maxTTL	V	V	S	S	S	SR	IL	P/O	MW/HL	ED/FL	TL/TTL
			♂	♀	♂	♀	♀						
T. couchii	ep; int	1062	174.5	169.4	91.6	79.9		21-21-17	11 N 10 S	1	.89	.66	.253 .236
T. ditueti	none	856	159.9	154.4	70.6	64.7		23-21-17	10	2	—	—	.237 .218
T. hammondi	int	1068	168.4	162.3	81.2	71.5		21-19-17	10	2	1.00	.73	.229 .210
T. hammondi esp.	ep	1016	170.0	163.8	80.0	71.9		21-19-17 21-21-17	10	2	—	.64	.233 .220
T. giles	etr N; ep S	1626	162.4	157.6	76.3	70.0		23-21-17	10	1	.96	.64	.243 .218
T. a. hydrophilus	ep; int; etr	916	163.6	159.0	87.5	76.3		21-19-17 19-19-17	10	1	.99	.65	.268 .250
T. a. aquaticus	int; etr	875	159.9	150.5	82.9	74.4		19-19-15	10	1	—	—	.267 .244
T. a. atratus	etr	1016	154.2	147.0	79.4	70.3		19-19-15	10	1	—	—	.262 .241
T. a. zexanthus	etr	902	157.6	151.8	79.3	71.4		19-19-15	10	1	—	—	.259 .242

ep = spotted; etr = etriped; int = spotted and striped; MW/HL = muzzle width over muzzle length; ED/FL = eye diameter over frontal length

Table 8. Characteristics of members of the *Thamnophis couchii* complex.

Fig. 22. Distribution of the *Thamnophis couchii* complex. red: *T. couchii* ; blue: *T. hammondi* ; gray: *T. gigas* ; orange: *T. digueti* ; yellow: *T. atratus*.

Variation (n=313): Variation was analyzed on a north-south axis, using three population groups: Kern Co. to Madera Co. (S), Tuolumne Co. to Nevada Co. (C), Plumas Co. to Shasta Co. (N). The following clinal trends were noted from south to north: mean TL decreases (0.266, 0.242 in S for males and females respectively, 0.245, 0.230 in N); ventrals increase (171.9, 168.3 in S, 178.2, 172.4 in N); subcaudals decrease (92.6, 80.0 in S, 89.8, 76.1 in N); MSR increase (21 in 46% of S, in 96% of N); IL are usually 10 in S and C, 11 in N; anterior genial length increases ($AG/PG = 0.85$ in S, 0.99 in N); eye diameter decreases ($ED/FL = 0.69$ in S, 0.65 in N); the muzzle is more pointed in northern snakes ($MW/ML = 0.93$ in S, 0.86 in N). Of these eight characters, the south to north trend is followed through into *T. a. hydrophilus* only by eye diameter and subcaudal count. The others are reversed at the Pit River contact zone between the two taxa. All characters but TL and S are followed through into *T. hammondii* from *T. couchii* S. Eye diameter is the only character which follows a continuous cline from *T. hammondii* to *T. atratus*, via the Sierra Nevada.

There may be a step within the cline of *T. couchii*, but my data are incomplete for C. Relative TL, though intermediate between N and S, is closer to the latter. V are closer to N, while IL and S are not significantly different from S. There is a north-south difference in color pattern. Northern snakes have a dorsal stripe continuous to the tail, and moderately distinct lateral stripes. Dark markings are extensive on the ventral sutures, and the throats are whitish to dusky. Snakes from the vicinity of Fresno, south, usually have a faint dorsal stripe, visible only on the neck, distinct, yellow lateral stripes, reduced black on the venter, and yellow throats. They bear a strong resemblance to *T. hammondi*.

Snakes from the Owens Valley may have dark spots on an overall dusky ground color, with indistinct stripes (MVZ). Few snakes were seen from this area to determine if this is typical.

Distribution (fig. 23): The Sierra Nevada region; occurs north to the Pit R. above Deep Cr., Shasta Co., and west to the Sacramento R. in Tehama Co.; occurs on the east edge of the Central Valley near Chico, Butte Co., Fresno, Fresno Co., and Porterville, Tulare Co.; occurs east of the Sierran Crest along the Susan R., Lassen Co., Lake Tahoe, the Truckee, Carson, and Walker Rivers into Nevada, and

Fig. 23. Distribution of *Thamnophis couchii* in California.

the Owens R., Inyo Co.; occurs along the Tehachepi crest to Cuddy Valley, Ventura Co., and Gorman, Los Angeles Co. (San Andreas rift zone). Snakes were collected at Fresno in the 1890's, and near Porterville in the 1930's. Restricted water flow in the Kaweah, Kings, and Kern Rivers has probably led to their extirpation on the east side of the San Joaquin Valley. The Owens R. population is nearly extinct (R. E. Macey, pers. comm.).

Thamnophis hammondi, Two-striped Garter Snake

Eutainia Hammondi Kennicott, 1860: 332 Type locality: "Fort Tejon" "San Diego"; restricted to the latter by Fitch, 1940: 73. Lectotype: USNM 894

Diagnosis: maximum total length, 1068 mm; ventrals, males: 160-179 (mean 168.4, $n=45$), females: 156-171 (mean 162.3, $n=38$); subcaudals, males: 74-88 (mean 81.2, $n=29$), females: 62-78 (mean 71.5, $n=22$); ASR 21 (44%), 23 (26%), 22 (26%), rarely 20; MSR 19 (59%), 21 (26%), rarely 20; PSR 17, rarely 15 or 16; SL 8; IL 10, rarely 9 or 11; preoculars equally 1 or 2, rarely 3 (single preoculars are often creased or incompletely divided); dorsal stripe absent; lateral stripes prominent, often bright yellow; dorsum gray, brown, or olive; a row of small, dark spots above the lateral stripe, and occasionally a row of smaller spots alternating above these; muzzle moderate in width ($MW/ML = 1.00$); eye and pupil moderate or large ($ED/FL = 0.73$); top of head gray brown with paired, black neck blotches, smaller than in *T. couchii*. parietal spot present; pale area at angle of mouth fails to reach the temporals; preoculars and lower postocular pale; narrow, dark marks present on some SL sutures; suture between SL 6 and 7 slants towards eye; venter pale gray or dusky, often with a yellow or pink tint; throat yellow; dark marks at ventral sutures reduced or absent; tail relatively short, 22.9% TTL in males, 21.0% TTL in females.

Variation (n=297): Snakes from the Santa Lucia Mtns. are markedly different in morphology and coloration. These are described as *T. hammondi* ssp. in the next account.

To analyze variation, typical *T. hammondi* was divided into southern (S = San Diego Co. to Los Angeles Co.) and northern (N = San Luis Obispo Co. to San Benito Co.) population groups. South to north clinal variation was noted for the following characters: relative tail length decreases (TL/TTL mean .236 and .223 in S for males and females, respectively, .225 and .213 in N); subcaudals decrease (mean 87.2 males, 72.2 females in S, 77.9, 70.0 in N); MSR decreases (21 in 46% of S, 21 in 6% of N); 6th SL squared in N ($R^2 = 1.00$), taller than wide in S ($R^2 = 0.87$); preoculars are less frequently divided (60% S, 40% N); snout blunter in N ($R^2 = 0.61$, $R^3 = 0.86$ in N, $R^2 = 0.52$, $R^3 = 0.79$ in S); posterior chin shields longer in S ($R^4 = 0.77$ in S, 0.81 in N); sides of frontal more nearly parallel in N (PF/AF = 0.85 in N, 0.66 in S); frontal and parietal more nearly equal in length in S (F/P = 0.91 in S, 0.83 in N); eye larger in S (E/G = 0.22 in S, 0.20 in N); head wider in S (IOW/G = 0.38 in S, 0.36 in N).

Values for R^2 , R^4 , F/P, eye size, and head width suggest that northern snakes bear cephalic proportions similar to *T. couchii*. Southern snakes show affinity towards that species only in possessing narrower muzzles (R^2 , R^3). Color and pattern were not noted to vary between N and S. The chief difference noted within populations was size of dorsolateral, dark spots. A specimen from Avalon, Catalina I. (CAS 63080) is unstriped.

Distribution (fig. 24): The southern Coast, Transverse, and Peninsular Ranges; occurs north along the Salinas R. to near Salinas, Monterey Co. and San Benito R. to the Pinnacles region, San Benito Co. This form is absent from the Santa Lucia Mtns., and I have seen none from west of the Salinas R. The northernmost coastal occurrence is in the Oso Flaco region, San Luis Obispo Co. It extends east into arid lowlands along semipermanent streams above Coalinga, Fresno Co., San Juan R., San Luis Obispo Co., desert slope of San Gabriel Mtns., Mojave R. near Victorville (probably no longer due to flow reduction; at least to 1936), Whitewater Can. and desert slope of San Jacinto-Santa Rosa Mtns., Riverside Co., and Sentenac Can., San Diego Co. Coexistence with *T. couchii* is in Cuddy Valley,

Fig. 24. Distribution of *Thamnophis hammondi* in California.

Ventura Co. (San Andreas rift). The only insular specimen, from Avalon, Catalina I., was collected in 1929. It is extirpated from many lowland areas of southern California (Stebbins, 1985). Most Baja California records are from the Rio Santo Domingo and Sierra San Pedro Martir. CAS 147723-24 are from San Pedro de la Presa in Baja California del Sur, nearly 500 miles south of the Rio Santo Domingo.

Thamnophis hammondi ssp., "nostripe garter snake"

Diagnosis: maximum total length, 1016 mm; ventrals, males: 167, 173 (n=2), females: 156-168 (mean 163.8, n=12); subcaudals, males: 79, 81, females: 68-75 (mean 71.9, n=11); ASR 21 (54%) or 23 (46%); MSR 19 (46%), 20 (8%), or 21 (46%); PSR 17, rarely 16; IL 10; preoculars 2 (80%) or 1 (20%); stripes absent; ground color olive-brown, with two rows of prominent, separated, black spots on each side; venter dusky, darker than typical of the two-striped form; cephalic proportions are similar to those of *T. hammondi*, except for a smaller eye ($E/G=0.18$ vs. 0.20); parietal spot faint or absent; tail moderate in proportion, 23.3% TTL in males, 22.0% TTL in females.

Variation: (19 specimens examined); a photograph of a brood of 25 snakes showed pattern variation only in the relative size and intensity of the dorsal dark spots (A. Ford and W. Hutchins, pers. comm.). This is reflected in preserved adults examined from throughout the range, but no quantitative analysis was made. A juvenile (CAS-SU 7602) from near Big Sur shows faint lateral stripes. The two largest females examined were overall dusky, with an indistinct pattern. CPS has several snakes that appear to be intergrades between this and the two-striped form. These have faint lateral stripes, darker ventrals than typical *T. hammondi*, and some have enlarged, nearly connected, dorsolateral spots.

Distribution (fig. 24): Permanent or semipermanent streams in the Santa Lucia Mtns., Monterey and San Luis Obispo Cos.; occurs north to the Carmel R. and south to the vicinity of Lopez Can.; No *T. hammondi* have been examined from the west side of the Salinas Valley. Apparent intergrades between the two forms have been seen from the upper Salinas R. and east of Arroyo Grande.

Thamnophis digueti, San Ignacio Garter Snake

Tropidonotus Diguetei Mocquard, 1899: 327 Type locality: "L'un des specimens provient de Mulege; les cinque autres de San Ignacio" (restricted to San Ignacio, Baja California del Sur, by Fitch, 1940: 81)
Syntypes: the five San Ignacio specimens at the MNHN.

Diagnosis: maximum total length 856 mm; ventrals, males: 155-170 (mean 159.9, n=8), females: 149-158 (mean 154.4, n=15); subcaudals, males: 65-74 (mean 70.6, n=5), females: 62-68 (mean 64.7, n=12); ASR 21, 22, or 23 (mean 22.2); MSR 21, rarely 19 or 20; PSR 17; SL 8, rarely 9; IL 10, rarely 9 or 11; preoculars 2, rarely 1 or 3; dorsal stripe absent; lateral stripe indistinct from ventral color; dorsum uniform olive; venter lighter, offset from dorsal color at 3rd scale row; dark spotting reduced or absent; muzzle moderately pointed; eye and pupil relatively small; top of head uniform olive or olive-gray; dark supralabial suture marks reduced or absent; parietal spot and neck blotches absent; tail moderately long, 23.7% TTL in males, 21.8% TTL in females.

Variation: (34 snakes examined): All but two of those examined are from San Ignacio. Variable intensity of a faint, anterior lateral stripe was noted. In none of the snakes did it approach the bright yellow found in *T. hammondi*. The two snakes from Comondu resembled *T. hammondi* in having a faint lateral stripe and small, black spots immediately above the lateral stripes. One of these, MVZ

13782, is badly darkened by formalin. Additional specimens from this locality may show it to be an intergrade population between *T. diqueti* and *T. hammondii*.

Distribution (fig. 22): Permanent water in the Sierra de la Giganta, Baja California del Sur.

Thamnophis gigas, giant garter snake

Thamnophis ordinoides gigas Fitch, 1940: 69 Type locality: "Gadwall, Merced County, California"

Holotype: MVZ 5428

Diagnosis: maximum total length 1626; ventrals, males: 157-168 (mean 162.4, n=16), females: 150-164 (mean 157.6, n=33); subcaudals, males: 73-81 (mean 76.3, n=11), females: 65-73 (mean 70.0, n=22); ASR 21 (33%) or 23 (54%), occasionally 22 or 24; MSR usually 21; PSR usually 17; SL usually 8; IL 10 (67%) or 11 (28%), rarely 9 or 12; preoculars 1, rarely 2; dorsum brown with two rows of alternating, dark spots on each side, the intensity of which varies; stripes distinct to indistinct (see variation); top of head brown; paired neck spots reduced in size; parietal spot absent; labial dark suture marks reduced; suture between 6th and 7th SL near vertical; muzzle moderate (MW/ML=0.96); eye and pupil relatively small (ED/FL=0.64); venter light dusky, unmarked; tail moderately long, 24.3% TTL in males, 21.8% TTL in females.

Variation: (44 specimens examined): Snakes were separated into a northern group (San Joaquin to Butte Cos.), and southern group (Merced to Kern Cos.). Southern snakes had slightly longer tails (TL/TTL=0.245 vs. 0.242 in males, 0.221 vs. 0.217 in females), and fewer ventrals (158.3 vs. 163.8 in males, 153.1 vs. 159.5 in females). Cephalic proportions and other scale counts were similar between the two groups. There is a marked difference in color: northern snakes have a nearly uniform, dark

brown dorsum with three distinct light stripes; southern snakes are lighter brown, spotted, and have dull or indistinct stripes.

Distribution (fig. 25): The Central Valley of California, in permanent, lentic water. Hansen and Brodie (1981) give the most complete summary of distribution. It occurs north to the vicinity of Chico and the Colusa Basin. Its occurrence is continuous in sloughs, south to the vicinity of Stockton and Antioch. No specimens have been collected in similar habitat in southern San Joaquin or Stanislaus Cos., although they are still found at numerous localities in central Merced Co., to near Burrel, Fresno Co. It formerly occurred as far south as Buena Vista Lk., Kern Co. Fitch found them in canals near Buttonwillow as late as 1936. MVZ 52254 was collected east of Fellows in 1949. The drainage of Tulare and Buena Vista Lks., and constant fluctuation of water levels entering the San Joaquin Valley basin, have led to the extirpation of this snake there.

Thamnophis atratus, Aquatic Garter Snake

The morphological tendency in this species is a north to south change from a highly aquatic to semiterrestrial morph. This consists of a decrease in relative tail length, number of scale rows, ventrals, subcaudals, and cephalic scales. There is an increase in relative muzzle width, eye and pupil diameter, interorbital width, and height of posterior supralabials. Pattern changes from drab, spotted, and unstriped to dark with bold stripes. Clinal variation within *T. atratus*, with respect to these characters, is summarized below.

Four geographic divisions are analyzed for variation. Area 1 is southwest Oregon and northwest California (Del Norte, Siskiyou, Humboldt, northern Trinity, western Shasta, Glenn, and Tehama Cos.), representing typical *hydrophilus*. Area 2 includes Mendocino, Lake, southern Trinity, and Colusa

Fig. 25. Distribution of *Thamnophis gigas*.

Cos., representing snakes intermediate between *hydrophilus* and *aquaticus*, or areas of overlap between the two. Area 3 includes my Areas A and B, representing typical *aquaticus*. Area 4 includes my Areas C-G, representing all snakes formerly included in the subspecies *atratus*.

Each of twelve characters examined were grouped among Areas with similar values (table 9, fig. 26). In eight of the twelve characters, typical *hydrophilus* possessed values unique from the other snakes: more S, SR, nearly square 6th SL (R1), longer and narrower snout tip (R2 and 3), and narrower IOW (R7). Typical *aquaticus* was unique only in possessing V counts intermediate between Areas 2 and 4, but not near either. The subspecies *atratus* was unique in half the characters: shorter tail (R5), lower V, S, ASR, and MSR, and tall 6th SL. The "intergrade" Area 2 snakes were unique in having the narrowest IOW. When Fox's (1951) concept of *aquaticus* (Areas 2 and 3) are grouped, uniqueness increases to four characters: S, MSR, PSR, and R1. Each of these, however, are intermediate between typical *hydrophilus* and *atratus*.

The determination of breaks in the characters is difficult due to the intermediacy of characters in Areas 2 and 3. Both *hydrophilus* and subspecies *atratus* are unique in at least 50% of these characters, besides color and pattern. Area 2 and 3 snakes are each unique in 8% of the characters, and together, are unique in only 33%. They are grouped with *hydrophilus* in 33% of characters, and to *atratus* in 67% of characters. Their "intergrade" status cannot, therefore, be disputed on a morphological basis. However, Lawson and Dessauer (1979) found *aquaticus* to be genetically similar to *hydrophilus*. Nei genetic distance between *aquaticus* and *hydrophilus* was 0.011, while that between *aquaticus* and *atratus* was 0.034.

An examination of more morphological characters and genetic evaluation of Area 2 are needed to determine whether there is broad intergradation, or whether there is an underlying genetic break in *aquaticus*.

The following character clines are observed from north to south in *T. atratus*: spotted pattern to striped; shortening of the tail; decrease in numbers of V, S, SR, and PrO; taller 6th SL, shorter and blunter snout; smaller ED,

	1	2	3	4
R5 (males)	0.268 (34)	0.264 (9)	0.267 (30)	0.261 (73)
V (males)	163.1 (41)	162.9 (12)	159.9 (59)	155.0 (157)
S (males)	85.9 (34)	83.2 (9)	82.9 (55)	78.8 (132)
ASR	19.9 (184)	19.0 (201)	19.5 (133)	19.3 (407)
MSR	19.6 (153)	19.0 (183)	18.9 (136)	18.4 (407)
PSR	16.4 (153)	15.5 (183)	15.7 (134)	15.1 (405)
PrO	1.1 (309)	1.0 (154)	1.0 (272)	1.0 (814)
R1 (males)	1.03 (11)	0.92 (9)	0.93 (29)	0.84 (84)
R2	1.12 (26)	1.08 (9)	1.08 (62)	1.07 (231)
R3 (males)	0.79 (15)	0.92 (9)	0.93 (31)	0.92 (106)
R6	0.187 (26)	0.191 (9)	0.179 (68)	0.182 (230)
R7 (males)	0.387 (15)	0.374 (8)	0.394 (33)	0.394 (101)

Table 9. Characteristics of *Thamnophis atratus* from 4 geographic areas.

Fig. 26. Similarity of characters by area. Per cent of similar characters are diagrammed. Per cent of characters unique to areas indicated at right.

larger pupil, darker iris, and broader IOW. Each of the following subspecies exhibits subvariation in some of these characters.

Thamnophis atratus hydrophilus, Oregon Garter Snake

Thamnophis ordinoides hydrophila Fitch, 1936: 648 Type locality: "Trail Creek 6 miles from its mouth, Jackson County, Oregon" Holotype: MVZ 18127

Diagnosis (fig. 4a,b): Maximum total length 916 mm; ventrals: males 151-171 (mean 163.6, n=77), females 148-168 (mean 159.0, n=71); subcaudals: males 77-95 (mean 87.5, n=62), females 65-82 (mean 76.3, n=60); ASR 21 (55%) or 19 (45%); MSR 21 (36%) or 19 (64%); PSR 15 (33%) or 17 (67%); SL 8; IL 10 (rarely 9 or 11); PrO 1 (95%) or 2 (5%); dorsal stripe narrow, less than 1 and 2 half scale rows wide, sometimes absent; lateral stripes absent to prominent; dorsum dark olive with varying amount of alternating black markings, producing a bold, alternating spotted pattern; muzzle moderately pointed (MW/ML mean = 0.99); eye and pupil relatively small (ED/FL=0.65); top of head olive to dark brown; paired dark neck blotches distinct or indistinct; parietal spot present; SL suture marks present but of varying intensity; demarcation between dorsal head color and pre- and postocular and SL light color less distinct than in *T. couchii*; venter light dusky with midventral orange or yellow wash; dark markings present on ventral sutures; tail long, averaging 26.8% TTL in males, 25.0% TTL in females.

Variation: (n=273 from Area 1 typical *hydrophilus*, n=460 from "intergrade" Area 2); a spotted morph is dominant in Oregon, northwestern California, and the inner Coast Range (fig. 4a and b). A striped morph is frequent in Siskiyou, Shasta, and Trinity Cos. (fig. 4c). Sympatry of pattern morphs occurs, and intermediates are frequent, but a quantitative analysis of pattern is lacking. Snakes from the Pit R. drainage, at the contact zone with *T. couchii*, have shorter tails (25.6% TTL in males) than remaining

hydrophilus (26.8% TTL). Variation in cephalic proportions has been examined by Rossman and Stewart (1987). Pit R. snakes had narrower, longer snouts ($MW/ML=0.98$ vs. 1.01 ; $ML/FL=0.85$ vs. 0.75) than Coast Range snakes, and smaller eyes ($ED/FL=0.64$ vs. 0.66). V and S counts were evenly distributed except as follows: V=161.5 in Siskiyou Co. males, 164-165 elsewhere; S=85.3 in Siskiyou Co. males and 84.8 in the Cache Cr. drainage, 86.6-87.2 elsewhere. ASR were 21 in over half the snakes from Oregon and Del Norte, Siskiyou, and Shasta Cos., but 19 in at least 80% of snakes from the inner Coast Range. MSR followed a similar pattern but were less frequently 21 overall. Snakes from Oregon and Del Norte and Siskiyou Cos. usually have 17 PSR, while snakes from the Trinity and Eel R. drainages usually have 15. Snakes from Oregon and Siskiyou and Shasta Cos. occasionally have divided PrO.

Distribution (fig. 27): Southwest Oregon and northwest California: occurs north to the Rogue R., South Umpqua R. (to near Tiller and Canyonville, Douglass Co.), and South Fork Coquille R. above Myrtle Point, Coos Co; occurs east to the junction of the Klamath and Shasta R., and headwaters of the latter, Pit-McCloud R. drainage to Clark Cr., Shasta Co., and, west floor of the Sacramento Valley along Cottonwood, Stoney, and Cache Creeks. The uncertain relationships between this subspecies and *aquaticus* make the southern distributional limits unclear. Snakes referable to *hydrophilus* have been collected from as far south as Rumsey, Yolo Co., Clear Lake, Lake Co., and Gualala R., Sonoma Co. It reaches the coast along major streams and rivers, but appears to be absent from the coastal lowlands between the Eel and Smith Rivers.

Thamnophis atratus aquaticus, North Bay Garter Snake

Thamnophis elegans aquaticus Fox, 1951: 493 type locality: "Dillon Beach, Marin County, California"
holotype: MVZ 48196

Fig. 27. Distribution of *Thamnophis atratus* in California.

Diagnosis (fig. 4d): Maximum total length 875 mm; ventrals: males 149-168 (mean 159.9, n=59), females 142-159 (mean 150.5, n=59); subcaudals: males 75-93 (mean 82.9, n=55), females 65-83 (mean 74.4, n=48); ASR 19 (76%) or 21 (24%); MSR 19, rarely 17; PSR 15 (72%) or 17 (28%); SL 8; IL 10; preocular single; dorsal stripe yellow to orange-yellow, and narrow, averaging less than 1 and 2 half scale rows wide in the thoracic region; lateral stripe prominent; dorsum olive-gray, with darker markings indistinct; muzzle moderately pointed (R2 mean=1.08); eye and pupil relatively small to moderate (R6 mean=.179); iris pale gray; top of head dark olive-brown with a distinct parietal spot; supralabial suture marks narrow when present; demarcation between dorsal head and supralabial color distinct; chin cream, becoming bright yellow in the gular region; venter pale olive-green with salmon suffusion midventrally; dark markings absent from ventral sutures; tail relatively long, averaging 26.7% TTL in males, 25.1% TTL in females.

Variation: (n=139); Fox (1951) referred snakes from as far north as Trinity Co. to this subspecies (fig. 4c). He distinguished *aquaticus* from *hydrophilus* by darker ground color of the former, lack of checkerboard spotting, distinct lateral stripes, broader and brighter dorsal stripe, and fewer V and S. Many of the snakes representing Area 2 would be considered *aquaticus*, and there is a 67% similarity of characters I examined. However, the color pattern and scale count differences between northern and southern *aquaticus* are as great as those between northern *aquaticus* and *hydrophilus*. In view of the complexity of characters in snakes from the northern California Coast Ranges, I have restricted the diagnosis of *aquaticus* to populations composed of snakes similar to the holotype. Variation in these snakes (Areas A and B) has been discussed in the Results and Discussion sections.

Distribution (fig. 27): The Coast Ranges immediately north of San Francisco Bay: extends to the edge of the Sacramento Valley in Suisun and Ulati Creeks, Solano Co. I have not located the northern limits of the distribution of typical *aquaticus*. Fox (1951) suggests northern limits in the Eel R.

headwaters and Gualala R. I have no records of it from the Sonoma or Napa Valleys, and it appears to prefer uplands.

Thamnophis atratus atratus, Santa Cruz Garter Snake

Eutainia atrata Kennicott, 1860: 296 Type locality: "California" (San Francisco according to Cochran, 1961:181 ; based on the original description, the lectotype and paralectotype [ANSP] are typical of snakes from the southern San Francisco Peninsula and Santa Cruz Mountains) Lectotype: USNM 970A (designated by Fitch, 1940: 89)

Eutaenia infernalis vidua Cope, 1892:658 Type locality: "San Francisco, California" (description based on cotypes of *Eutainia atrata*)

Diagnosis (fig. 3b): Maximum total length 1016 mm; ventrals: males 146-165 (mean 154.2, n=57), females 141-155 (mean 147.0, n=57); subcaudals: males 67-89 (mean 79.4, n=49), females 64-79 (mean 70.3, n=48); ASR 19 (90%), occasionally 17 or 21; MSR 19 (65%) or 17 (35%); PSR 15, rarely 17 or 13; SL 8; IL 10; preocular single; dorsal stripe yellow to deep, orange-yellow, and broad, averaging 4 scale rows wide in the nuchal area, 2.5 rows in the thoracic region; lateral stripes absent; dorsum olive-black, grading to dark olive at the ventrals; dorsal black spots obscure; muzzle moderately pointed (R2 mean=1.04); eye and pupil moderate in diameter (R6 mean=.185); iris dark brown; top of head dark olive-brown to olive-black, with a prominent parietal spot; supralabial suture marks narrow when present; demarcation between dorsal head color and dusky-olive supralabials indistinct; chin cream, becoming bright yellow in the gular region; venter rapidly becomes dark olive-gray in the thoracic region and may be nearly black posteriorly; yellow-orange midventral suffusion prominent; dark

markings absent from ventral sutures; tail moderate in length, 26.2% TTL in males, 24.1% TTL in females.

Variation: see Results and Discussion. Dark dorsal spots of juveniles are less obscured. Intergrades from Areas C and E have lateral stripes of varied intensity, yellower SL, and paler venters.

Distribution (fig. 27 and 28): Santa Cruz Mtns. to the central San Francisco Peninsula. Typical *T. a. atratus* occur north to near Half Moon Bay and San Andreas Lk. They occur south to the San Lorenzo R. drainage on the west, and headwaters of Alamitos and Uvas Creeks on the east slope. They do not extend onto the San Francisco Bay lowlands or Santa Clara Valley. Intergrades with *T. a. aquaticus* occur north of Moss Beach and Daly City. Intergrades with *T. a. zaxanthus* are found on the southeast slope of the Santa Cruz Mtns., in the Transition Zone, from Los Gatos Cr. south, and from Soquel Cr. east.

Thamnophis atratus zaxanthus, Diablo Range Garter Snake

new subspecies

Holotype: MVZ 207940, from 3 mi. So. of Gilroy Hot Springs, Santa Clara Co., California, collected 15 April 1986, by William P. Hutchins.

Description of holotype (from life; fig. 3d, frontispiece): Adult female, 448 mm SVL, 128+ TL (approx. 7 mm missing from tip); ventrals 149; subcaudals 62+; scale rows 19-19-15, all but first row keeled; SL 8-8; IL 9-9 (5th and 6th fused on each side); preoculars 1-1; postoculars 3-3; temporals 1+2+2 on each side; posterior chin shields longest; gulars 3; anal single; top of head flat; snout moderately blunt; eyes and nostrils with a slight upward tilt; pupil approx. half eye diameter; iris dark gray; ED/G=0.17; top

Fig. 28. Distribution of *Thamnophis atratus* in central California.

of head dark olive-gray, becoming lighter in the preocular area; parietal spot present; labials, and side of neck to about one head length posterior of jaw angle, deep yellow; slightly lighter yellow on ventrals to about two head lengths back; chin yellow-cream; thin black sutures between all SL except 1st and 2nd; upper half of SL dusky-yellow; venter pale gray-green, becoming darker posteriorly, with midventral yellow suffusion; olive-gray ventrolateral stripe on 1st scale row and tips of ventrals, beginning at the 11th ventral; small black markings on anterior edges of first 3 scale rows; lateral stripe on 2nd and 3rd scale rows, light olive-gray on yellow, the yellow fading posteriorly; dorsal stripe orange-yellow, 3 and 2 half scale rows wide on nape, narrowing to 1 and 2 half rows posteriorly; stripe becomes duskier, 2 half rows wide on tail, to end; ground color dark olive-brown, heavily suffused with black, giving an overall black appearance.

Diagnosis: maximum total length 902 mm; ventrals, males: 148-168 (mean 157.6, $n=57$), females: 140-167 (mean 151.8, $n=76$); subcaudals, males: 65-89 (mean 79.3, $n=47$), females: 59-83 (mean 71.4, $n=63$); ASR 19 (85%), rarely 17 or 21; MSR 19 (80%) or 17 (20%); PSR 15 (85%) or 17 (15%); SL 8; IL 10; preoculars 1; dorsal stripe relatively broad, averaging 3.3 scale rows on the nape, 2.2 rows in the thoracic area; dorsal stripe yellow to orange-yellow; lateral stripe conspicuous, pale greenish; dorsum dark gray to black, with obscured dark spotting; muzzle moderately pointed ($R2=1.08$); eye and pupil moderate in size ($R6=0.18$); iris dark gray to brown; top of head dark olive-black, with a prominent parietal spot; SL suture marks narrow when present; demarcation between dorsal head color and yellow SL distinct; chin cream, becoming bright yellow on throat, grading to pale green in the thoracic region; ventral color darkens slightly posteriorly; midventral suffusion of orange or yellow-orange; dark markings absent from ventral sutures; tail moderately long, 25.9% TTL in males, 24.2% TTL in females.

Variation: see Results and Discussion.

Distribution (fig. 27 and 28): Diablo and Santa Lucia Ranges. It ranges from the Carquinez Straits, to Tres Pinos Cr. in the Diablo Range, and Pinnacles region in the Gabilan Mtns. It occurs on the coastal slope of the Santa Lucia Mtns., from the Monterey Peninsula, to Lopez Can., near San Luis Obispo. Scattered localities in the southern Diablo and Transverse Ranges suggest a more extensive range there than presently determined. These include the Call Mtns., Salinas R. near Santa Margarita, and Alamo Pintado Cr. in the Transverse Ranges. Snakes typical of this subspecies occur in the Upper Sonoran Zone in the southeast foothills of the Santa Cruz Mtns., south of the Santa Teresa Hills. It is absent from major valleys except along certain streams, including Coyote Cr. south of San Jose, and the upper Salinas R. It is widespread and common in the northern Diablo Range, extending to the west edge of the San Joaquin Valley along Kellogg, Corral Hollow, Hospital, Del Puerto, Orestimba, and Romero Creeks.

KEY TO THE *THAMNOPHIS COUCHII* COMPLEX

- 1a. Dorsal stripe absent; usually 2 preoculars (2)
- 1b. Dorsal stripe present, at least anteriorly; preocular usually single (4)

- 2a. Lateral stripes and parietal spot present: *Thamnophis hammondi* (two-striped form)
- 2b. Lateral stripes and parietal spot absent (3)

- 3a. Dark spots present on dorsum: *Thamnophis hammondi* (unstriped form)
- 3b. No dorsal dark markings: *Thamnophis digueti*

- 4a. Thoracic scale rows usually 21 or more; dorsal stripe scarcely covers more than vertebral scale row; throat cream or dusky (5)
- 4b. Thoracic scale rows 19; dorsal stripe covers at least half of scale row adjacent to vertebral row; throat bright yellow (7)

- 5a. Dorsal dark spots, when present, smaller than interspaces; parietal spot absent; ventral dark markings absent; usually 21-23 scale rows on neck: *Thamnophis gigas*
- 5b. Dorsal dark spots larger than interspaces, sometimes overlapping at corners; parietal spot present; dark markings usually present on ventral sutures; usually 21 scale rows on neck (6)

- 6a. Broad, dark suture marks below eye; dorsal stripe vanishes posteriorly; paired dark neck blotches extend onto head, creating a distinct demarcation between temporal-supralabial color; 11 infralabials in the north: *Thamnophis couchii*

6b. Narrow, dark suture marks below eye; dorsal stripe present at least to tail; paired dark neck blotches reduced in size, not extending onto head; demarcation between temporal and supralabial color less distinct; 10 infralabials: *Thamnophis atratus hydrophilus*

7a. Lateral stripes absent; venter dark olive; supralabials dark olive, slightly paler than temporal color: *Thamnophis atratus atratus*

7b. Lateral stripes present; venter pale greenish; supralabials pale green or yellow, distinct from dark temporal color (8)

8a. Dorsal stripe covers not more than half of scale row adjacent to vertebral row; ground color dark gray; iris pale gray; salmon midventral suffusion: *Thamnophis atratus aquaticus*

8b. Dorsal stripe often covers more than half of paravertebral scale row; ground color blackish; iris darker gray to brownish; orange-yellow midventral suffusion: *Thamnophis atratus zaxanthus*

SPECIMENS EXAMINED

THAMNOPHIS ATRATUS (429): CALIFORNIA: ALAMEDA CO. (31): Berkeley, MVZ 1629, 47946, 48538; Strawberry Can., Berkeley, MVZ 2457, 47945, 47947-8; Berkeley Hills, near Berkeley, MVZ 3757; U. C. Berkeley, MVZ 10524; Thornhill Pond, Berkeley, MVZ 12857; Hamilton Gulch, Berkeley, MVZ 47943; head of Hilgard Ave., Berkeley, MVZ 47944; Calaveras, CAS-SU 4161; pond along Mt. Hamilton-Livermore Rd., CAS-SU 11913-4; Arroyo Mocho, 1900', MVZ 24897-8, 24905-6; Arroyo Mocho, 2000', 17 mi. NNE of Mt. Hamilton, MVZ 25200; Arroyo Mocho, 750', 6 mi. SE of Livermore, MVZ 32244; Arroyo Mocho, 7 mi. SE of Livermore, MVZ 38951-2; Mocho, MVZ 187625; Mines Rd. on No. slope of Crane Ridge, 2000', MVZ 111370; 5.3 mi. E. on Tesla Rd. from Mines Rd., MVZ 191323; 5 mi. So. of Livermore, MVZ 187622; 6 mi. So. of Livermore, MVZ 187626; 7 mi. So. of Livermore, MVZ 187623-4, 187649. CONTRA COSTA CO. (14): Mt. Diablo, CAS 43695; Rock City Camp, near summit, Mt. Diablo, MVZ 47951; Marsh Cr., 500', 4.6 mi. E of Mt. Diablo, MVZ 32885; 2 mi. SW of Walnut Cr., MVZ 4009; Las Trampas Cr., St. Mary's College, MVZ 47950; Wildcat Can. Dam, MVZ 19139; Wildcat Can., Indian Picnic Grounds, MVZ 47952; Wildcat Cr. Can., Richmond, MVZ 85208-9; Jewell Lk., Wildcat Can., MVZ 47949, 48973-5; Berkeley Res. site, 1760' 3750 Grizzly Peak Blvd., MVZ 111362. MARIN CO. (52): near San Anselmo, MVZ 40708; Rodeo Laguna, 2 mi. W of Sausalito, MVZ 206938; Nicasio Cr., MVZ 172251; 1 mi. W of Inverness, MVZ 47996; 2.2 mi. NW of Bolinas, 300', MVZ 68194; NE side of Bolinas Lagoon along Pike County Gulch, CAS 93771; Lake Ranch, No. of Bolinas, MVZ 47954-6, 47967, 47969; Rolland Pond, Dillon Beach, MVZ 18196, 18198; Dillon Beach, MVZ 36184, 47953, 47957-66, 47970-95, 48196 (holotype of *Thamnophis elegans aquaticus*). MERCED CO. (2): Romero Cr., 575', 6 mi. W of Hill Ranch, MVZ 39350; Romero Cr., 450', 4 mi. W of Hill Ranch, MVZ 39351. MONTEREY CO. (19): Seaside, CAS 13764-5; Pacific Grove, CAS-SU 1685, 5143, 5147, 5149, 10327-9; 2 mi. up Robinson Can., E of Carmel, SJSU R2660; So. side of Carmel Valley just E of hwy 101, CAS-SU 11316; 10 mi. W of Salinas, Rt. 156,

MVZ 66382; Malpaso Cr., 2000', 5 mi. So. of Carmel, MVZ 44865; mouth of Garrapata Cr., MVZ 125415; Pfeiffer Beach, CAS 149553-4; near spring, W slope, 1 1/4 mi. So. of Chalk Pk., about 3000', MVZ 7243; Pine Cr., 2500', head of Little Sur R., MVZ 26010; Salmon Cr., CPS 248. NAPA CO. (44): Petna (= Aetna) Springs, CAS-SU 6134; Berryessa Cr., CAS-SU 6310-14; 7 mi. SSW of Monticello, MVZ 42639-44; Soda CR., 6 1/2 mi. SW of Monticello, MVZ 47887-8; Pope Cr., 5 mi. NNW of Monticello, MVZ 47999-48008; 14 mi. W of Monticello Dam, MVZ 78049-51; 8 mi. W, 2 mi. So. of Monticello, Chiles Valley, MVZ 60234-5; Chiles Cr. Rd., 2.4 mi. No. of Chiles Can. X hwy 128, MVZ 149625; hwy 128, 3 1/2 mi. E of Muskovite Corner, SJSU R3035; 4 mi. W of Muskovite Corner, MVZ 78052; Dry Cr., 550', 2.1 mi. So., 1.6 mi. W of Oakville, MVZ 78817; Jameson Can., MVZ 48011; Curry Lk., MVZ 48012; 6 mi. W of Calistoga, MVZ 187630; Sulphur Can., 400', 1 mi. wsw of St. Helena, MVZ 85214; Sulphur Cr. Rd., 2 air mi. SW of St. Helena, MVZ 149606-9, 149621-3; Small Cr., Beagle's Ranch, 3 mi. NW of Napa, MVZ 48010. SAN BENITO CO. (6): Panoche Pass Rd., just E of Panoche Pass, SJSU R1590; E side of Panoche Pass, SJSU R1964; Panoche Pass Rd., 6 mi. E of Paicines, SJSU R1591; Panoche Pass Rd., 10 mi. E of Paicines, SJSU R1592; Pinnacles Nat. Mon., CAS 49212; E entrance Pinnacles Nat Mon., Chalone Cr., MVZ 83647. SAN FRANCISCO CO. (12): Lake Merced, MVZ 19118-20, 19122-3, 19125-8, 19133-4; No. side of Lincoln Park, MVZ 37138. SAN JOAQUIN CO. (3): Corral Hollow, 0.6 mi. E of county line, SJSU R2802; Hospital Can., 500', MVZ 28206-7. SAN LUIS OBISPO CO. (20): Salinas R., 7 mi. E of Santa Margarita, CPS 120; 5 mi. up San Simeon Cr., CPS 2420; Cayucos Cr. just up from hwy 1 bridge, CPS 2428; Perfumo Can., 8 mi. SW of Los Osos Rd., CPS 188-9; Perfumo Can. Cr., CPS 2426; 4 mi. in Perfumo Can., CPS 3218-9; Perfumo Can., 3 mi. SW of San Luis Obispo, CPS unnumbered specimen; San Luis Cr., 0.8 mi. NW of Cuesta Park, CPS 191; base of Rocky Butte just below Circle 3 Ranch House, CPS 2436; Reservoir Can., CPS 3220, 3227-8; Price Can., CPS 3224; Avila Beach, CPS 3217; 1 mi. So. of Laguna Lk., CPS unnumbered specimen; Lopez Can., CPS 2437, 3216, 3225. SAN MATEO CO. (144): San Andreas Lk., CAS-SU 10691-2, 10694, 10695-6, 10698, MVZ 9316; Jct. of Tanforan Rd. and Skyline Blvd., CAS-SU 10706; rd. betw. Half Moon Bay and Moss Beach, CAS-SU 10712; Moss Beach, MVZ 47893; vic. of Sharp Park Golf

Course, near San Bruno, CAS-SU 8157; Laguna Salado, Sharp Park, MVZ 47896; 1 mi. SE of Sharp Park, MVZ 47912, 47920; 1/2 mi. No. of San Francisco Co. Jail, MVZ 47883, 47889; 3 mi. No. of San Francisco Co. Jail, MVZ 47884; Skyline Blvd. at San Francisco Co. Jail, MVZ 47885-8, 47890, 47899-900, 47907-11, 47918-9, 47921-5; Skyline Blvd., 1 1/2 mi. No. of San Francisco Co. Jail, MVZ 47891-2, 47897-8, 47901-6, 47913-4, 47916-7; turnoff to San Francisco Co. Jail, MVZ 47915; McKay Radio Sta., 5.8 mi. So. of Half Moon Bay, MVZ 47894-5; 2 mi. So. of Half Moon Bay, MVZ 47882; Rt. 1 in El Granada, MVZ 93805; 2 1/2 mi. No. of Pigeon Pt., MVZ 32628; Pescadero, CAS-SU 1200-5; Pescadero Cr., CAS-SU 5183; 2 mi. No. of Pt. Ano Nuevo, MVZ 47926-8; Pilarcitos Lk., CAS-SU 10686-7; Mill's Lk., CAS-SU 10688; Crocker's Lk., CAS-SU 10897-9, 17906-7; Alma House Can. Rd., 1/2 mi. No. of County Home, CAS-SU 17867; Eisenberg Ranch, Skyline Blvd., CAS-SU 10827-8, 10831, 10833-4; Eisenberg Ranch, Yerba Buena Nursery, CAS 149585-617, 149677; La Honda, CAS-SU 1198, 4149, 4155; 1 mi. NE of La Honda, MVZ 187632-6, 187654-5; La Honda Rd., 1/4 mi. E of Stage Rd., MVZ 92508; Skylonda, CAS-SU 8105, 8109-12; Butano Basin, CAS-SU 5184; summit near Searsville Lk., CAS-SU 1654-5; Corte Madera Cr., CAS-SU 5180; near Portola, CAS-SU 13781; Bordin Ranch, No. of Portola St. Park, E of Evans Cr., CAS-SU 22949-51; 4 mi. So. of jct. with Page Mill Rd., within 1 mi. of county line, CAS-SU 22952; small lake on No. slope of Mindogo Hill, 4.75 air mi. W of Black Mtn., CAS-SU 25567-8; Alpine Cr. Ranch, Menlo Park, MVZ 14003, 16592; 2 1/2 mi. NW of Saratoga Gap, SJSU R3356. SANTA BARBARA CO. (1): 40 mi. So. of Santa Maria, CPS 94. SANTA CLARA CO. (103): Palo Alto, SJSU R724; Stanford University, CAS 54225, CAS-SU 4157, 6378-80, 8207-8; Corte Madera Ranch, near Stanford University, CAS-SU 13780; between Stanford University Campus and Spanish Town, CAS-SU 4322; Hidden Villa Ranch, 1.6 mi. up Moody Rd. from hwy 280, SJSU R1603; 1.1 mi. W of Stevens Cr./Mtn. View Rd. and Mt. Eden Rd., CAS-SU 18160-62; Sanborn Cr., 0.2 mi. So. of Saratoga Springs, SJSU R5680; Skyline Rd. at Castle Rock Park, SJSU R1958; 2 mi. NW of Saratoga Gap, SJSU R2801; summit, 2 mi. SE of Saratoga Gap, SJSU R2961, R4992; Lk. McKenzie, off Black Rd., SJSU R3355; hill NE of Lexington Dam, SJSU R3006-11; E side of Lexington Res., SJSU R5717; Sierra Azul Rd., Mt. Umunhum, SJSU R4943; upper reaches of

Guadalupe Cr., SJSU R727; Guadalupe Res., SJSU R850; near Guadalupe Res., SJSU R851; head of
 Guadalupe Res., SJSU R3299; 1/4 mi. below Guadalupe Dam, SJSU R3364; Hicks Rd., below
 Guadalupe Res., SJSU R852, R858; lower Hicks Rd., SJSU R853; Hicks Rd., SJSU R1593-6, 1608;
 Guadalupe Mines Dump, 1 mi. SE of Camden Ave. X Hicks Rd., SJSU R3384; Almaden Canal, 3/4
 mi. SW of Calero Dam, SJSU R5210; Almaden Canal, 1 1/4 mi. SW of Calero Dam, SJSU R5702;
 Santa Teresa Co. Park, SJSU R5005-6; upper Uvas Can., 2200', SJSU R868; upper Uvas Can., 1250',
 SJSU R869; Uvas Rd., 2 mi. No. of the end of Chesbro Res., SJSU R863; Uvas Rd. at Little Uvas Cr.,
 SJSU R862; Little Uvas Rd., SJSU R2379; Little Uvas Cr., 3 mi. W on Little Uvas Rd., SJSU 5355-6;
 Uvas Cr., CAS-SU 6520; Uvas, SJSU R726; No. end of Mt. Madonna Co. Park, SJSU R3018; San Jose,
 SJSU R721; Silver Creek Hills, SJSU R722; So. end of Silver Creek Rd., SJSU R854, 864-5, 867; 3 mi.
 So. on Silver Creek Rd., SJSU R855; Silver Creek Rd., 0.6 mi. So. of Yerba Buena Ave., Evergreen,
 SJSU R5211; San Felipe Rd., No. of int. with Silver Creek Rd., SJSU R849; Alum Rock Can., San Jose,
 CAS 41661-2; Penitencia Cr., Alum Rock Park, SJSU R5235; Smith Cr., SJSU R861, 1726, 1767, CAS-
 SU 4091; hwy 130, 11.2 mi. E of Alum Rock Ave., SJSU R3091-2; hwy 130, 7.5 mi. E of Lick
 Observatory, SJSU R3096-8; No. end of Kincaid Rd., NW of Mt. Hamilton, SJSU R2100; Kincaid Rd.
 at Mt. Hamilton., SJSU R1959, 3385; 10 mi. E of Mt. Hamilton, CAS-SU 22953-4; San Antonio Valley,
 1/2 mi. So. of The Junction, SJSU R860; Metcalf Rd., No. of Coyote, SJSU R848; Coyote Cr. at
 Metcalf Rd., Coyote, SJSU R1897; Evergreen Canal, 1 mi. E of Metcalf Rd. at hwy 101, Coyote, SJSU
 R1953; Coyote Canal at Riverside Golf Course, Madrone, SJSU R5701; E. Dunne Ave., 3 1/2 mi. above
 Anderson Res., SJSU R1610; Poverty Flat, Henry W. Coe St. Park, SJSU R2829, 3000-1; Upper Coyote
 Cr., CAS-SU 5852; Gilroy Hot Sprs., CAS 39652-3; 4 mi. SE of Gilroy Hot Sprs., SJSU R731; Coyote
 Cr., several mi. So. of Gilroy Hot Sprs., SJSU R2813-4; 3 mi. So. of Gilroy Hot Sprs., SJSU R3086; 2
 mi. So. of Gilroy Hot Sprs., SJSU R3386, 3394; Gilroy Hot Sprs. Rd., 4 mi. So. of Gilroy Hot Sprs.,
 SJSU R5212; Coyote Cr., near Gilroy Hot Sprs., MVZ 79576. SANTA CRUZ CO. (65): Waddell Cr.,
 CAS-SU 4150-3; Waddell Cr., 20', 1/2 mi. from ocean beach, MVZ 26988; Waddell Cr., 100', MVZ
 35545-53; Waddell Cr., 3 mi. E from the mouth, MVZ 48976-9; Waddell Cr. at hwy 1, MVZ 149624;

mouth of Scott Cr., 1 mi. No. of El Jarro Pt., MVZ 47941; 0.7 mi. up Bonny Doon Rd. from hwy 1, SJSU R1898; Little Cr., 1 mi. ENE of Swanton, MVZ 47935; Big Cr., 2 1/2 mi. NE of Swanton, MVZ 47936-40; between hwy 1 and ocean, 4 mi. No. of Santa Cruz, SJSU R733-4; hwy 236, 3 mi. NE of Big Basin, SJSU R856-7; Waterman Gap, SJSU R866; No. end of U.C. Santa Cruz on Empire Grade, SJSU R5128; Empire Grade, 2.4 mi. W of the W entrance to UCSC, SJSU R5233; Empire Grade, 3.2 mi. W of the W entrance to UCSC, SJSU R5234; Brookdale, SJSU R859; Felton, CAS 81547; Boulder Creek, CAS-SU 10817, MVZ 39443; Boy Scout Camp Lindblad near Boulder Creek, MVZ 100280; Loch Lomond Res., SJSU R4737; near Zayante, CAS-SU 7636-7; Pine Flat Rd., 3.2 mi. WSW of Ben Lomond, 1800', MVZ 62106-18; 5 mi. No. of hwy 17 and 2 mi. off Mtn. Charlie Rd., SJSU R732; Paul Sweet Rd., E. Santa Cruz, SJSU R1842; Soquel, CAS-SU 1675, 1679, 4148; 2 mi. W of Corralitos, SJSU R2767; Highland Rd. at the head of Soquel Cr., SJSU R5693; Buzzard Lagoon, Forest of Nisene Marks, SJSU R5359-60; SOLANO CO. (4): 3 mi. W of Vacaville, 700', MVZ 4006-8; Suisun Cr., 3.5 mi. WSW of Suisun, MVZ 48017. SONOMA CO. (39): Duncan Mills, CAS 27939; 2 mi. So. of Duncan Mills, 100', MVZ 69691-3, 69695-7; Skaggs Sprs., CAS 28019-21, 28024-5, 28029, MVZ 125414; Warm Sprs. Cr., 1 km W of Skaggs Sprs., CAS 149676; Warm Sprs. Cr., near Skaggs, CAS-SU 4256-8; jct. Wheatfield Fk. and Gualala R., CAS-SU 4219; Wheatfield Fk., Gualala R., CAS-SU 4229-31; Guerneville, CAS-SU 4323; 1 mi. W of Guerneville, MVZ 4913-4; No. bank of mouth of Russian R., CAS-SU 11038-41, 11044; Russian R., Summer Home Park, CAS-SU 10741-2; Healdsburg, Russian R., CAS-SU 10743; 4 mi. So. of Cazadero, MVZ 48042; Knight's Valley Cr., near Kellog, CAS-SU 4232; mouth of Russian Gulch, 2 3/4 mi. NW of Jenner, MVZ 48013; mouth of Kolmer Gulch, 1 mi. NNW of Ft. Ross, MVZ 48015-6; 8635 Starlight Ln., Sebastopol, CAS 156208. STANISLAUS CO. (8): Orestimba Cr., 300', 10 mi. W of Newman, MVZ 39349; Del Puerto Can. Rd., 9.5 mi. W of hwy 5, CAS 161384; Del Puerto Cr., 450', 5.8 mi. W, 3 mi. So. of Patterson, MVZ 78816; Del Puerto Can., 1/2 mi. E of Adobe Cr., SJSU R5304; Del Puerto Cr., 13.2 rd. mi. W of hwy 5, SJSU R5646-9.

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