Observations on the Ecology and Behavior of the Pacific Treefrog, *Hyla regilla*

Bayard H. Brattstrom and James W. Warren

The Pacific treefrog, *Hyla regilla*, is one of the most abundant amphibians in western North America. It is found from British Columbia to the tip of Baja California and from the Pacific Ocean east to western Montana, Idaho, Utah, and Nevada. It occurs from sea level to an elevation of 11,600 feet. Little is known, however, about the general natural history of this small treefrog. Early in the year of 1953, while working on the general distribution of some southern Californian amphibians and reptiles, data were also obtained on the ecology and behavior of this treefrog.

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Study Area

Unless otherwise mentioned, the data presented herein apply to treefrogs collected or observed in the various streams, ponds, or lakes along, and usually the result of, the San Andreas Fault from the town of Gorman (elevation 4,000 feet) to the town of Palmdale (elevation 2,000 feet), Los Angeles County, California (Fig. 1). Trips were made along the highway from Palmdale to Gorman about every 2 weeks from January 1 to July 25, 1953 and occasionally after that.

Temperature Data

The temperature of the lakes, streams, and ponds, as well as the air and soil was taken and the temperature and behavior of the hylas noted. All temperatures were taken with a Schultheis thermometer.

Water temperature was taken at 1-inch and 6-inch depths; that of the air was taken at 1 inch above the water and at 3 to 5 feet above both land and water. Though the data, resulting in more than 500 temperature readings, were taken at many places, only the data for one area, the ponds at Gorman, are reproduced here (Table I). Areas varied in their *Hyla* fauna according to the size and temperature of the habitat. For instance, small streams and ponds were occupied early in the season since they were heated sufficiently by the January and February sun and did not cool off greatly at night. The larger lakes were usually not utilized for singing or breeding because they did not become sufficiently warm until after the breeding season. Small, cold (3°–8° C.) streams from underground springs were not occupied by the hylas, though they were found in warm ponds or lakes within 1,000 feet.

In medium sized lakes the activity of the hylas was variable. Hidden Lake, for example, is supplied by an underground spring that seeps through the grass and dirt down a small hill; at the edge of the lake there are many grass-covered 4-to-10-inch-deep depressions made by the hooves of grazing cattle. If during a cold night, the small seeps or depressions about the lake fringe area freeze, the frogs concentrate in the lake proper. If the lake becomes too warm (20° C. or above) by mid-afternoon, the adults go to small pools or seeps where the water is cooler (average, 15° C.). When these small depressions cool off too much, the frogs return to the lake proper which held the heat for some time during the night.

When the frogs were singing, they would often be in water of 10° to 12° C. with just their heads above the surface in air with temperatures of 5° to 10° C. When the air was warmer than the water the frogs would sing from sticks, grass, etc., in the air. If air temperatures became too hot and the hylas too warm, they would jump into the cool water for a short time as a means of cooling off.

Artificial Lake Two Miles South of Palmdale.—This is a body of water approximately 100 by 500 yards. It is used for fishing and is stocked with bass and bluegill. It is bordered by cat-tails and a Creosote-Juniper-Joshua Tree association. Coots are usually present. Water temperatures varied from 9.4° to 15° C. No amphibian eggs or larvae were ever seen in or near the lake, but on February

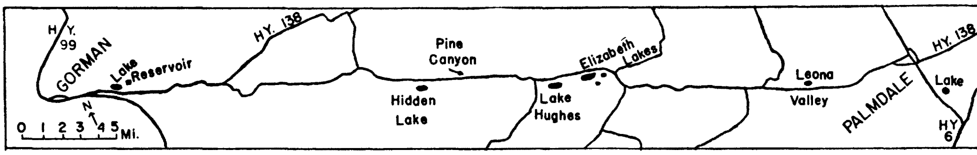

Fig. 1. Map of road between Gorman and Palmdale, Los Angeles County, California, showing places mentioned in the text.

2, at 5:40 PM, *Hyla regilla* was heard on the shore's edge and on July 18, a few hyla and many juvenile *Bufo boreas halophilus* were seen.

LEONA VALLEY.—In Leona Valley there is a pool approximately 20 by 60 feet and from 3 to 12 inches deep, and a shallow (1–2 inches deep) stream without vegetation. There were no hylas in the stream until March 7; on that date several adults were heard singing at 11:45 AM. In the grass-bottomed pond *Hyla* was not observed until February 2, when many were singing in it (water 11.5°, air over water 6° C.). On February 13, at 11:30 AM no hylas were observed in the pond (water temperature, 16.8° C.) but upon lifting up some dead tumbleweeds which had blown into the pond, a *Hyla* was uncovered sitting in the water (at 6.3° C.). After March 7 no adult amphibians were observed in the pond. On April 11, at 10:30 AM an aggregation of about 180 *Hyla* tadpoles was observed concentrated in a circle about 2 feet in diameter. A description of the aggregation will be given below.

FISHING POND EAST OF ELIZABETH LAKE.—This is a small (100 by 150 yards) artificial pond stocked with fish for use by members of a private club. Water temperatures varied from 9.7° to 13° C. No amphibians were seen or heard in the pond except for one *Hyla* heard on January 23 at 3:12 PM. The vegetation about the pond consists of a few planted trees, *Quercus agrifolia*, and grass at the water's edge.

PONDS AND STREAM SOUTH OF ELIZABETH LAKE.—In a grassy meadow and field, about one-half mile south of Elizabeth Lake (and up the hill from it) there are several small ponds, one large one (50 by 150 yards), and a small stream. The vegetation consists of several large poplars (*Populus fremontii*), grass and cattails. The temperature of a small pond 4 by 20 feet and 15 inches deep varied from 9.9° to 21.4° C. When the ponds were too warm, the hylas were often heard or found in the grass about 20 feet from the water.

TABLE I

OBSERVATIONS ON *Hyla regilla* IN PONDS AT GORMAN, LOS ANGELES COUNTY, CALIFORNIA, 1953

Date	Time	Temperature of water, °C.		Temperature of air over water, °C.		Remarks
		6 inches	1 inch	1 inch	3–5 feet	
1/3	1430	10.5 -12	...	9.0	15.0	Adults singing; no eggs; snow ¼ mile away.
1/11	1635	12.5	...	9.8	...	Many adults singing; freshly laid eggs.
1/24	1400	15.5	17.0	16.0	...	Adults singing; eggs.
2/2	2155	6.0	...	6.5	...	No *Hyla* singing in this pond; eggs.
2/2	2156	10.0	9.8	6.5	...	Hyla singing in this pond; eggs.
2/13	1505	13.0	14.0	9.0	7.5	Eggs; larvae; adults singing.
3/7	1710	14.2	...	17.5	...	Eggs; larvae; adults singing.
4/11	1525	10.8	13.0	...	12.0	Many tadpoles.
4/27	1250	15.0	13.0	...	12.0	Tadpoles ¾ to 1¼; no adults seen.
5/17	1400	15.0	17.2	21.0	17.0	Tadpoles in all pools; some with hind legs; fresh eggs in pools 15° or less.
6/20	0950	14.0	14.0	15.0	15.5	Adults seen; no eggs; larvae 10 mm. and up.

PINE CANYON.—The temperature of a small stream from an underground spring in Pine

Canyon varied from 5.0° to 18.6° C. It never contained *Hyla*, probably because it lacked vegetation.

HIDDEN LAKE.—This small lake (about 300 by 400 yards) was formed by the San Andreas fault. It is surrounded on the east and south by dense chaparral and on the west by a grass meadow. On the north the lake is bordered by *Artemisia tridentata*. There are cat-tails in the lake. On the west side there are many small depressions, made by cattle feet, that are filled with water and surrounded by grass. Water temperatures of the lake varied from 8° to 20.8° C. Hylas were heard on the first visit, January 11, and on every subsequent one.

LAKE, 2 MILES EAST OF GORMAN.—A large lake (about 500 by 1,000 yards) located 2 miles east of Gorman had temperatures that varied, from 8.2° to 12.0° C. It never contained hylas but they were present in streams leading into it (water temperature usually 10° to 15° C.).

RESERVOIR, 2 MILES EAST OF GORMAN.—A concrete reservoir or tank in a small valley about 400 yards northeast of the above lake is located on the east side of the valley 10 feet above a cold stream. The reservoir is about 20 feet square and 10 feet deep with vertical sides. The water depth varied from 12 to 35 inches and supported a growth of *Spirogyra* and water-cress (*Rorippa*). The reservoir also contained the branches of a small bush, and several boards. Water came into the reservoir through a small pipe located about 5 feet above the bottom. The outlet of this pipe was surrounded by water cress. Most of the observations of behavior mentioned below were made at this station. By lying on our stomachs we could observe the hylas without disturbing them.

Water temperature varied from 9.4° to 13° C. These low temperatures may be due to the fact that part of the reservoir was always shaded by the vertical walls.

GORMAN.—At Gorman, at an elevation of 4,000 feet, there are some marshy pools and a stream between a side road and the main highway (U. S. Hwy. No. 99). These ponds vary in size from one square foot to 25 or 30 square feet. The surrounding area consists of grass, *Salix* and cat-tails. Water temperatures, taken in a small pond 4 feet by one foot and 12 inches deep, varied from 6° to 22° C. (Table I).

SUMMARY OF TEMPERATURE DATA.—The following is a summary of the various body temperatures and associated behavior in *Hyla regilla* in response to various environmental temperatures. They are based on over 500 temperature records.

When air or soil temperatures get above 10° C. and *Hyla regilla* can warm up enough, they will emerge from hibernation or retreats and will go to water. If the water temperature is 8° C. or above, they will remain there. When in the water they do not sing until the water or the air temperature (and body temperature) reaches to 9.8° to 10.0° C. At temperatures of 9.8° to 9.9° C. they can barely vocalize and the sound is a weak croak. That they do not (or can not) sing below 9.8° C. was suspected, as we noted their behavior in the various lakes. We were convinced, however, when on February 3, at 7:15 PM we observed *Hyla* in the Richfield Oil Company's South Cuyama Oil Field in Cuyama Valley, Santa Barbara County. In a small canyon about 10 feet deep in an open meadow, hylas were found in a small stream 2 feet wide and about 12 inches deep. The air temperature in the canyon was 5° C. and the water temperatures varied from 9.7° to 10.2° C. We observed that male hylas in water of 9.7° or 9.8° C. did not call or sing, but in water (in small coves or pools of the stream) of 10° (body temperature of hylas, 9.9° C.) and 10.2° (body temperature, 10.2°) they did call.

Hyla regilla will sing or be active in the water or air until it gets too hot (20° C.). Above 20° C. they will seldom, if ever, sing. At this temperature they will go to cooler ponds or to shade in the grass.

Eggs are not laid until water temperatures at the site of egg-laying are 12° C. In water temperatures above 15° C. no eggs will be laid; instead, the frogs go, by random wandering, to other ponds (if available) where the water is cooler. The eggs, after laying, can survive temperatures of −5° to −7° C. for 2 hours and as high as 34° C., though the later stages of development (Neurula and tail-bud stages) can withstand 38° C. for 2 hours and survive (Schechtman and Olson, 1941). Of course the rate of embryological development increases with temperature up to the point of lethality. Tadpoles in continuously warm pools will develop and metamorphose more quickly than those in cool pools. Tadpoles apparently can stand low temperatures (0° to 2° C.) as well as high temperatures of 33° C. but they seem to prefer temperatures of 19°–20° C.

The optimum (preferred) body temperature appears to be about 15° C., though active individuals (hopping about on grass, leaves, etc.) varied from 14.3° to 22.2° C. (Body temperatures of hylas were taken either cloacally or by placing the thermometer between the appressed femur and body. There was no difference in temperature between the two methods on the same individuals.) Hylas were, of course, found in the water singing, with body temperatures as low as 9.9° and 10.2° C.[1] The lethal temperature for adults appears to be 38.1° C. (38° and 38.2° C. in two experiments). Schechtman and Olson (1941) found that tail-fin and pre-hatch stages of larvae were killed if kept at 39° C. for 2 hours while the lethal temperature of blastula, gastrula, and neurula appears to be 35.5°, 37°, and 38° C., respectively.

Logier (1952) found that *Pseudacris n. triseriata* did not sing in water temperatures below 47° F. (8.5° C.). We do not know how much acclimation occurs with respect to body temperature, lethal temperature, etc. It is probable that the temperature data given above (temperatures for singing, egg-laying, etc.) will vary several degrees with latitude and altitude (Jameson, MS).

Color Change

Any person who has collected or observed *Hyla regilla* in nature is impressed by the color variation. A study of the variation in *H. regilla* was given by Test (1898) who described five "styles of color." Though there are many variations, the two main colors of *Hyla regilla* are green and brown. Both of these color phases are found with or without black markings. These black markings are variable in size, shape, and number. Both of the colors occur in a light and a dark phase. The dark phase usually occurs only in the presence of spots, whereas light phases are found in individuals with or without spots. Occasionally individuals with red, or with brown backs and green sides are found, but these make up only about five percent of the population. In all the color phases, however, the characteristic black stripe along the side of the head is always present.

The majority of the workers on western amphibians remark on the amount of color change possible in this amphibian. For instance, Klauber (1934) says, "It has the capacity to change its color considerably and may be bright green, gray or brown in almost any shade." Stebbins (1951) stated, " . . . capable of marked color change (from dark brown to bright green); . . ."

To determine what factors caused the color change, a series of experiments were performed. In none of the experiments described below did a green *Hyla regilla* change to brown, or vice versa. As will be seen below, we could make a *Hyla* get light or dark (*i.e.* light or dark green and light or dark brown) and gain or lose its spots, but never could we produce a change in their basic colors. Under high temperatures and intensive illumination, both green and brown hylas appear yellow due to the extreme "contraction" of the melanophores. A person seeing one yellow *Hyla* turn brown after cooling, and another green, might mistake this for a brown *Hyla* changing to green, or vice versa (also see Noble, 1931). Apparently in all the previous reports (Klauber, 1934; Stebbins, 1951) hylas were generally assumed to be changing color. Perhaps individuals of mixed colors, in jars, moved about so that it appeared that each individual changed color. It is also possible that change from green to brown, or brown to green, does take place in other parts of its range, but most of the evidence is to the contrary (Jameson, MS). All the specimens used in the various experiments described below came from Gorman, Los Angeles County, though observations were made on some from other areas and no color changes from green to brown, or brown to green, were observed.

It is possible that the basic color, green or brown, is a genetic character (which seems to be the case, as indicated by experiments by Jameson, MS), and the lightening and darkening, or gaining and losing of spots is environmentally controlled. No counts have been made on the number of individuals of each color in each pool, but general observations have shown that green and brown phases occur in about-equal numbers. Test (1898) could find no geo-

[1] John Cunningham and Don Mullally (personal communication) have recently found *Hyla regilla* active with body temperatures of 1.5° C.

graphic correlation with the five styles of color described by him, though in some areas certain patterns tend to predominate. Mr. Arlan Smith, Department of Zoology, University of California, Los Angeles, reported to us that he observed a light green male and a light brown female in amplexis in the laboratory. We have observed matings between different color phases in nature about as often as between the same colors.

To determine if there is a selection of a background color to match the basic color of the frog, a glass aquarium 3 feet long, 1 foot wide, and 15 inches high was filled with 4 inches of water. Half of the tank was surrounded on the top, bottom and sides by apple-green paper, and half by light brown paper. In the aquarium a piece of glass 5 inches high was placed across the aquarium to separate green algae and pondweed on the side with the green paper, and brown sticks and leaves on the side surrounded by brown paper. Hence the frogs had access to all parts of the aquarium. Four brown-spotted and four green-spotted adults were placed in the aquarium and their positions noted at least once a day for 3 weeks. At each observation the distribution of the green- and brown-colored hylas in the tank was at random. It is possible that this was due to the small size of the aquarium, but we also observed in nature that there was no color selection. In the small concrete reservoir, 2 miles east of Gorman, mentioned above, about half of the reservoir was covered with *Spirogyra*. This green alga was predominantly on one side of the reservoir. The remainder of the pond was covered with brown sticks and boards. Green and brown frogs were randomly distributed in the pond; both phases were observed sitting for long periods of time on top of the green algae (partly or entirely out of the water) or on the brown sticks. It is possible that the variation in color and color pattern is sufficient so that in normal activity, most of the individuals of each population will be in areas where by chance they will be protectively colored. Though an individual may be caught by an enemy on a different colored background, the variation itself is of survival value to the population and the species. It is our opinion that *Hyla regilla* is composed of such panmixic, variable, interchanging populations that no subspeciation has yet occurred.

In the following experiments all animals used were from Gorman, Los Angeles County. Usually from 6 to 40 animals were used in each experiment with controls used in all. The frogs were kept in the experimental situations for several hours and occasionally for several days.

Some hylas have small bumps on their back associated with color change (light to dark, with or without spots) but it appears to us that this is associated with high temperatures or desiccation.

SEGREGATION.—In each experiment green and brown (spotted or unspotted, light or dark) frogs were kept separate or, if not, they were marked, usually by toe clipping. No individuals were observed to change from green to brown or vice versa. As mentioned above a small percentage of the population may be mixed green and brown (*i.e.* brown on back and green on sides) in these individuals the color of the respective areas did not change.

LIGHT AND DARK.—In a lighted aquarium most of the frogs (green or brown) became lighter and in a darkened aquarium (covered by black paper) they became darker. Exposure to long periods of light or dark does not affect the basic color of green or brown as it does in *Hyla versicolor* (Edgren, 1953). Water temperatures in both tanks, as with all temperatures except those dealing with temperature, was approximately the same (25.0° and 25.8° C).

EXCITED AND NON-EXCITED.—With one tank as a control, frogs in another were disturbed continuously for about 20 minutes by stirring the water in the tank by hand and not letting any individual stand still or crawl on the glass for more than 5 seconds. No color change was noted from green to brown or vice versa or from spots to no spots or vice versa. One brown-spotted individual became lighter but kept its spots. Temperature of the water 24.2° C.; control, 23° C.

COLOR OF THE BACKGROUND.—Eleven marked, mixed-colored *Hyla* were put in an aquarium with apple-green paper all around it and eleven were placed in an aquarium similarly enveloped with light brown paper. In one hour's time no color change was noted. The following day the *Hyla* were segregated by color, light-dark, spots-no spots, into separate glass dishes 4 inches deep and 12 inches in diameter. These dishes were covered with tan, or black paper; the control dishes were not covered. Frogs in the tan-covered dish grew lighter and one lost its spots; most of the individuals in the black-covered jar grew darker. Those in the control dishes remained unchanged. If hylas are placed in an aquarium with an even colored background and in one with a variegated (*i.e.* cross-hatched) background, they loose their spots in the first situation and gain spots in the second. (The writers wish to thank Mr. Arlan Smith of our department for some of these data which were obtained as part of a project in the course in herpetology.)

TEXTURE OF SUBSTRATE.—It has been shown by Hargitt (1912), Biedermann (1926) and others that the texture of the substrate effects color change in some species of *Hyla*. Three experiments were performed in which *Hyla regilla* was placed on smooth and rough-textured substrata, but no color change was noted. Controls and experimental animals were placed in transparent glass dishes 12 inches in diameter. In one dish a 4 × 4 × 4-inch, ¼-inch-mesh basket was placed, the bottom of another was covered with pebbles, and that of another sand. The latter two were covered by wire screen to prevent the frogs from reaching the smooth glass. In two of the controls sand or pebbles were placed under the glass dish so that the visual clue would be the same as the experimentals but the texture smooth. No color changes were noted in any of the situations. Again, the temperature was essentially the same in all containers (24.8° to 25.2° C.).

BEHAVIOR AND SEX.—Allen (1950) reported that *Hyla cinerea* and *H. crucifer* change color while calling. No such color change was noted in *H. regilla*. The various colors appear to be equally distributed in the two sexes of *Hyla regilla*.

TEMPERATURE.—In general, in brown hylas medium high temperatures (32° C.) cause darkening and loss of spots; very high temperatures (above 32° C.) cause lightening and loss of spots; very cold (below 14° C.) temperatures cause darkening and gain of spots. In green hylas, medium high temperatures (32° C.) cause loss of spots and lightening of color, while cold (14° C. and lower) causes gain of spots, but the body color remains light. At medium temperatures green hylas are dark with spots.

SUMMARY OF COLOR CHANGE.—*Hyla regilla* does not change from green to brown or vice versa. The color changes noted are caused by one or more factors. This hyla becomes spotted on variegated backgrounds and loses spots on even-colored ones. Individuals lose spots at high temperatures and gain them at low ones. They become dark in dark areas or on dark backgrounds and light on light-colored ones. Brown hylas become dark at low and medium high temperatures and light at very high temperatures. Green hylas become light at both high and low temperatures and dark at medium temperatures. Intensive illumination and/or heat cause both green and brown hylas to become yellow; this is due to the extreme melanophore contraction, and these individuals return to their basic color when cooled.

In nature (and occasionally in laboratory experiments) the general pattern presented above is sometimes obscured because individuals may respond to one condition more readily than to another, or respond to one set of conditions and then move to another (from a light-colored, warm leaf to a dark-colored, variegated leaf). If these individuals are observed by the investigator before a new response is completed, erroneous conclusions may be formed.

BEHAVIOR

"SINGING".—Storer (1925) stated, "If a person walks out into a marsh where hylas are chorusing the notes quickly cease. . . . If the intruder remains quiet the hylas will usually resume after a few minutes, one individual beginning in a rather hesitating manner, then being joined by others one by one until the full chorus is under way once more." Some simple experiments at the reservoir, 2 miles east of Gorman, convinced us that the frogs detected us, and presumably its enemies, by our movements. We hid behind the wall of the reservoir on January 11 at 2:00 PM and were quiet until the chorus was under way. We then shouted and yelled, but there was no diminution in the volume of the chorus. Then, still hidden, we threw small stones, sticks, etc., into the reservoir with no decrease in singing. Pounding on the concrete wall in order to set up vibrations in the water yielded negative results as well, but as soon as we raised our heads above the rim the frogs stopped singing at once. We stood still, fully exposed to the view of the frogs and after a few minutes they began to sing again. Still in their view, we repeated the above experiments with noise, vibrations, and stones (with movements of our hands hidden) with the same negative result. However, if we moved our heads even a few inches, the singing would stop. We repeated these experiments at this and other localities, at different times of the day and night with the same results: the frogs did not stop singing unless the observers moved.

The main function of the singing of male *Hyla regilla* appears to be to attract females already within the pond. On January 11 at 2:00 PM we observed a female swim directly toward a male that had just commenced to sing. Amplexis resulted Females (caught later to determine sex) swimming toward singing males in response to his singing were observed many times. Hence, it appears that the singing of the male helps in localizing the mating site, or perhaps more correctly attracts the female to the male. If the female could distinguish between the calls of several species, this would aid in species recognition in a pond containing many calling species. We are not convinced that the singing functions to attract females to the pond, but rather that its function may be for localization within the pond. It is probable that hylas reach ponds in the Spring by random searching or by some hydrotaxis.

SEX DISCRIMINATION.—As mentioned above, when a female hyla approaches a singing male, the latter usually stops singing and commences to mate. Should, however, a male happen to swim past a singing male, the singing male will often attempt to mate with it. Presumably an oncoming frog acts as a releaser and denotes to the singing male that it is a female (*Cf.* sticklebacks, Tinbergen, 1951). When amplexis between males occurs, the lower of the pair, usually the swimming male, begins to croak and inflate its vocal sacs. As soon as this is done, the male on top will usually immediately release his hold. The croak and/or the vocal sacs serve as a releaser in sex discrimination. We observed this many times on January 11 and on other days and in other areas. Similar types of sex discrimination have been recorded in other species of anurans (Noble, 1931; Noble and Aronson, 1942; Aronson and Noble, 1945; Stebbins, 1951). It was noted on March 8 at 3:30 PM at the reservoir 2 miles east of Gorman that occasionally the top member of a pair of amplexing males would not release its hold when the lower one croaked, but would begin to scratch the abdomen and vocal sacs of the lower. This action suggests some aggressiveness, but as it is not associated with any definite area, territoriality is probably not involved.

SPATIAL LOCALIZATION.—Martof (1953) suggested that a "primitive territoriality" in eastern *Rana clamitans* is indicated by spatial localization. We do not think that his conclusions are completely justified by the facts as presented. If the term territory is to have any significance, it should be restricted to Noble's (1931) definition of "Any defended area." We believe that the data presented by Martof and our observations on *Hyla regilla* suggest a home range rather than any defended territory.

That spatial localization is present in *Hyla regilla* was indicated on certain occasions. When individuals of a peculiar coloration were disturbed or forced into the water, they would return after a few minutes to within a few inches of their original position. We interpret this as a home range, spatial localization, or local learning of an area, but not as a "primitive territory."

INTERSPECIFIC RELATIONSHIPS.—As far as we have been able to determine there is no competition between other anurans whose distribution is sympatric with *Hyla regilla*, with the possible exception of *Hyla arenicolor*. In those streams containing *Hyla arenicolor*, *H. regilla* is either absent or seems to be less abundant. *H. regilla* has a lower temperature preference and range for normal activity (8.0° to 22.0°; mean 16.2° C.) than does *H. arenicolor* (15.8° to 26.2°; mean 20.9° C.). It is possible that this temperature preference, plus (or is the cause of) the later breeding of *arenicolor* in southern California than *regilla*, allows these two forms to occur together in the same stream but not in competition due to differences in time of activity.

We have observed *Hyla regilla* singing in pools with calling *Bufo boreas halophilus* and *Scaphiopus h. hammondi* with the different species apparently taking no notice of each other. We have also observed them singing with groups of *Rana catesbeiana*, but never closer to them than about 4 feet.

SEX RATIO.—In any one pond the number of females changes throughout the day. In the early morning almost all the frogs are males; by early afternoon a few females enter the pond. The number of females increases throughout the evening as more females come to the pond.

TADPOLE AGGREGATION.—Bragg (1945, 1946, 1948) and Carpenter (1955) have recorded and discussed aggregations in anuran tadpoles. As mentioned above, we observed an aggregation of *Hyla regilla* tadpoles in the pond in Leona Valley, Los Angeles County on April 11 at 10:30 AM. The pond at this date was from 3 to 6 inches deep and most of the bottom was covered with grass. Water temperature varied from 9.7° C. in the shade to 19° C. in the sun. The air temperature over the water was 10.2° C. One hundred and fifty to 180 tadpoles averaging 25 mm. in total length were aggregated in a circle about 2 feet in diameter. Occasionally a few individuals would leave the aggregation and swim about. They never swam more than 7 feet away from the center of the aggregation and would always return to the group after a few minutes. The water was 3 inches deep where the tadpoles aggregated and most of them were on or within a half-inch of the bottom. The water temperature above the center of the aggregation was 16.5° C. (one-half inch below the surface), and 19.0° C. at or within a half-inch of the bottom (and within the center of the tadpoles). The bottom temperature was 19° C. for about a five-foot radius from the center of the aggregation. The edges of the pond had water temperatures of 9.7° to 17° C.

Many of the tadpoles in the aggregation were in contact with each other and no cannibalism was noted. At least two-thirds of the tadpoles were oriented with their heads to the northwest. If radiant heat was an additional factor in causing the aggregation, this alignment of the tadpoles provided the maximum dorsal area of each individual to be exposed to the early morning sun which was directly to the southeast, the direction toward which most of the tails pointed. It is also possible that the mass of tadpoles would absorb more heat in the early morning than would single individuals, and though cannibalism occurs at this stage in nature and in the laboratory (Bragg, *supra cit.*), this "social" aggregation might be advantageous in regard to body temperature.

A similar aggregation in this species was reported to the writer by Mr. William McFarland at Lake Hughes, Los Angeles County at 3:00 PM on May 13, 1953, in water 5 inches deep.

NATURAL HISTORY

FOOD AND FEEDING.—Needham (1924) reported on the stomach contents of 18 specimens of *Hyla regilla*. In 14 individuals from Gorman we found coccinellid, carabid, curculionid and gyrinid beetles, teridipediid midges, tabanid flies, mesoveliid hemipterans, cicadellid leafhoppers, as well as occasional unidentifiable beetle larvae, Hymenoptera, and Diptera. Needham's report supports our findings and the observation that *Hyla regilla* feeds predominately above water. We have observed hylas crawling up in bushes or sticks in ponds to about 2 feet above the surface and there eat insects. These frogs often sit on floating *Spirogyra* and feed on insects crawling or alighting on the mass. Since *Spirogyra* is usually in the sun, the frogs often become too warm or dry. They then push down into the algal mass until they are almost completely covered by water. After a few minutes they again appear on top of the algae. Thick *Spirogyra* is quite an obstacle to the swimming frogs; many were seen struggling through it, especially those that came from underneath. At the reservoir 2 miles east of Gorman, the hylas would often congregate in the leaves of the water cress growing about the 2-inch supply pipe. The hylas sit in the shade near the base of the leaves of the water cress, but come out momentarily to feed on the occasional insects that alight.

SEASONAL ACTIVITY.—The seasonal activity of *Hyla regilla* seems to vary locally with temperature and the availability of water. In general, choruses in southern California are heard from November to July. Though occasional individuals are active in other parts of the year, the majority go into hibernation or hiding. At higher elevations and latitudes breeding is later in the season (Livezey, 1953; Stebbins, 1951; Storer, 1925). Storer reported hiding places such as piles of debris, burrows of meadow mice and other terrestrial mammals, crevices in boulders, artificial drains, basements of buildings, etc. In southern California, at least, the frogs must seek hiding places where they will not desiccate during the hot and dry months of July to October. In general, our observations support those of Storer (*op. cit.*). We have even found 40 adult hylas in the cranial and nasal cavities of a horse skull lying 3 feet from a stream.

On January 11 on the south-facing, rolling, grassy hills about 500 to 1,000 yards north and about 200 feet above the lake 2 miles east of Gorman, we heard hylas calling all about us. After searching for some time, we discovered males coming out of small (one inch in diameter) holes in the ground. They would sing a few notes and then retreat down the holes. Of some 20 holes found, we excavated 5 and found that they were consistently alike. The holes went down at about a 45° angle throughout the depth which was about 20 inches. Some holes contained from one to five frogs and, as many times as not, a *Uta stansburiana* was present. Occasionally the holes were empty and occasionally only a *Uta* was present. Hylas were observed in these holes again on January 24, but after that we never found them again, nor did we hear them calling from the hills. It is probable that hylas occupy similar holes in other areas, but thick vegetation may prevent one from noticing them. Whether *Hyla* or *Uta* digs the hole is unknown. The hole is just large enough in diameter for each, and since the soil was soft humus it would probably not be too big a task for either one.

On both dates the temperature of the air in the holes varied from 14° to 15° C., and soil temperatures varied from 10.5° to 14.5° C. Outside the holes air and soil temperatures varied from 16.5° to 18.2° and 14° to 15° C., respectively. Body temperatures varied from 19° for those just outside the burrow to 14° C. for those back in the hole. The testes of a male caught on January 24 in the hole were smaller than those taken from Gorman, 2 miles away, on the same day. The gonads of the females from the holes were generally small, and none of them had yet ovulated.

ENEMIES.—In southern California the enemies of *Hyla regilla*, other than man, seem to be gartersnakes (*Thamnophis*), egrets, herons, and such nocturnal animals that frequent pools as raccoons, skunks, and opossums (Storer, 1925).

ALBINISM.—We wish to record here what appears to be the first record of an albino *Hyla regilla*. A metamorphosing albino *Hyla regilla* tadpole was brought to us at the University by Miss Barbara Sundberg who found it in a pool of the stream in Topanga Canyon, Los Angeles County. She found it along with several others, one of which she brought to us on another date. Many normal individuals were in the same pool which was about one mile from the mouth of the stream. In the laboratory, the first albino died just as the tail was beginning to be absorbed. The second specimen successfully completed metamorphosis but died within 2 weeks.

HYBRIDIZATION.—In many parts of southern California the distributions of *Hyla arenicolor* and *H. regilla* are sympatric. As mentioned above, where they occur in the same stream, *H. arenicolor* seems to be the more abundant. We have observed only one individual that appears to be a hybrid between these two species. This specimen (UCLA 6158) was taken on May 9, 1953 at the lowest grove of palms, Borego Palm Canyon, San Diego County. It is similar to *H. regilla* in color, except that it is mottled more than any *H. regilla* that we have ever seen. It approaches the granite coloration of most *H. arenicolor*. The skin is tuberculate as in *H. arenicolor* and the shape of the webbing of the feet (Salt and Stebbins, 1948) resembles that of *H. regilla*. The characteristic black bar through the eye and face of *H. regilla* is present only as a mottled outline. Though *H. arenicolor* was abundant, *H. regilla* was not observed in the canyon on this date, though it is known to occur higher up in the same creek. The presence of this probable hybrid does not mean that the species are invalid, but that on rare occasions *H. regilla* and *H. arenicolor* probably do hybridize in nature.

PROTECTION.—In addition to the advantages of the variation and changes in color, two activities that might be interpreted as protective behavior have been noted. When *H. regilla* is tossed or accidentally falls into water, it usually swims away, but if it should alight upside down, it will fold its legs along its sides and remain afloat in that position. We do not know the function of this behavior. It is possible that it is a symptom of nervous shock or disturbed equilibrium.

In nature, if flushed on land, these hylas will usually jump into the water, if it is near. They will make several jumps if necessary to reach water, even if the intruder is between them and the water.

REARING.—Through the courtesy of Arlan Smith, we would like to present here some suggestions on raising tadpoles through metamorphosis. Larvae are placed in large bowls of water containing about one inch of sand and mud taken from the same stream that the larvae were taken from. If this mud is not put in with the tadpoles, they will eventually develop a haemorrhagic condition in the gut and die. Apparently mud aids in the digestion of the plant material which these larvae normally eat. For food the young larvae are provided with green algae. As metamorphosis begins, blocks of wood are placed in the bowls. When many tadpoles are seen about these blocks of wood, they are then changed to a larger aquarium. This consists of a 5- or 10-gallon tank with a sand or gravel bottom. One end of the tank is elevated about 2 inches by placing a block of wood under one end and about 2 inches of water is placed in the other end providing both an aquatic and a moist area. A thin cloth or screen cover is placed over the aquarium at this time to prevent metamorphosed frogs from crawling out. Since the food habits change during metamorphosis (Munz, 1920; Wright and Wright, 1949), the larvae are supplied with adult fruit flies (*Drosophila*). We use, if available, vestigial-wing mutants of *Drosophila* because they are easily caught by the young hylas. Drosophila can also be fed to adult hylas in the laboratory. An egg shell broken into several parts is also usually provided for the larvae. The small bit of albumin sticking to the shell is eaten by them. Only a small amount of water is necessary during metamorphosis, as the larvae are changing to air breathers.

SUMMARY

Observations on the ecology and behavior of the treefrog, *Hyla regilla*, made in the spring of 1953 in Los Angeles County, California are presented. Temperature appears to have a strong effect on its habits and behavior. *Hyla regilla* can not be made experimentally to change from green to brown or vice versa, though lightening and darkening, and gaining and losing spots, appear to be environmentally controlled and can be experimentally performed in the laboratory.

Singing by the male of *Hyla regilla* acts as an attraction to the female in the local confines of a pond. Sex discrimination is accomplished by voice and inflation of vocal sacs. Male aggressiveness and spatial localization appear to be present, though territoriality is not. *Hyla regilla* perceives its enemies by their movements. Tadpole aggregations, enemies, hybridization, albinism, and probable protective devices are described. Notes on feeding, seasonable activity, and suggestions for rearing tadpoles are presented.

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DEPARTMENT OF ZOOLOGY, UNIVERSITY OF CALIFORNIA, LOS ANGELES 24, CALIFORNIA.

Upper Lethal Temperatures in the Salamander *Taricha torosa* as a Function of Acclimation

WILLIAM N. MCFARLAND

IN recent years a topic of extreme interest to experimental zoologists is that of acclimation of animals with respect to their environmental temperature. It has been shown in many invertebrates and fishes that the past thermal history of a given subject has a marked effect on its physiologic patterns (Prosser, *et al.*, 1950). Such phenomena as oxygen consumption are so adjusted that animals living at a lower temperature when compared to those living at a higher one show a relative increase in the rate of metabolism when compared at the same temperature (Wells, 1935; Scholander, *et al.*, 1953). It also has been demonstrated that fishes acclimated to cold water are less tolerant to higher temperatures than those acclimated to warm water (Hathaway, 1927; Fry, 1947; Brett, 1944). That such a phenomenon is characteristic of most aquatic poikilotherms is now well established (Bělehrádek, 1935; Prosser, *et al.*, 1950). The effect of temperature acclimation on amphibians has been studied but little; in fact in the entire class little is known about lethal temperature limits.

Davenport and Castel (1895) working on tadpoles of *Bufo terrestris* Bonnaterre were able to demonstrate differences in the upper lethal temperatures depending upon the temperature of acclimation. They showed that groups raised at 15° and 25° C. had average upper lethal temperatures of 40.3° and 43.5°, respectively. The differential between the two groups was lost when readapted to the other temperature. However, this loss was not rapid, the upper lethal temperature of a 25° group being 41.5° after 17 days reacclimation at 15° C. Hathaway (1927) working with tadpoles of *Bufo terrestris americanus* Le Conte was able to show the same phenomenon, *i.e.*, the lower the acclimation temperature the lower the upper lethal temperature.

Mellanby (1940) has shown low temperature acclimation to exist in *Rana temporaria* and *Salamandra salamandra*. In his work adults that had been acclimated to 10° and 30°, respectively, were transferred to a 0° environment. The high-acclimated group proved to be inactive at 0°, but the other active. In addition Mellanby indicated that the length of exposure is an important factor in temperature acclimation, a factor that has been investigated quite extensively in fishes by Doudoroff (1942), Fry, Hart and Walker (1946) and Brett (1946).

A number of papers relate geographic distribution of some amphibians to rates of development, temperature tolerances, etc. (Moore, 1949; Volpe, 1952). These reports are not concerned with the individual adaptation of the organism, but deal, rather, with reactions of