A Comparison of the Life Histories of Coastal and Montane Populations of Ambystoma macrodactylum in California

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ABSTRACT: The disjunct, coastal endemic *Ambystoma macrodactylum croceum* was compared with two populations of *A. m. sigillatum* (1980 and 2450 m) from the Sierra Nevada of California. *A. m. croceum* and *A. m. sigillatum* 1980 m breed in temporary ponds, but *A. m. sigillatum* at 2450 m requires permanent ponds. The last has a 14-month larval period with a 2-3 month overlap of larval age classes, whereas the others have a short (3-4 month) larval period. *A. m. croceum* breeds in January and February, *A. m. sigillatum* from late May (1980 m) through June (2450 m). In all areas climatic conditions control the primary activities. Rainfall is the only important governing factor for *A. m. croceum.* It controls the breeding migration, dispersal of juveniles, time of breeding, and (because it determines the length of time the ponds persist) determines size attained at metamorphosis. For *A. m. sigillatum* the most important factor is temperature, determining the time of breeding (thaw) and the larval and adult growth rates.

A. m. croceum deposits eggs singly on vegetation near the surface in shallow water. In *A. m. sigillatum,* eggs are clustered under logs and bark near the bottom in the deeper portions of the ponds. Size at metamorphosis is approximately the same in *A. m. croceum* (37.5 mm S-V) and *A. m. sigillatum* from 2450 m (37.8) but the former attains this size in 90-140 days whereas the latter requires 14 months. The *A. m. sigillatum* from 1980 m metamorphose after 80-90 days, at 25.0 mm S-V, approximately the size reached by the 2450 m population after the first growing season. Metamorphosis seems to be triggered by intrinsic factors in *A. m. sigillatum* at 2450 m but by extrinsic factors (drying of the ponds) in the others. The larvae of *A. m. croceum* are secretive at all stages but their behavior varies and has been generally correlated with stage of development. Larval *A. m. sigillatum* (2450 m) are secretive in hatchling and metamorphic stages but active in open, illuminated portions of the ponds otherwise.

The breeding migration of *A. m. croceum* is stimulated by heavy rainfall and takes place only on rainy nights. The migration of *A. m. sigillatum* was not observed but occurs while snow and some ice are present. Sexual maturity is reached during the second year of life in *A. m. croceum,* during the third year in *A. m. sigillatum* from 2450 m.

Both *A. m. croceum* and the Sierran *A. m. sigillatum* are derived from ancestral populations to the north. The isolated *A. m. croceum* shows the greatest divergence in life history compared to present-day northern populations.

INTRODUCTION

The Long-Toed Salamander, *Ambystoma macrodactylum,* occurs in diverse habitats throughout its range, having been reported from moist coniferous forests, alpine meadows, sagebrush communities, and many intermediate situations. At the southern periphery of the range, *A. macrodactylum* extends into the Sierra Nevada of California to Tuolomne Co., but on the coast the main populations terminate in southeastern Oregon (Ferguson, 1961). An isolated subspecies (*A.*

m. croceum) occurs near the northern edge of Monterey Bay in Santa Cruz Co., California (Russell and Anderson, 1956). This population is separated from the nearest coastal locality by nearly 400 miles and is approximately 150 mi SW of known localities in the Sierra Nevada. The Great Valley of California lies between the coastal population and the Sierran localities.

Salamanders illustrate a relict distribution pattern perhaps better than any other group of vertebrates (Darlington, 1957), having discontinuous distributions at practically every taxonomic level. The evolutionary significance of peripherally isolated populations has been stressed by Mayr (1954, 1963). Salamanders, furthermore, because of low vagility and dependence upon certain physical features of the environment are ideal for studying adaptations to local conditions. Since *A. m. croceum* lives far from the main species range, and in a very different habitat, its ecology was studied to discover the adaptations permitting its survival. The present report deals with a basic comparison of the life history and yearly activity cycle of *A. m. croceum* and *A. m. sigillatum* (Ferguson, 1961) of the Sierra Nevada. Other aspects of the ecology will be reported subsequently.

DESCRIPTIONS OF STUDY AREAS

COASTAL STUDY AREAS

Ambystoma macrodactylum croceum is known from only two localities, both in Santa Cruz Co., California; both localities were used as areas of intensive study. The principal study area was the type locality (Valencia Lagoon, Rio del Mar, Santa Cruz Co.) referred to henceforth as Valencia Lagoon. This area is described in detail by Russell and Anderson (1956:139-140). Little can be added except that in years of heavy rainfall, water enters the lagoon from an intermittent stream flowing from the southeast. At such times water may overflow into nearby Valencia Creek, a permanent stream flowing into Monterey Bay. Valencia Lagoon is a temporary pond, drying by late June, or earlier (1953-1959). It is oriented east-west, parallel with ridges to the north and south. The ridge to the south rises approximately 30 to 60 m above the pond and its north-facing slope is densely clothed with a humid oak forest. The northern ridge is somewhat lower and its south-facing slope is grassy and herbaceous. Terrestrial stages of *A. m. croceum* inhabit only the oak woods south of the pond. The pond area is separated from the open, grassy slope by California State Highway No. 1, and from the oak-covered slope by Bonita Road. This unpaved, sandy road, skirting the southern shore of the pond, provided an ideal spot for the observation of salamanders migrating to and from the pond.

In 1956, *A. m. croceum* was found at a second locality approximately 4 mi SSE of Valencia Lagoon. The designation for this locality is ½ mi NW Ellicott Railroad Station, 4 mi W Watsonville, Santa Cruz Co. The defunct railroad station at Ellicott is clearly marked on the Capitola Quadrangle of the U.S.G.S. topographical series. This study area, on the land of Mr. John Edwards of Watsonville, is referred to henceforth as Ellicott. The breeding pond at Ellicott is also temporary and variable in extent. It is not fed by streams but is a natural "Hog Wallow" depression collecting rain water and run-off from the surrounding hills. There are apparently springs in the ridge east of the depression, since seepage throughout the dry season maintains a high water table. The soil tends to hold moisture over the summer, so the pond is quickly filled when the rains become heavy in fall and winter. At its maximum extent the pond is oval shaped, approximately 90 m long and almost 45 m wide although both dimensions vary greatly. Like Valencia Lagoon, this pond normally dries by late June. The entire southern edge of the pond is bordered by a dense willow thicket somewhat over 840 m^2 in area. Most of the *A. m. croceum* population resides in this thicket during the terrestrial stages. The opposite shore borders on a grassy area where cattle are grazed.

The Ellicott pond is, like Valencia, temporary and has a similar invertebrate fauna. *Eleocharis* is also the dominant plant but forms denser, higher stands. *Polygonum* is abundant at Valencia but here is scattered and less dense. There are no tules at Ellicott, a major difference between the two areas.

At Valencia Lagoon *Hyla regilla* and *Rana aurora* were the only amphibians sharing the pond with *A. m. croceum.* In addition to these, *Ambystoma tigrinum californiense* utilized Ellicott Pond for breeding. Both *Thamnophis elegans* and *T. sirtalis* were observed in the spring but were seldom encountered at other times.

Ellicott Pond, somewhat more open, and closer to the sea, attracts more water birds than Valencia. Killdeer, Mallards, Cinnamon Teal, and Coot were common and flocks of Dowitchers, Long-Billed Curlew, and Willet were occasionally seen in spring. Bonaparte, Western and California Gulls, Green Heron, Pied-Bill and Eared Grebes fed at the pond sporadically.

During terrestrial stages, *A. m. croceum* shares the willow grove at Ellicott with *Aneides lugubris, Batrachoseps attenuatus, Hyla regilla* and *Rana aurora. A. tigrinum* was never found in the willows, apparently spending its terrestrial life underground in the open slopes around the area.

SIERRAN STUDY AREAS FOR *A. m. sigillatum*

BIG MEADOW, 1980 M, CALAVERAS CO., CALIFORNIA

The small (64 x 27 m) temporary pond at this locality is formed almost entirely from melting snow each spring and dries completely by late July or early August. The pond is situated in a heavily forested area overlooking the north fork of the Stanislaus River. Sugar Pine, White Fir, Yellow Pine, Incense Cedar and Lodgepole Pine are important members of the surrounding forest. The pond itself is surrounded by large trees (predominantly White Fir, Yellow Pine, Lodgepole Pine and Aspen) that provide shade most of the day. The pond bottom is littered with twigs, branches, cones and needles of these conifers. The acidic water (*p*H 5.9) lacks aquatic vegetation. In addition to *A. m. sigillatum, Hyla regilla* and *Rana muscosa* utilize the pond. *Thamnophis elegans* preys upon the larvae of all three species.

Ponds near Mosquito Lakes, 2450 m, 2 mi W Lookout Peak, Alpine Co., California

A series of small ponds comprising the local breeding centers for a large population of *A. m. sigillatum* are situated on a granite ridge 140 m NE of the lakes across Highway 4. Two of the five permanent ponds in the group were studied intensively. They may be partially spring-fed although much of the water is derived from melting snow and the depth tends to decrease slightly in late summer. In three years of observation, however, they never lost sufficient water to affect the salamander population. Most of the ponds are in natural depressions between low, parallel granite ridges characteristic of this locality. The forest near the ponds tends to be sparse because of the outcropping granite but trees bordering the ponds provide considerable shade. Lodgepole Pine, White Pine (*P. monticola*) Red Cedar and Mountain Hemlock are abundant and form dense forests where the soil is deep.

The largest pond (designated as pond 1 in the field notes) is roughly triangular in shape with the apex directed northeast. It is 37 m wide at the base, 55 m long, and 9 m across at the apex. When freshly filled from melting snow some water overflows to the northeast, down approximately 300 m into Pacific Valley. Maximum depth is about 75 cm and average depth 60 cm. The bottom is soft and littered with needles, cones, and twigs from surrounding conifers. Many logs and tree trunks are present in the water, some submerged and others floating. These tend to be concentrated at the apex of the triangle, which is a tangle of floating and submerged logs, branches and twigs. Since the water is clear and vegetation almost entirely lacking, it is possible to observe salamander activity in all but the deepest portions. The pond is bounded on three sides by low granite ridges and on the fourth by the steep drop into Pacific Valley. The ridge to the northwest separates it from pond 2. The granite outcrops are devoid of soil and vegetation and hinder dispersal of salamanders. *Hyla regilla* and *Rana muscosa* are the only other amphibians found in this and other ponds in the region. *Thamnophis elegans* is present but not abundant.

Pond 2 is similar in most respects, although smaller and more shallow than pond 1. It is roughly figure 8-shaped, 45 m long and 15 m wide. Greatest depth is approximately 75 cm, average depth about 30 cm. Trees are more numerous, so that one end is always shaded. The pond is oriented east-west and separated from pond 1 by about 45 m and a granite ridge. A tangle of logs, branches, etc., has accumulated at the northwest portion although others, floating and submerged, are scattered throughout.

Other ponds in the area are similar but slightly smaller. All are bordered by the same species of trees as ponds 1 and 2. Some are enclosed by thicker growth and thus almost continually shaded.

Almost all field observations were made in ponds 1 and 2 although spot checks were made in all the others. All larval samples, whether for food studies, growth samples, or for experimentation, were drawn from pond 1. Adults were taken from ponds 1 and 2. Supplementary collections were made in the others but none was utilized in growth measurements.

LIFE HISTORY PATTERNS

The three species of *Ambystoma* inhabiting western North America, *A. gracile, macrodactylum* and *tigrinum* are more variable in life history than most species in the east. In various parts of the west, for instance, *A. tigrinum* may have a "normal" one-season larval period, a two-season larval period or may be paedogenic. Snyder (1956) reported similar variations in *A. gracile* and correlated the patterns with altitude. Kezer and Farner (1955) observed three life history patterns in *A. macrodactylum* in Crater Lake National Park. Stebbins (1951) indicates that approximately one year is required for *A. macrodactylum* to achieve metamorphosis at high elevations in the Sierra Nevada of California, whereas only a few months are necessary in coastal Oregon.

The life history of *A. m. croceum* consists of a simple one-season larval period. The length of larval life, however, is variable, since the coastal ponds are temporary and dependent upon the winter rains. Breeding cannot take place until the ponds fill. Furthermore, variations in the quantity of rainfall determine the length of time that water remains and, therefore, the time available for larvae. During one season (1957) rainfall was scattered and insufficient to allow normal egg deposition and larval development. In other years (1955-1960) the ponds persisted between 94 and 140 days. The single-season pattern of *A. m. croceum* is facultative since the ponds always disappear, and transformation occurs when the ponds begin to shrink. Since temperature conditions are rather uniform and moderate near the coast, the life cycle is controlled by, and dependent upon, rainfall.

At least two distinct life history patterns are evident in the Sierra Nevada: a short facultative one-season larval period and a two-season larval period. The Big Meadow pond was available to larvae from late May or early June, when the snow melted, to late August or early September when the pond dried. At this locality, between 80 and 90 days would represent the average time from egg deposition to metamorphosis. The same situation probably occurs in other snowmelt ponds at this elevation. Larger, more permanent bodies of water at similar elevations might permit a longer, single-season larval period, such as that described by Kezer and Farner (1955) for Lake West in Crater Lake Park.

A two-season larval period was observed at the Mosquito Lakes locality where 14 months elapsed between egg deposition and transformation. The growing season is so short, and the average summer temperature so low, that larvae are unable to reach the critical size for metamorphosis in a single season. They spend winter under the ice and transform in August or September of their second year of life. These larvae, therefore, overlap the greatest part of their second growing season with the next season's young.

Temporary ponds at high elevations (2450-2750 m) proved unfavorable habitat for *A. macrodactylum* in this area. Few breeding adults were seen and eggs were found only once in such ponds. The few larvae that hatched did not achieve metamorphosis. In extremely favorable years (long, wet summers) some larvae might reach metamorphic size in temporary ponds but this did not occur during the present study. Most successful reproduction at high elevations therefore takes place in permanent ponds where the larval period exceeds one year. There is no evidence of paedogenesis or a larval period longer than two seasons anywhere in the species range although a longer larval period might be possible in large, cold lakes.

BREEDING SEASON

Temperature and rainfall are the principal environmental factors influencing the time of breeding in amphibians. In various areas anurans, for example, have adjusted their breeding cycles to the prevailing climates. Moore (1939) has shown that species of *Rana* in the eastern United States respond to the temperature progression evident in that region. during the spring. In more arid regions breeding seasons may be adjusted to prevailing rainfall patterns, with temperature of lesser importance. Little is known of geographic variation in breeding cycles where species occur in areas of differing prevailing climate In the present study, the coastal and mountain populations of *A. macrodactylum* were found to be adjusted to radically different environmental stimuli for breeding.

The breeding season of *A. m. croceum* varies depending upon the rainfall pattern of a given year but normally falls between mid-January and mid-February (Table 1). Mating might possibly take place earlier if the ponds filled earlier, since the adults may migrate to the breeding areas long before they become inundated (see sub-

TABLE 1.—Breeding dates *A. m. croceum* 1955-1959

Year	Main breeding effort	Field observations
1955	Early February	Hatchling larvae, 27 Feb.
1956	Late February	Hatchling larvae, 16 Mar.
1957	Sporadic—no success	Eggs on 9 Mar., 100% mortality
1958	Early February	Eggs 9 - 16 Feb.
1959	Mid-January	Eggs 15 - 21 Jan.

TABLE 2.—Total monthly precipitation (inches) during the breeding season of *A. m. croceum* 1955-1958[a]

	1955-56	1956-57[b]	1957-58	Av. 1931-52
October	0.05	1.83	5.34	1.51
November	3.74	0.02	0.97	2.91
December	21.07	0.96	5.48	7.38
January	9.34	5.90	7.70	6.73
February	1.46	4.90	13.86	6.10
	35.66	13.61	33.35	24.63

[a] Data from Weather Bureau records for Santa Cruz, Santa Cruz Co., California.

[b] Breeding efforts failed during 1956-57 season but were successful the other years.

sequent discussion). It is doubtful, however, that successful breeding occurs much after February, since rainfall begins to slacken in March and ponds not filled to capacity by then tend to dry very rapidly. The breeding season of 1957 is instructive in this respect. Rainfall in the winter of 1956-57 was subnormal and erratic, although the months of October, January and February were about average (Table 2). A prolonged dry spell during November and December prevented the accumulation of moisture in the pond areas and the later rains were not sufficient to make up the deficit. Pools began to form in late February and early March and were utilized for a limited amount of mating and egg deposition. These pools, however, dried before the end of March, causing 100% mortality of remaining eggs and those larvae that had hatched.

Although there is considerable annual variation in time of breeding, in any given season mating and egg deposition take place over a relatively short span of time. In 1958 and 1959, when breeding activities were followed closely, eggs were deposited from 9 to 16 February and 15 to 21 January, respectively. No eggs were found prior to those dates and no freshly deposited eggs seen subsequently. The rather uniform size of larval samples in other years substantiates the assumption that breeding activities are performed rapidly once proper conditions are established in the ponds.

Temperature (Table 3) presumably plays a minor role in controlling and influencing the breeding season. Although there is a slight drop in temperature during December and January when breeding activities commence, freezing temperatures are rare and never of sufficient duration to curtail mating activities for more than a day.

In the Sierra, however, an entirely different situation prevails, rising temperatures being the primary factor controlling the breeding season. At the Mosquito Lakes area the ponds are frozen and covered by a deep snowpack until late May or June. Table 3 indicates that temperature conditions comparable to those of the breeding season

TABLE 3.—Temperature data[a] for coastal and Sierran study areas (°F)

	Santa Cruz[b]			Twin Lakes[c]		
	Mean min.	Mean max.	Mean temp.	Mean min.	Mean max.	Mean temp.
January	37.9	60.4	49.5	11.7	35.6	23.7
February	40.1	62.0	51.4	12.3	37.2	24.9
March	41.3	65.0	53.5	15.1	42.0	28.6
April	42.8	68.2	56.1	22.1	48.5	35.3
May	45.1	70.7	58.5	28.1	54.0	41.0
June	47.6	74.3	61.5	34.6	61.9	48.2
July	50.0	75.1	63.1	40.6	71.5	56.0
August	50.2	75.3	63.3	40.1	71.8	55.9
September	48.6	76.8	63.0	35.4	65.8	50.6
October	45.6	73.3	59.6	28.6	54.8	41.7
November	41.2	68.0	54.8	21.0	45.7	33.4
December	38.5	61.7	50.8	15.9	38.7	27.3
Annual	44.0	69.2	57.1	25.4	52.3	38.8

[a] From Weather Bureau Bulletin W-supplement 1931-1952. 20-year averages.

[b] Weather Bureau data taken at Santa Cruz, Santa Cruz Co., California.

[c] Weather Bureau data taken at Twin Lakes, 7,829 feet (app. 2385 m), Alpine Co., California.

of *A. m. croceum* are not generally reached until June at this elevation. The Big Meadow pond does not become available for breeding until extensive melting has occurred.

A. m. sigillatum emerges as soon as the first thaw reduces the snow cover and opens the ponds; courtship and mating commence almost immediately. The breeding season is variable, depending on the time of thaw and also, less directly, on the past winter. In some years prolonged periods of high temperature are required to produce suitable conditions for breeding; in other years with less accumulated ice and snow less time is necessary to open the ponds. The breeding seasons of 1958 and 1959 illustrate the range of variation. In 1958, the ponds at Mosquito Lakes were half covered by ice and surrounded by snowdrifts on 28 June. Most females had mated and eggs were being deposited. On 27 June 1959, by contrast, the ice had gone and only scattered patches of snow remained. The larvae had already begun to hatch and adults had repaired to their terrestrial haunts. The breeding season was thus late June one year and late May or early June the following year.

I have no direct observations on the exact time of breeding at Big Meadow but from differences in early samples of larvae, it is likely that breeding takes place two weeks earlier at 1980 m than at 2450 m. The breeding season of *A. m. sigillatum* in the Sierra Nevada can therefore be stated as May at low elevations and June at high elevations. Since this species is rare or absent below 1830 and above 2750 m, the May to June designation probably characterizes the breeding season for all Sierran populations.

COURTSHIP BEHAVIOR

The courtship behavior of *A. m. croceum* has been discussed elsewhere (Anderson, 1961). In overall pattern of behavior it differs markedly from other species of *Ambystoma* except for members of the *A. jeffersonianum* complex (Mohr, 1931; Kumpf and Yeaton, 1932; Uzzell, 1964). The clasping behavior of these species is similar to that of certain salamandrids (Smith, 1941) and is possibly a specialized behavior derived from the generalized pattern (Noble, 1931) evident in most species of *Ambystoma.* It may represent, within the genus, an evolutionary trend from a mass courtship to one with more specific pairing and more elaborate behavior by the male in stimulating the female and leading her to pick up a spermatophore.

The spermatophore of *A. m. croceum* is most like that of *A. jeffersonianum* (Anderson, 1961). The similarities in courtship and structure of the spermatophore indicate a close relationship between *A. macrodactylum* and the *jeffersonianum* complex, as proposed on morphological evidence by Tihen (1958).

Courtship was not studied in the other subspecies but a cursory report by Knudsen (1960) indicates that the pattern is similar in *A. m. macrodactylum.*

EGGS AND EGG DEPOSITION

Slater (1936:235) states that *A. macrodactylum* lays its eggs in shallow portions of small ponds and that if no shallow areas are present "eggs may be fastened to grass hanging in the edge," otherwise they are deposited on the bottom. Presumably Slater referred to ponds at sea level in Washington (subspecies *macrodactylum* ?) but this is not made clear. Fitch (1936) reports eggs laid in ponds, ditches, and creeks in southern Oregon but gives no details. At 1890 m in the Crater Lake region, eggs of this species, deposited in ponds, are attached to vegetation near the edge of ponds (Kezer and Farner 1955:128, 129).

At Valencia Lagoon and Ellicott Pond the eggs of *A. m. croceum* were always found in shallow water, (7.5-22 cm) 1 to 14 m from the shore line. At any depth, the eggs were well off the bottom, generally attached within 5 to 8 cm of the surface. With but one exception, eggs were attached to stalks of the Spike Rush (*Eleocharis*), the most abundant plant in shallow water. Most were found on new sprouts but some were seen on mats of dead stalks of this plant. The eggs were always laid singly and usually at least 2.5 cm apart, most often separated by 5 to 8 cm. In areas of heavy, new growth of *Eleocharis* the eggs were placed one to a stalk, close to the pointed tip of a sprout that had not yet grown to the surface (Fig. 1a). Although eggs were slightly more dense on mats and clumps of dead stalks of *Eleocharis,* they were usually spaced 2.5 to 5 cm apart. Moreover, in such places eggs tended to be arranged linearly along horizontal stalks. The most crowded group consisted of nine eggs lined up on a dead stalk of *Polygonum* 35 cm long (Fig. 1b). Being small, transparent, and scattered, eggs were difficult to locate in any of these situations. The water was frequently silty during the rainy season and intense effort was required to locate eggs, since silt adhering to the jelly colored the egg brown, blending with the silty background. The difficulty in locating eggs may be one reason that *A. m. croceum* escaped discovery for so long.

Although detailed observations were made during only one season, *A. m. sigillatum* clearly deposits its eggs in a very different manner. All but a few eggs were deposited on the undersides of large logs and thick branches floating free or resting partly on the bottom. The eggs were completely hidden from view unless the log was lifted to the surface and turned over. The few exceptions were eggs laid on bark, twigs and branches forming a tangle of debris near the bottom. Even on these objects, however, they were invariably on the lower surfaces (Fig. 1c). Twigs and branches less than 2.5 cm in diameter were not utilized although they littered the bottom. Slabs of bark 15 cm or more in length were favored sites. Logs or branches 12 cm or more in diameter and with bark still attached were also distinctly preferred. If a log had the bark remaining in patches, eggs were invariably affixed to the rough surface of the bark. Eggs were not found on the bottom nor on scattered patches of vegetation and were also absent from objects resting directly on the bottom.

The eggs of *A. m. sigillatum* were never found in water less than 25 cm deep and thus were never near the edge unless the shore line

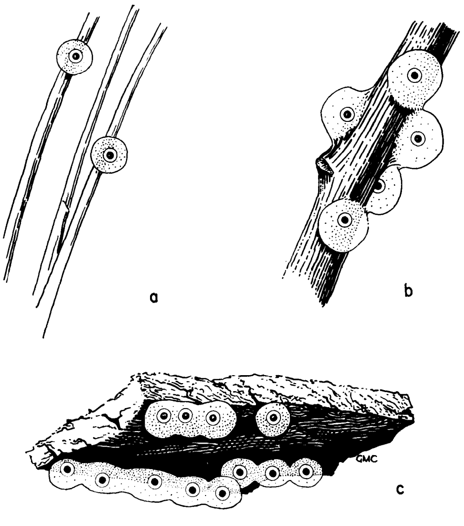

Fig. 1.—Eggs of *Ambystoma macrodactylum. a,* eggs of *A. m. croceum* attached to stalks of *Eleocharis; b,* eggs of *croceum* attached to a branch of *Polygonum; c,* eggs of *A. m. sigillatum* (Mosquito Lakes) attached to underside of a slab of bark. Jelly capsules are diagrammatic.

dropped rapidly to deep water. Some logs bearing eggs were in water up to 75 cm deep. On a floating log, however, eggs might be only 12 to 25 cm below the surface although in most instances they were 25 to 40 cm below. Those eggs attached to bark, branches, etc., were frequently 50 to 65 cm below the surface.

A few isolated, single eggs were found but most were in loose clusters (Fig. 1c). Since the word "mass" has been used for groups of eggs having a common outer capsule (as illustrated by Salthe, 1963, for several species of *Ambystoma*), it cannot be applied to these eggs. The outer envelopes of *A. m. sigillatum* eggs adhere to one another but are individually distinct (Fig. 1c). The clusters were usually arranged in linear fashion in one or, rarely, two layers.

Many eggs were often found under a single object. Approximately 500 were counted under a log 20 cm in diameter and about 1.5 m long. It was not unusual to find 100 eggs per square foot in favorable sites. On less favorable objects, branches 5 to 12 cm in diameter for instance, only five to ten eggs might be found, and the rare single eggs were usually in such locations. As a rule the flatter and rougher the surface, the more numerous the eggs. The greatest aggregations were found in or along the furrows in thick bark, indicating that females tend to follow furrows when depositing eggs.

This information was secured primarily at the two principal ponds at Mosquito Lakes. Cursory observations at other Mosquito Lakes ponds indicated that deposition sites were similar. On 3 July 1958, eggs were collected at approximately 2750 m at the summit of Ebbett's Pass, Alpine Co.; no exceptions were noted to the details presented above. Freshly laid eggs were not observed at Big Meadow. On 25 June 1958, however, egg capsules from which larvae had just escaped were noted under floating logs at this locality. They were arranged similarly to those of Mosquito Lakes. The manner of egg deposition seems therefore to be similar at all elevations in the Sierra Nevada.

Females were observed in the process of egg deposition on the night of 2 July 1958 at pond 2 of the Mosquito Lakes group. They were, unfortunately, disturbed by lights and did not deposit while being observed, although remaining in deposition postures. One female, for instance, remained in position for three hours and was checked eight times during that interval. Each time I returned new eggs were present. By means of such periodic checks, 10 females with fresh eggs were located and observed. All ten (and several others not definitely associated with new eggs) were clinging to the undersides of logs 25 cm or more in diameter. In this upside-down position the tail was held about 45° below the horizontal. One female clung to the log with her hind limbs only, whereas the others used all four. Two females, with their freshly laid eggs, were seen inches apart under the same log and another observed depositing eggs under a log bearing eggs from the previous night; both observations indicate that several females utilize favorable sites and that deposition sites are not defended. Ice and snow covered part of the pond at this date and the water temperature ranged between 3.4 and 4.0 C. Although several females were observed in the ponds during the day, none was seen at deposition sites or in the act of deposition.

Egg capsules, although not studied in detail, appear similar to those described for *A. jeffersonianum* by Salthe (1963). One major exception is that the outer jelly layer is restricted to individual eggs in these populations of *A. macrodactylum.* In both *A. m. croceum* and *sigillatum,* the outer layer is soft and loose, being much less firm than that of *A. gracile* or *A. maculatum,* and becoming distorted when removed from the buoyancy of water. One or more tough, firm inner capsules maintain shape when the egg is removed from the water. In this respect the eggs are similar to those of *A. jeffersonianum, A. tigrinum,* and possibly *A. talpoideum.* The rather fluid outer capsule is very sticky in both *A. m. sigillatum* and *croceum,* perhaps more so in the latter. Silt and other debris adhere to the sticky outer surface, and small organisms (copepods and cladocerans) frequently become trapped in it. In *A. m. croceum,* silt from the pond water often covers the jelly so completely that the egg or embryo is not visible. The only species, to my knowledge, with an equally sticky outer capsule is *A. opacum.* It is important to note that the stickiness of the outer coat is responsible for the formation of clusters, as described, in *A. m. sigillatum.* When several eggs of *A. m. croceum* are placed in a finger bowl they form clusters by adherence, although clusters were never seen in the field.

Ferguson (1961) reports that near Corvallis, Oregon, the eggs of *A. macrodactylum* (subspecies *macrodactylum*) are seldom laid singly. He records masses of between 5 and 25; the greatest frequency seemingly between 9 and 15 per mass. Most authors mention groups of between 2 and 10 eggs per mass. None of these workers, however, mention the nature of fusion of jelly capsules but it is assumed that a "mass of eggs" means a common outer jelly capsule. A captive female from Corvallis, Oregon, in my possession, laid small egg masses having a common outer capsule. Although observations on the northern subspecies (*macrodactylum, krausei* and *columbianum*) are inconclusive there does seem to be geographic variation in the nature of egg deposition: masses in the north, clusters (as described herein) in *sigillatum* and single eggs in *croceum.* A comparable situation pertains in *A. tigrinum* with the eastern subspecies, *tigrinum,* depositing masses, the California form (*californiense*) depositing single eggs, and other subspecies apparently variable in this respect (Bishop, 1943). *A. texanum* also varies in the manner of egg deposition, but has not been studied adequately to determine whether or not the variation is geographical. Bragg (1957) has postulated that variation between single eggs and masses results from the utilization of different types of egg supports and that the egg laying pattern is greatly modified by the available supports. Although the environment may induce modifications in deposition behavior in certain instances, such is not the case with *A. m. croceum* and *sigillatum* under natural conditions. In both regions a variety of supports, sufficient for the deposition of masses, clusters or single eggs, are present. One may assume some adaptive significance to the manner of egg deposition and further that the nature of the "mass" is determined by the female, governed in turn by natural selection.

The adaptive significance of deposition site in *A. m. sigillatum* is obvious. The ponds, partly covered with ice when breeding commences, would completely freeze with a sudden drop in temperature. Eggs of *A. m. sigillatum* under logs in deeper water are safe and would probably survive a prolonged return to winter conditions, whereas exposed eggs near the surface like those of *A. m. croceum* would be killed with even a slight drop in temperature.

The adaptive significance of the single, well-spaced eggs of *A. m. croceum* is less clear. Water temperature in the shallow portions of coastal ponds may rise fairly rapidly and under such circumstances the single eggs allow a better diffusion of respiratory gases than would a mass or cluster. It is significant that *A. t. californiense,* breeding in similar situations, lays its eggs singly whereas *A. t. tigrinum* breeding in colder regions in early spring deposits its eggs in masses.

The symbiotic alga, *Oophilia amblystomatis* is unknown in this species. Thousands of eggs of *A. m. sigillatum* and *croceum,* examined in field and laboratory, showed no algae of this type.

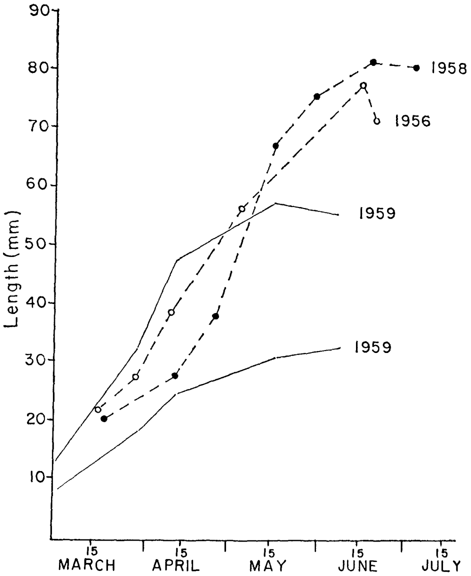

Fig. 2.—Growth curves for larval *Ambystoma m. croceum* at Valencia Lagoon. Interrupted line with open circles — 1956; Interrupted line with solid circles — 1958; Solid line — 1959. The lowest curve for 1959 represents increase in snout-vent length, all others represent total length.

The egg complements of five large *A. m. croceum* averaged 307 (range 215-411); counts were not made for *sigillatum.* Ferguson (1961) reports counts of 130 to 219 in six *A. m. macrodactylum*; 85, 87 and 145 for three *A. m. columbianum;* and 198-345 for two *sigillatum* from the Crater Lake area of southern Oregon. Although the data are obviously incomplete the southern forms, *A. m. croceum* and *sigillatum,* from rather extreme environments, apparently produce the greatest number of eggs.

SIZE AT HATCHING

Nine larvae of *A. m. croceum,* measured in the laboratory within a few hours of hatching, had an average total length of 10.9 mm (range 9.6-12.4). A series of 19 taken on 1 March 1959 at Valencia Lagoon, in the process of hatching, averaged 12.6 mm (range 10.9-14.6). Newly hatched larvae were not taken at Big Meadow or Mosquito Lakes. A series of 20 from the latter locality that hatched in the laboratory averaged 10.3 mm in total length (range 9.2-11.1) and, thus, only slightly smaller than hatchling *croceum.*

TABLE 4.—Growth (mm) of larval *A. m. croceum* at Valencia Lagoon 1956-1959

Date	Sample size	Total length	
		Mean	Range
1956			
16 March	13	21.3	14.0-26.0
29 March	12	27.0	16.0-35.0
10 April	14	38.1	26.4-47.8
5 May	14	56.3	34.5-68.2
16 June	10	78.1	70.0-87.1 (transforming)
21 June	7	72.0	67.1-80.4 (terrestrial)
1958			
18 March	4	20.0	17.3-22.7
11 April	16	27.6	20.1-36.0
26 April	17	47.4	41.0-60.0
17 May	12	67.1	51.0-81.4
31 May	6	76.0	74.5-80.0
20 June	8	82.1	75.5-91.5 (transforming)
5 July	3	81.4	78.2-86.5 (terrestrial)
1959			
1 March	19	12.6	10.9-14.6
30 March	17	32.0	27.8-36.4
12 April	20	47.2	39.8-56.6
17 May	12	57.8	47.8-65.6
9 June	2	55.6	55.1-56.2 (terrestrial)

GROWTH TO METAMORPHOSIS

Because of the discrepancy in length of larval life, the three populations are considered separately with respect to growth to metamorphosis.

The larval growth curves for *A. m. croceum* (Fig. 2 and Table 4) are similar for 1956, 1958 and 1959 (breeding was unsuccessful in 1957), however, the time of breeding and the maximum size attained varied considerably. Breeding, as indicated earlier is affected by the nature and extent of rainfall, which controls the time when water becomes available for reproduction. The amount of rain largely determines the length of time the ponds retain water and therefore time available for growth. In extremely favorable years, *A. m. croceum* breeds early and the ponds provide larval habitat into June; larvae thus attain large size because of the prolonged growing season. The higher water temperatures during May and June probably accentuate growth. The data on increase in total length is most nearly complete for 1958, (Table 4) and the curve for that year approximates the sigmoid (Fig. 2). Dempster (1930) has shown that increments of weight and length of embryonic and larval *A. maculatum* approximate the sigmoid curve from early cleavage stages through metamorphosis.

Table 5 includes data on increase in snout-vent length, and Fig. 2 compares growth in snout-vent and total length for 1959. In any year they are similar except for the decrease in total length as the larvae approach metamorphosis.

During 1959, larval growth was followed in both ponds. The growth curves are similar (Fig. 3) but for any date the larvae are larger at Ellicott Pond. This pond fills earlier in the season, perhaps because of greater runoff and underground seepage. In 1958, for instance, the first eggs appeared at Ellicott on 9 February but not until 16 February at Valencia Lagoon. Since the ponds dry at about

TABLE 5.—Proportional changes in larvae of *A. m. croceum*

Date	Snout-vent (mm)	Weight (g)	Tail/Total	HW/SV	HL/SV	HW/HL
		1958—Ellicott Pond				
19 March	16.8	....	.411	.310	.388	.804
11 April	24.6	....	.476	.296	.393	.754
26 April	32.1	....	.492	.298	.374	.797
11 May	39.0	....	.517	.275	.354	.776
17 May	41.1	....	.513	.261	.351	.742
		1959—Valencia Lagoon				
1 March	7.8	0.017	.396	.384	.412	.933
30 March	18.0	0.278	.434	.301	.359	.838
12 April	24.5	0.801	.464	.296	.361	.817
17 May	30.7	1.500	.468	.282	.351	.806

HW—head width; HL—head length; SV—snout-vent length.

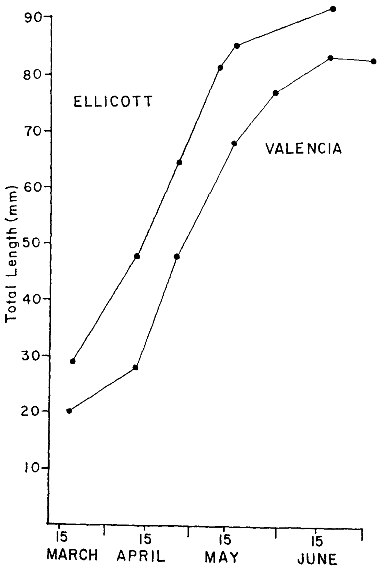

Fig. 3.—Comparison of larval growth in two populations of *Ambystoma m. croceum* during 1958. The last point on each curve represents recently transformed individuals.

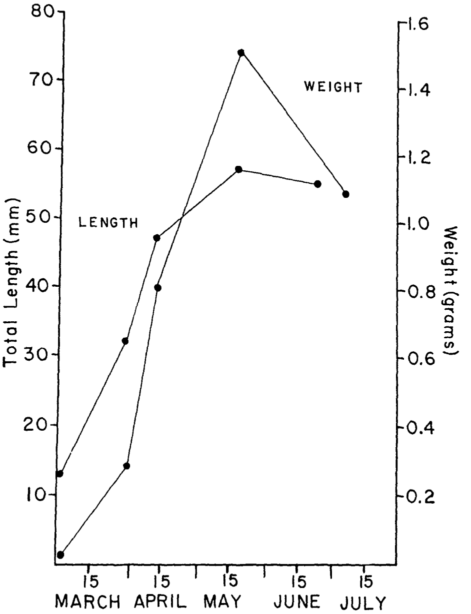

Fig. 4.—Curves representing increase in total length and weight of larval *Ambystoma m. croceum* at Valencia Lagoon during 1959. The last point on each curve represents recently transformed individuals.

the same time, the difference in size of larvae is probably due to the slightly greater time available for growth at Ellicott.

Accurate weights of larval samples were taken only in 1959. Fig. 4 shows the general relationship between length and weight. Most noteworthy is the rapid gain in weight during later larval stages, resulting in a high peak on the weight curve. At and soon after metamorphosis the total length declines slightly but weight decreases markedly. Changes in water content of the body during metamorphosis are probably partly responsible for the rapid loss of weight. Dempster (1930) found differences in weight at metamorphosis of *A. maculatum* in two years. One year the pond studied allowed a long growing season and the length-weight curves had a relationship similar to that of *A. m. croceum,* the curves crossing because of the late peak in the weight curve. In another year, however, the pond dried early and the *A. maculatum* metamorphosed at a lesser weight and length. The larvae, interestingly, did not show the late spurt of weight increase, the growth curves maintaining the relationship observed in early stages of growth. The same type of variation probably exists in *A. m. croceum* since metamorphosis may occur at various sizes from year to year in one population depending on the pond conditions.

The growth data are scanty for *A. m. sigillatum* at Big Meadow but during 1958 three samples (Table 6) indicate growth in that population. For a gross comparison of the three study areas, these samples are plotted with 1958 data for *croceum* and Mosquito Lakes *sigillatum* (Fig. 5). As indicated earlier, breeding was delayed at Big Meadow in 1958 yet the larvae attained sizes in excess of 40 mm in about 60 days.

A two-year larval period at Mosquito Lakes was first indicated on 3 August 1957, when two size classes were noted in the ponds. Six large larvae, averaging 83.6 mm in total length, were collected, along with three others of about 50 mm. The smaller larvae were devoured by the larger animals before they could be preserved. The data for small larvae in Fig. 5 are thus approximations based on field observations and subsequent collections. The larger larvae taken on 3 August were approaching metamorphosis, and by the next collection date, 4 September 1957, animals of their size and age class

TABLE 6.—Measurements (mm) of larval samples from Big Meadow study area 1958

Date	Sample size	Total length	Snout-vent	Tail length	Tail/Total
2 July	15	19.7	12.1	7.6	.386
6 August	20	55.3	29.8	25.5	.461
20 August	20	51.9	29.6	22.2	.429
				(not transforming)	
20 August	20	55.4	32.3	23.0	.415
				(transforming)	

were no longer present in the ponds. Smaller larvae had reached approximately 60 mm in total length by September. The growth of this group was followed to metamorphosis in 1958 (Table 7) and larvae hatched in 1958 were followed until June of 1959. Larvae of the two age classes overlap only during the summer months, after the breeding season (late June) until the year-old larvae metamorphose in late August or early September.

Growth in this larval population occurs in two spurts (Fig. 5). During the first year the larvae attain a total length of 55 to 65 mm, approximately the size reached by the Big Meadow population at metamorphosis. Very little growth takes place over the winter although the actual amount varies depending on the severity of the

TABLE 7.—Measurements (mm) of larval samples from Mosquito Lakes study area

Date	Sample size	Mean length Total	Snout-vent	Tail	Tail/Total
	1956 age class (transforming)				
3 Aug.	6	83.6	42.7	38.5	
		1957 age class			
4 Sept. 1957	17	60.9	31.3	28.3	46.5
2 July 1958	14	64.2	33.1	30.2	47.4
6 Aug. 1958	15	77.4	39.2	35.8	46.3
20 Aug. 1958	11	82.0	42.1	37.1 (transforming)	45.3
		1958 age class			
6 Aug. 1958	12	21.5	12.7	9.0	41.7
20 Aug. 1958	15	35.1	19.7	15.4	43.8
23 Sept. 1958	20	57.4	30.9	26.5	46.2
27 June 1959	9	84.8	43.1	41.7	49.1

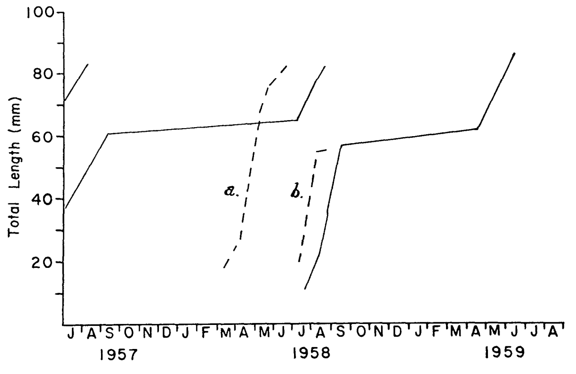

Fig. 5.—Larval growth in three populations of *Ambystoma macrodactylum*. Solid lines — Mosquito Lakes 2450 m (*sigillatum*); Interrupted line a — Valencia Lagoon (*croceum*); Interrupted line b — Big Meadow 1980 m (*sigillatum*).

winter. In 1958 when the winter was severe and the thaw was late, there was little difference between samples taken in September 1957 and July 1958. The winter of 1958-59 was milder and followed by an early thaw; these conditions are reflected in the large size of the June 1959 sample (Table 7). The larvae reach maximum size during their second summer and metamorphose before winter. Intensive collecting of larvae at high elevations in the Sierra Nevada has not revealed exceptions to this pattern. If larvae persist longer than two seasons they must do so in inaccessible portions of deep, cold lakes such as Lake Alpine, Alpine Co., or Lake Helen, Lassen Co. Based on the present study and knowledge of the species elsewhere, such neotenic tendencies seem highly unlikely.

PROPORTIONAL CHANGES

In all three populations (Tables 5, 6 and 7) the tail makes up a great portion of the total length as the larvae grow. This trend is slightly more pronounced for *A. m. croceum,* in which the tail may exceed 50% of the total length (Table 5).

As the larvae approach metamorphosis, however, the tail becomes proportionally, and then actually, shorter. The Big Meadow population, metamorphosing at the smallest size, has the shortest tail when first becoming terrestrial.

Head proportions were analyzed only for *A. m. croceum* (Table 5). The decrease in the ratio of head width to head length as body length increases indicates the more rapid linear growth of the head. The relative narrowing of the head throughout larval life is reversed at metamorphosis when the blunt-snouted condition typical of adult *Ambystoma* becomes established. Relative decrease in head width is also indicated by the decrease in ratio of head width to snout-vent length. The relationship between head length and body length varies during development but generally the head makes up less of the snout-vent length as the larvae grow.

SIZE AT METAMORPHOSIS

Table 8 summarizes the information on metamorphic size in the study areas. Year to year variations within each population can be attributed primarily to time available for growth, *i.e.,* persistence of ponds, in *A. m. croceum* and in *sigillatum* from Big Meadow, and to the severity and duration of winter at Mosquito Lakes. As indicated earlier, the Ellicott *croceum* are consistently larger at metamorphosis, since that pond forms earlier and provides a greater period for larval growth.

Table 8 indicates that Big Meadow *A. m. sigillatum* metamorphose between 30 and 35 mm (S-V), almost exactly the size attained during the first summer by Mosquito Lakes *sigillatum.* The latter, at metamorphosis, are similar in size to transforming *A. m. croceum* but require about 14 months to achieve the size that *croceum* attains in three months. Mosquito Lakes *sigillatum* vary only slightly in size but the time of metamorphosis may vary greatly. These facts suggest that a critical size (or stage) must be reached in this population before transformation occurs, and that it is reached earlier some years than others. Big Meadow *A. m. sigillatum* and *croceum*, however, are forced into metamorphosis by drastic changes in the ponds as the habitat dries out. Metamorphosis may be triggered by intrinsic factors in the first instance and by extrinsic factors in the others.

HABITS AND HABITAT OF LARVAE

Certain aspects of larval ecology (temperature tolerances, reactions to light and feeding behavior) will be discussed in another publication. The following observations, chiefly made while collecting samples for growth studies, provide the first information on habitat selection and activity, under natural conditions, in larval *Ambystoma*. In addition to field observations, several groups of *A. m. croceum* larvae were raised in the laboratory and observations on their behavior recorded from hatching through metamorphosis. In Table 9 development and laboratory behavior are correlated with field observations.

TABLE 8.—Size at metamorphosis in three populations of *A. macrodactylum* (mm)

Date	Sample size	Mean length and (range)		
		Total	Snout-vent	Tail
		Valencia Lagoon		
16-21 June 1956	17	75.6 (67.1-80.4)	37.5 (34.2-41.1)	37.2 (33.0-46.0)
20 June-5 July 1958	8	81.5 (78.2-88.2)	42.6 (38.5-45.2)	38.0 (33.5-41.3)
9 June 1959	2	55.6 (55.1-56.2)	32.6 (31.8-33.4)	23.0 (21.7-24.4)
		Ellicott Pond		
20-28 June 1958	9	90.8 (86.0-97.5)	45.1 (43.3-47.5)	42.3 (37.1-46.8)
		Big Meadow		
7 Aug. 1956	23	62.6 (57.6-70.0)	35.2 (32.4-37.8)	25.9 (23.7-28.7)
3 Aug. 1957	37	54.5 (48.7-61.4)	31.2 (28.6-35.4)	26.3 (18.5-25.6)
20 Aug. 1958	20	55.4 (48.8-59.9)	32.3 (30.1-34.2)	23.0 (17.0-26.5)
		Mosquito Lakes		
3 Aug. 1957	6	83.6 (76.8-91.5)	42.7 (38.8-46.0)	38.5 (35.2-44.0)
20 Aug. 1958	11	82.0 (76.8-87.5)	42.1 (39.9-45.7)	37.1 (35.0-40.2)

In the field, newly hatched *A. m. croceum* larvae were concentrated near the sites of egg deposition. When sampling with a dip net, as many as 10 hatchlings could be gathered in one sweep through a clump of *Eleocharis* near the edge, but in other portions of the pond no larvae were taken. Until the fins and tail musculature became better developed, the larvae remained aggregated in plant cover. In the laboratory, larvae moved very little at this stage, and when they began feeding took only moving objects that passed directly in front of them.

At about 20 mm total length the larvae began dispersing from the egg sites. In captivity, at this size, the larvae were more active and moved about in search of food. Under crowded conditions, the larvae often fought until gills, fins and limbs were lost. This aggressive behavior is probably one of the factors involved in the dispersal and subsequent spacing observed in the field. An attempt to mark and recapture larvae in order to study spacing was unsuccessful but the fact that larger larvae could only be taken singly with a dip net is indicative of the spacing. At metamorphosis the animals aggregated in favorable areas as the habitat became reduced. Transforming larvae in the laboratory ate very little and became more tolerant of other salamanders.

Throughout larval life *A. m. croceum* prefers shallow areas (Fig. 6). They were most abundant near clumps of vegetation, apparently feeding near the edges of *Eleocharis* patches and retreating to the

TABLE 9.—Correlation between linear growth of larval *A. m. croceum* and morphologic development and behavior

Total length	Morphologic development	Behavior in laboratory	Field observations
10–14	Balancer present. No limbs, tail fin poorly developed.	Few movements. Not feeding.	Near egg sites. Difficult to collect.
15–20	Balancer reduced or absent. Forelimb a bud only.	Few movements. Wait for food to pass by.	Near egg sites. Difficult to collect.
20–25	Balancer gone, forelimbs function as a balancer in crawling.	Swim more; begin to stalk prey by crawling.	Near egg sites but not concentrated. Easier to collect.
25–30	Forelimbs well developed. Hind limbs developing but nonfunctional. Fins well developed.	Swim and crawl after prey. Conflicts over food. Dispersal.	Away from egg sites. Easy to collect individuals.
30–60	All four limbs functional. Maximal development of fins.	Hunt food. Aggressive, conflicts if crowded; dispersed.	Well spaced, easy to collect individuals.
60–	Gills decrease in size. Fins reduced. Limbs strong.	Swim to surface, otherwise less active. Tend to hide, less aggressive.	Difficult to collect. Tend to be aggregated in favorable places.

vegetation when disturbed. Both field and laboratory observations indicate that the larvae remained at, or close to, the bottom during the day.

After mark-recapture methods were unsuccessful, I attempted to devise a system of traps in order to obtain information on movements of larvae in the field. Twelve funnel traps, similar to those described by Carpenter (1953), were constructed and set in Valencia Lagoon. The traps, placed on the bottom 2.5 m apart, formed a grid. The entrances to the traps were approximately 2.5 cm off the bottom. The traps were checked every two hours over a 24-hour period. This was done five times during the season when larvae were most active. Only three *A. m. croceum* larvae were taken, all entering the traps during the daylight hours. No explanation can be offered for the results since adult salamanders, tadpoles of *Hyla regilla,* and insects entered traps in great numbers.

Neither Valencia Lagoon nor Ellicott Pond was suitable for direct observation of undisturbed larvae because of the turbidity of the water and extensive plant cover. The Mosquito Lakes ponds, however, were clear and essentially devoid of vegetation. Although logs, dead branches and bark offered shelter for larvae, the opportunities for observation were excellent.

Newly hatched *A. m. sigillatum* were also secretive and remained hidden under bark, logs and other bottom debris until they reached 30 mm in total length towards the end of the first summer. Then these larvae were seen more and more in open, well-illuminated portions of the ponds when larvae from the previous year had left the ponds or were in the process of metamorphosis. The larvae of the

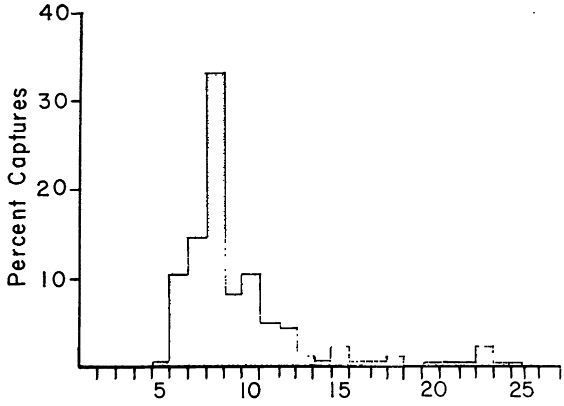

Fig. 6.—Depths at which 210 larval *A. m. croceum* were captured at Valencia Lagoon (1956 and 1958). Only larvae greater than 30 mm in total length are included.

year remained active on the bottom where they were seen foraging and feeding into September.

As the temperatures decreased the larvae once again became secretive. On 23 September 1958, for example, the water temperature at midday was 6 C, and no larvae were seen in any of the pools. When logs and bottom debris were moved, however, numerous larvae were exposed. Such retreats are presumably sites where the larvae spend the winter. In early spring, when adults were breeding and a film of ice covered part of the pond, larvae were found in similar places. They were best obtained, then, by turning logs or bark slabs several feet from the edge in water more than 30 cm deep. They generally occurred in small aggregations and tended to work their way down into smaller debris under larger pieces of cover. As temperatures rose in the spring, the year-old larvae dispersed from these winter retreats and were active in well-lighted portions of the ponds. Meanwhile, the new crop of larvae had hatched and restricted their activities to the logs and debris recently abandoned by larger larvae. As they approached metamorphosis the larger larvae again became secretive, remaining under cover within inches of the shore and in water 5 to 8 cm in depth.

The sequential behavior of these salamanders from hatching through metamorphosis the following year thus results in a selection of different habitats by the age classes of larvae. This plus the differences in diet (Anderson, 1960) serves to minimize intraspecific competition. The habitat differences may also prevent cannibalism, which was frequently seen under laboratory conditions.

POSTMETAMORPHIC GROWTH

Like most members of the genus, terrestrial *Ambystoma macrodactylum* is difficult to collect except during the breeding season. An exceptional favorable circumstance gave information on growth in *A. m. croceum* during the first year of terrestrial life. Following the wet winter and spring of 1958, the willow grove at Ellicott retained sufficient moisture to maintain newly transformed and juvenile *croceum* at, or near, the surface during the summer. Monthly samples of young were taken from June 1958 through January 1959 (Table 10). By January some of these juveniles had reached the size of the smallest (but older) breeding adults that appeared at that time and migrated to the breeding pond. The two groups were easily distinguished since young animals lacked the sexual characteristics (enlarged tail and swollen cloaca in males; great girth of gravid females) of migrating adults. The immaturity of presumed juveniles was later confirmed by examination of the gonads. Growth is probably always most rapid during the first year but was markedly so in 1958 when the pond remained into June allowing growth to large sizes at metamorphosis (Table 8). Moist surface conditions permitted a long period of activity and provided abundant food. In other years metamorphosis at a smaller size and drier surface conditions result in much smaller animals after a year of life. The young of 1958 overlapped in size animals at least a year older. An unusually early rain on 19 September 1956 offered another opportunity to study growth. Juveniles at Valencia Lagoon emerged from their summer retreats in response to this rain. The average snout-vent length of 17 newly metamorphosed young from the same area between 16 and 19 June was 37.5 mm, average total length 75.6. Approximately three months later, on 19 September, the mean snout-vent length of the 28 young was 40.1 mm and total lengths averaged 77.0 mm.

SIZE AT SEXUAL MATURITY

With the exception of the juveniles mentioned above and scattered individuals taken under special circumstances, all *A. m. croceum* were taken in the breeding ponds or during migration. All of the adults associated with the breeding ponds showed obvious external signs of sexual maturity, and for many the breeding condition was confirmed by examination of the gonads. Reproducing males ranged from 46.5 to 64.0 mm in snout-vent length; females from 51.8 to 63.0. It is best to consider 50 mm as adult size in this subspecies since few sexually mature *A. m. croceum* are under 50 mm SV (Table 11) and since some individuals reach 49 mm during their first year of life (Table 10) but are sexually immature. For example, juveniles from Ellicott, taken in January 1959, were almost one year old but the gonads were still immature; they would almost certainly breed the following year — their second year of life. Additional information confirming the attainment of sexual maturity in the second year of life was obtained from the recapture of marked animals at Valencia Lagoon. Approximately 100 juveniles were marked during 1956 and 1957, and only two later recaptured. Both had been marked on 19 September 1956, part of the group mentioned above. Number 23, a male, had a snout-vent length of 44.0 mm on that date and was recaptured on 24 January 1958 when it measured 55.2 mm.

TABLE 10.—Growth of juvenile *A. m. croceum* at the Ellicott study area following metamorphosis in June, 1958

Date	Sample size	Mean length (mm) Total	Snout-vent	Tail	Tail/Total
20 June	2	91.8	46.2	43.0	46.8
28 June	7	90.6	45.9	42.1	46.4
5 July	6	91.4	45.6	42.6	46.6
20 July	6	91.1	43.6	44.6	49.1
2 Aug.	8	92.6	45.6	44.2	47.7
29 Aug.	12	91.2	44.6	43.6	48.6
13 Sept.	11	77.4	47.3	47.0	48.1
14 Oct.	10	102.0	49.4	49.8	48.8
15 Nov.	7	97.5	46.3	48.2	48.5
27 Dec.	6	95.7	49.0	45.2	47.3
10 Jan. 1959	6	95.4	49.4	44.0	......

TABLE 11.—Percentage of breeding individuals in various size classes. (Both males and females are included)

Valencia Lagoon, n = 137
Mosquito Lakes, n = 32

Snout-vent Length (mm)	Valencia Lagoon (%)	Mosquito Lakes (%)
40-50	8.8	0.0
50-55	43.6	6.2
55-60	42.3	46.7
60-65	5.8	37.5
65-70	0.0	9.6

When recaptured, it was migrating to the pond and had the swollen cloaca and enlarged tail typical of breeding males. The other, a female, had increased from 36 to 53 mm in snout-vent length. It was recaptured on 16 February 1958 and was gravid when taken. Both had thus attained adult size and sexual maturity in their second year of life, having hatched from eggs laid in February of 1956 and metamorphosed in June of that year.

Growth is probably slower after the second year since the largest male measured was 64.0 mm snout to vent, the largest female 63.2. Of all the adults measured, these were the only two in excess of 60 mm. Table 11 gives the size distribution of adults at Valencia Lagoon. The data, although fragmentary, indicate that, on the average, *A. m. croceum* attains a snout-vent length between 40-45 mm the first year; 50-55 the second; and a maximum between 60-65 after the second year. The first year is probably the most variable due to extrinsic factors as indicated earlier.

Almost no comparable information is available for *A. m. sigillatum.* Some inferences can be made, however, based on size at metamorphosis and the size ranges of adults from Mosquito Lakes and other areas of similar elevation. A series of 32 breeding adults from the Mosquito Lakes ponds, all taken during the breeding season of 1958, provide some information on size at sexual maturity. Males ranged from 53.8 to 64.9 mm and females from 55.5 to 68.9 mm S-V. The size distribution of this sample is compared to that of *A. m. croceum* in Table 11. None of the breeding adults examined from other areas in the Sierra Nevada are less than 55 mm in snout-vent length. Sexual maturity, thus, seems to come at a slightly larger size in *sigillatum.* At high elevations in the Sierra Nevada, individuals of *A. m. sigillatum* are still larvae in their second year of life, metamorphosing just before winter at body lengths of 39 to 46 mm (Table 7). Assuming that the terrestrial stages, like the larvae, grow very little over the winter, it seems unlikely that they could reach the minimum size for breeding, approximately 55 mm, by the following spring. They probably breed for the first time a year later which would be the end of their third year of life.

HABITS AND HABITATS OF TERRESTRIAL STAGES

JUVENILES

The terrestrial habitats of *A. m. croceum* are extremely dry at the time of metamorphosis. As the ponds dry out the transforming larvae become concentrated in the center of the pond area. The newly metamorphosed animals are unable to disperse at Valencia Lagoon because of the arid summer conditions. They concentrate under debris, logs, and mats of dead vegetation on the former pond bottom or in willow thickets near the pond. Immediately after the pond dries up, almost any object in the area affords protection because the substrate retains moisture for at least a week. Young salamanders were found in numbers by rolling back mats of aquatic plants (mostly *Polygonum* and *Eleocharis*). These shelters, however, are temporary, since, by the middle or end of July, the former pond bottom is as dry as the surrounding region. The juvenile *A. m. croceum* make use of burrows as the habitat changes. It is not known whether they make their own burrows, but there is evidence that they utilize mammal burrows. Almost as soon as the water disappears other terrestrial animals begin to invade the area. The first to exploit the new habitat, as terrestrial plants move in, is *Microtus californicus*, followed soon by *Scapanus latimanus* and *Thomomys bottae*. Within a few weeks, the entire area is a network of runways and burrow systems of these mammals, formed quickly enough to enable the salamanders to exploit the burrow systems. Several *A. m. croceum* were dug from mammal burrows during the summer months, and others were observed emerging from burrows during the first autumn rains. Two other summer retreats were located at Valencia Lagoon. Several *A. m. croceum* were collected during the summer by digging out buried logs. One, for example, was found at the very end of a willow branch, 1.2 m long and 20 cm thick, that extended 0.5 m into the soil at an angle of 30°. On this date, 28 August 1958, the surface soil was powder dry, but water could be squeezed from the mixture of soil and rotting wood where the salamander was located. Numerous juveniles were found deep in a tule thicket during July and August. Near the center of the thicket, the salamanders were dug from the moist depths (25-30 cm) of mats of dead stalks. Microhabitats like this probably afford optimal temperature and moisture conditions throughout the dry season.

At Ellicott Pond, an extensive willow grove located right at the edge of the pond provided habitat for adults and juveniles. The canopy provided shade most of the day, and the high water table allowed high moisture content of the soil under the abundant logs, branches, stumps, etc. This permitted the newly transformed salamanders to disperse immediately upon leaving the water; none was found in the old pond bottom after it had drained. In addition, the soil in the willow grove was honeycombed with burrows of *Scapanus latimanus* that were extensively used by *A. m. croceum* (Anderson, 1964). Juveniles were taken in this thicket almost every month in 1958 when the area was studied most intensively.

The behavior of the salamanders changed as the soil became progressively drier. Until the latter part of August usually only one or two could be found under larger logs resting on the surface. After this time, however, they had to be dug from partly buried logs or from the burrows of *Scapanus*. They tended to form aggregations, individual animals being rarely collected. Throughout September, groups of three to nine were regularly taken by digging or breaking open rotted logs. In every case the animals were in bodily contact. One group of nine, found in the center of a rotted log, was so tightly entwined that it could be handled like a ball. A similarly entwined group was taken from under a log buried 15 cm under the soil. The physiological significance of such aggregations will be discussed in another report. The only amphibian found in contact with *A. m. croceum* was *Hyla regilla*, although *Batrachoseps attenuatus* and *Aneides lugubris* were found in similar places in the vicinity. With the onset of winter rains, aggregations were no longer typical and the juveniles became more active.

The onset of winter rains elicited quite a different response from juveniles at Valencia Lagoon. The terrestrial habitat is the oak woods on the hillside south of the breeding pond but separated from it by Bonita Road and an open grassy area dotted with *Baccharis pilularis.* Forty-five to 90 m of this open, dry habitat separates the transforming salamanders from the oak woods, apparently forming an effective barrier to dispersal all through the dry season. When the winter rains begin, the juvenile *A. m. croceum* disperse to the woods. The response may be immediate and spectacular, depending on the nature of the early rains. In 1956, for example, only a trace of rain had fallen in Santa Cruz Co. from June to 19 September, when 0.28 inches were recorded. The rain was light in the afternoon, heavier just after dark and sporadic later that night. Beginning at dusk, the road between the pond area and the oak woods was surveyed continually. Juvenile *A. m. croceum* began crossing this sandy strip about one hour after dark, moving from the pond area to the woods. Approximately 90 were counted between 8:30 and 11:30 PM and new individuals were continuing to appear when observations were terminated at midnight. Most observations were made on a 35-m stretch of road directly opposite the center of the former pond area. All but two of the salamanders were moving in a straight line from the pond to the woods, seemingly taking the shortest route to the terrestrial habitat. Temperatures near the ground ranged between 13.0 and 15.2 C. The following day there was no rain, but the ground was moist and, after dark, the relative humidity, measured with a sling psychrometer, was 98%. In four hours of observation that night, only two *A. m. croceum*, both juveniles, moving to the woods, were observed. On 6 October, a trace of rain fell after dark and 10 juveniles were observed. Seventeen were noted on 30 October when rainfall after dark was slightly heavier. In numerous subsequent trips only a few juveniles were observed, the main emigration having coincided with the first rains of the season. By the time adults began their breeding migration, the juveniles had already passed into the terrestrial habitat. In other years (1957-1959) observations were less complete, but essentially the same pattern was observed. On a few occasions when the first rains came late in the season, juveniles were seen moving to the woods while adults crossed the road moving to the breeding pond. After reaching the terrestrial habitat the young establish themselves and move little. They were seldom encountered on the surface at night after the emigration.

No comparable information was obtained for *A. m. sigillatum* at Mosquito Lakes, but at Big Meadow newly metamorphosed animals were found in great numbers. Immediately after transformation when the pond had dried, the tiny juveniles were observed under almost any piece of cover from large logs to bits of bark a few square inches in size. Almost all the animals were found within the depression marking the old pond area. For the first few weeks after metamorphosis they were found singly or in groups of up to 10 animals. At this time, with abundant soil moisture, they were seldom in contact and never entwined. Later in the summer, when conditions became drier, large aggregations ranging from 15 to 43 individuals were observed, frequently so entwined as to form a ball. Although many juvenile *A. m. sigillatum* may spend the summer this way, some dispersal probably occurs during the summer. The summer thunder showers in the Sierra probably facilitate dispersal of juveniles.

ADULTS

Adults of both subspecies can be collected easily only during the breeding season, being underground most of the year. A few adults of *A. m. croceum* were found up to 6 weeks after the breeding season in habitats like those occupied by juveniles during the summer. Adult *A. m. sigillatum* were found only when breeding in the ponds.

The breeding migration of *A. m. croceum* was observed by the same methods as described for the emigration of juveniles. The areas were frequently visited at various times of day and night and under a variety of climatic conditions. Breeding migrations took place on rainy nights only.

Adults require heavy rainfall before emerging and moving to the breeding ponds (a light rain will stimulate emigration of juveniles). In four years of observation adults did not migrate until the total seasonal rainfall had exceeded 4.2 inches. In the two years when it was certain that the first movements were being observed, heavy rains (1.8 and 2.5 inches) fell on the day and during the night of the initial migration. Once migration had begun, such heavy rains were not essential although the time of day it rains is of great consequence. For example, after the main migration in late January 1957, 1.24 inches fell during the day of 21 February, stopping just before dark.

No salamanders moved that night although the ground was soaked and the relative humidity was 98%. On the following night when only 0.24 inches fell between dusk and midnight, 22 *A. m. croceum* migrated. Temperature conditions were virtually identical on both nights. Similar observations were made throughout the study. Table 12 summarizes the pertinent observations on the breeding migration of *A. m. croceum*. Only those nights when three or more individuals were seen are included. The numbers recorded naturally reflect only the magnitude of movement since only a portion (approximately 135 m) of the road was patrolled. The data clearly indicate the great range of time over which migration occurs. Heavy, soaking rain, sufficient to affect the animals in their summer retreats, and to produce runoff, is necessary to trigger the migration, and continued rain, falling at night, is required to sustain the migration. The erratic nature of the rains, especially early in the season, results in the variability in time of migration each year and the span of time within a season when animals migrate.

Heavy rainfall early in the season may result in salamanders reaching the pond area long before sufficient water has accumulated for breeding. In 1957, stimulated by unusually heavy, early rain, adults moved to the pond area in October and November, but the pond did not form until mid-January. In these circumstances, salamanders must seek shelter at or near the pond area during the interim, since in frequent patrols of the area none were seen moving back to the oak woods until after eggs had been deposited.

Both sexes respond to the rainfall at the same time, but the cumbersome, gravid females move more slowly than the males and

TABLE 12.—Observations on the breeding migration of *Ambystoma macrodactylum croceum*. (Only those nights when three or more salamanders were observed are included.)

Date	Time (PST)	Precipitation[a] (inches)	Temperature[b] (° C)	Males	Females
2 Dec. 1954	9:15-11:30	1.28	12-14	12	1
25 Jan. 1957	6:00- 9:30	0.04	6.0-6.6	3	10
22 Feb. 1957	6:45-11:30	0.24	12-14	12	10
13 Oct. 1957[c]	6:00- 8:30	2.49	14-15	4	1
18 Nov. 1957	6:00-10:45	0.22	11-13	26	00
15 Dec. 1957	7:00-11:15	1.52	13-14	11	8
23 Jan. 1958	11:15- 1:45	3.70	8.0-8.6	00	3
5 Jan. 1959	5:00-10:35	1.00	8.6-9.6	15	2

[a] Precipitation is the total for the 24-hour period as recorded by the weather bureau at Santa Cruz, Santa Cruz Co.

[b] Temperatures are air temperatures recorded ¼ inch above ground where salamanders were collected.

[c] Animals observed on 13 Oct. 1957 were in the oak woods and not on Bonita Road. Remainder recorded as they crossed Bonita Road by Valencia Lagoon, Rio del Mar, Santa Cruz Co.

appear at the pond slightly later. On 18 November 1957 when only males were observed crossing Bonita Road, observations in the oak woods some distance from the road, revealed that females were moving toward the pond. On 22 February 1957 and 15 December 1957, almost all the males had been observed before females began to cross the road. Table 12 also shows a predominance of males migrating from October through January, but females predominate later in the season. Since most of the migration takes place before the pond has filled, the differential migration of the sexes does not affect their equal representation at the pond when there is sufficient water for breeding.

Few observations were made on the return from the breeding pond. Since no mass emigration was observed, postbreeding dispersal appears more gradual than migration to the ponds. Rain at night is also required for the return trip. One male marked as it migrated to the pond was recaptured 15 days later as it returned to the woods. It was recaptured less than 9 m from the original point of capture. *A. m. croceum* clearly differs from other *Ambystoma* that have been studied with respect to breeding migration. The only important factor affecting *croceum* is rainfall. The other species are affected by temperature and possibly interaction between temperature and moisture (Blanchard, 1930; Baldauf, 1952; Peckham and Dineen, 1955). The few species that have been studied are from the eastern U. S. and breed in early spring.

The breeding migration of *A. m. sigillatum* was not observed, but at Mosquito Lakes adults were found soon after their arrival at the ponds and before most of the eggs had been laid. The stimuli for migration and the conditions under which it occurs are clearly different than in *A. m. croceum.* As indicated earlier, the ponds were partly covered with ice and surrounded by snow as *A. m. sigillatum* reproduced. At best, only 1.5-2.0 m of bare ground was present near the water, and in some places drifts over 2 m deep were present at the edge of the pond. Rising temperatures producing a partial thaw seem the most probable stimulus to the breeding migration. Moisture is provided by water from the melting snow. It is very possible that *A. m. sigillatum* migrates to the ponds under the snow.

Concerning the nonbreeding habitat of *A. m. sigillatum,* little information can be added to that provided by Stebbins (1951). Adults are extremely difficult to collect when not at the ponds. They apparently spend most of the year underground or inside large, rotting logs. To collect large series for experimental or systematics studies, it is essential to visit known breeding areas as soon as the ice begins to clear from the ponds.

CONCLUSIONS

The populations of *Ambystoma macrodactylum* that were studied live in drastically different climatic zones: coastal, Mediterranean for *A. m. croceum*; moderate subpolar (Köppen classification) for *sigillatum.* They are southern terminal forms apparently derived from ancestral populations in the Crater Lake region of southern Oregon (Russell and Anderson, 1956; Ferguson, 1961). The Sierran populations of *A. m. sigillatum* are probably continuous whereas *croceum* is disjunct from northern populations. The major features of the life history of each are adaptive to the prevailing climatic regime. Important differences are apparent in the timing of events in the life history. Different environmental stimuli trigger these events, and there are different adaptations to conditions prevailing during breeding, development and metamorphosis. The result is different activity patterns for these peripheral populations.

Demes within each area show minor differences depending upon prevailing conditions in a particular pond or type of pond. Such differences are most pronounced in the Sierra where altitudinal changes over short distances mean distinct environmental changes. These changes are sufficient, for example, to prevent the species from utilizing small temporary ponds at high elevations whereas such ponds are regularly used at midelevations. Moreover, a single-season larval period is characteristic of midelevations whereas a two-season period seems typical of higher elevations.

Although life history of the species has not been studied in detail elsewhere, the breeding pattern seems variable throughout the species range and correlated with the prevailing climatic regime as in the present study (see Ferguson, 1961, for a review of life history for the entire species). As indicated, both *A. m. croceum* and the Sierran *sigillatum* are probably derived from ancestral populations in the Crater Lake region, *croceum* having diverged sufficiently in isolation to be recognized as a distinct subspecies whereas *sigillatum* grades clinally from the Crater Lake area into the Sierra. The life history in the Crater Lake region, although variable, (Kezer and Farner, 1955) is basically of the same type reported herein for Sierran populations, and very different from that of *A. m. croceum.* It is highly probable that some Pleistocene pluvial permitted the maximal southward penetration of coastal populations and that with subsequent increasing aridity these populations became isolated pockets following withdrawal and extinction. One of these has survived as *A. m. croceum,* now adapted to a climatic situation different from that of any other populations of the species. Released from genetic influence from the north, *croceum* has diverged most strongly in life history. Whereas *A. m. croceum* might have remained throughout the Pleistocene, the Sierran populations were probably restricted to the north during the glaciation of the Sierra, and reestablished the present distribution subsequent to the last glacial maximum. Although the coastal populations may have been *in situ* for a longer period, adaptations to increasing aridity may be fairly recent (post-Pleistocene). The ancestral *A. m. croceum* population, endowed with the plasticity characteristic of the species, has adapted to a different habitat and a different climatic regime through modifications of behavior and life history. Physiological adaptations are also apparent (Anderson, 1960) and will be reported subsequently. This is a good example of a peripherally isolated population assuming a way of life and evolving adaptations different from those of the main species populations in which gene flow exerts a conservative influence.

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