

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN NO. 160

**The Life History, Social Organization,
and Parental Behavior of *Hyla rosenbergi*
Boulenger, a Nest-Building Gladiator Frog**

by

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INTRODUCTION

The disparity between theory and empiricism is particularly conspicuous in anuran ecology and behavior, where detailed studies of natural populations are rare. With few exceptions, the available data are qualitative and limited to few parameters, do not document individual variation, and were taken during one breeding season. Moreover, the tropics, where anuran diversity is greatest, largely have been neglected. It was for these reasons that I undertook the study of Neotropical gladiator frogs of the genus *Hyla*, family Hylidae¹.

The focus of this paper is the relationship of territoriality to parental care in *rosenbergi*. Similar research on other gladiator frogs, *boans*, *crepitans* and *pugnax*, will be published separately. The meaning of the terms territoriality and parental care are not universally agreed upon, and to avoid misinterpretation I adopted the following definitions:

Territoriality—any overt defense of an area against intruding conspecifics that allowed the resident exclusive or priority access to the limited resources contained therein.

Parental care—any behavior exhibited by a parent toward its offspring that increased the offspring's chance of surviving (and hence becoming reproductive) at the cost of the parent's ability to invest in other offspring (Trivers, 1972).

Most of the literature cited in the remainder of this section formed my introduction to gladiator frogs, and the observations that I summarize were what excited and compelled me to initiate my field study of their biology. Goeldi (1895) described nest building in Brazilian *faber*. He observed an individual, almost certainly a male, diving below the surface of the water, scooping up mud with its snout, placing the spoil at the side of a depression, and shaping that material with its hands into a rampart which eventually rose above the water. Goeldi also stated that it took an individual at least two nights to complete a nest, during which time it did not advertise for mates, and not all of the several basins clustered together at the edge of a shallow pond had eggs deposited in them. Further, he observed an amplexed female deepening a basin and raising its wall.

Lutz (1960a, 1960b, 1961) confirmed Goeldi's observations on nest building, and described fighting among male *faber*. The aggression occurred in or near nests, with the combatants wrestling for long periods in a chest-to-chest position with their arms locked around the opponent's neck and head. Lutz concluded that wrestling bouts took place when a resident's nest was approached or entered by an in-

¹*boans* (Linnaeus), *circumdata* (Cope), *crepitans* Wied, *faber* Wied, *pardalis* Spix, *pugnax* Schmidt and *rosenbergi* Boulenger.

truder. She stated that one male died after a fight, most likely having been stabbed to death by its opponent's dagger-like prepollical spines. All male gladiator frogs have a large bony spine on the medial surface of each thumb (Duellman, 1970).

In the Darien of Panama, Breder (1925a, 1925b, 1946) observed male *rosenbergi* building nests with ramparts of mud and litter, and using these water-filled basins as calling stations (see also Noble, 1925). Breder found eggs deposited as a surface film in the depressions, and he observed a female initiating amplexus and behaving as if she were deliberately choosing among adjacent calling males. Breder suggested (1927a) that the nests protected the frog's embryos from predatory fishes such as *Rivulus chuncunaque*.

Crump (1974), Duellman (1970), and Lamotte and Lescure (1977) stated that *boans* built nests, and Kenny (1969) reported female *boans* excavating nests after amplexus. Cochran (1955) and Nemuras (1978) provided additional observations on nesting and fighting in *faber*. Lutz documented nesting (1960c) and fighting with prepollical spines (1973) in *pardalis*. The breeding habits of *crepitans* have been observed at several localities throughout its vast geographic range and it does not appear to build nests (Duellman, 1970; Fouquette, 1968; Kenny, 1969; Lutz, 1973; Stebbins and Hendrickson, 1959). Similarly, Lutz (1973) did not report nests for breeding *circumdata*. Cochran (1955), Crump (1974) and Lamotte and Lescure (1977) reiterated Breder's (1927a) hypothesis that the nests of *boans* and *faber* protected their embryos from predatory fishes. However, Lamotte and Lescure also suggested water temperatures in nests might be higher than in the surrounding water and that this would be advantageous in increasing rate of development. It is not clear from the available literature whether gladiator frogs have a mating system of male dominance or resource defense polygyny (Emlen and Oring, 1977).

Recently, McDiarmid (1978) and Wells (1981) reported paternal care in the form of nest guarding and embryo protection in *rosenbergi* based on my unpublished research. Curiously, Salthe and Mecham (1974) stated that *faber* "might" guard their embryos, but gave no supporting evidence. Their opinion could have been based on Merten's (1960) contention that nest building by *faber* constitutes a form of paternal care, a point of view I do not share (pp. 116-125).

MATERIALS AND METHODS

ORIGIN OF SAMPLES

I began long-term field studies on the *boans* complex in 1975 with my son, John Kluge. We spent the summer surveying possible research areas in southern Costa Rica and central Panama, and per-

fecting individual frog marking techniques. The study was restricted to Panama, largely because of logistics and species abundance. Relatively well protected field sites were found in the Canal Zone where the wet season breeding *crepitans* and *rosenbergi* could be studied in sympatry and allopatry.

In 1976, I marked and observed individual *crepitans* and *rosenbergi* on a nightly basis throughout most of June, July and August at Chiva Chiva Quarry, Canal Zone, but *rosenbergi* were too rare to justify continued study. The remainder of the research on *rosenbergi* was shifted to the Obispo Diversion Study Site, hereafter abbreviated ODSS (Figs. 1-2). While most of the data and discussion are based on the ODSS population, I have included relevant information obtained

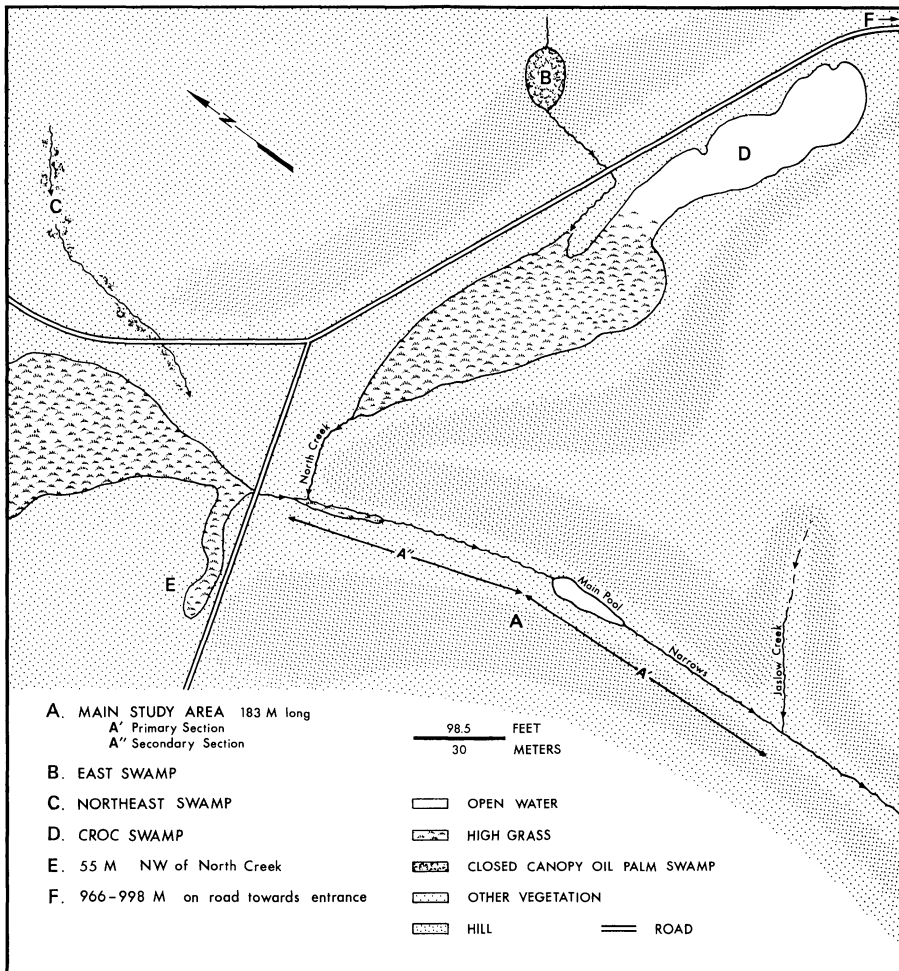


Fig. 1. Diagrammatic aerial view of the ODSS where most of the *rosenbergi* research was conducted. Letter symbols indicate chorus locations. See also Fig. 2.

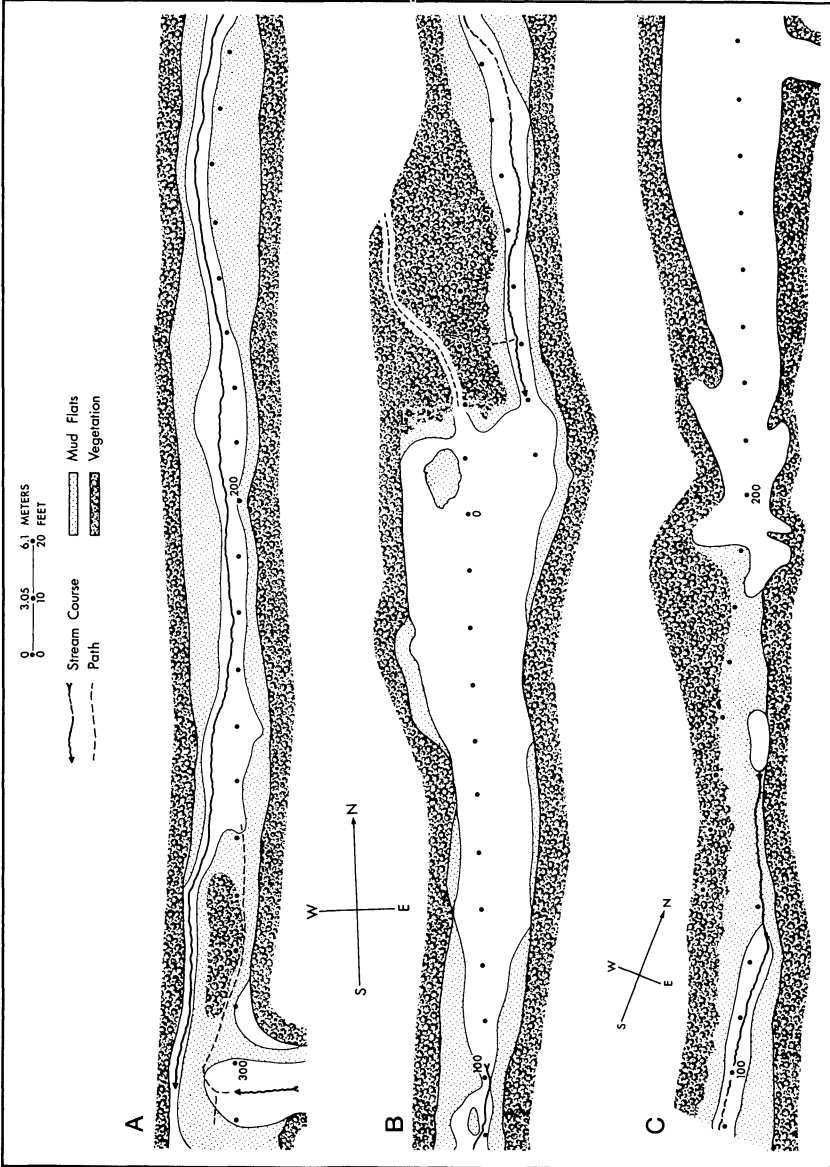


Fig. 2. Diagrammatic aerial view of the water course along the main *rosenbergi* study area labeled A in Fig. 1. Each panel represents part of the water course; A is the panel farthest south, C the farthest north, and B connects A to C. Dots represent stakes set at 10 ft intervals.

at Quebrada Benjamin, Costa Rica (8° 58' N lat, 83° 28' W long, 30 m elev) and elsewhere in Panama, particularly at the Chiva Chiva Quarry (9° 03' N lat, 79° 34' W lat, 50 m elev). The geographic source and sample size of all marked reproductively mature *rosenbergi* are listed in Table 1.

The amounts and patterns of rainfall at ODSS in 1977 and 1978 represented extremes that considerably altered the density of *rosenbergi*, which in turn affected many aspects of the frog's life history and social behavior. Therefore, the 1977 and 1978 data are presented separately, unless otherwise indicated.

TABLE 1
GEOGRAPHIC ORIGIN AND SIZE
OF *ROSENBERGI* SAMPLES USED IN THIS STUDY

CANAL ZONE: Obispo Diversion Study Site (Figs. 1-4)						
Year	Primary Section (A')		Secondary Section (A'')		Other Localities (B-F)	
	Males	Females	Males	Females	Males	Females
1977	67	53	38	20		
1978	22	24	35	2	19	13
			Chiva Chiva Quarry			
1976	17	2				
1977	8					
1978	1	1				
			Miscellaneous ¹			
1975-76	7					
			COSTA RICA: Quebrada Benjamin			
1975	5					
1976	6					

¹Includes specimens from Rio Frijoles (9° 9' N lat, 79° 44' W long) and Summit Gardens (9° 4' N lat, 79° 39' W long).

ODSS VARIABLES

From June 3 to November 11, 1977, two observers (Alan Jaslow and Arnold Kluge) spent 390 hr during 87 nights at the ODSS. From April 22 to December 15, 1978, three investigators (Jaslow and Arnold and John Kluge) accumulated 536 hr of observation during 142 nights. The distribution of study nights is shown in Figs. 29-30.

Observations usually began each evening about 1815 hr, approx 20 min before males called and descended from their diurnal resting

places. Regular and rapid transects of the study site were made by one or more of the investigators until all major areas of frog activity were located and all new recruits were marked, weighed and measured. Most males were located by their calls, while females and non-calling males were discovered by their eyeshines. A grid system was installed on the main study area of the ODSS and all frog locations were mapped according to it. Observations of individual behavior usually continued until about 2300 hr, after which time there was little frog activity. The observers' movements were concentrated along the middle of the water course to reduce habitat alteration and nest destruction. Animals were touched as little as possible, but handling and frequent observations did not appear to change their normal behavior. Males commonly resumed courting or fighting immediately after being toe-clipped, weighed, measured and banded, all of which took about 10 min.

Locations of all nests were recorded with reference to the study grid (Fig. 28) and most were marked with a galvanized metal stake and numbered aluminum plant tag. Nest identification provided data on occupancy and reproductive success within and between years. The following nest measurements usually were taken: (1) surface area of the water calculated from major and minor orthogonal axes; (2) water depth at its deepest point; (3) average rampart height and width (at the base).

A spring driven Stevens Type F Water Level Recorder (Model 68) was placed in the main pool of the ODSS on June 10, 1978, and it ran until September 8, 1978. Continuous water temperature recordings in degrees Celsius ($^{\circ}\text{C}$) were made simultaneously in and immediately outside nests with a dual channel, 12-volt battery-driven Rustrak Recorder (Series 400). Also, dissolved oxygen was measured (ppm) in and immediately outside nests with a portable YSI Meter (Model 57). All individual frog vocalizations recorded were taped at 9.5 cm/sec with a single-track monaural Nagra 4.2L. An AKG (C451E) microphone with a cardioid condenser usually was employed. However, an American (D33) microphone was substituted to avoid the static developed by the AKG in high humidity.

The female choice experiments utilized two Kudelski Paudex (DH 0002) speakers played simultaneously, each powered by a separate Nagra sound recorder. Speakers were played directly at 4.4V and 3k ohms. The Nagras (4.2L and 4L) were played at equal volume at the point of the female's release (approx 3 m from each speaker). The equal volume was determined with a third Nagra and either AKG or Senzheiser (MKH 104) microphones. The contrasting signals were played at -2 to 0 db peak value on the Nagra modulometer. Females were housed in a styrofoam container before being released between the two speakers. All other playbacks, eg, the tests of paternal care behavior, employed the 4.2L Nagra internal speaker and/or a

separate Kudelski Paudex. The audiospectrograms were made with a Kay Sonagraph 7030A at 40–4000 Hz. The frequency scale was determined with the Nagra 4.2L internal one kHz signal. The temporal scale was determined with a stopwatch.

STATISTICS

Most data manipulation and tests of significance were performed with the Michigan Interactive Data Analysis System (MIDAS) designed and programmed by the Statistical Research Laboratory of The University of Michigan (Fox and Guire, 1976; Staff of Statistical Research Laboratory, 1976). Data (standardized and normalized) were considered normally distributed when they formed a straight line in a normal probability plot. The null hypothesis of equal variances was rejected with a F-distribution statistic at $P \leq .05$. When data sets met the parametric assumptions of normality and equal variances, the Student's T-test, ANOVA and product moment correlation coefficient (r) were employed. When either of these assumptions was falsified, nonparametric tests were used (Conover, 1971). Many of the data sets included large numbers of tied observations and I was often forced to apply the median test rather than the more sensitive Mann-Whitney statistic (U). In some instances, I present the results of both analyses. The Sign, Binomial (z) and Fisher's Exact Probability tests were applied to special cases. Spearman's rho (r_s) was used to assess degree of bivariate correlation. A nonparametric modification of Levene's approach to estimating equality of variances was employed (Levene, 1960; McCauley, 1979). The absolute difference of each observation from the same mean was determined and these values rank-ordered. Such transformed data sets then were compared with the Kruskal-Wallis test, because it is especially sensitive to differences among means (now removed) in k -populations. I used the G statistic in most cases where goodness-of-fit was in question (Mood and Graybill, 1963). All values of $P \leq .05$ were considered significant, and $P < .001$ can be assumed when the results are said to be significant and when no value is given in the text. $df = 1$ unless otherwise stated. I numbered the days of the year consecutively for convenience of data analysis, rather than employ the conventional monthly calendar, and my figures and graphs reflect that change of scale.

INDIVIDUAL MARKING TECHNIQUES

Each frog was toe-clipped when first encountered. No more than one digit per hand or foot was removed, and the inner-most finger, the one bearing the prepollical spine in males (Figs. 13–16), was never amputated. At least one half of the digit's length was removed, which required cutting slightly into the interdigital webbing (Fig. 16).

I am confident that when apparently unmarked *rosenbergi* were observed in the field, they were individuals that had not regenerated amputated digits. To test for regeneration, the outer-most left finger and toe were amputated from two *rosenbergi* males, and the four stubs were soaked in a solution of 0.1 Normal Beryllium Nitrate for 1.5 min. Heatwole (1961) found that this solution completely inhibited regeneration of salamander toes. The treated *rosenbergi* digits showed no regeneration after nearly eight months in captivity, while an untreated amputated toe and finger on the right side of each male showed no increased length and only slight regrowth of the terminal fleshy pad. Regeneration in untreated field animals was limited to the terminal toe disc. However, as in the captive experimentals, the toe disc never regained its normal diameter. Individuals observed for over one year in the field and over two years in captivity showed no noticeable regeneration of digit length or webbing.

Each frog was given a waist band for individual recognition without handling (Breder, 1927b). The band made of plastic surveyor's tape was 16 mm dia \times 7.5 mm width, and a number corresponding to the toe-clip was printed on it with Pelikan Tusche K ink. This ink did not erode or fade, but occasionally bands had to be replaced, because they were lost or twisted. The frogs' narrow hips and even smaller waists allowed the bands to be slipped into position with little difficulty in the field. All frogs received the same size band because of the small variance in body size within and between the sexes (Figs. 17-19). Few frogs showed any sign of skin abrasion or cutting. None was observed attempting to remove the band, and bands did not appear to impede the frogs' normal behavior.

SIZE MEASUREMENTS

All frog weights were taken in the field to the nearest 0.1 gr with a 50 gr Pesola scale. Excess water on the skin was removed; few individuals emptied their bladders prior to weighing. The only length variable scored was taken with a plastic ruler, to the nearest 0.1 mm, from the tip of the snout to the posterior-most extreme of the anus while the individual's long axis was held straight. Some individuals were reweighed and remeasured when a body band became twisted or lost or when a marked male was found in amplexus with an unmarked female. Investigator error was determined from data collected from the same individual within a span of four days. Sequentially taken estimates within that period were subtracted from each other and these values were considered the error term. The differences in WT (Δ WT) and SVL (Δ SVL) were not normally distributed. WT and SVL were estimated with between 0-11% and 0-6% accuracy, respectively (Table 2). There were no significant differences between the sexes, and accuracy did not change significantly with size. SVL

TABLE 2
 INVESTIGATOR ERROR
 IN THE ESTIMATION OF *ROSENBERGI* WT AND SVL ¹

Variable	N	x_{\min}	x_{\max}	\bar{x}
Δ WT	50	-2.9	+3.70	-0.02
Δ SVL	33	-4.0	+5.00	+0.07
Δ WT/WT	50	0.0	0.11	0.04
Δ SVL/SVL	33	0.0	0.06	0.02

¹WT in gr; SVL in mm.

was used as the independent variable in the statistical analyses, because of its slightly lower error variance.

Eggs and larvae were manipulated with a plastic turkey baster. All stages were sampled in the field and fixed in 10% buffered formalin. Eggs and tadpoles were measured with an ocular micrometer to the nearest 0.1 mm. SVL was taken from the tip of the snout to the anterior margin of the vent; tail length (TL) from the anterior margin of the vent to the end of the tail. Only undamaged and unregenerated tails were measured. The total length (TTL) of a tadpole is SVL + TL. I used Gosner's (1960) normal table to stage premetamorphic *rosenbergi*; stage number was based only on general morphology of preserved specimens.

THE OBISPO DIVERSION STUDY SITE

Most of the data on *rosenbergi* presented in this paper were collected along a man-made water course, the Obispo Diversion, Panama Canal Zone. The study site was 9° 05' N lat and 79° 41' W long, 87 m elev, 300 m E of and nearly parallel to the Panama Canal, and 200 m W of the Gaillard Highway. At the time of this study, the area was administered by the Panama Canal Company and access controlled by the United States Navy. Apparently, the Diversion was begun by the Compagnie Universelle du Canal Interoceanique, a French concern, and later expanded by the Panama Canal Company to direct excess runoff away from the isthmian canal excavations (McCullough, 1977:465-6, 549). I believe the Diversion was not entirely successful and the man-made cut soon reverted to its naturally vegetated state after approx 1910.

The plant formation covering the Obispo Diversion is Tropical Wet Forest according to the Holdridge classification (Holdridge and Budowski, 1959). The tropical climate is typical of low latitudes and elevations. Temperatures and humidity are moderately high throughout the year. At the Balboa meteorological station (65 years of records)

the average monthly temperature varied from 26.2°C (October–November) to 27.9°C (April), with average monthly minima and maxima of 22.1°C (January–February) and 32.6°C (March), respectively. The average annual relative humidity was 83.3%, with an average monthly low of 73.5% (March) and high of 87.9% (September). Rainfall was abundant, with violent thunderstorms producing most of the measurable precipitation. The year was usually divided into a four month dry season, mid-December to mid-April, and an eight month wet season when rain occurred almost daily. The average annual rainfall at the Summit meteorological station (38 years of records) was 215.4 cm, with lowest and highest monthly averages of 1.0 cm (February–March) and 32.0 cm (November).

Fig. 1 is a diagrammatic aerial view of the ODSS and the region surrounding it. The area was hilly, and steep banks occurred along most of the water courses that drained the numerous swamps. A mature forest, with little evidence of human disturbance, covered much of the region, and the larger trees formed a nearly complete canopy. *Corozo oleifera* (HBK), the oil palm, was a common understory tree along the swamp and creek margins, and I believe the litter-filled bases of the fronds were a diurnal retreat of *rosenbergi*. In 1977, most *rosenbergi* occurred along the main area (Fig. 1A). One or two males occasionally called along the Diversion about 30 m S of Jaslow Creek. However, in 1978, *rosenbergi* often were found in nearby swamps at the places labeled B–E, in addition to the main area (A'–A''). It is likely that this species rarely if ever occurred at these other localities in 1977, because males calling at D–E could be clearly heard by an investigator working the main area in 1978. Unless otherwise stated, all data and discussion pertain to the main area.

The flow of water along the Diversion was markedly affected by rainfall. There was no standing water during most of the dry season, and a downpour of about 25 mm during the rainy season raised the water table about a centimeter and caused a rapid flow between the partially isolated pools. The outline shown in Fig. 2 defines the approx width of the water course at its average height during the rainy season. The riparian understory consisted of a wide variety of plants, with *Heliconia* species being the most numerous, particularly on the extensive mud flats. *Heliconia* plants often formed miniature canopies over *rosenbergi* nests.

The main area was mapped with wooden stakes (Fig. 2). Most of the grid followed the middle of the water course. Stakes were set at 10 ft (approx 300 cm) intervals, but all distances have been converted to meters. The main study area extended slightly more than 180 m, approx 90 m S and 90 m N of the zero stake shown in panel B of Fig. 2.

Calling and nesting *rosenbergi* were discontinuously distributed along the main area in both years of the investigation. Accordingly,

the main area, as shown in Fig. 1(A), was divided into primary (A') and secondary (A'') sections. In the more detailed view of the main area shown in Fig. 2, the primary section includes all of the top panel and most of the middle (40 m N of the 0 stake). The most intensive study focused on the primary section (A' of Fig. 1), because frogs were more numerous and easier to observe. Also, the vegetation was relatively sparse, and the mud shelves on which nests were constructed were more extensive. The northern secondary section (A'') usually was traversed only once or twice each night. All data and discussion pertain to the primary section unless otherwise stated. The most prominent feature of the primary section was the large pool shown in the middle panel of Fig. 2, which was approx 0.5 m deep during the wet season and surrounded by steep banks and relatively few mud flats (Fig. 3). The more extensive mud shelves shown in the top panel of Fig. 2 (see also Fig. 4) adjoined a narrower and shallower flow of water.

RAINFALL AND FLOODING

GENERAL CHARACTERISTICS

The pattern and amount of precipitation affected much of *rosenbergi's* biology. Rainfall and its conspicuous result, flooding, determined the temporal pattern of breeding and nest-clutch survivorship.

An hourly recording meteorological station was located nearby at Las Cascadas (9° 05' N lat and 79° 41' W long), on the W bank of the Canal, approx 600 m WSW of the primary area. The near perfect correlation between time of water level rise at the main pool and the time of recorded rainfall at Las Cascadas documented the relevance of the station's records. Only one of 39 storms of more than 2.5 mm rainfall was not simultaneously recorded at both the main pool and Las Cascadas.

The Las Cascadas pre-1977 monthly average rainfall plotted in Fig. 5 indicates the dramatic change from dry to wet seasons in April, and the return to dry in December. This figure also illustrates that June, July and August were slightly drier than the other wet season months. In the monthly rainfall records for 1977 and 1978 (Fig. 5), the following features are important: (1) the beginning of the wet season was unpredictable, 1977 being one of the two latest recorded at Las Cascadas, and 1978 the earliest; (2) June through September exhibited considerable monthly variation between years and between months within a year; (3) there was little monthly variation in precipitation as the wet season closed. The cumulative monthly rainfall records shown in Fig. 6 illustrate the magnitude of the difference between the



Fig. 3. View of the main pool looking south from stake 0 in 1978 (section A' of Fig. 1). The water level meter is in the foreground; a row of eight *rosenbergi* tadpole growth pens is in the background.



Fig. 4. View of the primary section of the main *rosenbergi* study area (this is the region labeled "narrows" in A' of Fig. 1) looking south from stake 150 in 1977. The water course is about one meter wide at this point.

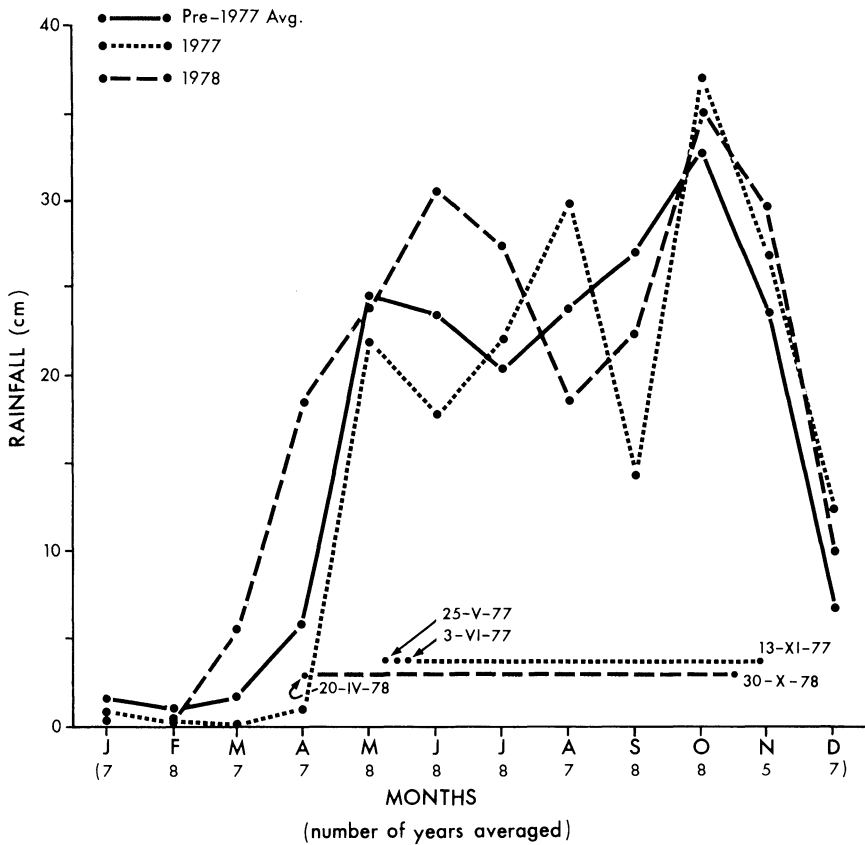


Fig. 5. Average monthly rainfall recorded at the Las Cascadas meteorological station plotted according to year (pre-1977, 1977 and 1978). Beginning and end of the *rosenbergi* breeding seasons are illustrated with horizontal lines and dates. The dotted portion of the line represents the more likely beginning date for 1977.

“drought” year of 1977 and the wet 1978. The Obispo Diversion *rosenbergi* exhibited several adaptations to this relatively unpredictable water resource.

Most rainfall occurred in the afternoon (Fig. 7) with peaks at 1500 hr in 1977 and 1600 hr in 1978. In both years, 58% of the storms occurring during the breeding season (May–November) dropped measurable precipitation in only six hours, from 1300–1900 hr. Fig. 8 plots flood height, as measured by the rising water level recorded at the main pool, against rainfall. It appears that for every millimeter of rainfall, the water level rose about 3 mm. As noted earlier, nearly all thunderstorms were short but intense, and produced nearly instantaneous rises in water level followed by slow returns (Fig. 9). For most storms lasting 1–2 hr, the average drop at one, two, four, eight, 16 and 32 hr after the peak of the storm was 35, 54, 69, 81, 91 and 100% of the total rise in water level due to that storm. For example, the flooding profile of a typical storm of 13 mm recorded rainfall on July 20, 1978 is shown in Fig. 9. This precipitation raised the water level

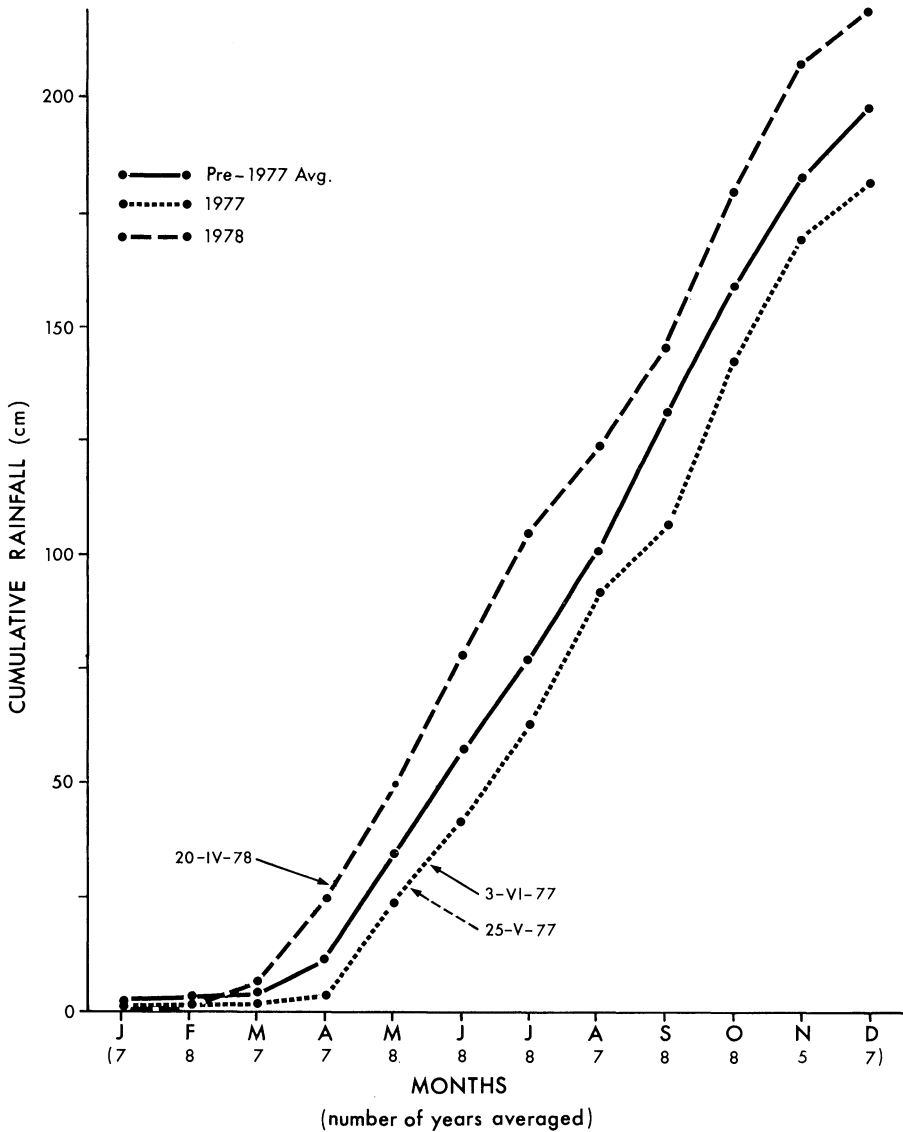


Fig. 6. Cumulative average monthly rainfall records obtained at the Las Cascadas meteorological station plotted according to year (pre-1977, 1977 and 1978). Arrows and associated dates denote times the *rosenbergi* breeding seasons began. The dashed arrow is the more likely date of origin in 1977.

nearly 40 mm in about one hour. By 1900 hr (one hour after peak flooding) the water level had dropped 14 mm and at midnight it was still 12 mm above average.

CORRELATES OF BREEDING ACTIVITY

On the first visit to the ODSS in 1977, on June 3, three male *rosenbergi* were calling approx 2 m above ground. No nests were

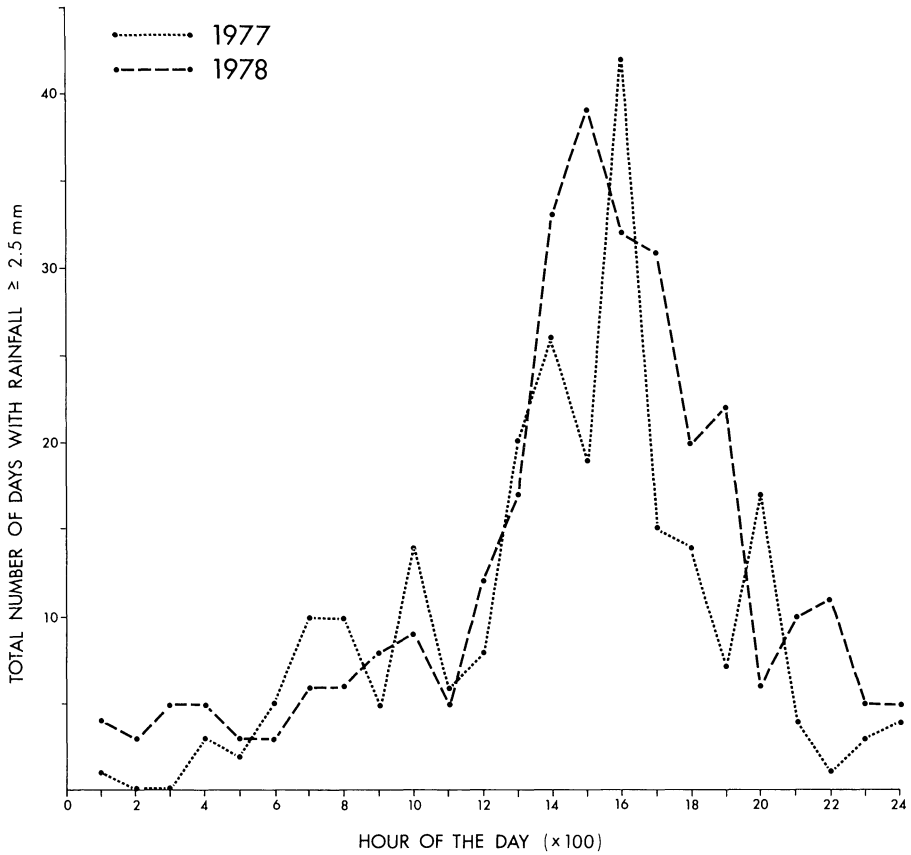


Fig. 7. Total numbers of days during the wet season (April–November) with rainfall ≥ 2.5 mm plotted according to hour of day. Less than 2.5 mm rainfall was difficult to measure accurately and it was considered only a trace. Data were obtained from the Las Cascadas meteorological station.

found. Since the main pool had not yet filled, breeding activity could not have begun much earlier. I selected May 25 as the earliest date of breeding activity in 1977, because it was the first night immediately following the major storm (36 mm rainfall) that probably filled much of the main pool. I believe the three significant rainfalls occurring earlier in May, initiating the wet season, were spaced too far apart to have increased the standing water level along the Obispo Diversion to a point where *rosenbergi* could have constructed and used water-filled nests.

The beginning of the 1978 breeding season was more accurately delimited. The dry season ended with large storms of more than 48 mm rainfall on two consecutive days (April 16–17). There were several calling males and nests present on April 22. The size/age and developmental stage of tadpoles present in two nests indicated the first complexes occurred on April 19 or 20 (see data on growth rates; pp. 55–60). My selection of May 25, 1977 and April 20, 1978 as the

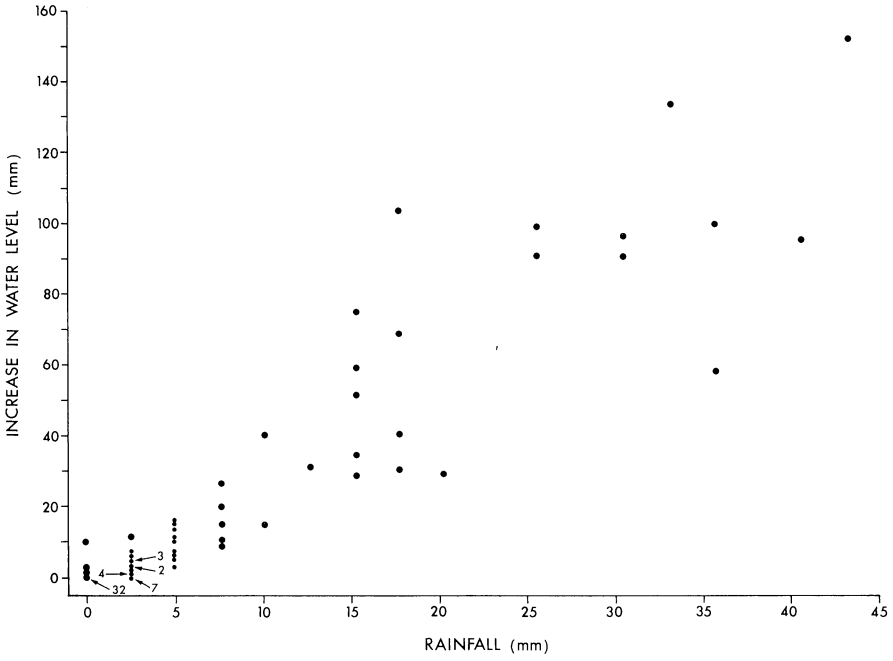


Fig. 8. Increases in water level of the main pool (see Fig. 3) plotted according to the coincident rainfall measured at the Las Cascadas meteorological station. An exceptional storm of 58.4 mm rainfall was not included. Dots indicate individual records, except where numbered.

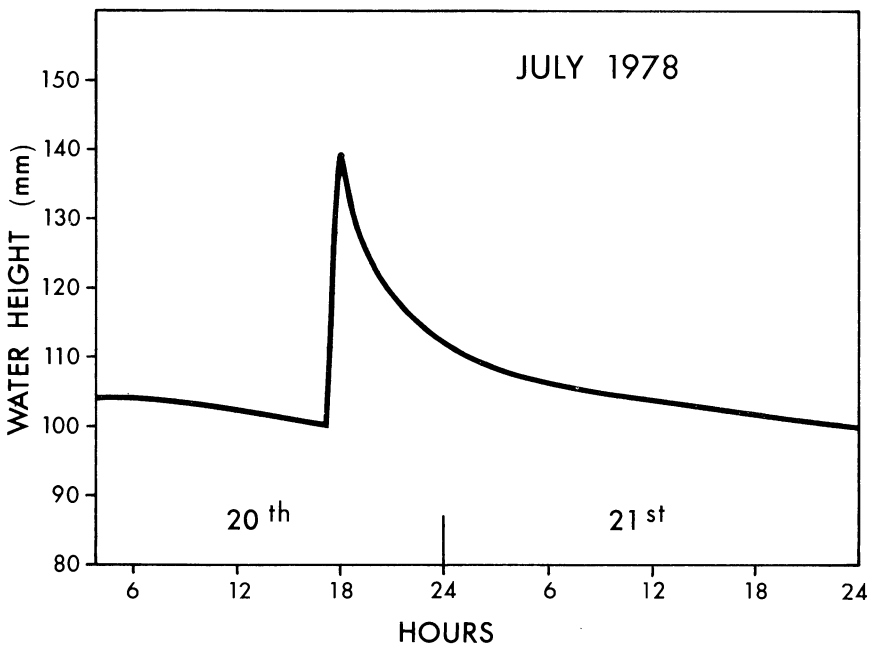


Fig. 9. Tracing of the actual rise and fall of the water level recorded on July 20-21, 1978. The average water level was about 100 mm at this time of the year, and the storm, which abruptly flooded the area with an increased height of almost 40 mm, began at 1700 hr on the 20th.

beginning of the breeding seasons coincides with nearly identical amounts of accumulated rainfall (approx 25 cm; Fig. 6). It probably takes this accumulation each year to raise the water table along the Obispo Diversion to a favorable nest building and flooding environment.

A conspicuous feature of *rosenbergi*'s behavior was the effect heavy rainfall had on breeding activity. From July 5 to August 22, 1977, many males were present. Total numbers of males observed, number of males calling from nests, and amount of rainfall in the preceding daylight (0600–1800 hr) were recorded each night (N = 48). Rainfall and numbers of males present were significantly negatively correlated (total males, $r_s = -.580$; males in nests, $r_s = -.609$; Fig. 10). Log transformations did not improve the correlation. The relationship shown in Fig. 10 indicates that 17.8 mm was the minimum rainfall that kept all male *rosenbergi* silent and out of sight above ground. If the minimum storm of 17.8 mm occurred in mid-afternoon (Figs. 7–9), the area was still moderately awash by the time the frogs usually descended from their daytime retreats. For the purpose of my later discussion of nest flooding, I refer to all rainfalls of 17.8 mm or more as significant. From May 24 to November 24, 1977, significant rainfalls occurred an average of every 6.8 days (163 hr); in 1978, every 6.3 days (151 hr). I interpret the high standard deviation of these estimates ($s_{1977} = 5.41$; $s_{1978} = 4.74$) and the exceptional length of a few intervals (29 and 23 days) to mean this phenomenon was unpredictable.

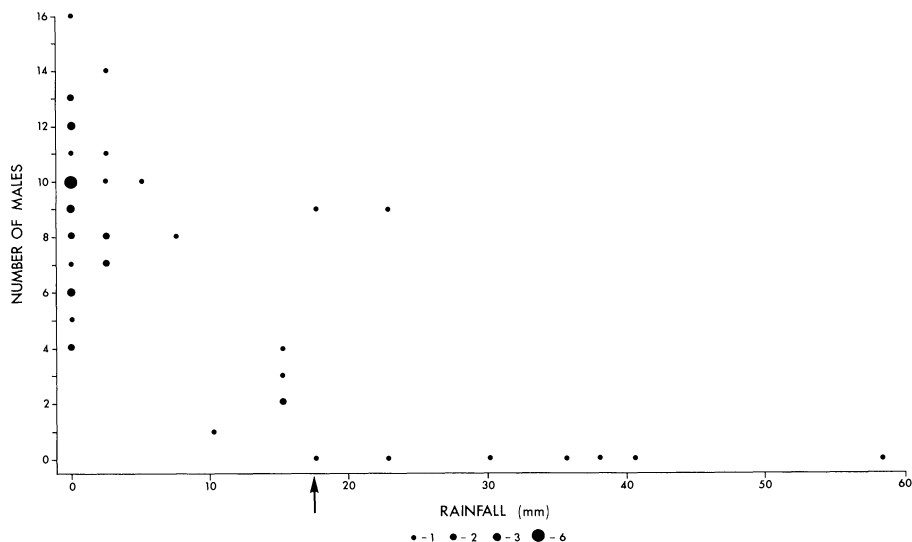


Fig. 10. Numbers of *rosenbergi* males observed each night (July 5–August 22, 1977) plotted according to the amount of rain that fell during the preceding 0600–1800 hr. Dot size denotes number of coincident records. The arrow indicates the minimum amount of rainfall that kept all *rosenbergi* from descending to the ground. Individuals heard but not seen were excluded.

In 1977, the last *rosenbergi* observed on the ground was on November 2, but a single male called from the trees on November 13. The last male observed in 1978 was found calling in a nest on October 30. The Obispo Diversion water table remained high until mid-December of both years; the final wet season rains of more than 2.5 mm fell on the 12th (1977) and 11th (1978) of December and the main pool held considerable water until the third week of that month. These data indicate that *rosenbergi*'s breeding season terminated before the wet season peak was reached in late November and well before the ground water for nesting disappeared. Also, I conclude that male *rosenbergi* were reproductively active for at least 173 (1977) to 194 (1978) days in central Panama. Females were found in amplexus (Fig. 11) from June 25 to October 20, 1977 (118 days), and April 19 to October 2, 1978 (167 days). Reproductively mature *rosenbergi* of either sex have been collected from mid-February through November in the Darien of eastern Panama, from March through September in southwestern Costa Rica and western Panama (Puntarenas and Chiriqui Provinces) and from March through October in Valle Department, Colombia. All of these intervals occurred during the local wet season, except for February and March when Breder (1946) studied *rosenbergi* in the Darien.

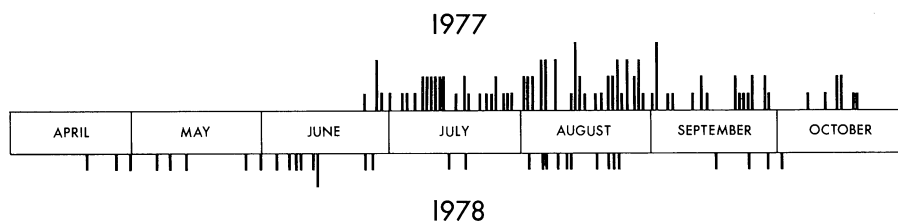


Fig. 11. Dates of *rosenbergi* amplexes ($N = 105$ in 1977 and $N = 33$ in 1978). The shortest vertical line equals one mating.

ADULT CHARACTERISTICS

COLOR AND PATTERN

Males usually had much more pigmented throats than females, and hormonal control of that coloration was suggested, because individuals appeared to become darker in proportion to their calling activity. The female's dorsal color was conspicuously yellower than the male's, a difference which may be the product of sexual selection (pp. 111-115). Both sexes had a pattern of dark brown marks and a thin mid-dorsal stripe, and several lateral body bars were particularly obvious and usually present (Fig. 12). All color faded to a light gray or tan during the day and most of the pattern disappeared. The

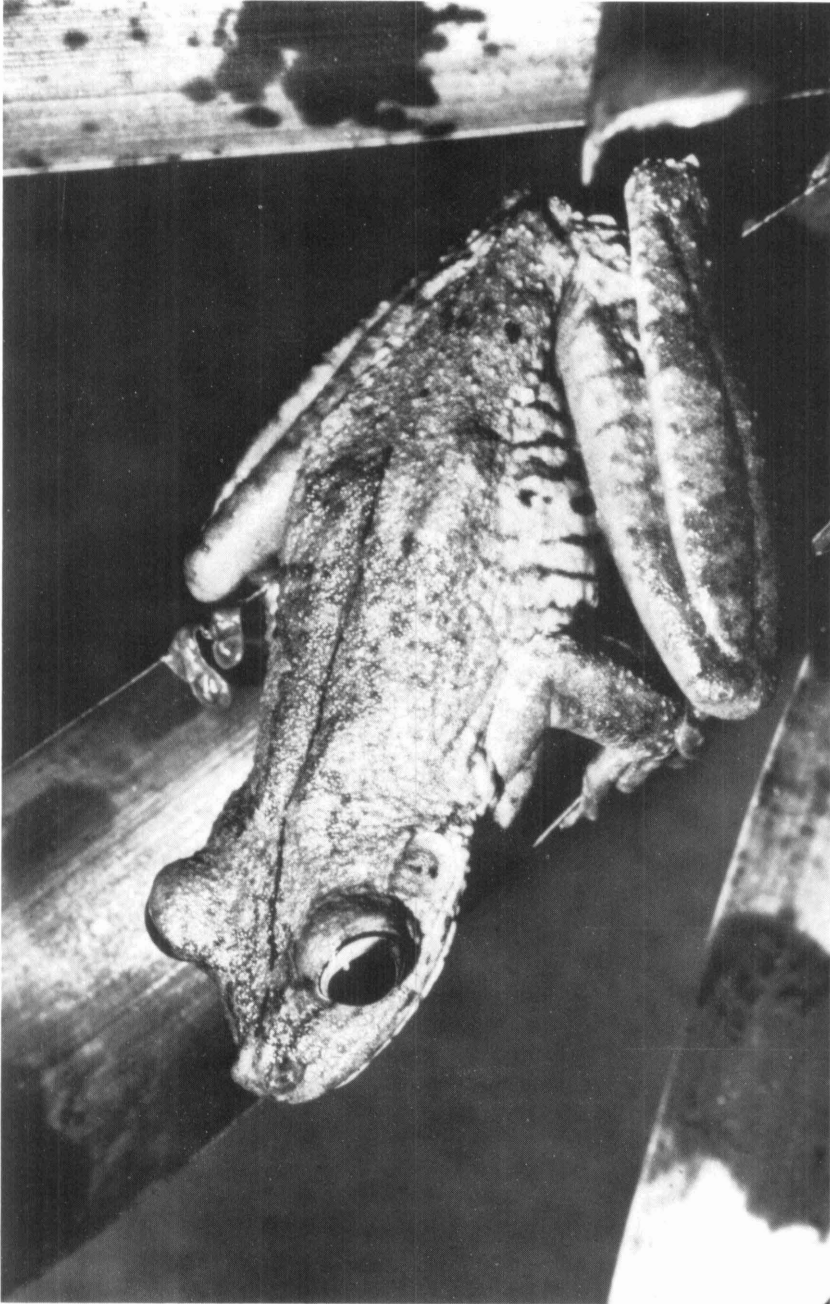


Fig. 12. Dorsolateral view of an adult male *rosensbergi* collected at Summit Gardens, Canal Zone in 1976. Photograph by R. W. VanDevender.

female's lateral body wall immediately anterior to the groin was nearly transparent and when the black eggs were oviducal or in the egg sac they were easily seen.

PREPOLLICAL SPINE

Prepollical spines possessed by males (Figs. 13-15) are bony neomorphs, and only slight ossifications in the comparable thenar regions were observed in some adult females. The male's extremely pointed spines had sharp inner margins along the distal scythe-like portions (Fig. 15). The complicated musculature and articular facets associated with a spine's base suggests males had control over its position and the retraction of the fleshy sheath usually encasing the scythe-like extremity (Fig. 16). Occasionally, a male withdrew a sheath and voluntarily jabbed his spine into an investigator's hand. While the skin was rarely cut or punctured, my first reaction was to drop the beast.

Shine (1979:302) stated that "sexually dimorphic development of [prepollical] spines . . . in male anurans is an adaptation to male combat rather than to amplexus." This conclusion appears to be logically untenable for the earliest phases of spine evolution. Assum-



Fig. 13. Positive print of a radiograph of the head and forelimbs of an adult male *rosenbergi* (no. 10). Note the prepollical spine on the medial aspect of the hand. He was marked on June 29, 1977 (WT = 25.9 gr; SVL = 81.0 mm), and he died on July 12, 1977 as the result of a fight with male no. 33.



Fig. 14. Enlargement of the left hand of the male *rosenbergi* illustrated in Fig. 13. Note the prepollical spine.

ing gradualistic evolution, the initial steps in the transformation must have involved only a slight swelling of the medial aspect of the thumb, with small increases in keratinization or ossification. It seems most unlikely that there was an advantage to such weakly developed structures in male-male combat. Prepollical spines probably became useful in intrasexual aggression after the structures had evolved to a considerable size and stiffness. I accept Noble's (1931) and Pope's (1931) conclusions that amplexus formed the adaptive basis for the origin of prepollical spines.

SIZE

Size was estimated from WT and SVL measurements taken at first capture (Fig. 17), and all of the *rosenbergi* samples listed in Table 1, except those with $N \leq 4$, were employed in the analysis. WT

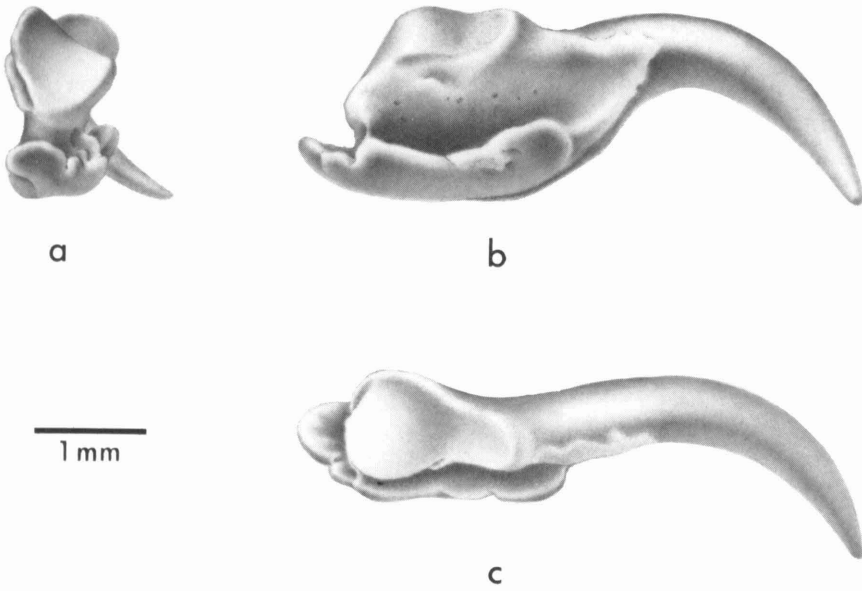


Fig. 15. Views of a left prepollical spine removed from a dermestid beetle-prepared skeleton of an adult male *rosenbergi* (WT = 30.3 gr; SVL = 83.0 mm) collected on Pita Road, Canal Zone (UMMZ 143401) in 1976. In situ (according to Figs. 13, 14 and 16), the views are: a. lateral, b. dorsal, c. anterior.

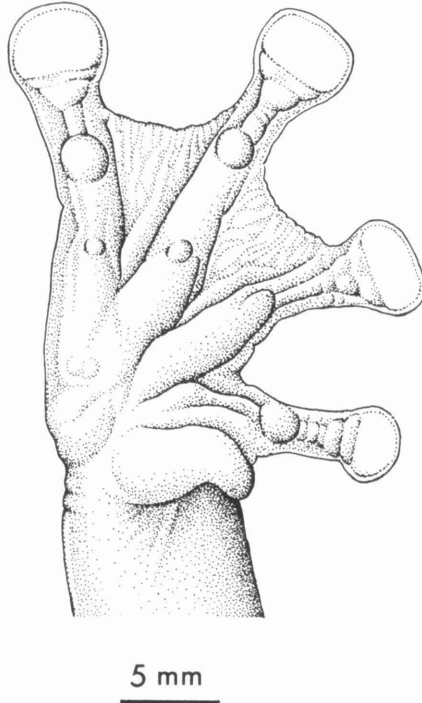


Fig. 16. Ventral view of the right hand of an adult male *rosenbergi* showing the fleshy sheath encasing the prepollical spine (from Kluge, 1979).

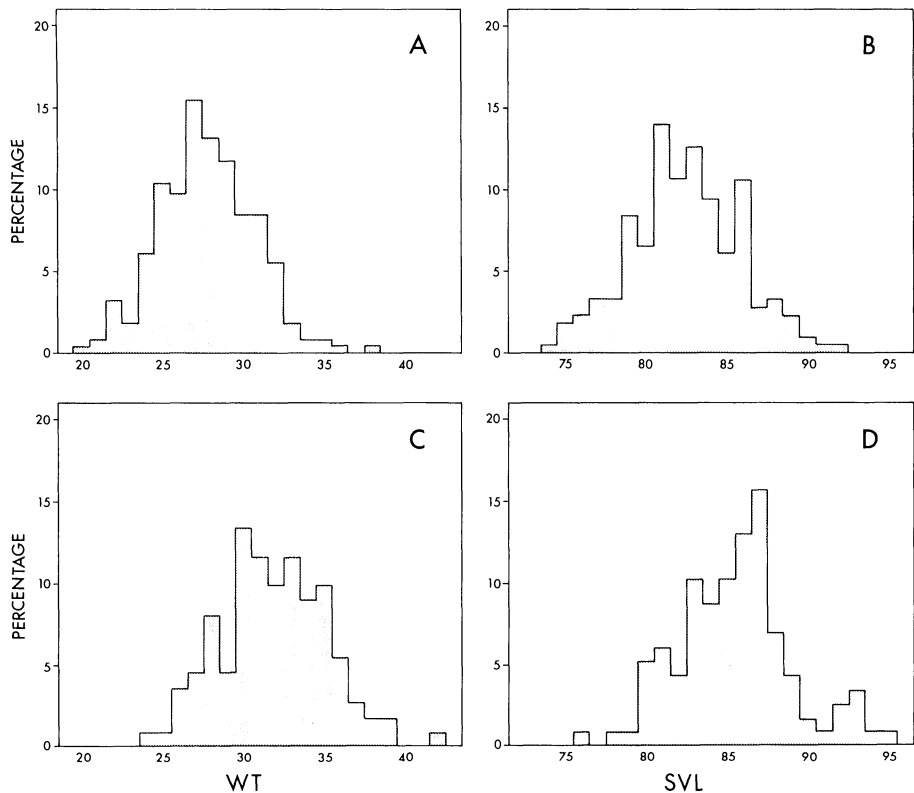


Fig. 17. Histograms of live male and female *rosenbergi* WT and SVL. A. Male WT: \bar{x} = 27.7 gr, s = 2.98, N = 214. B. Male SVL: \bar{x} = 82.4 mm, s = 3.59, N = 214. C. Female WT with eggs: \bar{x} = 31.8 gr, s = 3.37, N = 111. D. Female SVL: \bar{x} = 85.3 mm, s = 3.53, N = 115. All specimens were from the Canal Zone (see Table 1).

and SVL were significantly correlated in both males ($N = 191$, $r = .765$) and females ($N = 108$, $r = .817$). The most strikingly different samples were the Costa Rica males (no females were recorded). Compared to the Canal Zone material (Fig. 18), they were significantly smaller in both WT and SVL (Table 3). Costa Rica and western Panama (Chiriqui Province) populations were phenotypically homogeneous and geographically contiguous. They are separated by approx 300 km from the nearest *rosenbergi* in the Canal Zone.

Table 3 summarizes the remaining significant sex, locality and year differences in WT and SVL among the Canal Zone samples. Females always averaged slightly longer than males (Table 3), but they were heavier only when they possessed eggs (Figs. 17-20). The average clutch weighed 7.2 gr (5.8-9.5), and was 22.7% (18.8-29.9) of the female's WT with eggs (Fig. 20). The fact that clutch WT was not significantly correlated with the female's WT (with or without eggs, $N = 15$, $r_s = .366$ and $r_s = .033$, respectively) will be discussed later (pp. 32-35). The males from Chiva Chiva Quarry were slightly

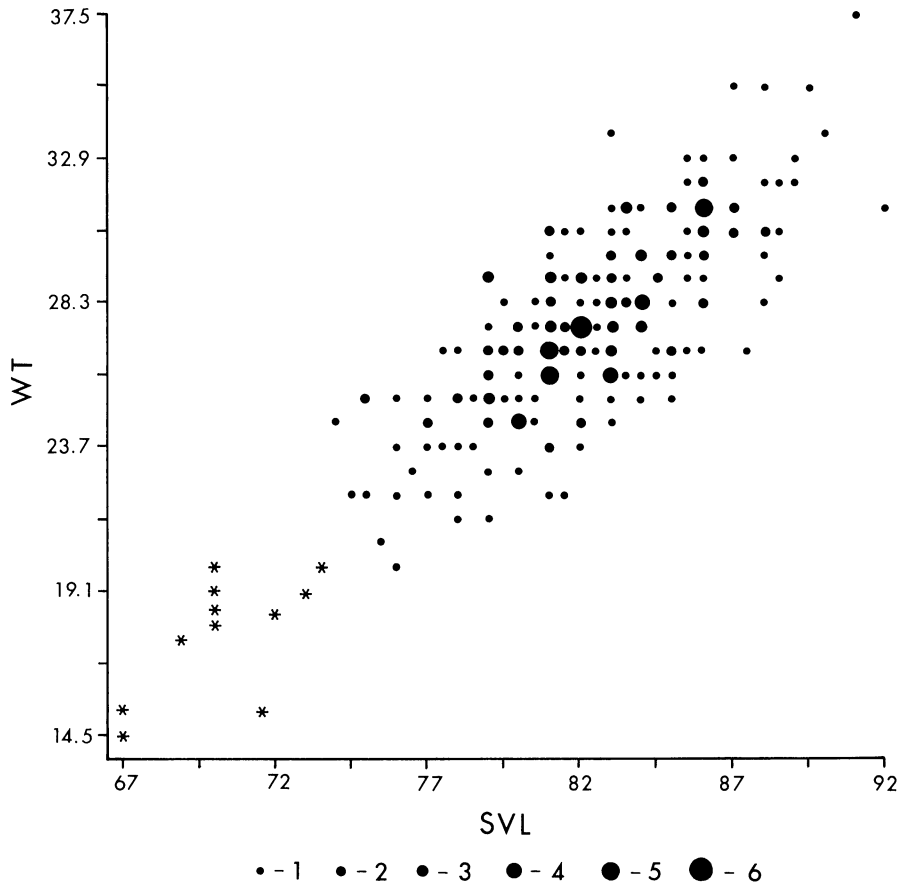


Fig. 18. Live *rosenbergi* male WT plotted according to SVL. * = Costa Rica sample. • = Canal Zone sample. Dot size denotes number of coincident Canal Zone records.

shorter than those from the Obispo Diversion. However, there was no corresponding difference in WT (Table 3). Within the ODSS, males and females from the primary section usually were significantly smaller than samples collected elsewhere (Table 3). Only females showed between-year differences, those from 1978 were larger (Table 3).

One might hypothesize that individuals captured later would be exhausted recruits from other choruses, and thus weigh less, or that toward the end of the breeding season individuals were more likely to enter the choruses regardless of not having grown to some large size. The correlations between date of first capture and WT and SVL were investigated with the yearly samples of males and females from the primary section or elsewhere to test these possibilities. Only the male 1977 primary section ($N = 67$, $r = -.310$, $P < .01$) and the female 1978 other than the primary section ($N = 20$, $r_s = -.534$, $P < .01$) samples

TABLE 3
ROSENBERGI SAMPLES
WITH SIGNIFICANTLY DIFFERENT AVERAGE WT AND SVL¹

MALES ONLY								
Between Countries								
Samples	WT ²				SVL			
	N	\bar{x}	t	P	N	\bar{x}	t	P
Canal Zone	214	27.7			214	82.4		
Costa Rica	11	17.9	10.83	.000	11	70.3	11.70	.000
Within Canal Zone								
Obispo Diversion Study Site					181	82.6	2.98	.003
Chiva Chiva Quarry					26	80.5		
Within Obispo Diversion Study Site								
1977 Primary Section					67	81.9	2.51	.01
Other areas					38	80.4		
1978 Primary Section	22	27.3	-3.76	.000	22	82.6	-3.97	.000
Other areas	54	29.9			54	85.1		
FEMALES ONLY								
Within Obispo Diversion Study Site								
1978 Primary Section	23	33.3	-3.48	.001	24	86.9	-2.67	.01
Other areas	15	35.8			15	89.3		
Primary Section								
1977	50	30.8	-3.44	.001	53	84.6	-3.37	.001
1978	23	33.3			24	86.9		
SEXUAL DIMORPHISM								
Within Obispo Diversion Study Site								
1977								
Males	105	26.7	-9.11	.000	105	81.3	-6.29	.000
Females	70	30.6			73	84.2		
1978								
Males	76	29.2	-9.01	.000	76	84.3	-5.68	.000
Females	38	34.3			39	87.8		
1977 and 1978								
Females	108	31.9	-10.84	.000	112	85.5	-7.02	.000
Males	181	27.7	4.26	.000	181	82.6		
Females without eggs	19	24.6						

¹WT in gr; SVL in mm.

²Female's WT with eggs except where noted.

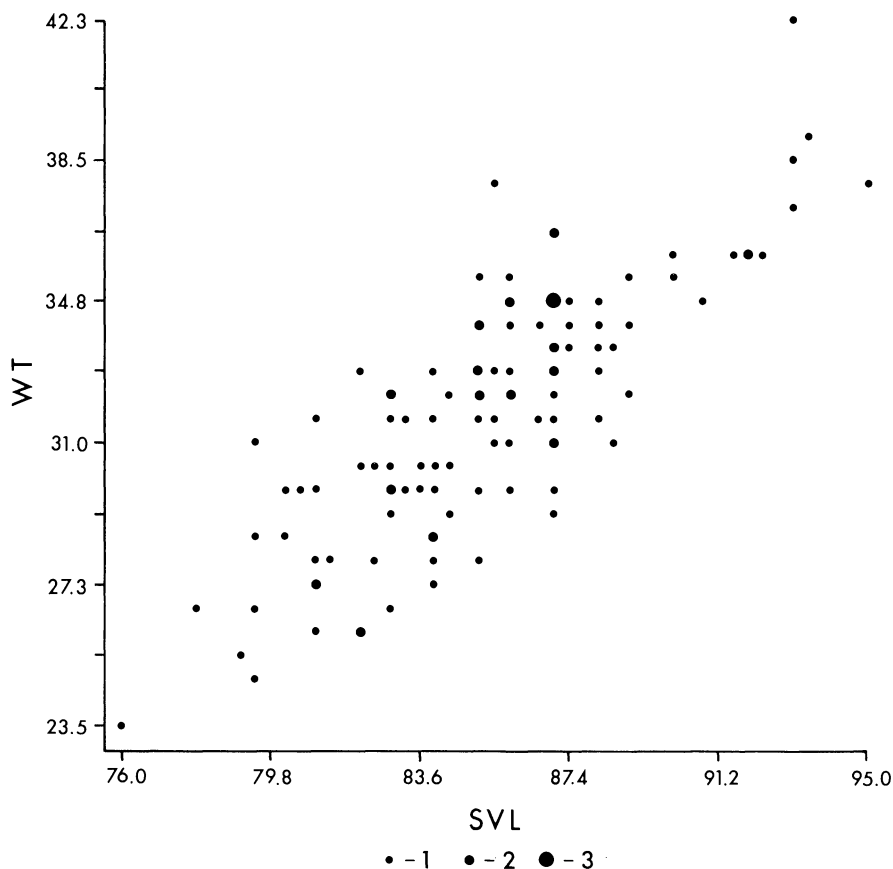


Fig. 19: Live gravid *rosenbergi* WT plotted according to SVL. Data were from the Canal Zone (see Table 1). Dot size denotes number of coincident records.

exhibited significant correlations between date of entry into the population and WT. These were not likely to be biologically significant, because so little of the variance is explained by the correlation. Furthermore, most samples did not indicate such a relationship, and SVL did not change with time. I conclude that *rosenbergi*'s size did not vary significantly with date of first capture.

GROWTH

Growth within a breeding season in reproductively mature *rosenbergi* was estimated from WT and SVL measurement data collected five or more days after marking. The interval between captures was 5–103 days ($\bar{x} = 18.5$). The change in WT and SVL was divided by the number of days, thereby transforming all measurements to the same scale, $\Delta\text{WT}/\text{day}$ and $\Delta\text{SVL}/\text{day}$. Few individuals

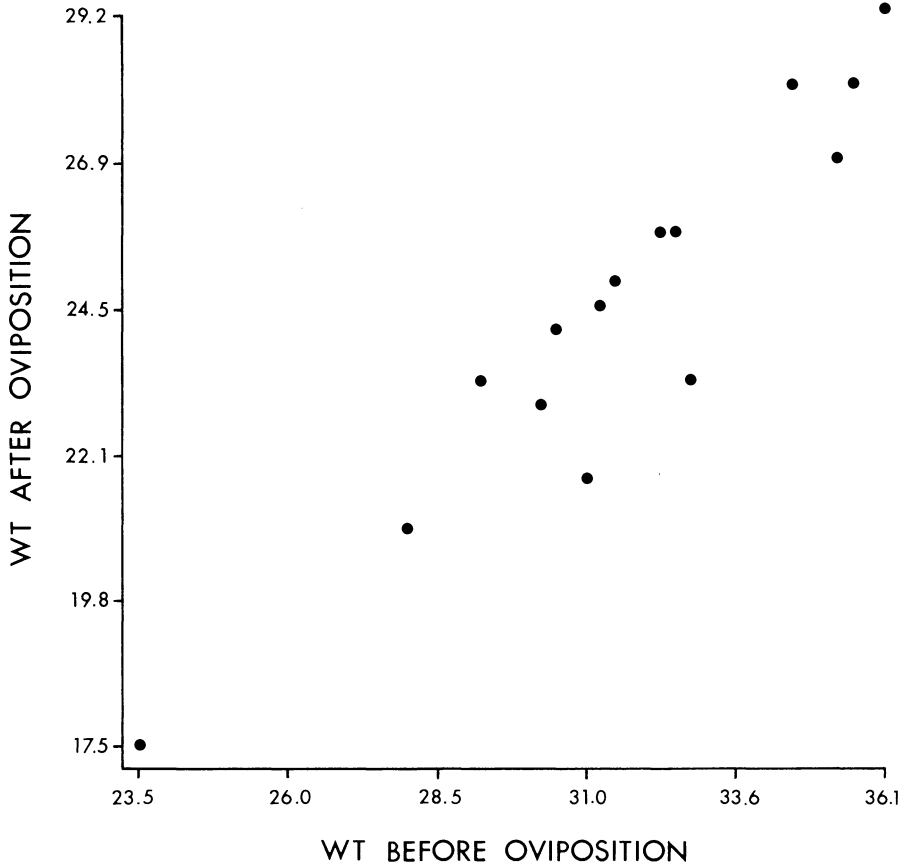


Fig. 20. Live female *rosenbergi* WT after oviposition plotted according to WT before spawning.

were remeasured more than three times and most intervals were short. Consequently, no attempt was made to identify individual growth rates.

Initially, the transformed data were analyzed within and between the following four samples: Chiva Chiva Quarry males, 1977 plus 1978 ($N = 7$); ODSS males, 1977 ($N = 56$) and 1978 ($N = 61$); and ODSS females, 1977 plus 1978 ($n = 23$). According to the median test, growth rates were not different among localities, or between years or sexes. It should not be surprising that male and female growth rates did not differ given the errors of estimation, small sample sizes and small degree of sexual dimorphism. Further, $\Delta WT/day$ and $\Delta SVL/day$ were not significantly correlated with date of capture or with size (WT or SVL). Considering all data together, $\Delta WT/day$ ($N = 143$) and $\Delta SVL/day$ ($N = 95$) did not differ significantly from zero (Fig. 21). In a further attempt to discover increasing size or loss of WT, the growth data were arbitrarily subdivided into those cases taken from intervals

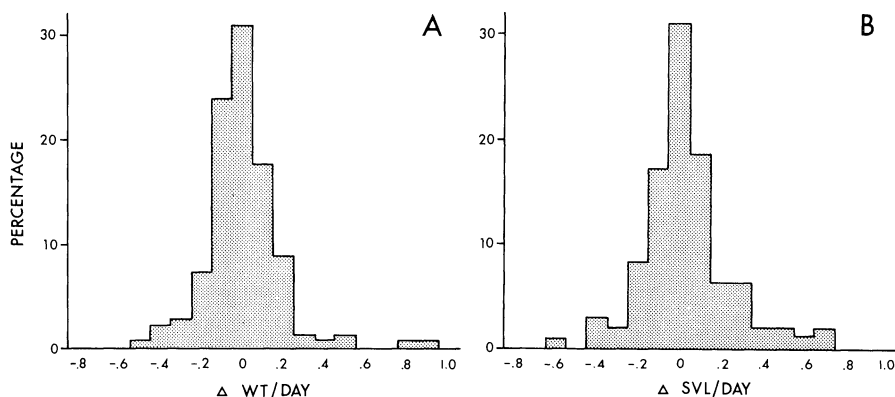


Fig. 21. Changes in *rosenbergi* WT (A) and SVL (B) per day.

of 5–17 (N = 87), 18–33 (N = 44) and 34–103 days (N = 13). Similarly, there were no significant differences in $\Delta\text{WT}/\text{day}$ and $\Delta\text{SVL}/\text{day}$ between these three intervals using the Mann-Whitney test; no sample differed significantly from zero. Thus, I conclude, that if growth existed, it was not sufficient to distinguish from error in measurement (Table 2).

Only three *rosenbergi*, all females, were recaptured in a second breeding season. The time between remeasurement of these individuals was 249, 256, and 273 days, and the following size changes were recorded: .013 gr, .001 gr, .026 gr $\Delta\text{WT}/\text{day}$; .009 mm, .000 mm, .018 mm $\Delta\text{SVL}/\text{day}$. While the sets of observations are all positive and the pair of variables perfectly correlated, the sample is much too small to consider further.

FOOD HABITS AND FAT BODIES

Ten males and two females with full term clutches were available from the Canal Zone wet season for a survey of *rosenbergi*'s food habits and fat bodies. This small sample of adults was obtained in July and August, 1975 and 1977 from the ODSS, Summit Gardens and Rio Frijoles, and all were preserved within six hours of collection. One male *rosenbergi* had no detectable abdominal fat, and the fat bodies consisted of only a few short thin lobes in the remainder of those sampled. The small intestine of each specimen contained trace to moderate amounts of organic material, most of which could be identified as fragments of arthropod cuticle. Four male *rosenbergi* had arthropod remains in their stomachs, and the stomachs were fully distended with prey in only two individuals. The identifiable contents are listed in Table 4. These prey taxa are most frequently encountered within 3 m of the ground according to I. J. Cantrall and T. H. Hubbell (pers comm).

TABLE 4
STOMACH CONTENTS OF *ROSENBERGI*
COLLECTED FROM THE WET SEASON IN THE CANAL ZONE¹

Orthoptera
Blattidae (1 adult)
Gryllacrididae, Gryllacridinae, <i>Abelona salvinii</i> (1 adult)
Gryllidae, Eneopterinae (1 adult)
Tettigoniidae, Pseudophyllinae, Cocconotini (1 nymph)
Copiphorinae (2 nymphs)
Arachnida
Araneida (2 adults)
Thelyphonida? (1 adult)

¹Removed from four adult male *rosenbergi* collected in July and August, 1975 and 1977.

Wolda's (1977, 1978) long term light trap census on nearby Barro Colorado Island, Canal Zone demonstrated that most of *rosenbergi*'s known or suspected insect prey reach peak abundance during the wet season. I conclude that the absence of growth in reproductively mature *rosenbergi* during the breeding season was not related to low food availability. The absence of growth in females during the breeding season probably resulted from diverting most food into calorie-rich eggs. Females left the breeding site after oviposition (pp. 53-55). When they returned to the breeding area in about 25 days they had formed a new set of eggs accounting for almost 23% ($\bar{x} = 22.7$) of their body weight. I predict females find the food necessary for this extraordinary conversion in or near the forest canopy. In contrast to females, males returned night after night during the breeding season to the bare ground or shallow water (rarely were they observed more than 4 m above the substrate), and the habits of the prey taxa (Table 4) suggest that males fed at lower heights in the forest. The absence of growth in males during the breeding season might have been due to low insect abundance at or near the ground, the males were too preoccupied with reproductive activities to feed, or the caloric intake was quickly expended with their advertising for mates, building nests and defending territories.

CLUTCH FREQUENCY

The number of days between clutches of eggs in a given female in a single season was 21-101, $\bar{x} = 35.8$, based on 22 recaptures during 1977 and 1978. Most of the intervals were less than 33 days, and they clustered around a mean of 25.4 ($N = 16$, $s = 3.26$). The conspicuous outliers in the between-clutch interval distribution were 42, 44, 46, 70, 79 and 101 days. Such long intervals may have been influenced by four factors. Local food abundance might have changed dramatically

during the wet season, or females might have varied in their ability to locate and physiologically process the prey necessary to complete vitellogenesis. Some females also might have delayed ovipositing until a favorable environmental condition (probably rainfall) was encountered, or they could have mated in the intervening period without being observed.

Other females were able to find food during the exceptionally long intervals, and environmental conditions were favorable to nesting. Also, one half of the females with the exceptional records completed vitellogenesis at other times in shorter intervals (21, 26 and 30 days). Therefore, it seems likely that the females with long intervals oviposited without being seen, especially since observers were not present every night.

Given the likelihood that the six longest spans were due to intervening unobserved matings, I estimated their interclutch intervals by dividing the total into the smallest nearly equal numbers of days between 20–33 (eg, $42 = 21 + 21$; $44 = 22 + 22$; $46 = 23 + 23$; $70 = 23 + 23 + 24$; $76 = 26 + 26 + 27$; $101 = 25 + 25 + 25 + 26$). Adding these estimated values to the observed (see Fig. 22), plus a recapture record of 27 days from Chiva Chiva Quarry yielded a new mean of 24.7 days between successive clutches ($N = 33$, $s = 2.72$). All female *boans* ($N = 1$) and *crepitans* ($N = 6$) recaptures were 24–31 days. The average interval between clutches in gladiator frogs is similar to that of temperate zone ranids, *Rana catesbeiana* and *R. clamitans* (Howard, 1978a; Wells, 1976).

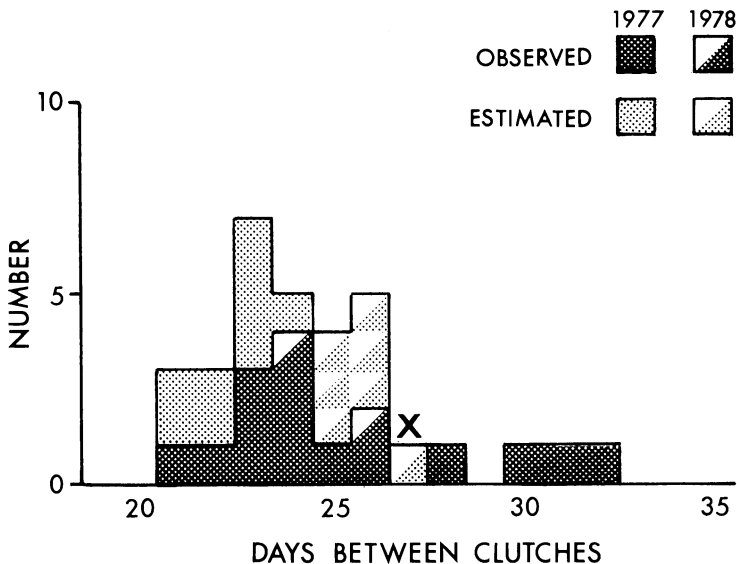


Fig. 22. Days between successive clutches laid by female *rosenbergi*. Data were collected on the primary section of the ODSS (squares) and Chiva Chiva Quarry (x), Canal Zone.

If mean clutch WT was 7.2 gr and the interval between ovipositions was 24.7 days, then adult females must have been able to process food into eggs at an average rate of 0.3 gr/day. The number of clutches laid by individual female *rosenbergi* will be considered under Mating Success (pp. 125–130).

CLUTCH SIZE

Clutch size was estimated from a direct count of eggs laid. Sixteen *rosenbergi* clutches were obtained from marked females after they oviposited in either a plastic shoe box in the laboratory or a naturally occurring nest. According to Davidson and Hough (1969), oogenesis is synchronous, and females usually laid their entire complement of eggs when they oviposited. I was unable to forcibly extrude eggs from spent females, and I saw only one individual in more than 100 that retained a noticeable number following oviposition. Clutch size was 1780–3057 ($N = 16$, $\bar{x} = 2350$, $s = 318$). These large numbers provide another exception (Crump, 1974) to Salthe and Duellman's (1973) generalization that clutch size tends to be small in tropical anurans. I interpret the large numbers of eggs deposited by *rosenbergi* to mean that it suffered heavy mortality (pp. 66–75). Clutch size in *rosenbergi* was not significantly correlated with either SVL or WT (with or without eggs). There appeared to be no significant relationship between clutch WT (an estimate of clutch size) and SVL at first breeding or date of oviposition. However, the sample size was small ($N = 9$) and the correlations might improve with more observations. A significant relationship between clutch size and body size was found in the closely related *boans* (Kluge, 1979) and when individual *boans*, *crepitans* and *rosenbergi* observations were lumped ($N = 59$, $r = .866$; Fig. 23). Salthe and Duellman (1973) also observed a correlation between clutch size and SVL when the analysis was done on species within a reproductive mode. However, Crump (1974) found a significant relationship in only 11 of 41 species of frogs she studied in the Amazonian lowlands of Ecuador. I believe there are two possible explanations for the absence of a correlation in *rosenbergi*; it was difficult to accurately count large numbers of eggs and to measure female SVL and WT, and the female size range was too narrow (SVL = 76–95 mm) to reflect a consistent clutch size trend.

Fig. 24 demonstrates that a female's clutch size (WT) varied in a systematic manner with time. Second and third clutches were nearly always smaller than the first, whereas later clutches (4–6) were invariably larger. The maximum amount of variation in clutch WT in a female in one season was considerable ($11.9 \text{ gr} = 7.2 + 4.7$) and without taking into consideration each female's clutch number (time of season), I believe a significant clutch size/body size correlation

would be obscured. Almost all of the clutch size data shown in Fig. 23 were obtained from females whose individual reproductive histories were incompletely known, and therefore I was not able to test my prediction that seasonal variation is sufficient to mask the expected correlation.

Crump (1974) observed temporal changes in a few species' fecundities in her extensive survey of Amazonian anurans. Unfortunately, it was difficult for her to identify a causal agent(s) for the variation, because she used destructively sampled population estimates rather than the individual female's reproductive performance. Crump could not eliminate the confounding variables of differential predation and age at maturity. Therefore, it seems worthwhile to speculate on the adaptive significance of the seasonal variation in *rosenbergi's* clutch size (= Δ clutch WT; Fig. 24) because these

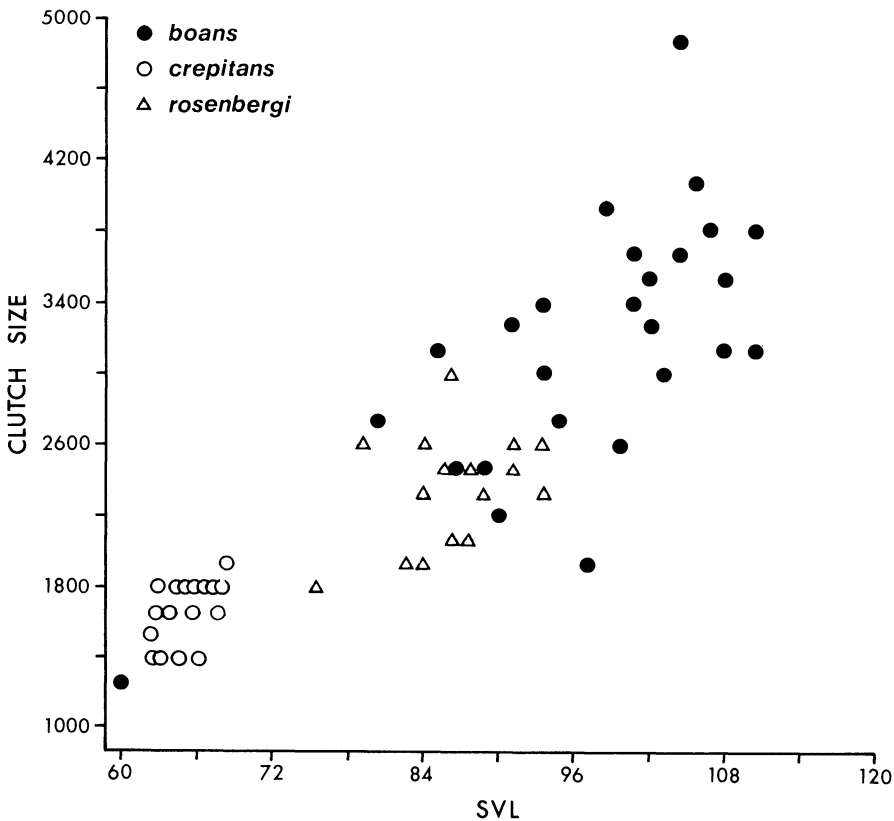


Fig. 23. Clutch sizes (number of eggs laid) of closely related species of gladiator frogs, *boans*, *crepitans* and *rosenbergi*, plotted according to SVL. The *crepitans* and *rosenbergi* data were from the Canal Zone, the *boans* records were from Ecuador, and used with the permission of M. L. Crump (1974, pers comm) and W. E. Duellman (1978, pers comm).

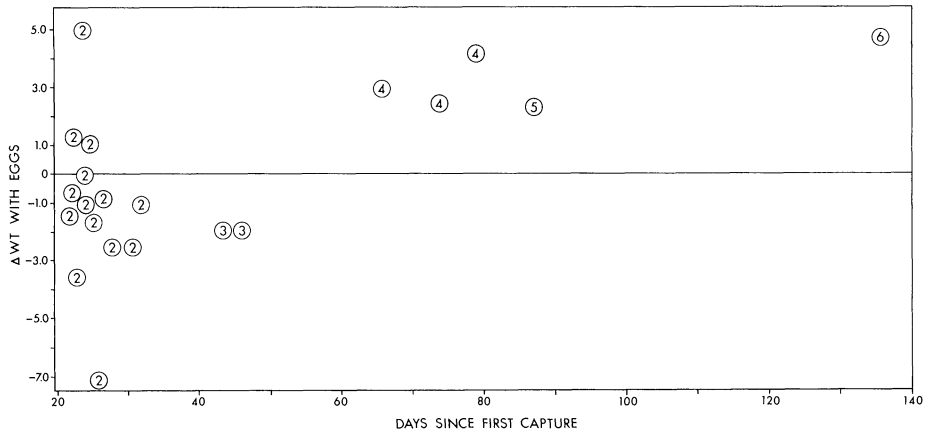


Fig. 24. Seasonal clutch size variation in individual female *rosenbergi*. Clutch size, Δ WT (with eggs), is plotted according to time since first captured. Clutch size was estimated from the difference between a female's weight with her first and her weight with some subsequent clutch (number 2, 3, 4, 5, or 6).

complications do not apply. My explanation for the origin of the variation (Fig. 24) involves two factors, the first creating the condition on which the second operates. My thesis assumes that (1) clutch size was positively correlated with time, a smaller set of eggs took less time to complete vitellogenesis than a larger set, and (2) the probability of adult survival declined during the breeding season (Fig. 56; see also pp. 86–90). Thus, I believe smaller, more frequently laid, clutches were an adaptation to the pattern and amount of rainfall. A significant rain occurred with little predictability on the ODSS on any given day during the wet season (an average daily probability of 0.31–0.17 for the months of May–August). Each clutch had a low probability of surviving a significant rain and the flood following it. However, the likelihood of one reaching the hatching stage improved as the number of clutches increased.

Eventually, this advantage may have been replaced by that of the second factor. It appeared that most mortality among adult *rosenbergi* resulted from predation on or near the ground (pp. 88–90), and more frequently oviposited smaller clutches only would tend to increase the female's rapidly diminishing chances of survival, particularly with predator densities growing during the anuran breeding season. The larger clutches at the end of the breeding season may be viewed as an adaptation related to the female's decreasing probability of survival. The residency-survivorship curve of *rosenbergi* (Fig. 56), with its rapidly declining initial phase and relatively long tail, is consistent with my two-part hypothesis.

Another explanation for the larger clutches is also available. The

female's chances of entering the dry season containing a partially developed egg mass increased toward the end of the wet season, because fewer males were available (Fig. 71) and a favorable breeding environment became less certain. If a female were to commit her effort to a larger, longer to mature, clutch in August-early September (Fig. 11), her life-time reproductive success would probably be greater than if two smaller clutches were projected for the remainder of the breeding season. The second clutch was not likely to be fertilized, because males were rare and may have disappeared altogether. A favorable breeding environment became more unpredictable toward the end of the wet season as well.

Only one *rosenbergi* has been collected in central Panama outside the breeding season. The specimen (UMMZ 152605), an adult female (SVL = 82.0 mm) without fat bodies and with an empty stomach, was found at the water's edge of the Rio Frijoles, Canal Zone during the night of January 21, 1978. She had ovarian masses of eggs, each 21.0 mm long. The largest oocytes were approx 0.3 mm dia, and they appeared to be developing normally. Numerous large black pigment masses were also present below the *theca externa*, and these were evidence of a reabsorbed clutch of eggs. Thus, this female apparently failed to deposit her last clutch of the 1977 breeding season.

EGG SIZE

Egg size was estimated by its greatest yolk diameter. Average egg size in a clutch was based on a randomly chosen sample (N = 6-10) preserved at developmental stages 9-12 (after Gosner, 1960). Twenty-nine clutches were sampled, each from a different female. All clutches were collected on the ODSS in 1977 (N = 22) or 1978 (N = 7). The median test was used, because of the small numbers of ova available and the small within-sample variance. Egg size was 1.6-2.1 mm within the total sample (N = 283), and the sample medians were 1.8-2.1 mm. The eggs of *rosenbergi* were larger than most other tropical hylids (Crump, 1974), and according to Moore (1942) a large egg permits attainment of a larger size before an external food source is sought by the larva. Average ovum size in *rosenbergi* was not correlated with day of oviposition, clutch size or weight, or female size (SVL or WT with eggs). No significant differences were observed between years or between first and second clutches. I interpret these data to mean that, while individual clutches differed in median egg size, they did not vary in a predictable manner.

Duellman and Crump (1974) proposed a special index, called the ovarian size factor (OSF), for relating egg mass to female size. The

factor is calculated by multiplying average clutch size by average ovum diameter and dividing that product by the average female SVL. Crump (1974) used OSF to compare a large number of anuran species with diverse reproductive habits from Amazonian Ecuador. However, she used maximum ovum diameter in her calculations. The OSF ranged from 0.7 (*Colostethus sauli*; Dendrobatidae) to 97.3 (*Bufo marinus*; Bufonidae) in Crump's sample of 66 species. The only gladiator frog scored was *boans*, and it had the second highest OSF with 63.7. OSF values for individual *rosenbergi* from the ODSS were calculated and, using average sample ovum diameter, I found considerable variation, 42.2–56.7, and a much lower mean OSF than *boans*' (*rosenbergi*: $\bar{x} = 49.9$, $s = 4.74$, $N = 7$). However, when average clutch size and SVL, and maximum ovum diameter were employed in the calculations, the OSF for *rosenbergi* became 58.2, a factor not very different from *boans*' 63.7. Crump (1974) found OSF increased with increasing female size within a reproductive mode, larger species having proportionately much larger egg masses. Such a relationship could not be demonstrated in *rosenbergi* using r_s . I suggest that future studies evaluate the meaning of OSF values in the context of individual variation. It seems that much is hidden by the Duellman and Crump (1974) method of estimation.

TIME OF OVULATION

Few data were collected on time of ovulation in *rosenbergi*. One female ovulated shortly after amplexus (2130 hr), as indicated by eggs protruding from her vent. Eggs had moved into the egg sac (Rugh, 1951) of another amplexed female by 2300 hr, while at least one had not committed her eggs to the oviducts approx one hour after being clasped by a male. I predict that most female *rosenbergi* delay ovulation until well after courtship, because of the many factors that can interrupt a preferred mating (Bragg, 1960). A female did not always reestablish contact with her preferred mate when they became separated. Separation in *rosenbergi* occurred as the result of a predator attack, aggression by a competing male, and probably successful courtship by an intruding female. I assume that eggs located in the egg sacs (uteri) are likely to be accidentally extruded or physiologically damaged when the female must take an additional 24 hr before remating and finally ovipositing. Secretory cells are present throughout the walls of anuran oviducts, except in the region of the dilated egg sac. Presumably the female has little physiological control over the water content of her reproductive products after they reach the egg sac (Ecker, 1889:344–347).

THE NEST

MATERIALS AND CONSTRUCTION

A *rosenbergi* nest is a water-filled excavation from which one male attempted to exclude all other males. The resident usually was stationed within the nest when he emitted territorial and advertisement calls (Figs. 25–26; pp. 96–100). The small but vigorously defended territory was the site of oviposition. Ordinarily, nests were built with a rampart (Figs. 25 and 27) and located in the soft substrate adjacent to some large stationary or slowly moving, semipermanent body of water. Few were found near the narrower sections of the water course where currents were swift and water levels fluctuated considerably. Nests filled by seepage from nearby bodies of water and the levels were the same. As the main body of water flooded or dried up, so did nests. The location of nests tended to vary seasonally, as did the water table, and nests were found next to the steeper banks, except at the beginning and end of the wet seasons. Frequently occupied nests developed a distinctive deep basin and shallow calling platform (Fig. 25). The platform appeared to form naturally as a result of the male stationing himself night after night in one or two radians of the nest. The platform location was a good predictor of the direction the resident most frequently called toward.

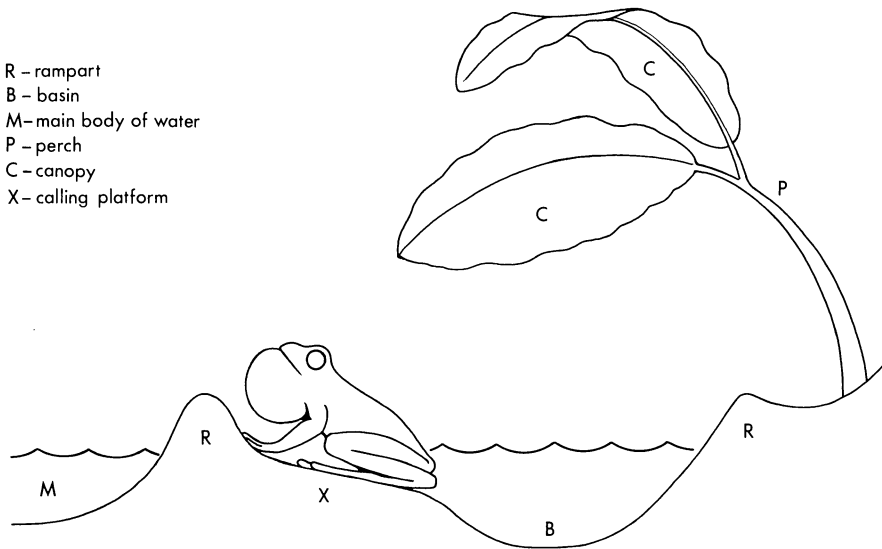


Fig. 25. Diagrammatic profile of a typical *rosenbergi* nest and its resident calling male. The miniature canopy (C) was usually formed by *Heliconia* (not drawn to scale).



Fig. 26. Male *rosenbergi* no. 144 giving the advertisement call from nest no. 127 on August 14, 1978. Note the fully extended vocal pouch. The relatively clear water indicates little or no renovation had occurred that evening.

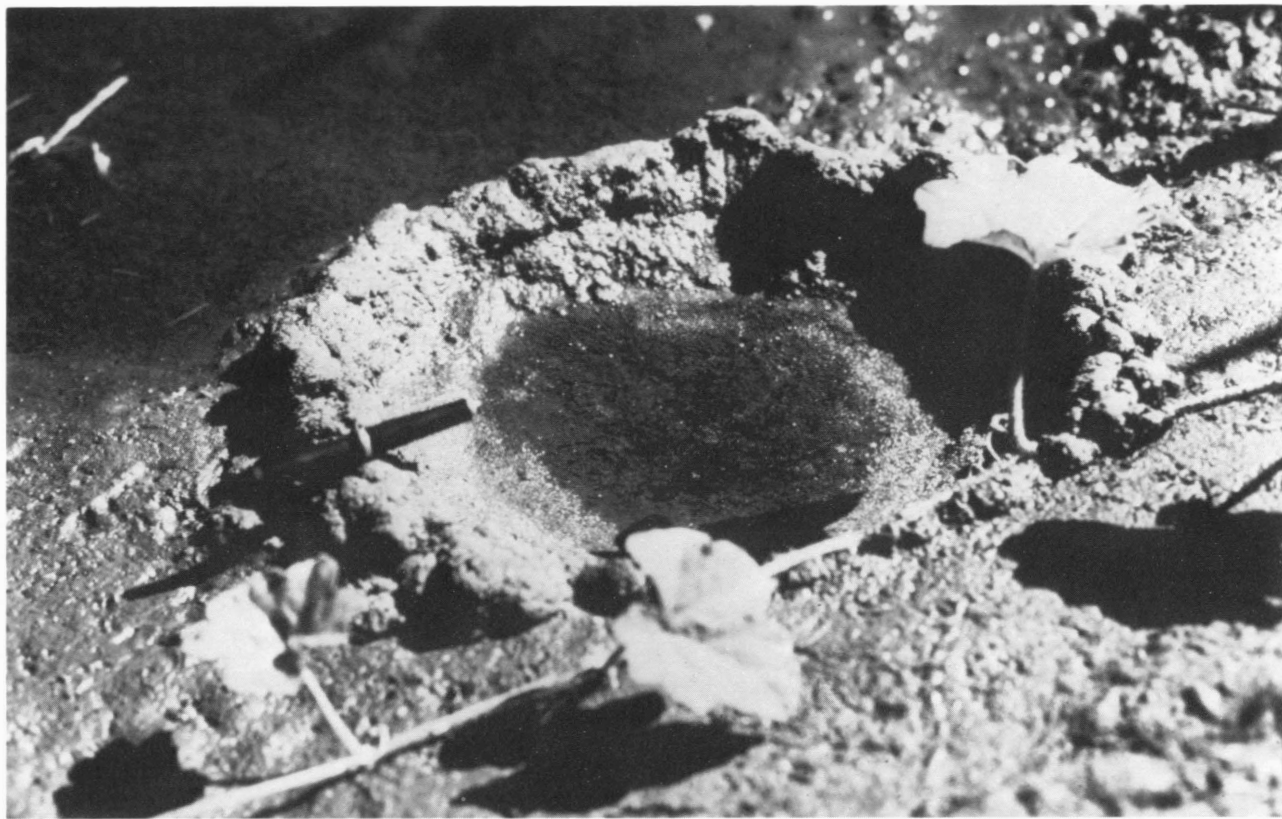


Fig. 27. A *rosenbergi* nest with high mud ramparts at Balzapamba, Ecuador. The 13 cm long rapidograph pen serves as a scale. Note the recently hatched larvae in the nest, and the proximity of the nest to the main body of water. Photograph by John Lynch.

Only males constructed new nests, but both sexes renovated them. Construction and renovation behavior were not obviously different. Like Breder (1946), I found the behavior of both sexes when involved in these activities to be affected most by the observer's presence. A nest was formed and maintained by the frog as it pivoted on its belly, pushed out with its palms and kicked backward with its feet. Except for immovable objects, such as large rocks and roots, everything was forced away from the center of the nest. A substantial amount of debris was lifted out of the depression with the frog's snout. Males rarely initiated nests on perfectly flat ground; most were started in natural depressions, boot prints (Breder, 1946) and even the vague impressions left from previous years' nests (pp. 52-53). Two of the four holes dug by *Leptodactylus pentadactylus* for their foam-egg masses during 1977-1978 on the ODSS were subsequently used as oviposition sites by *rosenbergi*. Approx 75% of all new *rosenbergi* nests were built in one night, and less than 10% were begun before 2200 hr, by which time males usually ceased giving advertisement calls. Only 2-3 new nests took three days to complete. Males did not call and build at the same time, and an extended interval of nest construction sacrificed some of the limited time available for mate advertisement. The substantial reproductive and energetic costs of new nest construction probably were why intruding males competed so aggressively with residents for their nests.

Unoccupied nests usually deteriorated rapidly. The fluctuating water table eroded the ramparts, and naturally falling vegetation (mostly leaves) filled the basin. Some renovation was performed almost every night by the resident male, and the more frequently this was done the more the mud rampart was capped by the leaves and other debris that had fallen into the nest. The female almost invariably deepened and widened the nest after she entered into amplexus with the resident male. Her renovation behavior seemed to be much more vigorous and sustained than the male's. Although females spent considerable time "inspecting" a nest during courtship (pp. 111-115), one was never observed actually renovating it prior to amplexus.

Nests varied considerably in size, shape and materials (Figs. 26-27). Nest surface area was an important variable, because the eggs were laid as a film on the water and the marginal rows were more likely to desiccate in a smaller and/or narrower basin. One might expect the builder's SVL to determine the diameter of the nest. However, the following data suggest that the condition of the substrate was much more important. The average male *rosenbergi* at Quebrada Benjamin, Costa Rica was 70.3 mm SVL (67.0-73.5 mm, N = 11; Table 3) and the average nest had a maximum diameter, between the tops of the rampart, of 121.3 mm (100-200 mm, N = 12). Comparable measurements from the Darien, Panama, population

studied by Breder (1946) are 79.2 mm SVL (73.0–87.0 mm, N = 22) and 269.9 mm nest diameter (203–330 mm, N = 16). The most obvious reason why the Costa Rica nests were proportionately smaller than expected is that all were built in dense grass. The more the male *rosenbergi* pushed outward the more the grass became matted into an immovable rampart much like the sides of a bird's nest. The Darien males constructed their nests in a soft muddy environment largely free of obstacles (Breder, 1946).

Another important size-related variable was the volume of water a nest held. Aquatic predators had free access to the nest's contents when it was completely full of water, and the lower the water the more likely the young were to die from desiccation after a few rainless days. The amount of water, as estimated from maximum depth and surface area, not only varied according to overall nest size but more importantly it changed markedly with the water table of the area. To illustrate the extent of this variation, 109 paired measurements of water surface area and greatest depth were recorded from 53 reproductively successful nests from July 5 to September 22, 1977, and May 14 to August 13, 1978. There were no significant differences between years, but as expected, surface area and depth were correlated ($r = .419$, $N = 109$, $P < .01$). In the total sample, surface area was 44–707 cm^2 ($\bar{x} = 282.9 \text{ cm}^2$) and depth 5–90 mm ($\bar{x} = 44.6 \text{ mm}$). Several of the repeatedly sampled nests exhibited nearly the same degree of variation. For example, nest no. 27 was 75–530 cm^2 and 5–55 mm ($N = 9$), and nest no. 48 was 44–314 cm^2 and 5–40 mm ($N = 2$). I conclude that the future volume of water must have been extremely difficult for the female to predict when she inspected the nest prior to amplexus. Such assessment would have been further complicated by differing nest shapes. Nearly 60% of the nests measured in 1977 and 1978 were conspicuously elliptical. Most non-circular nests were built against rocks, roots or a hard bank.

The maximum height and width of the rampart varied with degree of flooding and renovation. Mean rampart height and width in 22 nests sampled in 1977 were 31.7 mm (0–65 mm) and 63.8 mm (0–100 mm), respectively. All but one had ramparts, although the adjacent bank or some other large natural object formed part of the encirclement of several basins. The distance from the nest to the main pool varied according to degree of flooding. The same nest was as much as 2.5 m from the main body or awash with its waters. The nests in the secondary section of the main ODSS area were conspicuously different. The substrate tended to be harder and, accordingly, the basins shallower. Ramparts were rarely present and they usually were made from matted grass, much like those seen in Costa Rica. The nests seemed to be flooded more frequently. cursory study might lead to the conclusion that not all populations of *rosenbergi* build nests or that nesting behavior varies among individual frogs. The differences

between nests on the primary and secondary section seemed to be entirely due to local substrate and vegetation characteristics, because a few males built nests in both sections of the main area.

Egg surface films were often destroyed by rain, but canopies of *Heliconia* leaves provided some protection. For example, the surface film in one nest was undisturbed by a brief downpour of 15.2 mm on August 15, 1977, because of several covering *Heliconia* leaves, while all other egg masses in the area sank. Tree falls, wind and floods often and unpredictably altered the miniature canopies above nests.

NEST DYNAMICS

One hundred forty-nine nests were developed during the 1977 and 1978 breeding seasons. Most were located on shallow mud shelves (Fig. 28). The distribution for the secondary section (the lowest panel of Fig. 28) must be considered incomplete, because of the fewer surveys and denser vegetation. Nests tended to be clumped, and not all available shelves were used. Breder (1946) found a similar pattern in Darien, Panama.

Each nest's history is summarized in Figs. 29–30. There were 106 nests in 1977; the first was observed on June 6 and the last was added on October 16. Their location and number of amplexes in each are shown in Fig. 31. Not all amplexes led to an oviposition in the same nest. Occasionally, predation and intraspecific aggression interrupted amplexus or forced an amplexed pair to another basin. Only 43 nests were found in 1978, and 17 of these had been used in 1977. The 1978 breeding season began much earlier than the previous year. The first nest probably was built on April 20 (compared to June 6, in 1977) and the last one was added on October 2. Their location and number of amplexes in each are shown in Fig. 32. The rates of nest addition were extremely different in 1977 and 1978 (Fig. 33). Only those days that the primary section was surveyed or that a nest had to have existed given the size and stage of development of its reproductive contents were used in the estimation. The 1977 curve can be divided into four periods wherein the rate remained approx the same. Initially, nests were added about 1.2/day for a brief period, after which the rate nearly tripled to 3.4/day. The rate dropped to about 1.0/day following this interval of maximum activity and then ended with additions of only 0.4/day. The 1978 rate curve had three reasonably well-defined intervals wherein the rate remained little changed. At the beginning of the breeding season there was a long period of approx 0.6/day nest additions. This was followed by an even longer interval of only 0.2/day, and then there was a short period wherein the rate increased to 0.6/day. In the final section it slowed again to approx 0.1/day, and ended with a definite "upsurge" (due to 3–4 nests) of

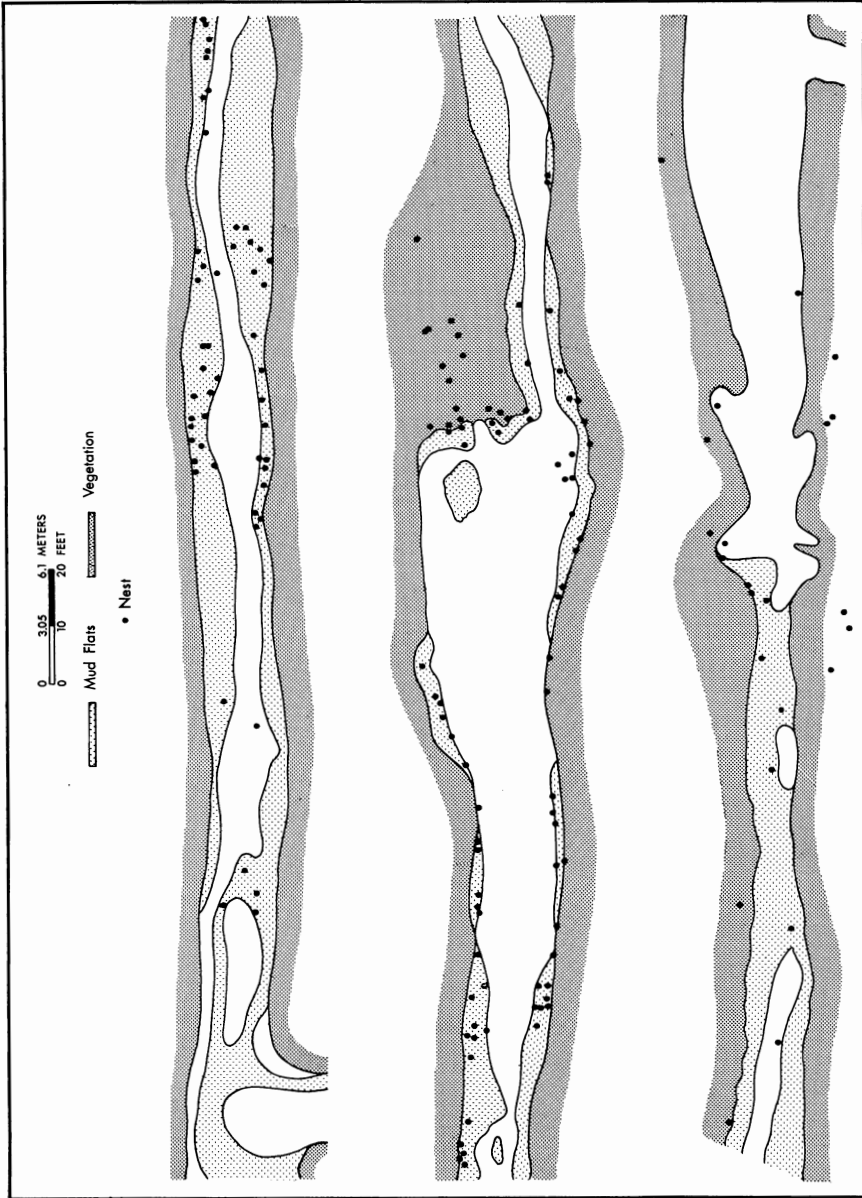


Fig. 28. Locations of all *rosenbergi* nests recorded on the main area. Nest distribution for the secondary section is incomplete, because of fewer surveys and denser vegetation.

0.7/day. Fig. 33 indicates that nest building did not increase at the end of the 1977 breeding season.

In addition to time of origin, the following variables were recorded for all but six of the 149 nests: (1) number of nights during which at least one male (almost always calling for females) was observed within the ramparts; (2) number of different males known to have occupied the nest; (3) number of nights where more than one male moved into the same nest; (4) number of days between first and last occupancy; (5) distance between an occupied nest and the nearest one with a calling male; (6) number of days between initial occupancy and first amplexus; (7) total number of clutches laid in the nest; and (8) number of days between successive clutches deposited in the same nest.

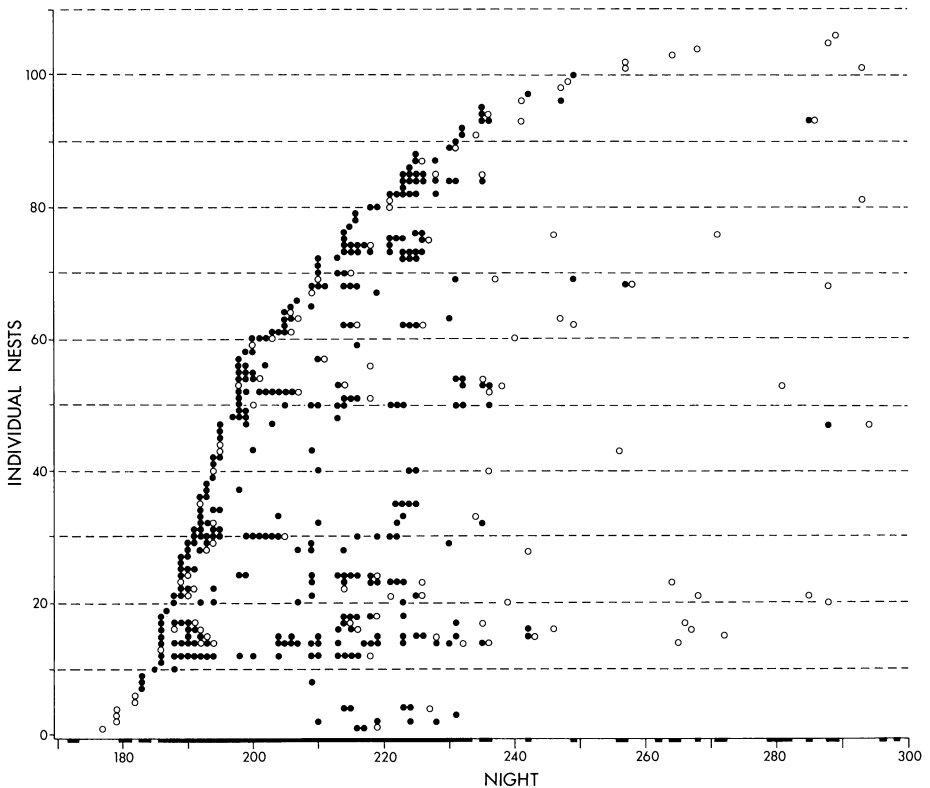


Fig. 29. Histories of *rosenbergi* nests in 1977. Open circles denote amplexes in nests, closed circles indicate presence of calling males that did not mate, and blanks no occupation by adults. Origin and subsequent occupancy of some nests were estimated from size and stage of development of the embryos it contained. The thickened portions of the horizontal axis were nights one or more investigators surveyed the primary section. Night 170 was June 19. Nightly surveys also were conducted on 301 (October 28), 303 (October 30), 306 (November 2), 309 (November 5), 311 (November 7), 313 (November 9), 317 (November 13), 322 (November 18), 324 (November 20), and 334 (November 30). However, new nests were not observed nor were old basins reoccupied.

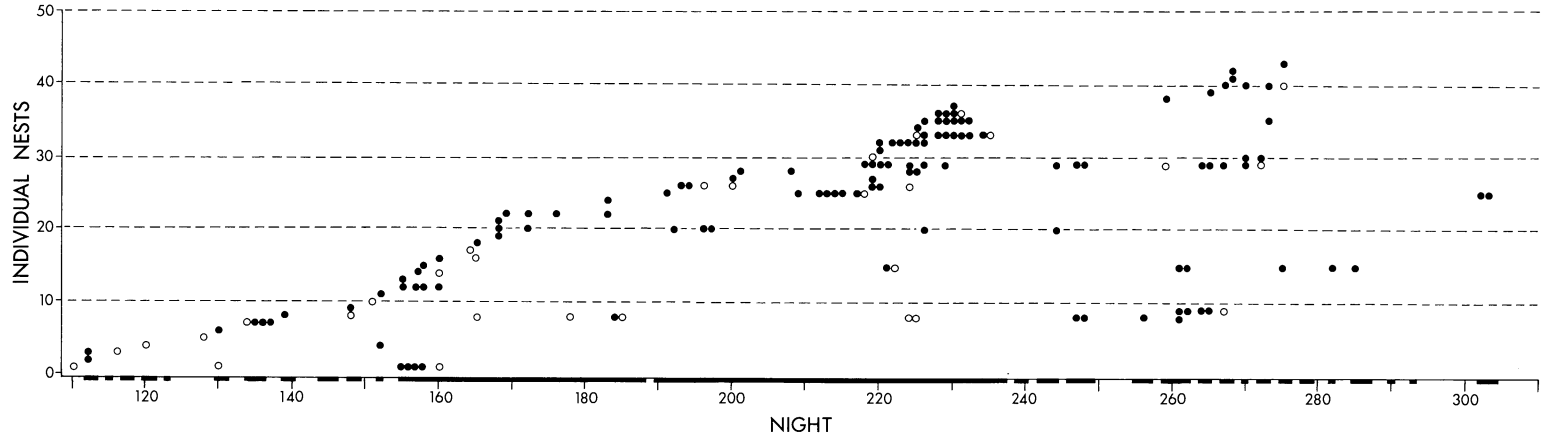


Fig. 30. Histories of *rosenbergi* nests in 1978. Open circles denote amplexes in nests, closed circles the presence of calling males that did not mate, and blanks no occupation by adults. Origin and subsequent occupancy of some nests were estimated from size and stage of development of the embryos it contained. The thickened portions of the horizontal axis were nights one or more investigators surveyed the primary section. Night 110 was April 20. Nightly surveys also were conducted on 314 (November 10), 323 (November 19) and 349 (December 15). However, new nests were not observed nor were old basins reoccupied.

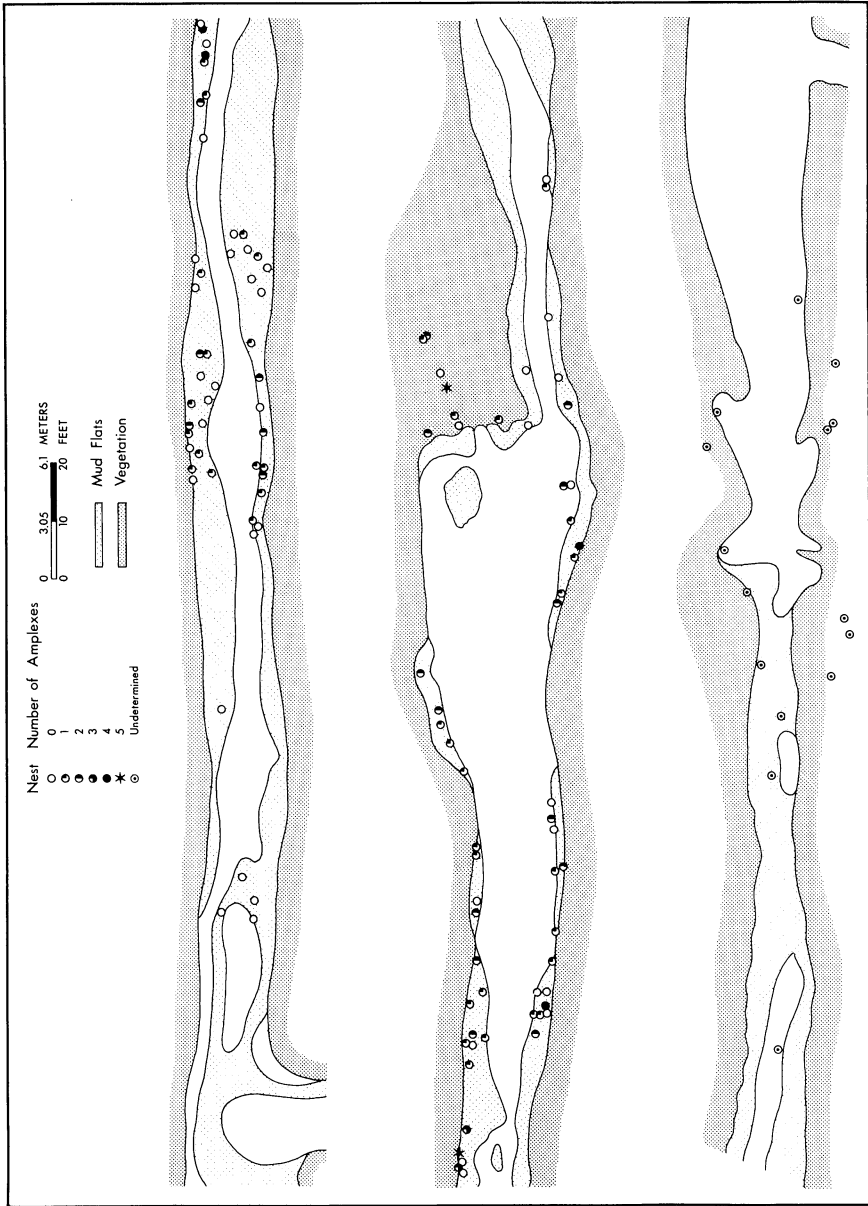


Fig. 31. Locations of *rosenbergi* nests in 1977, and number of complexes that took place in each.

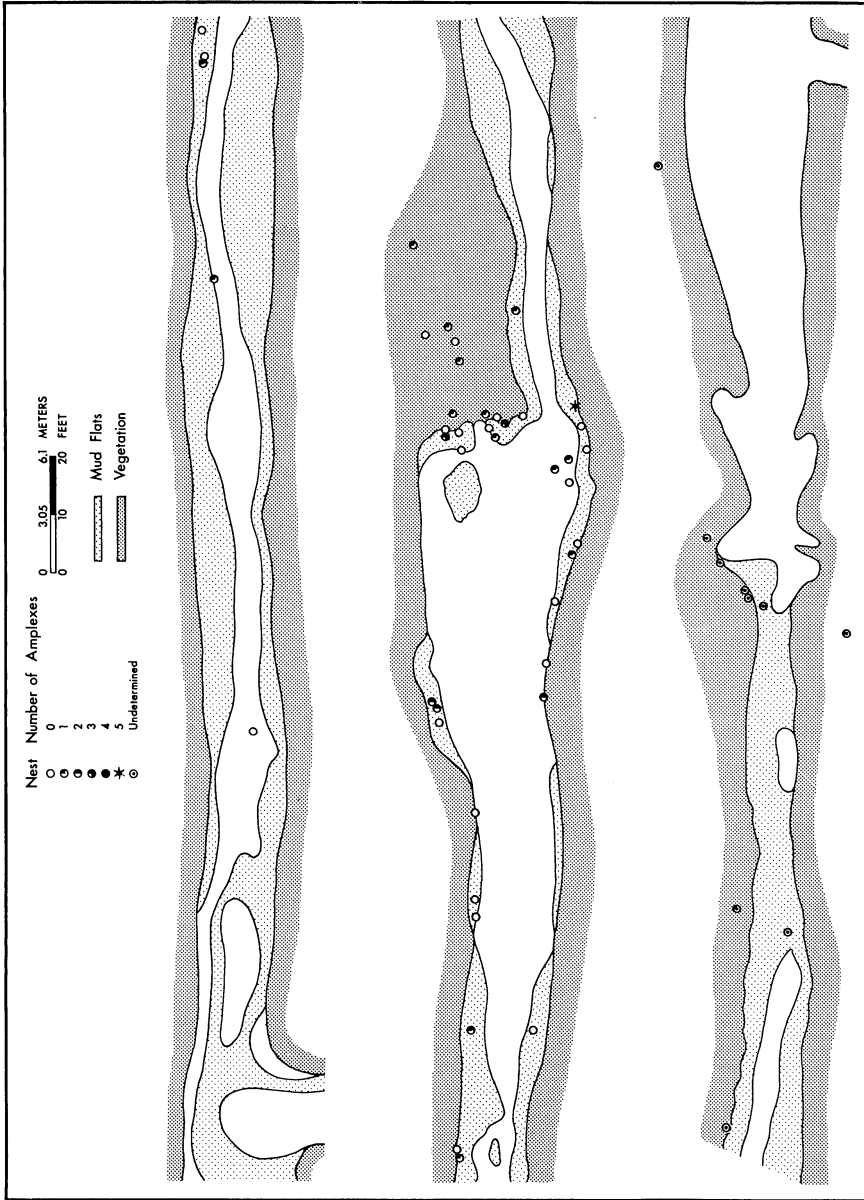


Fig. 32. Locations of *rosenbergi* nests in 1978, and number of amplexes that took place in each.

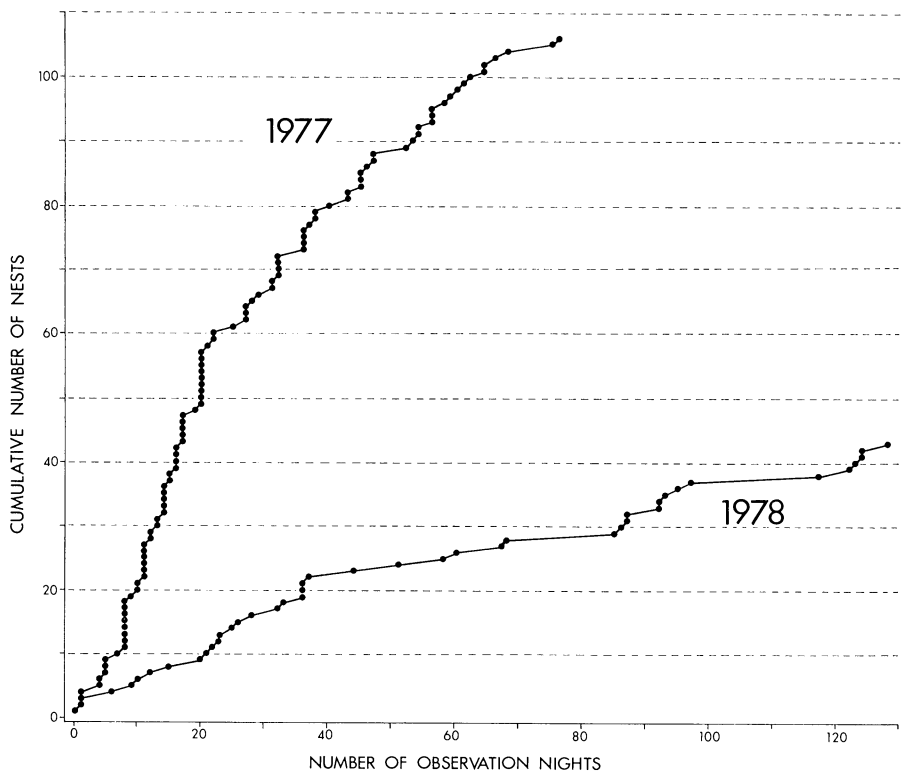


Fig. 33. Rates of new *rosenbergi* nest construction. The horizontal axis includes only those nights that the primary section was surveyed or that a nest was estimated to have existed, given the size and developmental stage of the embryos it held.

Nests were occupied 1–25 nights, ($\bar{x} = 4.1$, $N = 143$), with a mode of one. These values are particularly small considering the length of time between first and last occupancies ($\bar{x} = 22.9$, $ORV = 1-128$; Figs. 29–30). The extensive variation in length of time between first and last occupancy suggested that the raw data on nest occupancy should be transformed to a time-specific measure (per 100 nights; Fig. 34). Statistics for the adjusted data are $\bar{x} = 58.8$ and $ORV = 2.7-100$; the mean was inflated by the exceptionally high proportion of nests occupied only one night (35.9%). The surprisingly low use was due to rain, the shifting nature of the choruses (pp. 147–153), and the apparent avoidance of nests containing developing embryos. Nests were used as calling stations by 1–7 males ($\bar{x} = 2.0$, $N = 143$), and 64.3% were occupied by more than one male. The adjusted statistics (per 100 nights) are $\bar{x} = 45.4$ and $ORV = 1.7-100$. The existence of many nests used only one night and by one male inflated the mean (Fig. 35). The low multiple male use probably was due to territoriality and the shifting nature of choruses (see also Breder, 1946). Intruding males seldom displaced residents (pp. 102–111); there were only 17 nights

when more than one male occupied the same basin ($\bar{x} = 0.2$, ORV = 0-5). These data provide only a rough measure of male-male aggression associated with exclusive nest use, because all cases of multiple male occupancy were included, regardless of the individual's calling activity. An intruding male was able to enter a resident's nest without evoking an aggressive response, providing he remained silent (pp. 93-95).

The average nearest neighbor distance in 1978 was nearly double ($\bar{x} = 13.6$ m, ORV = 1.4-79.0 m, N = 112) that of 1977 ($\bar{x} = 7.0$ m, ORV = 0.2-50.1 m, N = 419). Several nearest neighbors were more widely separated in 1978, but more importantly, relatively few were close together (Fig. 36). The shorter nearest neighbor distance may have been due to a different mating strategy (pp. 150-153), as well as fewer males.

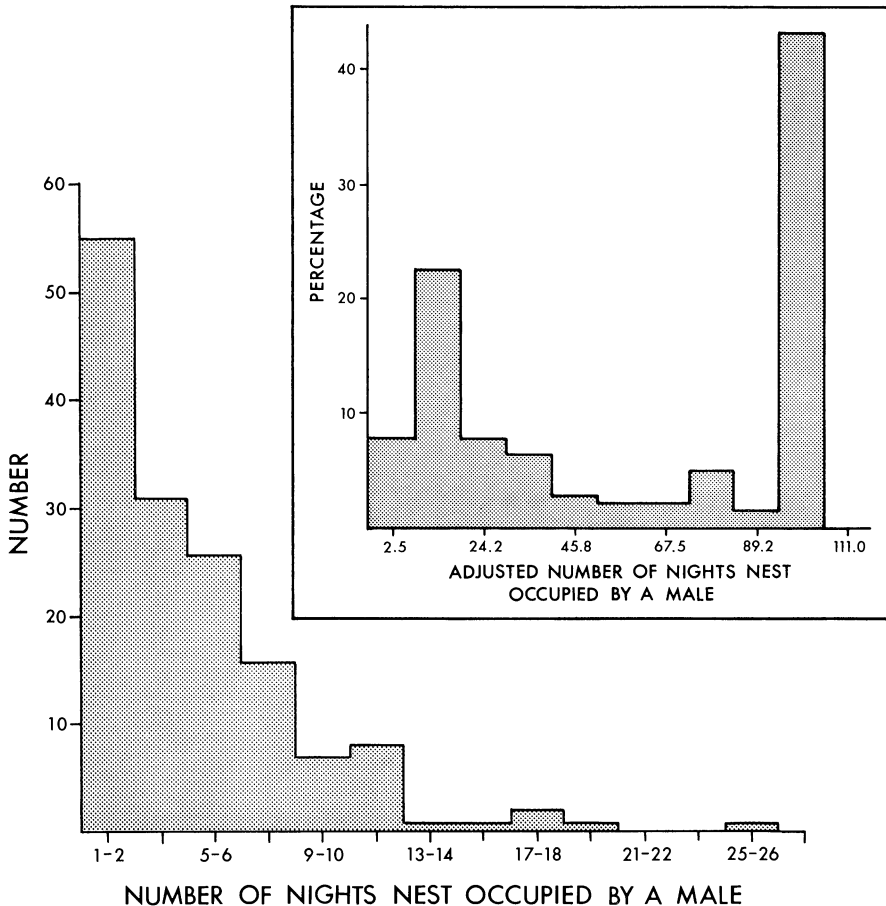


Fig. 34. Nights each *rosenbergi* nest was occupied by one or more males. The value for each nest was adjusted to a time-specific measure of 100 nights in the inset. The large percentage (43.4) at the right of the inset represents nests occupied one night by one male.

Nests were used 0–5 times for oviposition ($\bar{x} = 0.97$, $N = 143$). Number of clutches was significantly correlated with number of days the nest was occupied ($r_s = .603$), number of males known to have used the nest ($r_s = .663$), number of nights when more than one male entered the nest ($r_s = .223$, $P < .01$), and number of nights between first and last male visitations ($r_s = .675$). Number of clutches was not significantly correlated with the number of nights between nest origin and the first mating. The raw clutch data were transformed to a time-specific measure of 100 nights and the adjusted statistics are $\bar{x} = 15.7$ and ORV = 0–100 (Fig. 37). The mean was inflated because several nests (16) had eggs deposited in them on the only night they were occupied. The skewed distribution of number of clutches per nest (Fig. 37) might suggest that most basins were not suited for oviposition, but the distribution appears to be explained as well by

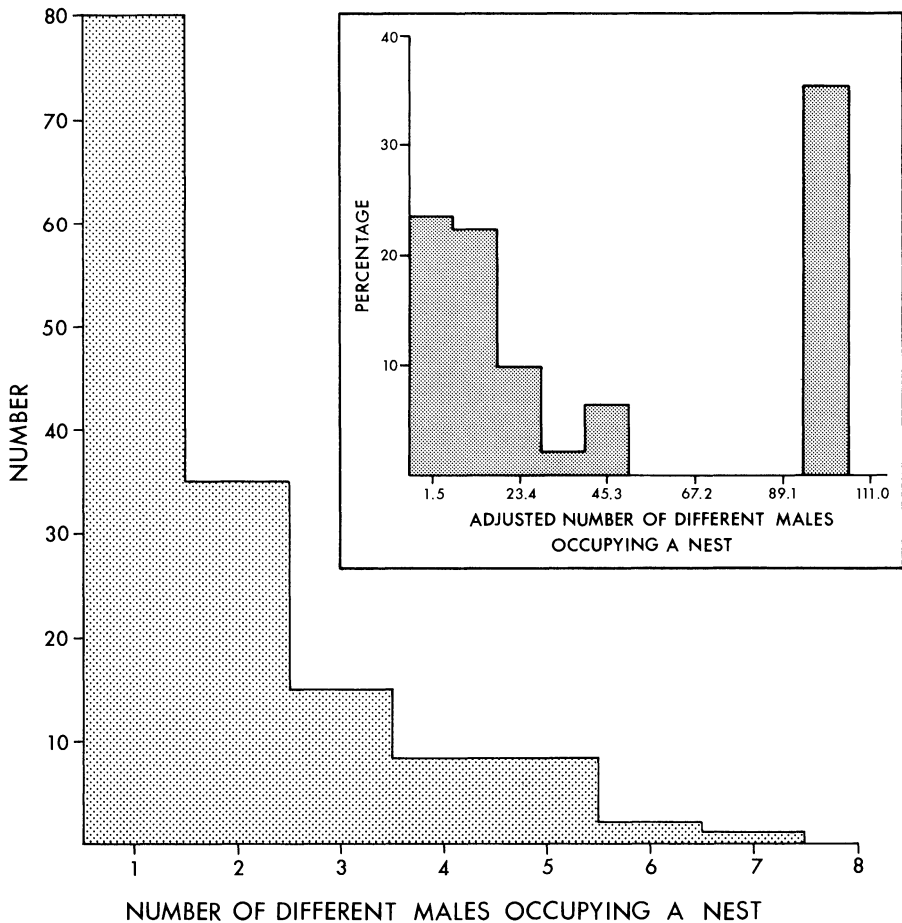


Fig. 35. Numbers of male *rosenbergi* occupying each nest. The value for each nest was adjusted to a time-specific measure of 100 nights in the inset. The large percentage (35.7) at the right of the inset represents nests occupied one night by one male.

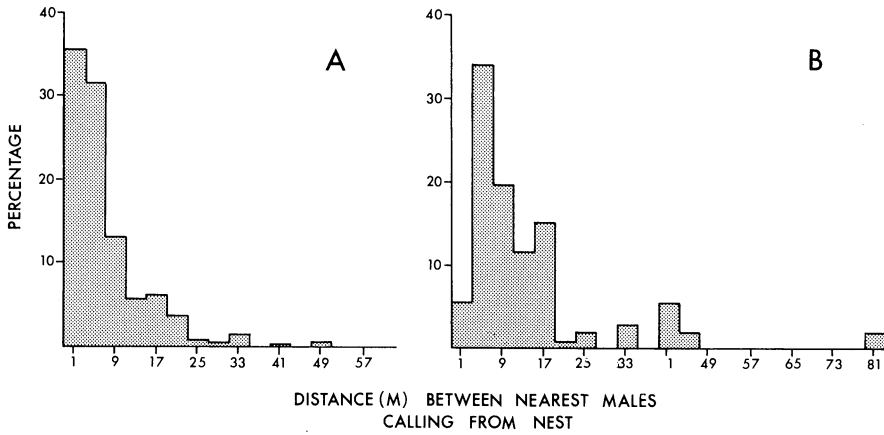


Fig. 36. Nearest neighbor distances (m) for male *rosenbergi* calling from nests on a given night in 1977 (A) and 1978 (B).

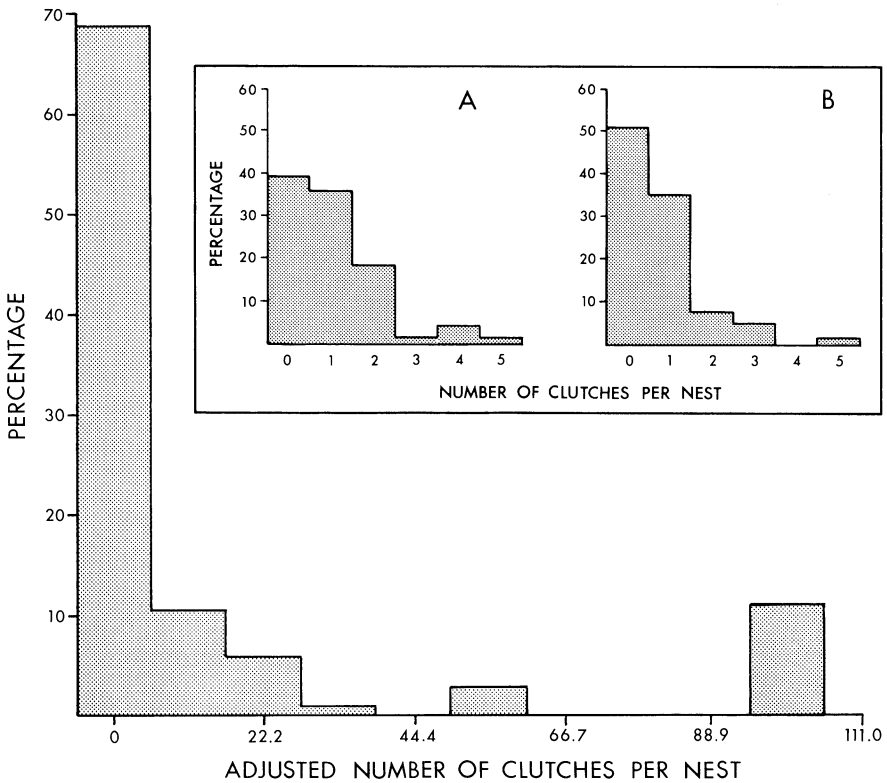


Fig. 37. Nests possessing different numbers of *rosenbergi* clutches in 1977 (A) and 1978 (B) are plotted in the inset. The value for each nest was adjusted to a time-specific measure of 100 nights in the larger graph. The percentage (11.2) at the right of this graph represents nests occupied one night and which had one oviposition. The raw data are slightly different from the number of amplexes illustrated in Figs. 29-32 (see text for explanation).

amount of male use, which in turn was related to chorus proximity. Breder (1946) reported that 11 of 26 nests (42%) were not used for oviposition, and my data are comparable (\bar{x} = 39.9%; 36.9% in 1977 and 47.5% in 1978).

Successive clutches were deposited in the same nest at intervals of 10–72 days (\bar{x} = 32.5, N = 48), and no nest was simultaneously used by different pairs of frogs. The shortest interval of 10 days (Fig. 38) occurred after predators completely consumed an egg mass sunk by rain. Cannibalism among tadpoles probably was the most important selective agent responsible for the lack of clutch overlap. It is possible that a second male might have benefited from occupying a nest with a surface film of eggs already present provided he destroyed the entire clutch. The intruder's offspring would have gained an advantage by feeding on organic matter left in the nest and would thereby have enjoyed more rapid growth. The growth rate advantage would have been particularly important at the beginning of the wet season when significant rains were infrequent and tadpole escape from the nest less predictable.

Identifiable males were observed in nests 582 times in 1977–1978. This is the sum of the nests each male entered each night of observation. In only 11 instances (involving nine males) was an individual found in a nest where he had once obtained a mating. Only two of the 11 male reappearances resulted in an additional mating. No female oviposited more than once in the same nest. These data suggest little quality variation between shelves. While variation in nest quality (eg, amount of water) might explain these results, no temporal changes were obvious. Furthermore, the low within-basin survivorship and frequent flooding make avoidance an unlikely explanation because of depleted organics.

I have complete histories of occupancy and mating success for 16 of the 17 1977 nests reused in 1978. Male *rosenbergi* appeared to use whatever depressions were available when initiating new territories. Many of the deep 1977 basins remained as slight but obvious cavities

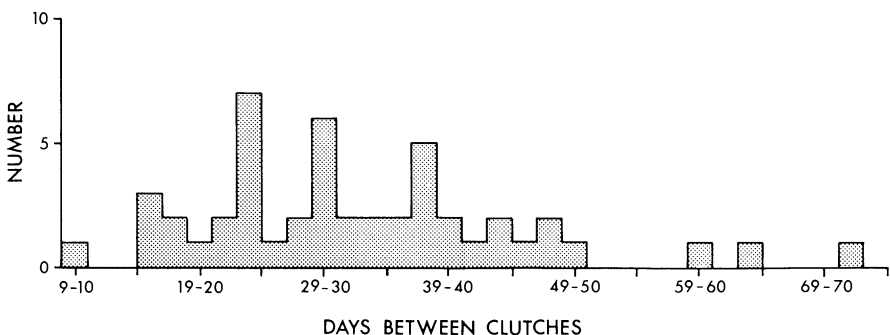


Fig. 38. Days between successive *rosenbergi* clutches. The smallest recorded interval (9–10) followed a clutch that suffered 100% mortality within 48 hr of oviposition.

in 1978. I suspect a male was able to complete a nest more easily by starting with an existing depression. There was no correlation between success of nests in 1977 and 1978 ($r_s = -.372$; Fig. 39). The four most successful nests in 1977 (four and five amplexes) were unsuccessful in 1978. Nest quality might have varied from year to year, but I found no obvious physical differences in the four nests between years. It seems more likely that differential mating success was due to differences in frequency of occupation and proximity to other calling males. The four nests in question were used on 25, 16, 11 and eight nights in 1977, but only one, four, four and one nights in 1978. Mating success in nests used in both 1977 and 1978 was significantly correlated with frequency of male residency ($r_s = .727$).

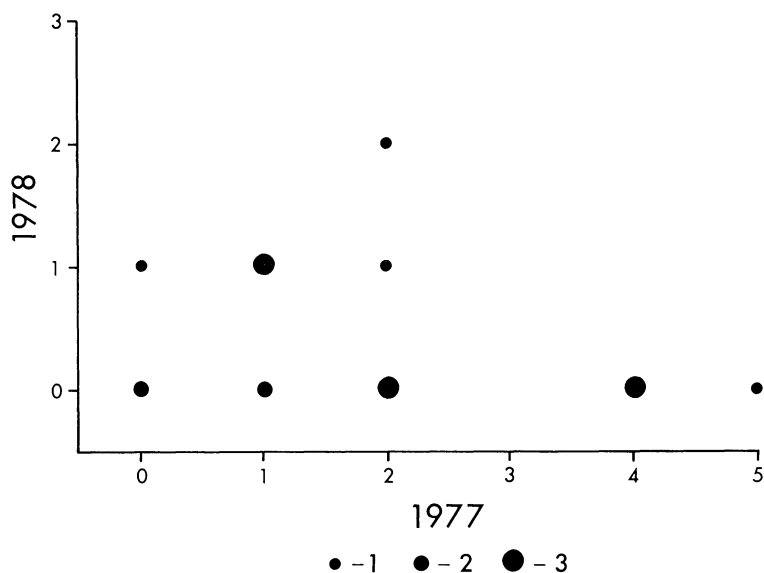


Fig. 39. Numbers of *rosenbergi* clutches laid in the same nest. Dot size denotes number of coincident records.

SUBADULT BIOLOGY

OVIPOSITION

Six pairs in amplexus began oviposition at 0230, 0245, 0255, 0407 and 0416 hr ($\bar{x} = 0301$) in 1977. Oviposition by five pairs in the laboratory occurred during the same time span. Females usually spent several hours renovating nests before depositing eggs (pp. 111-115). Furthermore, eggs probably had a greater chance of surviving

when they were deposited in the early morning after most males that might have disturbed the surface film had retired to their diurnal resting places. Either of these explanations for the long prespawning period of amplexus in *rosenbergi* appears to be more likely than the "female guarding" hypothesis usually cited for more explosive breeding species (Wells, 1977b). Also, it seems unlikely that guarding behavior would evolve in species like *rosenbergi* where the mating tempo is controlled by the female.

The events associated with egg laying were stereotyped, and the following description summarizes the most conspicuous behavioral acts observed. The male clasped both sides of the female's neck immediately behind the angle of her jaw. His palms were directed medially, and his thumbs and associated sheathed prepollical spines projected dorso-posteriorly. The male's back was arched downward, his head completely covered the female's snout, and his hindlimbs were held tight against his body. The soles of the male's hindfeet rested on the anterior surfaces of the female's thighs, a position which usually placed his cloacal opening immediately above his mate's. The male made no sound during oviposition, nor did he appear to forceably "strip" ova from the female. He remained nearly motionless. While ovipositing, the female was completely submerged, except for her cloacal opening which was at or just above the water's surface. She held her thighs horizontally at right angles to her body. The lower portions of her hindlimbs, as well as her extended arms, pressed against the bottom of the nest. Salthe and Mecham (1974:409) concluded for other frogs, that depositing eggs as a surface film often involves the cloaca being raised to the water's surface. In *rosenbergi*, a small cluster of eggs was extruded every 2–10 sec with a conspicuous contraction of the lateral body walls. Oviposition was completed in about 10 min. When first laid, the eggs usually formed a mound several layers high, particularly when the female's contractions were rapid. Within seconds, the eggs spread slowly over the surface of the water from the point of deposition, and eventually they formed a continuous monolayer. One female pivoted slowly during oviposition and thereby reduced the height of the mound of eggs she laid.

While eggs usually were deposited over the basin, the deepest part of the nest, they often spread to the shallowest inner edges of the ramparts. A freshly laid egg had a darkly pigmented animal pole and a yellow-white vegetal pole of yolk. As the eggs spread slowly over the surface of the water, those laid with the heavier yolk upward rotated within their jelly capsules. The combination of spreading and rotating was completed within 10–15 min. The male quickly released the female after her last contraction. He slid forward over the top of her submerged head, and rapidly leaped to an elevated perch near the nest (Fig. 66). The female slowly lowered her vent below the water's surface at the end of oviposition, raised her snout, and cautiously left

without touching the spawn. She paused briefly at the margin of the nest, and then quickly jumped toward the canopy and disappeared. Only two females were observed the night following oviposition. Both were in the process of shedding when located in the low vegetation adjacent to the stream. They appeared to be emaciated and did not attempt to escape. Fertilization was efficient in *rosenbergi*; no clutch had more than 25 undeveloped ova.

Zweifel (1968a) and Salthe and Duellman (1973), among many others, stated that the quantity and distribution of melanin covering frog eggs affects rate of development and shields the embryo from harmful ultraviolet radiation. They argued that a dense covering of dark pigment, such as found in *rosenbergi* (Fig. 40A), promotes absorption of radiant energy, particularly when the egg mass is at the surface of the water. However, Ryan (1978) reported that the temperature within the surface film of *Rana catesbeiana* eggs exposed to direct sunlight throughout most of the day was lower than the surrounding water. The fact that *rosenbergi* usually oviposited in well-shaded environments suggests that its darkly pigmented eggs may not be an adaptation for increasing rate of development or serve as a radiation shield. Darkly pigmented *rosenbergi* eggs probably are cryptic (pp. 69–70).

The eggs of *rosenbergi* appeared to be laid singly, each surrounded by two clear jelly-like capsules. The surface of the outermost capsule became sticky shortly after oviposition, and it was that property which appeared to hold the eggs together. Once the individual eggs came together, the contacting surfaces of the adjacent external capsules became indistinct (Fig. 42; see also Breder, 1946, Fig. 17B). The diameter of the inner capsule was approx 3.0–3.3 mm, with an egg of 1.8–2.1 mm dia located within it.

The location of the egg film (Fig. 40A) was almost certainly due to the surface tension of the underlying aquatic medium, because eggs sank when gently pushed into the water. The moderately high water temperature at which *rosenbergi* bred (pp. 62–64) probably was responsible for the low surface tension and the tendency for eggs to sink when disturbed.

PREMETAMORPHIC GROWTH AND MATURATION

Thirty-two clutches were used to estimate growth and development (Figs. 41–42). Clutches were sampled 1–4 times per day and for 1–21 days. Most samples consisted of 10 individuals. Clutches were assumed to have been fertilized at 0300 hr.

A measureable tail bud appeared about 40 hr after fertilization (Fig. 40B), grew rapidly until about 150 hr, and then lengthened more slowly thereafter. SVL increased much more slowly and linearly than did TL (Fig. 41). The decrease in SVL around 100 hr was due to

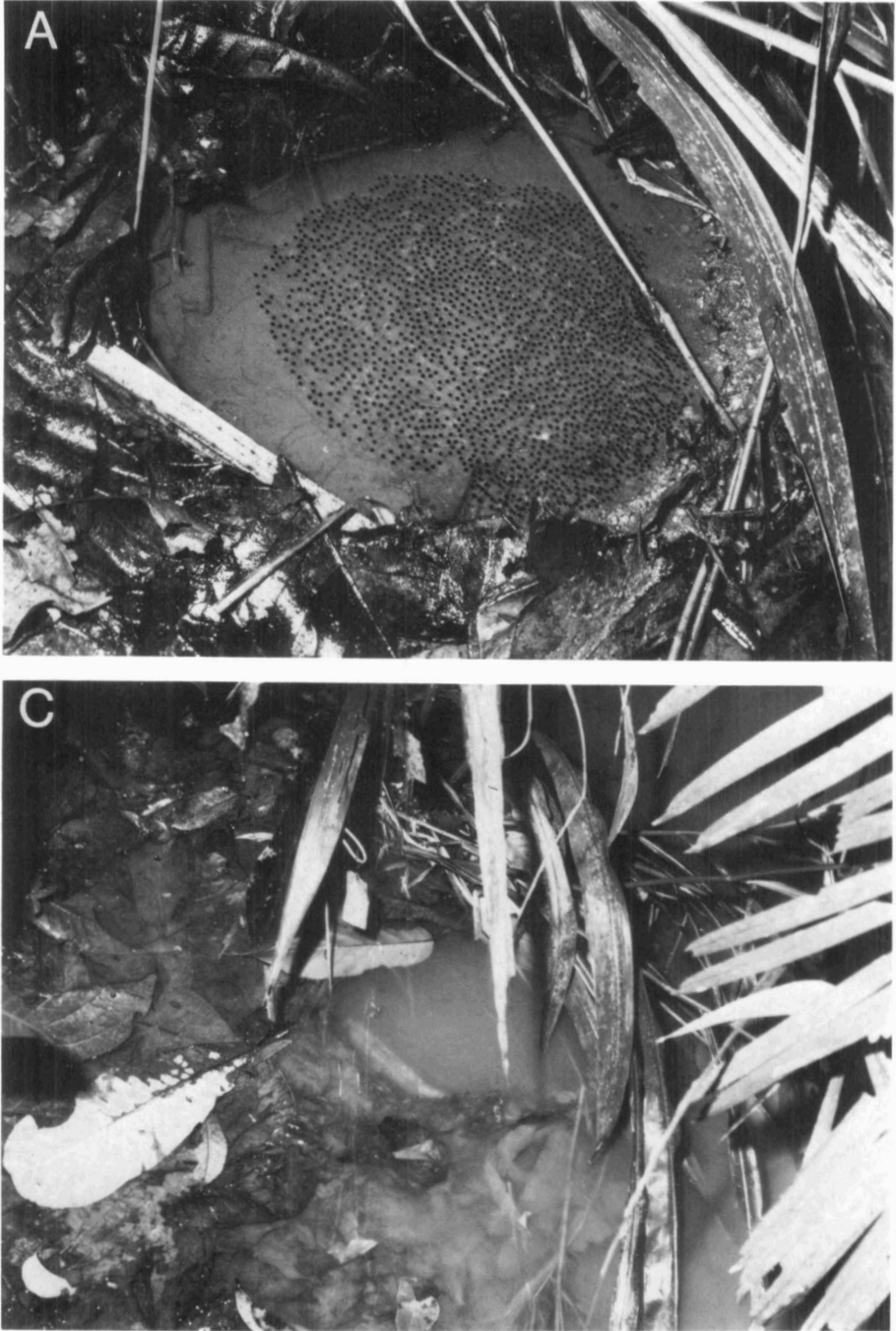
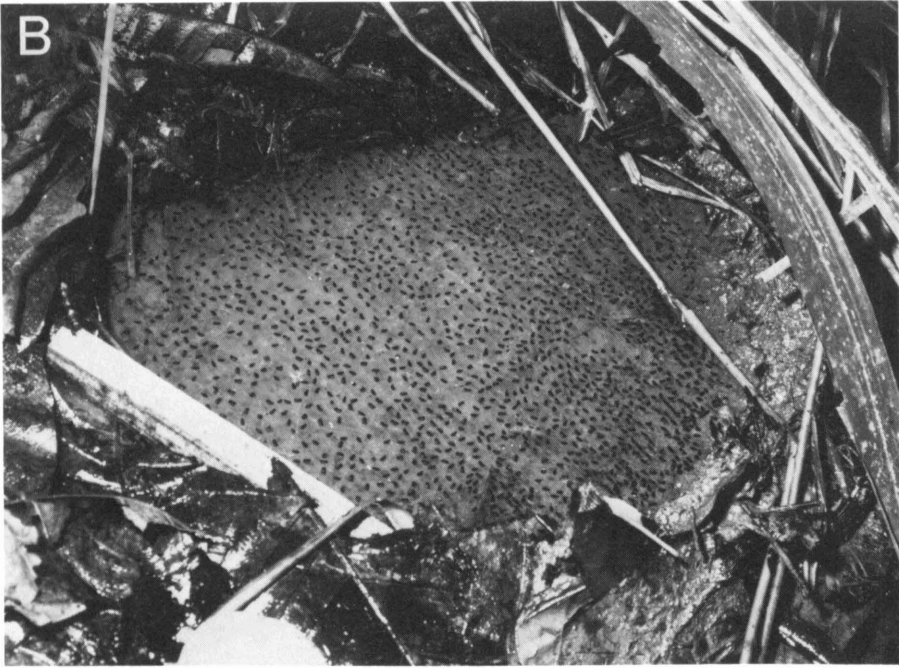


Fig. 40. Photographs of nest no. 45 containing offspring of *rosenbergi* male no. 111 x female no. 81, in 1978. A. Surface egg film deposited on June 17 (photographed 17 hr postfertilization). B. Embryos at stage 17, prior to hatching (photographed 41 hr postfertiliza-



tion). Average total length of embryos was 3.5 mm. C. The flooded nest which allowed the tadpoles to escape (photographed 185 hr postfertilization). D. The disturbed nature of the nest following the flood (photographed 25 hr after C).

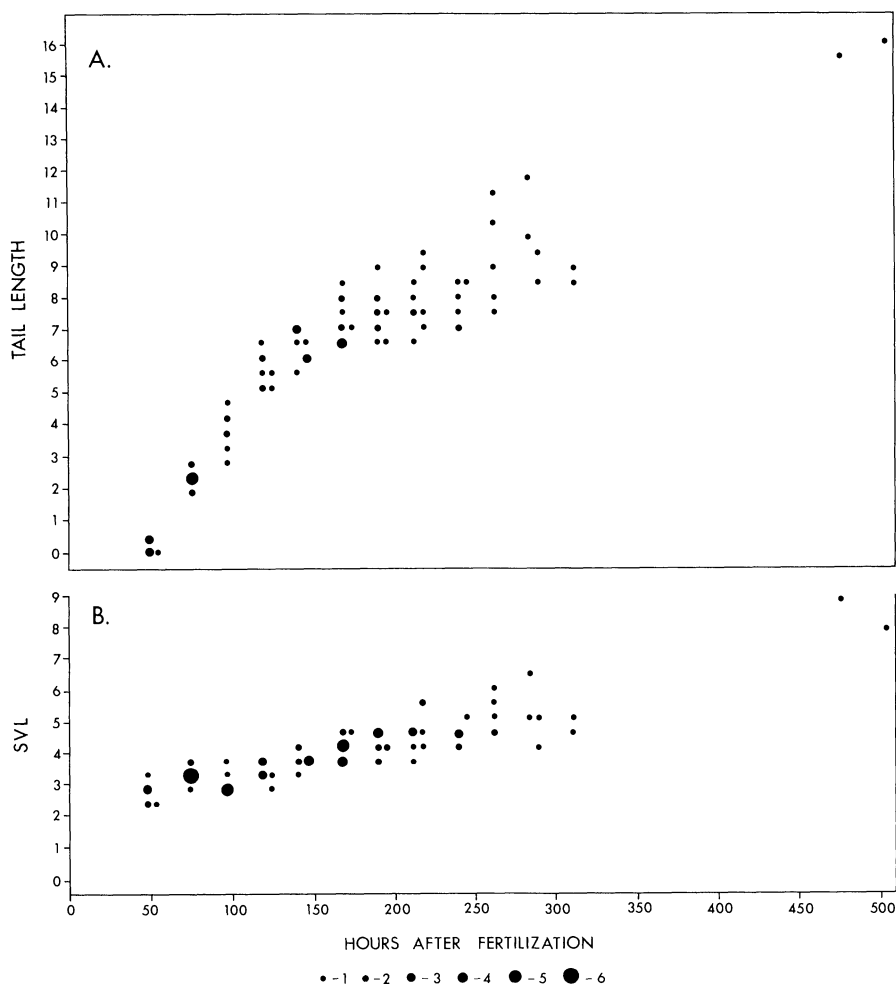


Fig. 41. Rates of TL (A) and SVL (B) growth in naturally occurring *rosenbergi* embryos. Measurements taken before embryos were 40 hr old were excluded, because the antero-posterior body axis had not been established. Dot size denotes number of coincident sample means.

difficulty in determining the end of the body as the belly-yolk shrank. The between-sample variance in size began to increase markedly after 150 hr postfertilization, and the same size and stage of maturation occasionally persisted for nearly 300 hr (150–450; Fig. 42). The absence of data in Fig. 42 between stages 26–28 and 300–500 hr almost certainly is a sampling artifact.

Hatching began with occasional flexures of the body at stage 17, about 40 hr after fertilization (Fig. 40B). All living embryos emerged from their jelly capsules by stage 19 (66 hr). Most larvae hung from (or rested on) the jelly mass which remained on or near the surface of the water during stages 18–19. There was increased tail movement

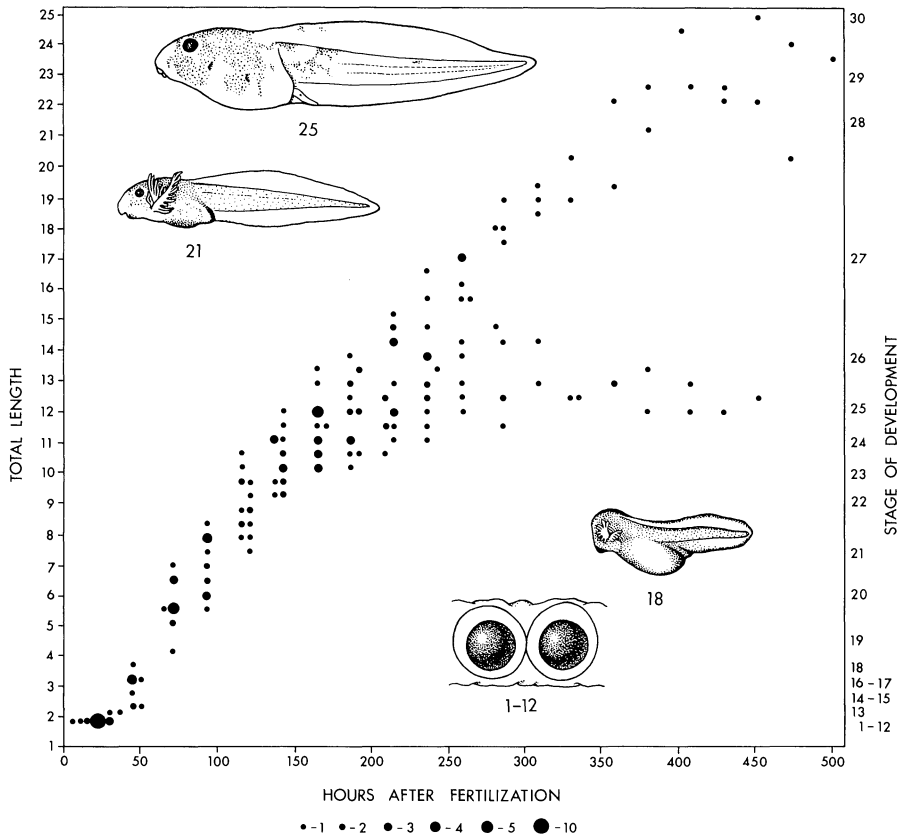


Fig. 42. Rate of TL growth in naturally occurring *rosenbergi* embryos. The sample mode of stage of maturation (according to Gosner, 1960) is shown on the right vertical axis. Dot size denotes number of coincident sample means. The four insets of embryos illustrate the important stages specified by their accompanying numbers.

within 65 hr, and by 85 hr there was rare and erratic swimming (fluttering) motion. The external gills of larval *rosenbergi* became exceptionally large and multibranching at stage 19 (Figs. 42 and 45) and they remained in that state until stage 23. Gill reduction and the formation of the overlying operculum characterized stage 24.

Noble (1927) appears to have been the first of several authors to argue that *rosenbergi*'s large filamentous gills are associated with low dissolved oxygen in the nest due to water stagnation and overcrowding. I measured oxygen content in 17 nests containing clutches at stages 19-23; oxygen content of nearby open water was recorded simultaneously. Average nest oxygen ($\bar{x} = 1.3$ ppm) was significantly lower than that in open water ($\bar{x} = 2.3$ ppm), but dissolved oxygen was low in both open water and in nests. It rarely reached 6.0 ppm, and this appeared to happen only after a flood or where the stream course narrowed and the water moved rapidly. Most stage 19-23

larvae hung from the surface with their gills spread out for maximum contact with the air. These structural and behavioral adaptations occurred during a period of exceptionally high growth rate and, presumably, high metabolism, before the larvae were capable of much coordinated locomotion.

By stage 24 (140 hr), *rosenbergi* larvae were active swimmers. They darted to the surface in a coordinated manner, gulped air, and often released bubbles during their descent to the bottom, where they remained stationary for long periods of time. Their behavior was similar to that of *Rana pipiens* under anoxic conditions (Wassersug and Seibert, 1975). *Rosenbergi* larvae began to mill around in the nest when they were 140–160 hr old; larvae often remained at the surface gulping air and releasing bubbles (Fig. 43). Stage 25 was reached between 150–165 hr, and well-formed mouth parts (beak and tooth rows) appeared. By stage 25, long, thin unpigmented lungs developed, external gills disappeared, and the operculum had completely formed. The larva definitely had become a free-swimming, feeding tadpole. Most tadpoles 150–165 hr (stage 25) or older swam from their nests during floods (Figs. 40C and 44). Larvae at earlier stages might have been washed out of a basin, but they never left on their own. In fact, stage 20–24 larvae appeared to return to the nest when swept only a few centimeters from it. Rate of growth and maturation to stage 25 (150–165 hr) appeared to be closely correlated with the average interval between significant rains (163 hr in 1977; 151 hr in 1978). If there is a causal relationship between periodicity of rainfall and rate of development, I predict the rate will be faster in other *rosenbergi* populations witnessing more frequent significant rains.

I was present on several occasions when broods of stage 25 *rosenbergi* tadpoles swam from their flooded nests. They usually moved together in a coordinated manner for several hours, and two such broods quickly returned to their nearby nests when I attempted to obtain a sample. One of the broods that returned was trapped for several days in the nest as the flood receded. Some clutches were confined to their nests for 150–165 hr (occasionally up to 350 hr; see Figs. 41–42), because of the unpredictable nature of rainfall during the breeding season (p. 18). The outcome of the rate of growth and maturation beyond stage 25 in those broods restricted to their nests for more than 150–165 hr appeared to depend on the tadpole density and, most probably, on the amount of nutrient in the basin. Where mortality in a clutch had been high and/or the nest was rich in food, the rate of growth and maturation was likely to be highest. When there had been little or no mortality and density of tadpoles was high, the nutrients in the nests appeared to be exhausted quickly, and rate of development slowed, if not stopped altogether (Fig. 42). The substrate appeared white in those nests that had been occupied



Fig. 43. The well-developed (stage 25) *rosenbergi* offspring of male no. 113 x female no. 78 in nest no. 119 on June 17, 1978, 161 hr postfertilization. The tadpoles were actively vacuuming the bottom, darting to the surface of the water and gulping air, and releasing bubbles upon descent. This clutch suffered about 70% mortality from a significant rain (17.8 mm) that fell 14 hr after fertilization. The tadpoles, still at stage 25, finally escaped from the nest when a significant rain of 30.5 mm fell 325 hr postfertilization. Note the light color of the nest substrate, the result of organic depletion by the tadpoles. Also note the bubbles released by the larvae.

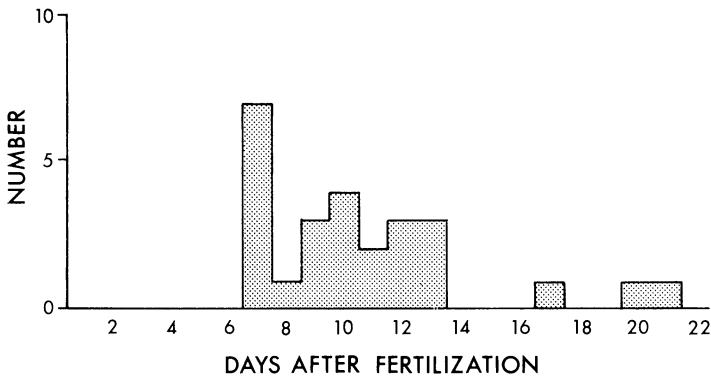


Fig. 44. Numbers of days after fertilization when more than one-half of a *rosenbergi* brood escaped from its nest. Observations were made between 1900–2400 hr, and fertilization was assumed to have occurred at approx 0300 hr of day number one.

for exceptionally long periods by a given brood (Fig. 43). These white spots were particularly conspicuous as a headlamp was shined along the gently sloping banks. It appeared that only the undigestible, crystalline, inorganic sediment remained after large numbers of tadpoles had repeatedly vacuumed the bottom of a nest.

Not only was there considerable between-clutch variation in size and stage of maturation when *rosenbergi* larvae were confined to their nests after stage 25 (Figs. 41–42), but samples taken from open water extended the range even further. For example, the largest of 10 tadpoles taken in a single seine haul from the main pool on August 3, 1977, exhibited the following stage of maturation, SVL and TTL: 31, 13.5, 34.0; 28, 12.0, 33.0; 27, 9.5, 26.0; 27, 10.0, 26.5; 26, 9.0, 24.0; 26, 8.3, —; 26, 7.5, —; 25, 7.5, 19.5; 25, 6.5, —; 25, 6.8, —. These data may suggest greater rates of development than those shown in Figs. 41–42, and cannibalism was a likely cause (pp. 70–75).

Duellman (1970) described a large *rosenbergi* tadpole collected by Breder in Darien, Panama. The blunt tail was different from any tadpole I collected from known *rosenbergi* parents, and it is unlike those illustrated by Breder (1946) as well. The specimen (AMNH 51791; TTL = 26.1 mm) is a typical *rosenbergi*, but the tail almost certainly is regenerated. Also, Duellman (1970) criticized Breder (1946) for not illustrating the fourth lower tooth row of a *rosenbergi* tadpole. This row of denticles rarely developed before stage 26 in my study, and it did not become conspicuous until stage 30. Breder's illustration probably is correct, the subject being at stage 25.

Water temperatures in nests and open water fell at night. The open water temperature underwent relatively more daily variation, probably because it had more opportunity to be warmed by the sun as it flowed downstream beneath occasional open spaces in the canopy. Lamotte and Lescure (1977) hypothesized that the water temperature

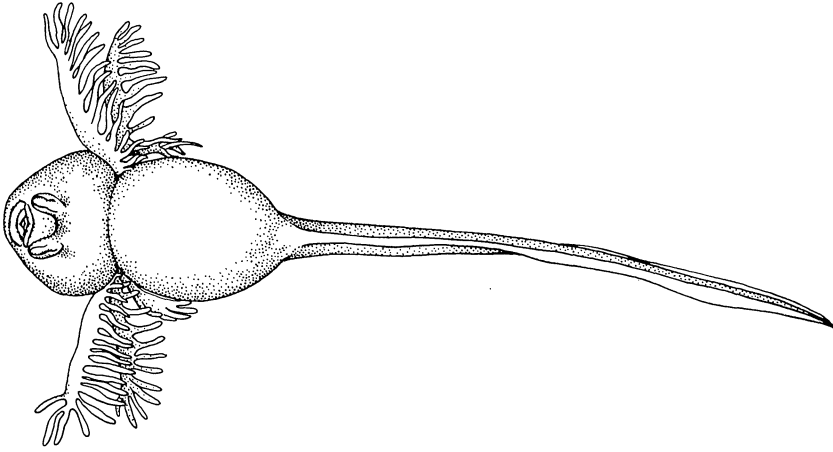


Fig. 45. Ventral view of a *rosenbergi* larva at stage 23. Note the exceptionally large external gills (redrawn from Noble, 1927).

of a nest is higher than that of the adjacent pond. I recorded temperatures with a Schultheis quick-registering thermometer at approx 10 mm below the surface in the nest and the nearby open water ($N = 298$). Thirty-six clutches were present in the nests, and nest temperatures were $24.3\text{--}27.5^\circ\text{C}$. These recordings were considerably lower than the $30\text{--}32^\circ\text{C}$ recorded by Wassersug (1971) for Costa Rica *rosenbergi*. There was little difference between the average nest site ($\bar{x} = 25.4^\circ\text{C}$) and open water temperatures ($\bar{x} = 25.8^\circ\text{C}$), and they were highly correlated, the nest being significantly lower. In fact, the nest temperature was higher than the open water in only one third of the cases. Hence, Lamotte and Lescure's (1977) hypothesis does not apply to *rosenbergi* at this site.

Some nests had significantly higher average temperatures than others. However, no pair of nests was monitored simultaneously and most, if not all, of the between-site differences could be accounted for by differences in sampling times. Future studies should better document between-nest temperature differences and correlate them with differences in rates of development and differential nest occupancy. Only a 2°C difference (eg., $24.0\text{--}26.0^\circ\text{C}$) between *rosenbergi* nests would vary the time to stage 20 by 15 hr, extrapolating from the average of the developmental rate curves constructed by Zweifel (1968a: Fig. 20). This would mean nearly a 20% change in time in this species, and strong selection for picking a warmer nest is implied.

Rate of development in *rosenbergi* was relatively slow compared to many anurans, which Crump (1974) predicted would make it more vulnerable to predation. It took *rosenbergi* about 77 hr to reach stage 20 at approx 25.5°C , a rate similar to the southwestern *Rana* "*pipiens*" studied by Zweifel (1968a), but considerably slower (26–47

hr) than *Hyla arenicolor*, *Bufo cognatus*, *B. debilis*, *B. punctatus*, *Scaphiopus bombifrons*, *S. couchi* and *S. hammondi*. Another Panamanian hylid, *Phrynohyas venulosa*, also investigated by Zweifel (1964), exhibited a much faster rate of development. Contrasted to *rosenbergi*'s 48 hr to stage 18 and 40 days to metamorphosis, it took *P. venulosa* 21 hr and 37 days. Some of these differences probably were due to the higher water temperatures (25–33°C) encountered by the latter species during the course of its development.

METAMORPHOSIS

Rates of growth and maturation were difficult to estimate in *rosenbergi* after tadpoles left their nests, because larvae could not be permanently marked (Ferner, 1979). To overcome this problem, I employed artificial enclosures containing tadpoles of known age and size which were allowed to complete metamorphosis. Four pens (76 cm × 76 cm × 38 cm) were completely screened with 1/8 inch hardware cloth and placed in the middle of the main pool (Fig. 3). They were left undisturbed for one week, whereupon a thick layer of sediment covered the bottom of each pen. On July 18, 1978, 10, 20, 30 and 40 *rosenbergi* tadpoles were placed in the enclosures. These samples were collected from a clutch deposited on July 12 (approx 0300 hr) and hence were about 159 hr (7 days) old when placed in the pens. The tadpoles were at stage 25. A separate sample (N = 18) was preserved and it had the following characteristics: $\bar{x}_{TL} = 7.5$ mm ($s = 0.42$) and $\bar{x}_{SVL} = 4.5$ mm ($s = 0.15$). Survivorship in the pens was 90–100%, and most (82/95) of the tadpoles left the water with well-developed forelimbs and shrunken tails on August 21. SVL of individuals with forelimbs was 19.0–22.5 mm ($\bar{x} = 20.7$ mm, $s = 0.96$), and there were no significant differences among pens, despite initial differences in densities. TL was 1.0–31.0 mm ($\bar{x} = 14.9$ mm, $s = 9.18$) among metamorphosing individuals and was not significantly correlated with SVL in any sample. I conclude that *rosenbergi* metamorphosed at about 21 mm SVL and 40 days after fertilization. Average daily growth in the pen samples (0.48 mm/day) was identical to that estimated for nest-bound individuals from stages 25–30 (an increase of approx 5.5 mm in 350 hr; Fig. 41).

Metamorphosing *rosenbergi* had extremely large fat bodies and macroscopically undifferentiated gonads. The froglets were covered with numerous small dark spots, unlike adults, which almost always possessed a thin but conspicuous mid-dorsal stripe and pattern of bars on the side of the body and dorsal surface of the thigh (Fig. 12; Kluge, 1979). Young *rosenbergi* also had much less webbing between the fingers than did adults. The metamorphosing specimen referred to *rosenbergi* by Breder (1946: Fig. 19) has a SVL of 15.5 mm, no spots or webbing between the fingers and toes, and it is almost certainly

misidentified. The series of 10 specimens (AMNH 79913 + 9) from which this individual probably was taken (R. Zweifel, pers comm) consists of at least two species of *Hyla*, *H. subocularis* (six specimens) and *H. cf. ebraccata* (four specimens). Both are conspicuously different from *rosenbergi* in the absence of dorsal spotting and smaller size at metamorphosis. If not misidentified, Breder's specimen was incorrectly illustrated, because some webbing was not indicated.

POSTMETAMORPHIC GROWTH AND MATURATION

Thirty-one metamorphosed *rosenbergi* were transferred from the field enclosures to 10 and 20 gallon aquaria and were held at 25–30° C until November 1, 1978. The froglets were fed daily with baby crickets dusted with Pervinal (vitamin supplement). SVL was recorded at intervals of 16, 21, and 35 days. Average growth rate was 0.21 mm/day ($s = 0.04$, $N = 60$; Fig. 46). If average SVL was 20.7 mm at metamorphosis then this growth rate would have produced an 89.0 mm long adult 325 days after metamorphosis.

Clearly, *rosenbergi* can reach sexual maturity in one year. The ovary was large and highly convoluted at 90 days of age, while the testis was long and slender. Only three of the *rosenbergi* used to determine postmetamorphic growth exhibited any sign of the typical adult mid-dorsal stripe and lateral body bars by November 1. There were equal numbers of males and females among 22 specimens available for dissection. This appeared to be a random sample (it was taken from a single mating) and I conclude that there was no bias in *rosenbergi*'s primary sex ratio.

Metamorphosing froglets quickly disappeared once they left the water (Breder, 1946). Where the juvenile period was spent and what the froglets ate was not determined. Only eight subadults were present in a sample of nearly 300 *rosenbergi* collected in Costa Rica,

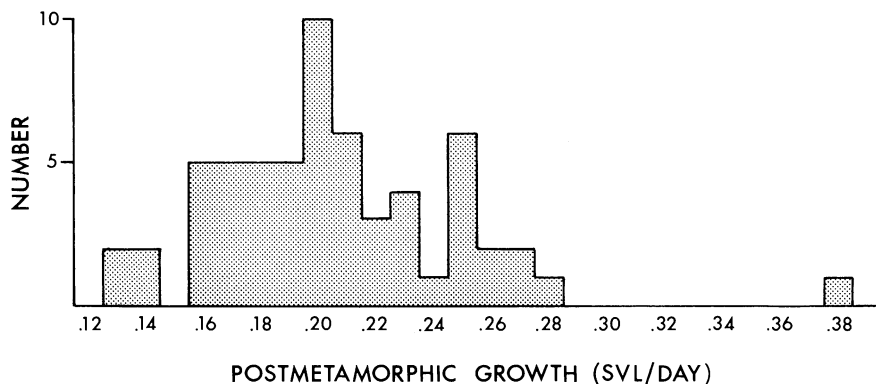


Fig. 46. SVL growth of subadult *rosenbergi* reared in the laboratory from time of metamorphosis.

Panama and Colombia (Kluge, 1979). Four subadults were obtained in the Canal Zone, and they had the following collection data: July 26 (female; FSM 29101) and August 12 (male; FSM 29102), 1968, Chiva Chiva road 0.3–2.7 km E of the Gaillard Highway; April 8, 1949 (female; FMNH 67822), 0.8 km S of Juan Mina; November 8, 1917 (male; MCZ 17582), Las Sabanas, Panama City. All four possessed fully webbed fingers of adult *rosenbergi* (Fig. 16) and yet they were still covered dorsally with the juvenile pattern of small dark spots. The mid-dorsal stripe characteristic of adults (Fig. 12) was absent. All had empty stomachs. FSM 29102 had a SVL of 45.5 mm and its testes were approx 1.8 mm long. The fleshy sheath encasing the prepollical spine was sufficiently well-developed that sex could have been determined without resorting to gonad examination. FSM 29101 had a SVL of 44.0 mm. Each of her ovaries was 11.5 mm long and contained conspicuous oocytes 0.14 mm dia. Probably both of the Chiva Chiva Road juveniles were young of the year, according to the estimates for average rate of growth. Strictly applying the average postmetamorphic growth rate estimate to the two specimens we must assume they came from eggs deposited on February 25 and March 7. These would be exceptionally early breeding dates for *rosenbergi* in the Canal Zone. The two specimens could have grown a little faster than average, 0.27–0.31 mm SVL/day would have placed their oviposition early in April when the wet season began, or they might have come from eggs deposited in late February when the Fort Clayton meteorological station records showed a rainfall of nearly 30 mm, an usually large amount for the dry season. FMNH 67822 and MCZ 17582 were 47.0 and 53.0 mm SVL, respectively. I have not attempted to interpret their birth dates in the absence of relevant rainfall records.

SUBADULT SURVIVORSHIP

The probability of an embryo surviving from fertilization to hatching (through stage 18, about 48 hr postfertilization) appeared to be extremely low (Table 5). Of 49 clutches surveyed, only 24% suffered little or no mortality, and all embryos died in 22%. Most early embryo mortality occurred immediately after the surface tension of the egg film (stages 1–18) was disturbed and the embryos sank to the bottom of the nest. Moore (1942) suggested that laying eggs as surface films is an adaptation for meeting embryonic oxygen needs in a low oxygen environment, and Zweifel (1968a) concluded that a monolayer provides the maximum gas exchange for each embryo (Fig. 40A). Salthe and Mecham (1974:410) implied that a muddy substrate is anaerobic and that frog eggs resting on it may suffocate. The actual cause of death in *rosenbergi* can be attributed to oxygen starvation and/or a

TABLE 5
 NUMBER OF CLUTCHES AND THEIR PERCENT SURVIVORSHIP
 THROUGH HATCHING (STAGE 18) IN *ROSENBERGI*

	Percentage Of Clutch Surviving			
	0	1-49	50-99	100
1977	6	9	6	8
1978	5	7	4	4

substrate contamination (bacterial or chemical) that blocked normal development. The following set of laboratory experiments, designed and implemented by Alan Jaslow, tested these two possibilities.

Eggs were collected from a field-deposited clutch about 18-22 hr after fertilization. In the first experiment (August 24-25, 1978), approx 500 eggs were placed in a one-gallon jar of pond water on a wire platform covered with silk cloth. The platform was held at the air-water interface, 56 mm above the bottom, by glass vials. A second gallon jar contained a similar number of eggs, but the platform rested on the bottom of the vessel. A third gallon jar was like the second, except that air from an aquarium pump was continuously bubbled through the water. The three containers were placed in a shaded courtyard where the water temperature reached 26° C during the day. The dissolved oxygen in jars 1, 2 and 3 was 5.2, 4.8 and 7.0 ppm, respectively. The fact that 99-100% of the embryos survived to stage 19 in all three containers suggested no significant effects occurred due to handling or experimental materials (pond water, jars and platform). The amount of dissolved oxygen in all jars was much higher than any field recorded values (maximum = 3.2 ppm), and death due to oxygen starvation would be unexpected.

Eggs for the second experiment were collected on September 25, 1978, and mud from the main pool was placed on the bottom of each jar to a depth of 35 mm. The mud was covered with 60 mm of pond water. The eggs were held at the air-water interface by the wire-silk platform in jar 1. In jars 2 and 3, the platform rested on the mud. Air was added continuously to jar 3. The containers were placed in the shaded courtyard where the water temperature reached 27° C during the following day. Dissolved oxygen in jars 1, 2 and 3 was 3.7, 4.1 and 7.4 ppm, respectively, and again higher than field values. Significant mortality occurred only in jar 2, to which oxygen was not added. It seems likely that death due to chemical inhibition associated with contacting the substrate can be eliminated as cause of death. How-

ever, bacterial infection cannot be ruled out entirely, because anaerobic bacteria can be killed with high concentrations of oxygen.

The following field observations seemed to eliminate the possibility of bacterial infection. In two nests, water dropped a few millimeters and the marginal rows of eggs in the surface films rested on the moist mud for several hours while those in the center floated. No differential mortality among marginally and centrally located eggs was detected. Thus, I predict that dissolved oxygen varies systematically in an undisturbed water column, with that at or near the bottom being the lowest and insufficient for normal *rosenbergi* development. I hypothesize that microorganisms in the mud create an anoxic environment and, as a result, a steep oxygen gradient forms within the adjacent water column. The shallow nests did not appear to be thermally stratified, and I doubt if there was much circulation except during flooding. The fact that not all sunken clutches showed the same level of mortality might be explained by certain nests being flooded with more oxygen-laden water. Nests at lower elevations along the stream course remained flooded longer. I suspect that the low oxygen concentrations in nests ($\bar{x} = 1.3$ ppm) and open water ($\bar{x} = 2.3$ ppm) were insufficient to maintain a normal rate of growth and maturation under ordinary conditions. The results from jar 2 (Table 6) also suggested that an oxygen deficiency was most important at earlier stages of development, particularly those prior to neural tube formation (stage 14). While these experiments must be repeated before a definitive statement can be made, I tentatively conclude that oxygen deficiency was responsible for much of the mortality observed prior to hatching, and that the probability of death increased when the surface tension was interrupted and the eggs sank within the first 20–30 hr after fertilization.

Only rain and intruding male *rosenbergi* were observed disrupt-

TABLE 6
NUMBER OF *ROSENBERGI* EMBRYOS SURVIVING
CONTACT WITH MUD AND LOW OXYGEN TENSION

Jar No. ¹	Oxygen Conc. ppm	Orig. Nos.	Died at Stages		Alive at Stages
			12–13	14–16	17–18
1	3.7	308	29	1	278
2	4.1	351	242	30	79
3	7.4	507	40	8	459

¹Embryos in jar 1 were held at the air/water interface, while in 2 and 3 they contacted the mud substrate. Air was added to jar 3 but not 1 or 2.

ing the surface tension of *rosenbergi* egg films, sinking clutches, and ultimately causing embryos to die. Heyer (1973) also observed rain destroy floating egg masses of SE Asian anurans. There were several other possible sources of egg film disturbance on the ODSS. An armadillo (*Dasyus novemcinctus*) and a large fresh water crab were seen once in empty nests, and the following large vertebrates frequented the banks and adjacent shallow water and they too must be considered possible, if only rare, sources of disturbance: *Chironectes minimus* (Didelphidae); *Butorides virescens* (Aroleidae); *Leptodeira annulata* (Colubridae); *Kinosternon leucostomum* (Kinosternidae); *Leptodactylus pentadactylus* (Leptodactylidae). *Leptodeira annulata* are known frog egg predators (Duellman, 1978). In addition to unintentional destruction, I suspect the other species, except adult *L. pentadactylus*, also fed on the eggs and larvae of *rosenbergi*. The destructiveness of rain on an egg surface film depended on its intensity and duration and the completeness of a canopy, while that of an intruding *rosenbergi* was related to how much it moved around in the nest. While there was little doubt that rain and intruding male *rosenbergi* were the most frequent causes of embryo mortality, it was extremely difficult to assess their relative importance. Each new clutch would have to be observed continuously, at least from dusk to dawn, to determine exactly how often an intruding male was responsible. A given rain and associated flood did not necessarily affect all surface films equally, because of the different nest exposures relative to the canopy and water level, and continuous monitoring of all clutches would be required to determine the importance of these destructive forces. Seventy-five to 80% of the surface films suffered some disturbance (Table 5). Five (22%) were caused by intruding *rosenbergi*, four males and one female, in 1977, but no early embryo mortality in 1978 could be attributed to this cause. The greater mortality in 1977 almost certainly was a function of higher adult densities.

Several invertebrates and vertebrates are known to eat *rosenbergi* eggs and tadpoles. Wassersug's (1971) tadpole palatability experiments suggested that *rosenbergi* has few toxic compounds in its tissues to discourage predators. On one occasion, a large number of an unidentified planarian were observed moving over a surface film of eggs. They appeared to feed on the jelly capsules, and some eggs seemed to sink as a result of the predator's activity. Villa (1979) also found planarians on frog eggs (*Rana maculata*) in Middle America, but he could not experimentally demonstrate they were feeding. The fishing spider, *Ancylometes valentine* (Pisauridae), was extremely abundant and it was often found on the water surface in a *rosenbergi* nest. The spider's common association with nests containing clutches, as opposed to empty ones, suggests they fed on *rosenbergi*,

but I observed only one successful predation of a larva. Occasionally, a water bug, *Belostoma porteri* (Belostomidae), was found in a nest, but only twice was it seen feeding on eggs and larvae. A large *B. porteri* (23.0 mm TTL) was placed in a water-filled gallon jar for 24 hr with several *rosenbergi* tadpoles 12.0 mm TTL. Prey were consumed at an average rate of only 0.3 tadpoles/hr. Odonate nymphs (Libellulidae) were rarely encountered, but I observed a successful predation of one *rosenbergi* tadpole.

The swamp eel, *Synbranchus marmoratus* (Synbranchidae), was common. However, it was found only twice in a *rosenbergi* nest and only once was I certain it was feeding on recently hatched embryos. The only other species of fish found in *rosenbergi* nests were identified by W. Bussing as *Poecilia gillii* (Poeciliidae). Specimens were taken from several nests at Quebrada Benjamin, Costa Rica and near the Rio Frijoles, Canal Zone, Panama. *P. gillii* feeds on diatoms and decaying organic matter and is an unlikely predator of frog eggs and tadpoles, according to R. Bailey and Bussing (pers comm). Breder (1946) reported *Rivulus chucunaque* (Cyprinodontidae) in a *rosenbergi* nest in Darien, Panama. *Rivulus* are known carnivores which freely migrate overland (Breder, 1946), and probably eat early developmental stages of frogs. I never encountered *Rivulus* in or near *rosenbergi* nests in Costa Rica and central Panama.

The tadpoles of *Leptodactylus pentadactylus*, *Physalaemus pustulosus* (Leptodactylidae) and *rosenbergi* were the most significant predators of *rosenbergi* eggs and larvae. Their carnivorous habit appeared to be widespread, and Wells (1979) argued that the exceptionally explosive breeding system of *Bufo typhonius* is an adaptation to the presence of predatory *L. pentadactylus* tadpoles. It was not always clear how predatory tadpoles gained access to *rosenbergi* nests. Nevertheless, a flooded basin containing a submerged clutch rarely was without several large tadpoles, particularly those of *rosenbergi*, feeding on the embryos. More predatory *rosenbergi* tadpoles than prey were often found, and such size diversity probably gave Breder (1946) the erroneous impression that more than one *rosenbergi* clutch co-occurred in a given nest.

Predators soon discovered eggs and prehatching larvae placed in open water, and I suspect they quickly located their prey by olfaction. For example, at Chiva Chiva Quarry in 1976, six large *L. pentadactylus* tadpoles ate an entire *rosenbergi* egg mass in less than 24 hr. The predators were not in the isolated nest before oviposition and must have reached the basin by moving up a gentle slope and over several meters of moist leaf litter. Presumably, the predators took advantage of the flooded forest floor produced by the same rain that sank the clutch. It was unlikely that all six predators found the clutch by searching randomly during the short period of flooding. Heyer, et

al. (1975) also suggested that *L. pentadactylus* tadpoles have well-developed olfactory senses.

P. pustulosus were encountered infrequently and, of the three predatory species of tadpoles, they were the least often observed in *rosenbergi* nests. In 1977, *P. pustulosus* deposited their foam-egg masses on the water surface of two empty *rosenbergi* nests. Adult *rosenbergi* were not seen in these particular basins until the *P. pustulosus* larvae disappeared.

Typically, the tadpoles of all three species darted to the water surface and tore one or more encapsulated eggs from the film. The surface tension was always disturbed by such attacks and the egg mass sank to the bottom. It also was typical of all three species to eat the jelly coats by spinning the sphere in their mouths. Unlike *L. pentadactylus* (Fig. 47), *P. pustulosus* and *rosenbergi* tadpoles did not appear to ingest whole eggs, and they scraped the proteinaceous surface, often leaving behind hard balls of yolk. *L. pentadactylus* had little trouble devouring whole tadpoles up to stage 25, and large *rosenbergi* tadpoles confined to a nest frequently cannibalized each other's tails. The efficiency of cannibalism by *rosenbergi* tadpoles was impressive. For example, I observed a heavy rain sink about 80% of a clutch, and the remaining tadpoles that hatched consumed all of the dead eggs in three days.

I am not aware of any beak and denticle modifications in *L. pentadactylus*, *P. pustulosus* or *rosenbergi* tadpoles, like those found in *Scaphiopus* (Bragg, 1965), that suggest specializations for feeding on eggs and larvae. Heyer, et al. (1975) speculated that the long tail,



Fig. 47. Lateral view of a *Leptodactylus pentadactylus* tadpole (stage 39, SVL = 19.0 mm, TL = 45.0 mm) which had eaten many whole *rosenbergi* eggs. No dissections were made. The predator was collected in *rosenbergi* nest no. 48 on August 11, 1977. Photograph by Karna Steelquist.

shape of mouth and oral disc, and well-developed lateral line system in *L. pentadactylus* is related to its predatory habits. However, these same characteristics are found in many other filter-feeding species (Duellman, 1970). Thus, carnivory in *L. pentadactylus*, *P. pustulosus* and *rosenbergi* probably is a facultative response to high larval densities and low productivity (Heyer, et al. 1975).

Several sets of laboratory trials were run to determine the efficiency of *L. pentadactylus* tadpoles in capturing and eating different size *rosenbergi* embryos. One-gallon glass jars, 15 cm dia, were filled 50 mm (640 ml) with cured tap water. The diameter and volume were similar to nests. However, the rough substrate of natural basins could not be duplicated, so prey may have taken longer to secure. The jars were placed on white paper and covered with opaque plastic during the trials.

Only *L. pentadactylus* tadpoles voluntarily emerging from two frothy egg masses were used in the experiments. One starved predator was placed in each jar. The number of prey introduced into each container was 1-160. Water temperature in the jars was 22.0-27.0° C. Several replicates of seven different trials were run (Table 7). The sizes and stages of maturation of predators and of prey were similar among replicates in trials 1-6. Each trial ran from 12-48 hr. The number of uneaten prey was scored at the end of four, six, eight, 16, 18 or 24 hr intervals. The predators and most prey (all but those at stage 25) grew and matured slightly during a 12-48 hr run. Prey capture rates were standardized by dividing the number of prey eaten by the number of elapsed hours. These rates were further standardized to eliminate the apparent density effect (see immediately below) by dividing by the

TABLE 7
A SUMMARY OF LABORATORY EXPERIMENTS INVOLVING
PREDATORY *LEPTODACTYLUS PENTADACTYLUS* TADPOLES
AND THE EGGS AND LARVAE OF *ROSENBERGI* AS PREY

Trial No.	No. Replicates	Prey		Predator		average standardized prey capture rate
		modal stage of maturation	average total length	modal stage of maturation	average total length	
1	7	15	2.5	28	42.9	.06
2	7	20	6.6	29	47.2	.04
3	6	22	9.0	31	40.1	.07
4	17	25	13.6	31	44.3	.001
5	10	25	12.3	35	52.1	.01
6	10	25	13.1	37	57.1	.08
7	8	21	8.0	31	44.3	.08
	10	25	14.2			

number of prey present at the beginning of the sampling interval (1-160).

L. pentadactylus (stages 28-31) fed on *rosenbergi* eggs and small larvae (stages 15-22) at about the same rate (0.04-0.07; Table 7). In all experiments involving prey at stages 15-22, predation rate went up monotonically as the density of prey increased from 3-35 per container. Experiments 4-6 seemed to indicate that only the largest predators (stage 37) had a significant impact on larger prey (stage 25). This was corroborated by experiment seven in which equal numbers of small (stage 21) and large (stage 25) prey were placed in the same container. The smaller prey were captured and eaten much more quickly. My field observations confirmed that prehatchling embryos were most vulnerable.

Heyer, et al. (1975) documented the inverse relationship between probability of capture and prey size. Moreover, they concluded that predator-prey systems involving tadpoles are rare, especially where fish occur. I have found that tadpoles usually eat each other's eggs, even in areas such as the Obispo Diversion which contained many species of fishes, several of which take frog eggs offered to them (M. Robinson, pers comm).

The last factor affecting egg and tadpole survivorship was desiccation. Breder (1946) found only one of 15 *rosenbergi* clutches in Darien, Panama, (7%) died because of desiccation, and my findings were similar (5%). One of five clutches (20%) observed at Chiva Chiva Quarry in 1976 died because of desiccation, four of 67 (6%) on the primary section of the ODSS in 1977, and none (0/24) in 1978. Hence, desiccation seemed to be a relatively insignificant factor in subadult survivorship, except perhaps at the beginning of the wet season when rains were infrequent and less predictable.

THE ADAPTIVE SIGNIFICANCE OF THE NEST

Lamotte and Lescure (1977) reviewed the extensive literature on anuran life cycles which differ from the usual sequence of egg deposition in large open bodies of water and a typical aquatic tadpole stage preceding metamorphosis. The structural and behavioral adaptations described in their world-wide survey were numerous and often involved forms of direct development, parental care and nest building. The Obispo Diversion had at least 20 species of frogs breeding along its course, and most of them had one or more of the adaptations that Lamotte and Lescure described (Table 8). The overwhelming conclusion is that many anurans avoid placing their offspring, particularly eggs and prehatchlings, in large open bodies of water, and that predation is responsible for the evolutionary divergences.

The small shallow "nests" excavated in temporary pools by

TABLE 8
A LIST OF THE ANURANS THAT BRED ALONG THE OBISPO
DIVERSION, AND A SUMMARY OF THEIR BREEDING HABITS

Family	Species	Developmental Program ¹
Dry Season Breeders		
Dendrobatidae	<i>Colostethus</i> sp.	1
Ranidae	<i>Rana palmipes</i>	x
Wet Season Breeders		
Bufo	<i>Bufo granulosus</i>	x
Bufo	<i>Bufo typhonius</i>	x
Centrolenidae	<i>Centrolenella fleischmanni</i>	2
Hylidae	<i>Agalychnis callidryas</i>	2
Hylidae	<i>Hyla boulengeri</i>	3
Hylidae	<i>Hyla ebraccata</i>	2
Hylidae	<i>Hyla microcephala</i>	4
Hylidae	<i>Hyla phlebodes</i>	4
Hylidae	<i>Hyla rosenbergi</i>	5
Hylidae	<i>Hyla rubra</i>	3
Hylidae	<i>Phrynohyas venulosa</i>	4
Hylidae	<i>Smilisca phaeota</i>	4
Leptodactylidae	<i>Eleutherodactylus</i> spp.	6
Leptodactylidae	<i>Leptodactylus bolivianus</i>	7
Leptodactylidae	<i>Physalaemus pustulosus</i>	7
Microhylidae	<i>Chiasmocleis panamensis</i>	8

¹x = Ordinary aquatic egg-tadpole development in large body of water. 1 = Terrestrial egg development; parents carry well-developed tadpoles to water. 2 = Eggs laid on leaves above water; tadpoles fall into water upon hatching. 3 = Ordinary aquatic egg/tadpole development but in small temporary pools. 4 = Eggs laid on surface of water, usually in weed-choked areas. 5 = Open mud nest. 6 = Terrestrial oviposition and direct development. 7 = Foam nest wherein early development is passed. 8 = Eggs laid in holes in the bank above average water table.

bottom-dwelling tadpoles of several species (Black, 1975) are not likely to represent an incipient stage in the evolution of nest building in the *boans* complex. It was the largely immobile and endogenously feeding egg and larval stages that the *rosenbergi* nest protected, not the bottom-scouring later tadpole stages. Moreover, in *rosenbergi*, adults built nests and most aquatic habitats they used tended to be permanent during the wet season.

The nest-building habit of *rosenbergi* has been repeatedly cited as an adaptation to avoid predation (eg, Breder, 1946), but until now it was not clear what predators were involved nor how effective they could be. It seems illogical to cite large terrestrial and aerial predators as selective agents for nest evolution, because the concentrated, stationary (hence more predictable), and exposed nature of the prey would make them more vulnerable. Even semiaquatic predators, such as water bugs, odonates, crabs and turtles, scaled the nests' low

ramparts. Even swamp eels burrowed into basins. I believe that predation by tadpoles and small fish and cannibalism played the key role in the origin and evolution of nest building in *rosenbergi* and its close relatives. Cannibalism probably was a much stronger selective force than interspecific predation. *L. pentadactylus* co-occurs with *rosenbergi* throughout much of its vast geographic range (Kluge, 1979; Cochran and Goin, 1970; Heyer and Peters, 1971; Heyer, 1979), and its larvae are efficient predators on *rosenbergi* embryos. However, *L. pentadactylus* tadpoles were never as common in nests or in open water as were cannibalistic *rosenbergi* tadpoles. Only four *L. pentadactylus* foam masses were encountered in 1977 and 1978 and the number of potential predators in two of the clutches was small (21 and 36 larvae were at stage 25 or older). Elsewhere in central Panama and Costa Rica, I always found *rosenbergi* tadpoles to be more common than *L. pentadactylus*. No doubt, the explosive breeding congregations seen in *L. pentadactylus* (Rivero and Esteve, 1969; A. S. Rand, pers comm) would greatly alter relative abundances of predators and cannibals, but these mass reproductive events appear to be unusual.

The nesting habit of *rosenbergi* is an excellent example of the numerous reproductive costs often accompanying the evolution of a novelty, as shown by the following list of possible disadvantages related to nesting: (1) decreased survivorship due to greater terrestrial-aerial and semiaquatic predation, (2) increased mortality due to the destructive affects of flooding and oxygen deprivation, (3) greater probability of desiccating in the small volume of water held by the nest, (4) increased intraspecific competition for food, particularly in clutches confined to basins for long periods of time, and probably smaller size at metamorphosis, and (5) increased probability of within cohort cannibalism. Other important costs were the reduced time males had for mate acquisition. Males did not advertise for mates when building and defending nests against other males, nor did they actively solicit females when caring for young. I believe it is reasonable to conclude that the selective pressure(s) imposed on the system by small aquatic predators, such as tadpoles, must have been great considering these several factors.

ADULT POPULATION BIOLOGY

DENSITY AND MOVEMENT AMONG AREAS

One hundred and five males were toe-clipped in 1977, whereas only 73 were marked in 1978. Breeding males appeared to be restricted to the water course within the Obispo Diversion itself in 1977 (A of Fig. 1, Table 9A). In 1978, many males occupied nearby swamps (B-F

TABLE 9
 NUMBER OF ROSENBERGI MALES RECORDED FROM THE
 OBISPO DIVERSION STUDY SITE (FIG. 1) IN 1977 (A) AND 1978 (B)¹

		A. 1977		B. 1978						
		Areas		Areas						
Areas		A'	A''	A'	A''	B	C	D	E	F
A'		69	9	26	2	2	0	0	0	0
A''		4	48	1	13	2	0	1	1	0
	A'			2	0	18	0	4	0	0
	A''			0	0	0	4	0	0	0
	B			1	0	1	0	12	0	0
	C			0	1	0	0	0	1	0
	D			0	0	0	0	0	0	0
	E			0	0	0	0	0	1	0
	F			0	0	0	0	0	0	13

¹Seasonal totals are located on the diagonal, those numbers below the diagonal represent immigrations from one area (vertical axis) to another (horizontal), and those above it are emigrations from one area (vertical) to another (horizontal).

of Fig. 1; Table 9B) as well as the Diversion water course. The difference in population size observed in these years was probably an artifact of limited geographic sampling. In spite of the wider distribution of males in 1978 the investigation continued to concentrate mostly on the main study area (A of Fig. 1). Nineteen seventy-eight was exceptionally wet (Figs. 5-6) and favorable nesting sites were widespread. However, large bodies of slow moving water with wide muddy shelves appeared to be limited to the main water course along the Diversion during the exceptionally dry 1977 breeding season.

In 1977, only 12 of the 105 marked males (11.4%) moved between the primary and secondary sections of the main study area, a distance of only a few meters (Fig. 2). One returned to his original section, for a total of 13 separate moves in 1977 (Table 9A). Twelve of 73 marked males (16.4%) moved among the seven choruses recognized in 1978 (A', A'', B-F of Fig. 1). Three moved more than once between areas, and they accounted for 50% of the 18 interchanges (Table 9B). Considerably fewer males moved to different areas than would be expected by chance ($P = Q = 0.5$) in both 1977 and 1978 ($z_{1977} = 7.81$, $z_{1978} = 5.62$), and the proportions of males moving in the two years was not significantly different ($G = 0.91$). However, the proportion (total number of moves/number of males not moving) was slightly higher

in 1978 ($G = 3.71$, $P = .05$). These data suggest that once an individual entered a chorus he was not likely to migrate to another. Breder (1946) also found little movement by *rosenbergi* males in the Darien. One might predict that males shift from high to low density choruses when the probability of mating is inversely related to number of males. Such a move might become even more likely as a male becomes physiologically exhausted from male-male competition. Alternatively, females might be attracted to larger choruses, thereby improving the probability of a male mating in a high density chorus. Under these conditions, more males would shift from small to large choruses. I divided the 1977 and 1978 areas that exchanged males (Fig. 1) into high (A', B) and low (A'', D, E) density groups, and determined the total number of movements made from one density to the other. Seventeen of 24 (71%) shifts between high and low density areas involved males leaving high density choruses and moving to lower densities (sign test, $P = .03$).

The total number of males present on the primary and secondary sections dramatically differed between 1977 and 1978 (Table 9). However, the proportion of migrants was not different between years ($G = 0.74$). The primary section was favored over the secondary 1.4–2.0 times in both years, and a similar proportion (9–11%) of the individuals made the shift between the choruses.

Two (C, F) of seven areas (Fig. 1) did not interchange males with any other chorus. This absence of movement was particularly surprising in the case of area C which was only about 150 m from A'' and E; these three choruses occurred along the same small drainage system.

Nine *rosenbergi* (eight males and one female with eggs) were released in the low vegetation surrounding the main pool of the primary section on August 31, 1978. The introduced individuals were taken from the following areas of the ODSS, or elsewhere: B (male nos. 141, 174), D (male nos. 152, 159, 161, 164); and Summit Gardens area, 3300 m SE of the ODSS (male nos. 172, 173, female no. 101). Immediately before the releases there had been 2–3 males on the primary section. Only three males, one of them the introduced male no. 152, remained on the primary section the day following the introductions. Male no. 152 was the only introduction that had previous experience with the main area. He was a regular resident of the primary section from August 2–21, 1978, during which time he obtained a mating. On August 30, he was rediscovered in area D. After male no. 152 was returned to A' he remained a regular resident until September 24, 1978. He was reproductively successful once again on A' and he re-used nests nos. 35 and 125, which had been his regular territories before moving to area D. The introduced female and seven other males never returned to the main area. Male no. 164 was found on September 4, 1978 in the same nest he had been removed from. I

interpret these data to mean that site familiarity was extremely important to *rosenbergi*, and that few individuals moved to a different area because of this lack of familiarity.

Seventy-three female *rosenbergi* were marked in 1977, and 36 in 1978. Three of the 1978 sample (nos. 22, 42 and 63) were recaptures. The proportions of males and females marked in the two years did not differ significantly ($G = .001$). This finding was surprising, because I expected females to be much more difficult to locate than males when the population is widely dispersed. The 1977 and 1978 females almost certainly laid a minimum total of 98 and 48 clutches, respectively. Not all of these matings were actually witnessed; 14 were estimated from the frequency of days between unobserved ovipositions (Fig. 22). The proportion of clutches unaccounted for was not significantly different in either year ($G = .01$).

At least 53 females oviposited one or more times on the primary section in 1977, and 26 did so on the adjacent secondary area. In 1978, at least 24 laid on the primary section while 17 used other areas, including the secondary section. The proportion of all females returning to any one of the areas (A', A'', B-F of Fig. 1), as opposed to depositing their next clutch elsewhere, did not differ significantly between years ($G = 1.43$). However, the proportion of females returning to the primary section to deposit a new clutch was greater in 1977 (Fisher's exact test, $P < .04$). The proportion of different females ovipositing on the primary area was not significantly different between years ($G = 0.85$). Seven of 73 females (9.5%) marked in 1977 were known to have migrated between the primary and secondary sections, and six of 36 females (16.7%) marked in 1978 moved among the several choruses recognized that year (A', A'', B-F of Fig. 1). There were no significant differences in the proportion of males and females moving in 1977 ($G = .02$) and in 1978 ($G = .06$).

DENSITY AND MOVEMENT WITHIN AN AREA

The first three males were observed on June 3 in 1977, all calling from well above ground; no nests were seen at that time. The first two males were marked on June 15, 1977 (Fig. 48), and the last individual was sighted on October 28, 135 days later. One nest was successful by June 26 and one as late as October 21 (Fig. 29). The first female was marked on July 5, 1977, and the last one was captured on October 17 (Fig. 49). Fig. 29 indicates that five females visited the primary section between June 26 and July 1, but they were not marked. No females or other successful nests were observed between June 15 and July 4, and I doubt that the number of unmarked females during this initial period was greater than five. At least three unobserved females mated on October 20-21 (Fig. 29). A total of 69 males and 55 females were observed on this part of the Diversion in 1977 and, despite the high

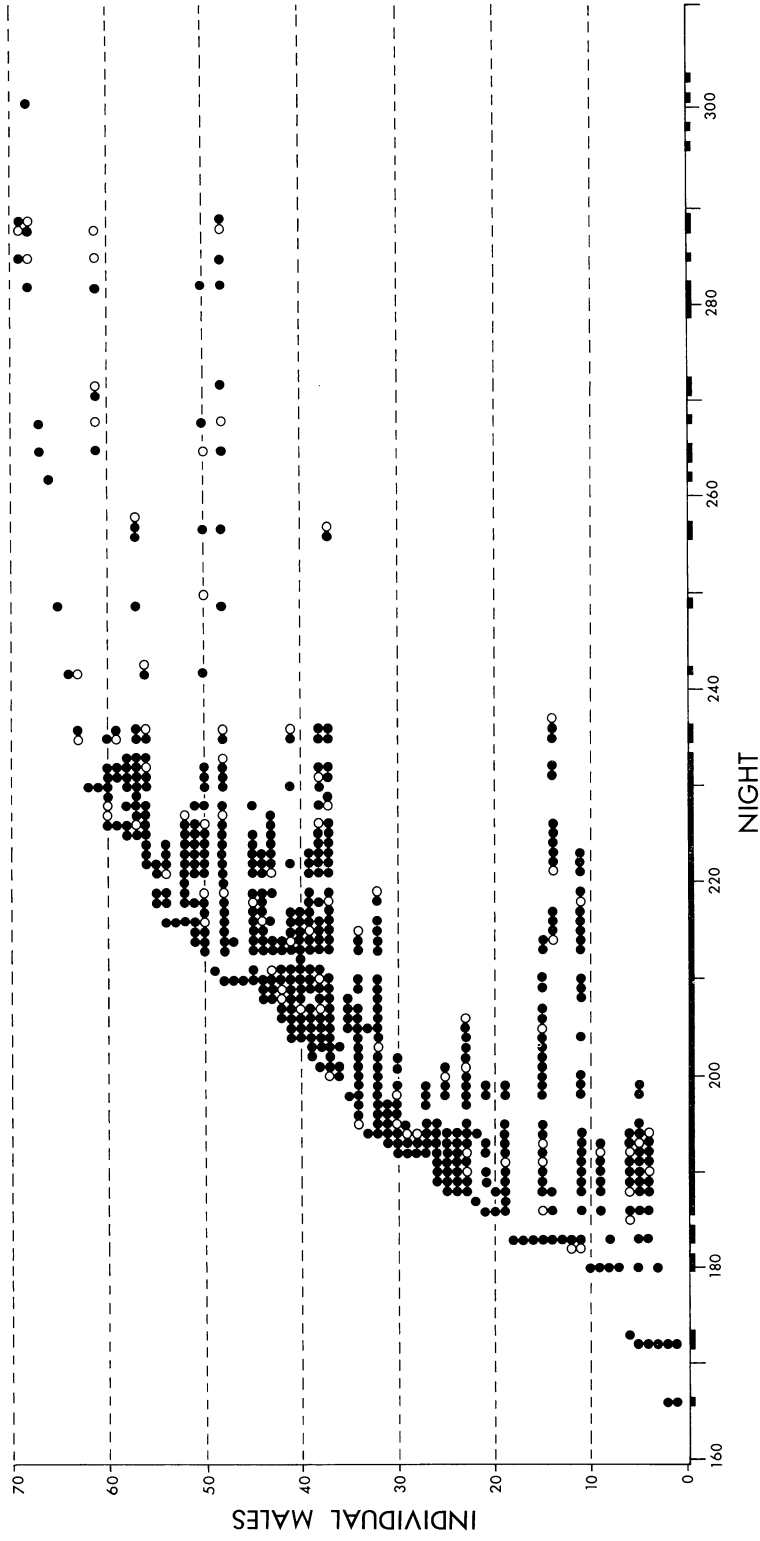


Fig. 48. Histories of marked male *rosenbergi* in 1977. Open circles denote nights of amplexes, closed circles males present, blanks males absent. The thickened portions of the horizontal axis are nights one or more investigators surveyed the primary section. Night 160 was June 9.

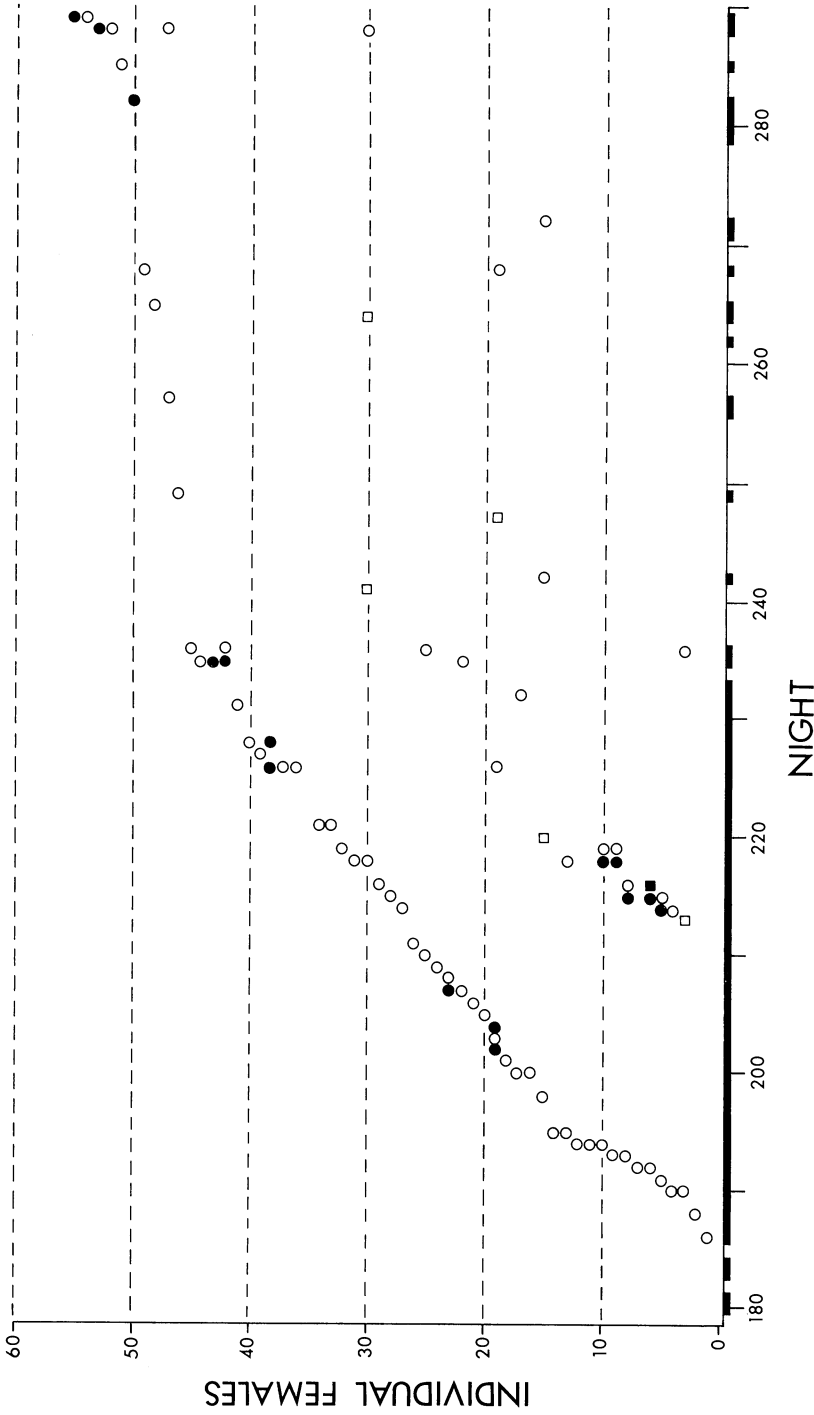


Fig. 49. Histories of marked female *roseberry* in 1977. Circles denote nights females present, open circles amplexes, blanks females absent. Appearances symbolized by open boxes are interpolations from data presented in Fig. 22, and closed boxes indicate known ovipositions on the secondary section. The thickened portions of the horizontal axis are nights one or more investigators surveyed the primary section. Night 180 was June 29.

probability of undersampling females, the cumulative (seasonal) sex ratio was not significantly different from 1:1. More nearly equal numbers obtained when the unmarked females were added to the sample.

The recruitment of both males and females was gradual rather than pulsed in 1977 (Fig. 50), probably because there was an upper limit to growth rate which most individuals attained. Earlier (pp. 65-66), I observed that it took about one year to reach adult size and sexual maturity, and hence I hypothesize that individuals entered the breeding population approx in proportion to their birth dates. Also, the general shape of the recruitment curves, rapid at first and slow later, may be affected by positively skewed individual growth rate frequency distributions. Males probably arrived at their first breeding site as quickly as possible in order to maximize the length of time they spent advertising for mates. As the season progressed, their arrival rate declined, probably as a function of increasing mortality. Increasing individual movement between breeding areas may have offset this decline. I interpret the 1977 female curve like that of the male except

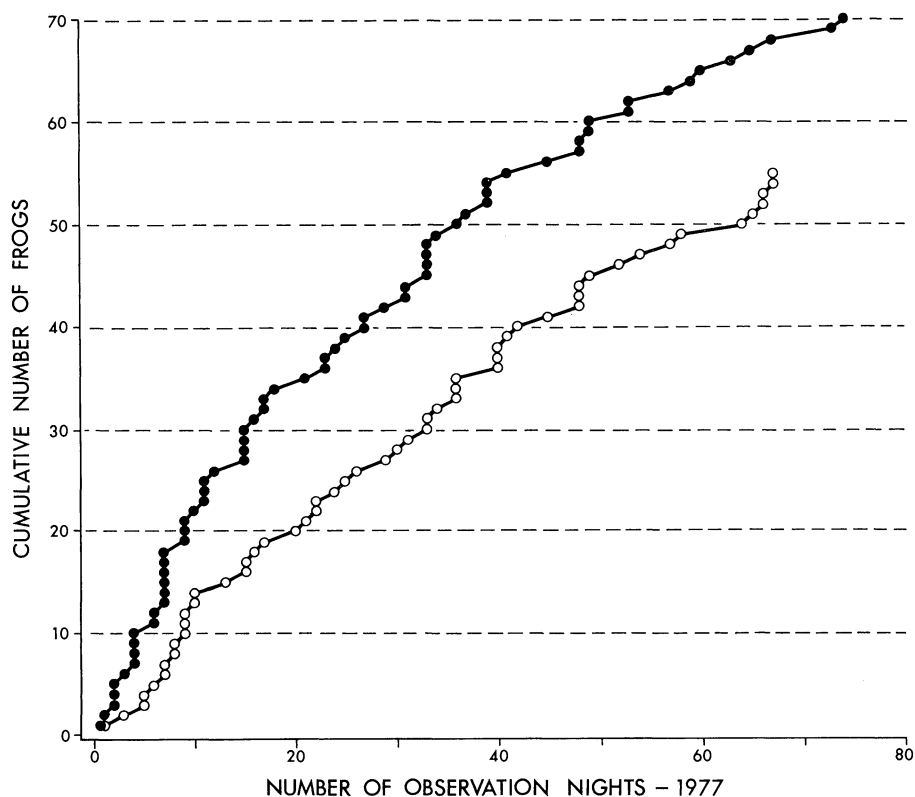


Fig. 50. New male (closed circles) and female (open circles) *rosenbergi* arrival rates in 1977. The horizontal axis includes only nights the primary section was surveyed or a frog's presence was estimated.

for the unique opening and closing rates. The opening rate probably was related to some females waiting until the unpredictable beginning of the wet season was over. Also, a part of this low recruitment rate may reflect some females having waited until they maximized the size of their clutch in proportion to their body size (Fig. 20). I believe the more rapid concluding interval was related to females anticipating the end of the breeding season. Reabsorbing an unlaidd clutch would be a significant loss in fitness (pp. 32-35), although perhaps not as great as a clutch destroyed by desiccation.

In 1978, the first *rosenbergi* mated on April 19 or 20, as estimated from the size/age and developmental stage of the tadpoles present on April 22 when observations began (Fig. 51). The last male was observed in a nest on October 30. The first female was seen on May 10 (Fig. 52); the number of nests used successfully before that date (see Fig. 30) indicated that at least four were missed. The last female to be observed was on September 25. However, two unobserved individuals deposited eggs on September 29 and October 2. The total numbers of males and females actually observed were 26 and 23, respectively. Adding only a few of the unobserved females would bring the cumulative sex ratio even closer to 1:1.

Neither male or female 1978 recruitment curves (Fig. 53) showed the exceptionally long uninterrupted trends observed in 1977, and I believe the rate changes that could be identified in the low density year were sampling artifacts associated with small numbers. Both male and female curves were fitted rather well with a straight line of approx 0.2/day. I believe the lower rate of immigration in 1978 was due to the species' hyperdispersion, which in turn was related to the greater rainfall and more widely available breeding environments. Further, the absence of long-term recruitment trends in 1978 probably was due to the smaller number of individuals using the primary section.

Much of the 1977 female recruitment curve regularly lagged behind the males' (Figs. 48-49), especially between nights 195-233 (July 14 to August 21). A delay of 10-25 nights remained even when the five unmarked females were added. Assuming most individuals entering the population were one year old and male and female growth rates were similar, I predict the lag resulted from differential investment in gametes. The females' delay was similar to the period between clutches within a breeding season (21-32 days; Fig. 22). The absence of a well-defined lag in 1978 may have been a sampling artifact associated with small numbers.

Movement between areas was infrequent in *rosenbergi* during the breeding season (pp. 75-78), and the level of philopatry also was assessed with the number of consecutive nights a male was not observed. Only nights 186-233 (July 5 to August 21, 1977; Fig. 48) and 155-237 (June 4 to August 25, 1978; Fig. 51), except for 189 (July 8),

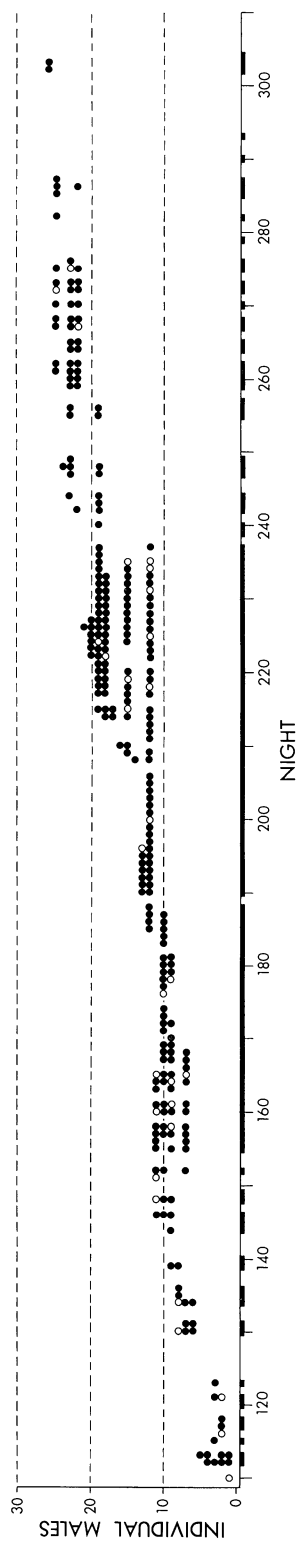


Fig. 51. Histories of marked male *rosenbergi* in 1978. Open circles denote nights of amplexes, closed circles males present, blanks males absent. The thickened portions of the horizontal axis are nights one or more investigators surveyed the primary section. Night 110 was April 20.

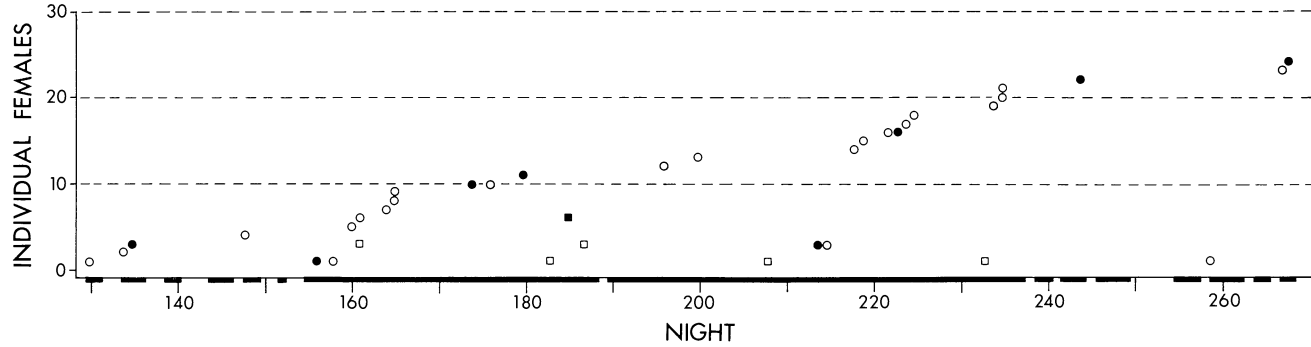


Fig. 52. Histories of marked female *rosenbergi* in 1978. Circles denote nights females present, open circles amplexes, blanks females absent. Appearances symbolized by open boxes are interpolations from data presented in Fig. 22, and closed boxes indicate known ovipositions on the secondary section. The thickened portions of the horizontal axis are nights one or more investigators surveyed the primary section. Night 130 was May 10.

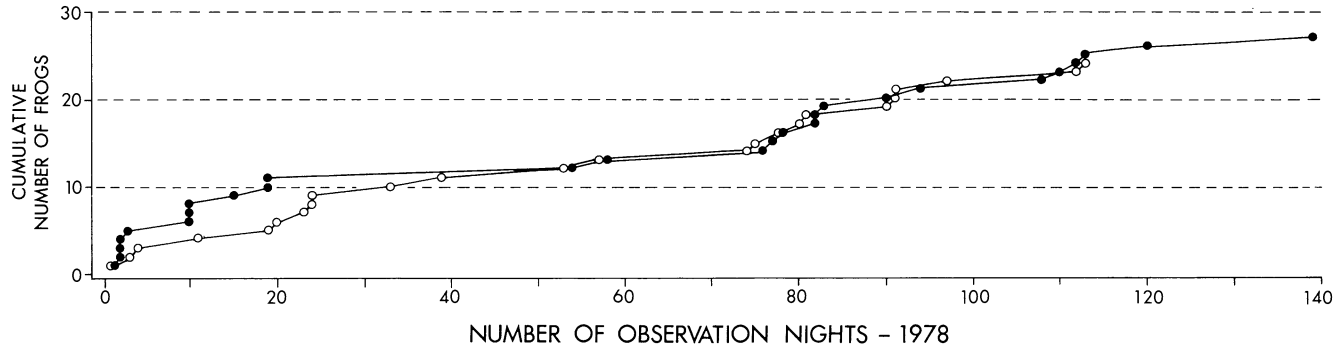


Fig. 53. New male (closed circles) and female (open circles) *rosenbergi* arrival rates in 1978. The horizontal axis only includes nights the primary section was surveyed or a frog's presence was estimated.

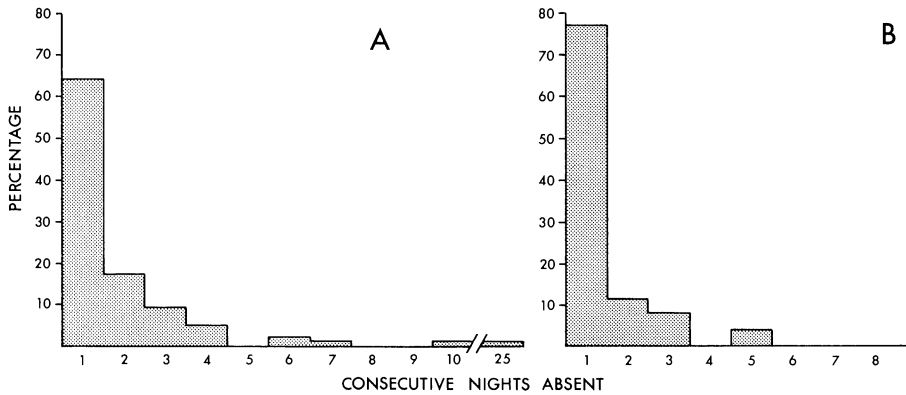


Fig. 54. Consecutive nights marked male *rosenbergi* were not observed. A. 1977; sampling period July 5–August 21. B. 1978; sampling period June 4–August 25. Fig. 22 is a comparable plot for females.

were surveyed, because they represented long uninterrupted intervals. In 1977, 51 males were present 610 of 698 possible frog nights. “Frog nights” for one individual was the number of nights from the first to the last time it was sighted. Few males were absent two or more consecutive nights in 1977 ($\bar{x} = 2.1$; Fig. 54A). One male’s 25 day absence (the individual 14th from the bottom in Fig. 48) was 2.5 times greater than the next longest record (Fig. 54A). I believe the exceptional absentee spent this time recovering from the bone-deep slash across the dorsal surface of each thigh he received from a predator on the night he disappeared, rather than in an unsampled chorus. His wounds had healed upon his return, and he had not grown. In 1978, 14 males were present 191 of 217 possible frog nights, and even fewer were absent two or more consecutive nights ($\bar{x} = 1.4$; Fig. 54B). However, both median and Mann Whitney statistics ($U = 983.5$) indicated the between-year difference was not significant. Such persistence in male *rosenbergi* probably was related to the importance of acquiring a nest, defending it and obtaining mates.

Thirty-nine males were observed 352 nights in 1977 and nine males 89 nights in 1978. Males returned nightly to the same nest 62% (243/393) of the time without visiting another basin; the difference between years was not significant ($G = 1.38$). Site specificity was more impressive considering 33% (49/150) of the moves to different nests followed nights of reproduction; the resident male would not be expected to reuse the same basin because of tadpole cannibalism (pp. 70–75). Males moved to another nest only 10% (46/441) of the nights, and movement to more than two basins per night was extremely rare (2/441); between-year differences were not significantly different in multiple nest occupancies per night ($G = 0.01$).

The distances males moved within an area were estimated from

the shortest interval between nests occupied by the same individual; measurements were made without regard to intervening "obstructions" (water, bank and vegetation). The distances moved between nights, including return to the same nest, were not significantly different in 1977 ($\bar{x} = 0.7$ m) and 1978 ($\bar{x} = 1.0$ m; $U = 12265.0$, $N = 393$). However, males traveled slightly farther within a given night in 1978 ($\bar{x}_{1977} = 1.0$ m, $\bar{x}_{1978} = 3.0$ m; $U = 117.5$, $N = 53$, $P = .01$). The average distance actually moved between and within nights was 1.8 m, but it was 0.8 m (Fig. 55) when those nightly returns to the same nest were included. The first nest occupied by a male after a successful mating was significantly farther in 1978 ($\bar{x}_{1977} = 1.4$ m, $\bar{x}_{1978} = 3.8$ m; $U = 85.5$, $N = 48$, $P = .004$). The combined two year average ($\bar{x} = 2.0$ m) was not significantly different from the distance traveled ($\bar{x} = 1.8$ m) when new calling stations were established without prior mating success ($U = 3502.5$, $N = 198$). Surprisingly, the few movements male *rosenbergi* made in the breeding habitat were short, considering the length of the primary section was only 120 m, with nests found throughout most of the central portion (Fig. 28), and a male's daytime retreat probably was 15–30 m from his nest. Familiarity with a few meters of breeding area appeared to be extremely important, probably because it improved the resident's chances of successfully defending his territory and escaping predators.

LENGTH OF RESIDENCY

Residency was calculated as the number of days from first to last observation. No male marked in 1977 on the ODSS was recaptured in

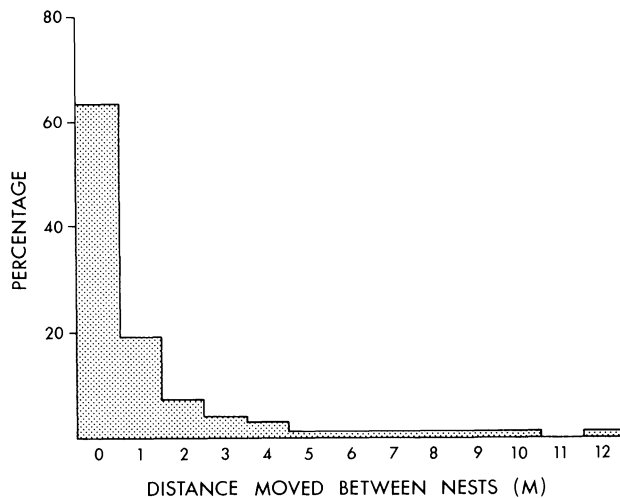


Fig. 55. Distances male *rosenbergi* moved within and between nights. All distances were rounded to the nearest meter.

1978. Similarly, none of the 17 males marked at Chiva Chiva Quarry in 1976 was recaptured in 1977 or 1978. Only males and females entering the primary section were included in the following analysis, but all of their observation dates were considered regardless of location. Male residency was 1–80 days ($\bar{x}_{1977} = 16.5$; $N = 69$) and 1–55 ($\bar{x}_{1978} = 23.3$; $N = 26$). The two years were not significantly different ($U = 678.5$, $P = .07$), and the combined average was 18.3 days. Also, when 10 day intervals were used the yearly differences were not significant ($G = 10.4$, $df = 67$, $N = 95$).

The few observations on 1978 females were lumped with those from 1977, including the three individuals found in both breeding seasons with residencies of 289, 340 and 404 days. The average was 23.2 days ($N = 75$). The male and female distributions, using 20 day intervals with the three exceptional female records lumped in the last cell, were marginally significantly different ($G = 8.52$, $df = 3$, $N = 167$, $P = .04$). Whether the two residency distributions were really different, with females tending to live longer than males on average, requires much more data. The average residency for years and sexes combined was 20.5 days (Fig. 56).

I believe residency data can be used to estimate *rosenbergi* survivorship for the following reasons: (1) marked individuals never regenerated amputated toes so that they could not be distinguished from an unmarked frog, (2) individuals moved infrequently between

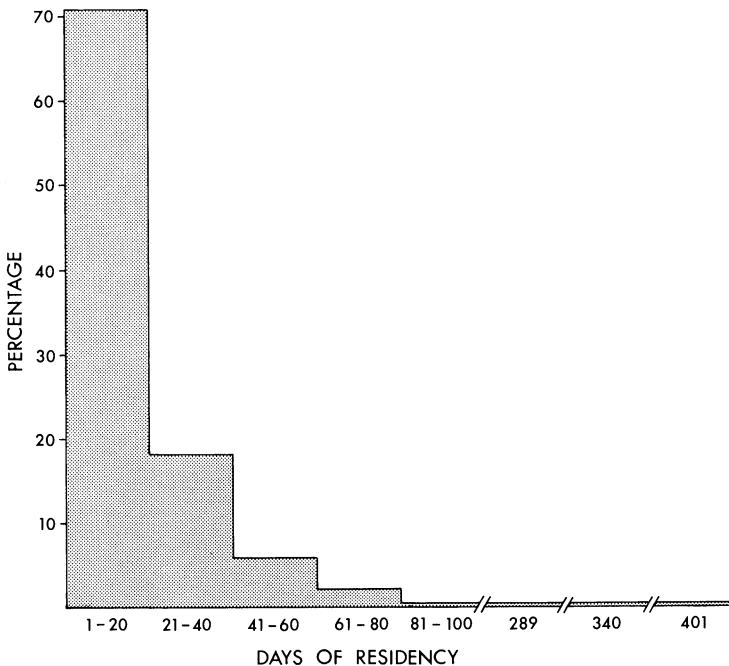


Fig. 56. Spans of days during which individual male and female *rosenbergi* were observed.

choruses and, the few that did, covered little distance, (3) males moved only a few meters within a breeding area, and they were rarely absent between the time they first entered it and when they permanently disappeared, (4) death due to predation and fighting among males was often observed (pp. 88–90, 102–111), (5) the local densities of known and suspected predators were extremely high, and the behavior of most of these species strongly suggested that they actively pursued *rosenbergi*, particularly calling males, and (6) other members of the *boans* group (*boans* and *crepitans*) studied in the Canal Zone were never recaptured between years, and their residency statistics were similar to *rosenbergi*'s. Additional relevant evidence may include wounding due to fights among male *rosenbergi*. The extremely low incidence of combat scars in individuals at first capture probably indicated that most had not been chorus residents elsewhere that year (pp. 104–105).

If residency was a good measure of survivorship, *rosenbergi* is one of the shortest-lived anurans known (Collins, 1975; Turner, 1962). It appeared to take one year to reach sexual maturity, and most adults died before their second breeding season. Further, predation and fighting probably were the principle causes of adult mortality, rather than some inherent genetic-physiological limit, because *rosenbergi* lived much longer than two years. I maintained two wild-caught adult males in captivity for nearly two years, and Bowler (1977) reported five wild-caught adult males living over 3.5 years in the Philadelphia Zoo.

PREDATORS

Predation on adult anurans is rarely observed in the field and it usually is inferred from only weak circumstantial evidence. A snake, *Leptodeira annulata* (Colubridae), and a frog, *Leptodactylus pentadactylus* (Leptodactylidae), were predators on *rosenbergi*. The large number of known and suspected attacks, the predators' search behaviors, and their occasional abundances suggested these two species were responsible for much of the adult mortality implied by the residency-survivorship data (Fig. 56).

L. annulata and congeners were considered predator specialists on anurans by Duellman (1958). *L. annulata* has a pair of enlarged deeply grooved rear maxillary fangs and well-developed venom (parotoid) glands, which it uses to kill its prey. The predator is nocturnal, rarely found away from water and exhibits peaks of abundance that "may be correlated with amphibian activity" (Duellman, 1958:120). It was frequently observed along the Obispo Diversion in 1977. At least five *L. annulata* were present; three of the four marked individuals were recaptured several times. In spite of the many more hours spent on the ODSS in 1978, only one subadult (46.5 cm TTL) *L. annulata* was observed, and it was dug out of a rotten log. I

believe these snakes were, like their prey, more widely dispersed in 1978. *L. annulata* was usually encountered on the bank or in the dense riparian vegetation within 2 m of the ground. They were almost always found in the vicinity of calling male *rosenbergi*. Wever's (1978) research on the cochlear potentials of several colubrids (no *Leptodeira* were investigated) indicated that all species have their greatest sensitivity to the low frequency range (80–700 Hz) of either airborne sounds or substrate vibrations, and that they are capable of locating a sound source. *L. annulata* may have located their prey by using auditory cues, because much of the energy in a male *rosenbergi*'s advertisement call was in the low frequency range (200–700 Hz, Fig. 61A; Kluge, 1979).

In 1977, a gravid female and three male *rosenbergi* were observed being killed and eaten by *L. annulata*. The sizes of the four predators were: $\bar{x}_{TTL} = 65.0$ cm (ORV = 61.0–72.5) and $\bar{x}_{WT} = 29.0$ gr (ORV = 26.5–30.6). These relatively small snakes exhibited no difficulty in subduing their prey; it took about 20 min for each frog to die, apparently as the result of envenomation, and two undisturbed ingestions lasted 50 and 70 min. All of the snake attacks involved an initial chewing (venom injection?) of the prey's hindlimbs. The female was preyed upon while in amplexus. Her mate must have been struck by the predator, because he perched limply on a small branch above his nest, and remained in a torpid state for several hours after the attack. He seemed fully recovered the next night.

Adult *L. pentadactylus* were extremely abundant on the primary section in 1977; far fewer were encountered in 1978. The predator's density may have changed, because of the different prey distribution, or both species' reproductive behaviors could have been affected by the same environmental factor. A *L. pentadactylus* ate a male *rosenbergi* (SVL = 86.0 mm and WT = 28.6 gr) in 1977, and a male and gravid female, the pair almost certainly in amplexus, were eaten in 1978. The female's size was not recorded; her presumed mate was SVL = 86.0 mm and WT = 30.8 gr. The size of five adult *L. pentadactylus* from the ODSS, $\bar{x}_{SVL} = 151.0$ mm and $\bar{x}_{WT} = 275.0$ gr, indicated that a single ingestion of two *rosenbergi* was an amazing feat. I doubt that *rosenbergi* made sounds while being attacked by *L. pentadactylus*, because ingestion was quick and apparently always head first.

When *L. pentadactylus* were encountered they usually faced a calling *rosenbergi*. It was not uncommon to find a male *rosenbergi* perched in the vegetation above his nest, where he had called earlier in the evening, with a *L. pentadactylus* below him in or near the basin. The fact that the dominant frequencies of the advertisement calls of both *L. pentadactylus* and *rosenbergi* were between 200–800 Hz (Straughan and Heyer, 1976) suggested that the predator used the prey's vocalization as a locational cue. Jaeger (1976) also described an

anuran predator-prey (*Bufo marinus*, *Physalaemus pustulosus*) system where vocal cues were involved. However, the mating calls of the two species were fundamentally different.

One female and five male *rosenbergi* had large deep cuts, torn skin and/or massive abrasions. These wounds almost certainly were made by predators with larger and sharper teeth than *L. annulata* and *L. pentadactylus*. Two of the males and the female were never seen again. I believe the animals responsible for these attacks were mammals, *Chironectes minimus*, *Philander opossum* and *Metachirus nudicaudatus*, and a crocodilian *Caiman crocodilus*. Occasionally, *Chironectes* were seen swimming along the ODSS where *rosenbergi* occurred, and *Philander* and *Metachirus*, which are known frog eaters (Walker, 1964), were often observed, usually above ground and as high as 15 m. In 1978, a *Philander* tried for nearly two hours to capture a male *rosenbergi*. The frog called occasionally from an oil palm. The opossum systematically investigated each frond in the vicinity of the *rosenbergi*. When it moved along the branch with the frog on it, the prey jumped to a new perch, and the predator excitedly ran back to the trunk and proceeded along another frond. Ryan (pers comm) demonstrated that *Philander* use acoustic cues to locate calling males of some frog species.

Several *Caiman* were seen in isolated swamps on the ODSS. At least one juvenile (approx 60 cm TTL) was present in the main pool of the primary section from July 6 to August 11, 1977. It was often observed near a *rosenbergi*. *Caiman* were extremely shy in this area of Panama, probably because they were hunted. Our nearly nightly presence must have added to their shyness and rarity.

No doubt, some predation of *rosenbergi* occurred during daylight. However, I believe most attacks took place at night when the frogs were active. Perhaps the most obvious indication of the importance of nocturnal predation was that most calling males, including amplexed pairs, left the ground whenever it started to rain. Predator noises probably were much more difficult to hear in the rain.

DAILY ACTIVITY PATTERN

I found only one *rosenbergi* during the day. Even this individual was encountered accidentally at Chiva Chiva Quarry. It was asleep in the forest litter. I believe *rosenbergi* were rarely observed during the day because they were inactive and hidden above ground. Freshly caught aquarium-held individuals were rarely awake when it was light. They usually were tightly pressed against the vertical glass at the corner of the container, as far above the substrate as possible. Moreover, the first *rosenbergi* calls given each evening in the field were almost invariably issued several meters above ground, and it was

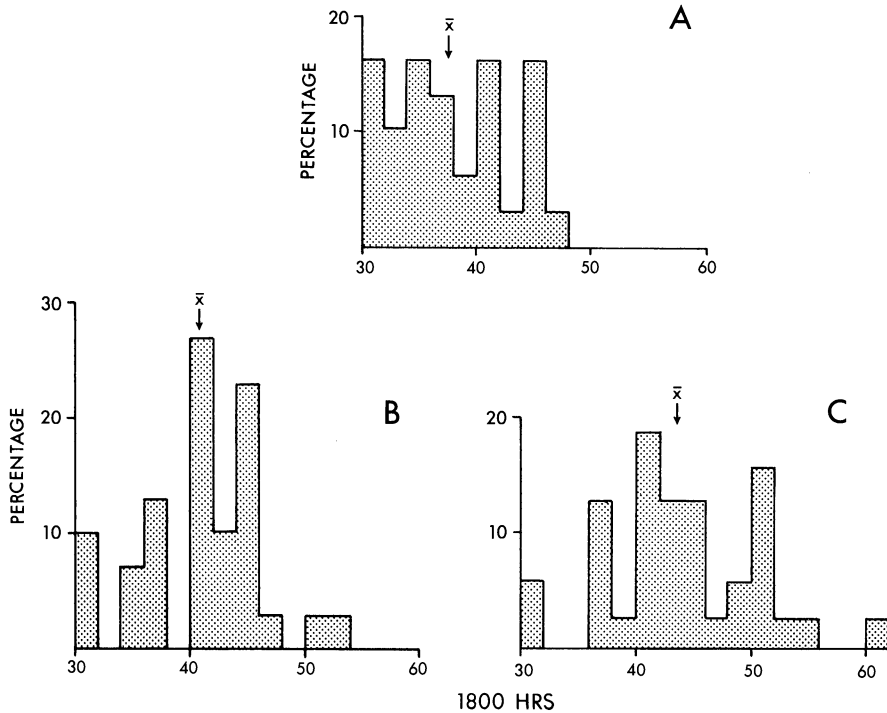


Fig. 57. Behavior of male *rosenbergi* when first observed in the evening in 1977. A. First territorial calls given from elevated sites (\bar{x} = 1837.0 hr, N = 31). B. First territorial and/or isolated advertisement calls given within or near nests (\bar{x} = 1840.6 hr, N = 30). C. First sustained chorus of advertisement calls given within or near nests (\bar{x} = 1843.6 hr, N = 32).

not uncommon at dusk to see individuals descending from the canopy.

The nightly pattern of activity varied little in *rosenbergi*. Few males descended from their daytime retreats without calling first. Fig. 57 illustrates the little variance in times males began calling (A), descended to nests (B), and subsequently formed active choruses (C). Rain retarded or inhibited mating activity in *rosenbergi* (p. 18), and a completely overcast and dark sky caused males to call much earlier than usual. To standardize the data in the following analysis, rainy or dark days were excluded. The average time when the first calls of the evening were given was 1837.4 hr in 1977 (Fig. 57A) and 1839.4 hr in 1978; the two were not significantly different. These first calls were almost invariably territorial and issued from elevated sites. Within minutes males descended to their nests (Fig. 57B), where they re-issued territorial calls and/or gave occasional advertisement signals. In 1977, males usually began descending by 1840.6 hr. To accomplish their descent so quickly, they moved noisily, and individuals often took several meter-long jumps, some landing in the water or on the investigator. It was an eerie feeling to be standing

quietly at twilight in a jungle stream and have a large wet frog suddenly jump on my arm or face. Males were significantly slower in 1978, with an average of 1853.1 hr. I believe the urgency of males getting to their nests was related to the number of competitors they heard giving the first territorial calls; there were far more males present in 1977 (compare Figs. 48 and 51). Fig. 57C illustrates that the first sustained chorus of several male *rosenbergi* giving advertisement calls from in or near their nests averaged 1843.6 hr in 1977. This third phase was impossible to score in 1978, because few males were present each evening, and they usually did not descend to the ground before issuing the advertisement signal. Also, I believe the yearly differences were a function of the number of sexual competitors present.

There was a significant between-year difference in the time females first appeared each evening ($\bar{x}_{1977} = 2002.5$ hr, $\bar{x}_{1978} = 1918.8$ hr; $U = 405.0$, $N = 73$, $P = .01$). The yearly samples of the females' time of descent were lumped together and contrasted to comparable data for male *rosenbergi* (Fig. 58), and they were found to differ significantly ($\bar{x}_{\text{males}} = 1848.2$ hr, $N = 76$; $\bar{x}_{\text{females}} = 1933.7$ hr; $U = 601.5$). Some of the difference in arrival time must be a function of females not being as readily located by the investigator, largely because they did not vocalize and usually moved more quietly. However, females might be expected to spend considerable time at an

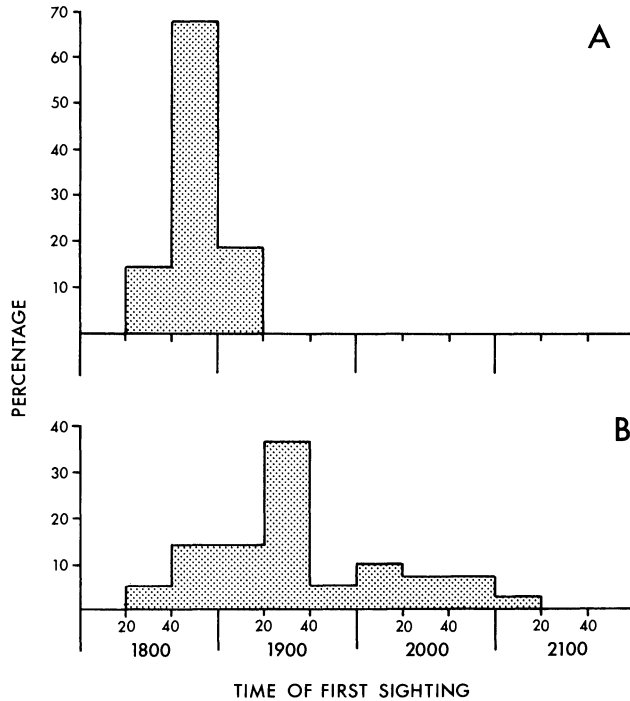


Fig. 58. Times the first male (A) and female (B) *rosenbergi* were sighted each evening. The average time was 1848.2 hr for males; 1933.7 hr for females.

elevated site surveying the competing males before finally descending and becoming apparent to the scientists on the ground (pp. 144–149). The females' earlier appearance in 1978 probably was due to the fewer males they had to choose among.

The time between the first sighting of a female and when she was amplexed was 2–104 min. Females made their choice more quickly in 1977 ($\bar{x} = 18.9$ min, $N = 17$) than they did in 1978 ($\bar{x} = 28.6$ min, $N = 11$); however, this yearly difference was not significant ($U = 71.0$). The amount of time females spent in nests before being clasped by resident males averaged only 10.6 min and was similar in both years ($U = 52.0$; 1977, $N = 17$; 1978, $N = 9$; Fig. 59).

There were no significant between-year differences in the times pairs were first observed in amplexus ($U = 328.5$; $\bar{x}_{1977} = 1941.4$ hr, $N = 40$; $\bar{x}_{1978} = 1927.8$ hr, $N = 21$). The samples were combined in Fig. 60, and the average time of amplexus, $\bar{x} = 1937.7$ hr, was only 54 min after the average time when males began advertising for females (Fig. 57C). Also, it was only shortly after the average female appeared on the study site ($\bar{x} = 1933.7$ hr). I conclude that females usually chose their mates shortly after entering the chorus.

SOCIAL BEHAVIOR

BEHAVIORAL DIFFERENCES AMONG MALES

Male *rosenbergi* were classified each night according to nest use, movement, calling, and distance from other calling males, and some

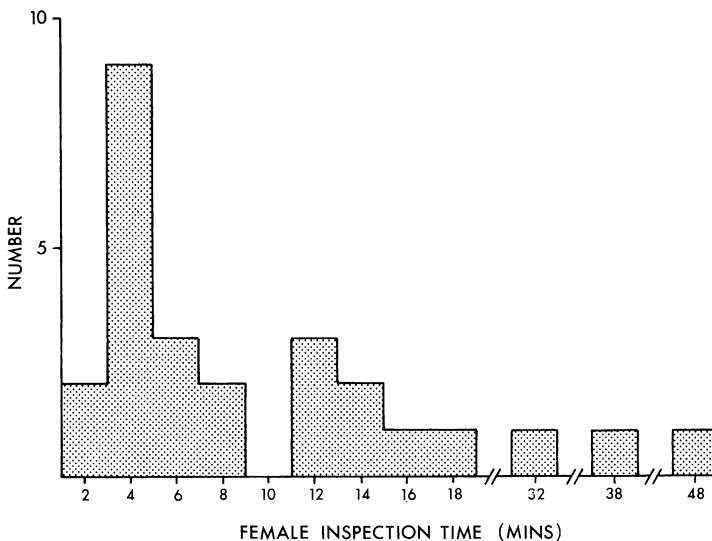


Fig. 59. Amounts of time female *rosenbergi* spent in nests before mating with the resident ($\bar{x} = 10.6$ min).

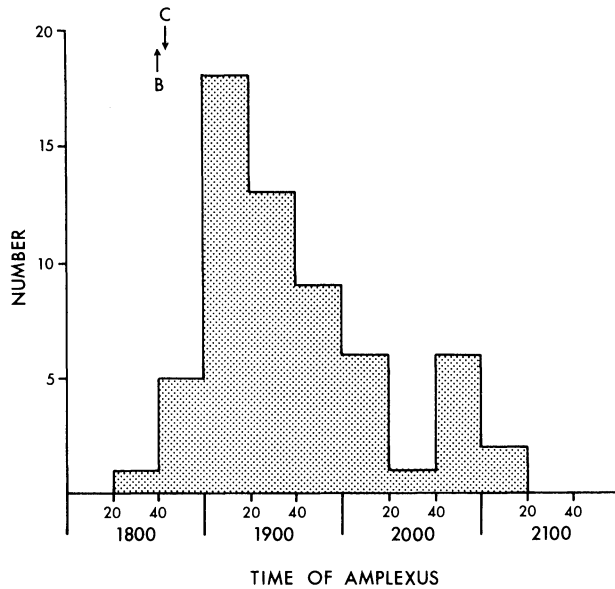


Fig. 60. Times of amplexus in *rosenbergi* ($\bar{x} = 1937.7$ hr). The B and C arrows refer to the average times of male arrival and chorusing summarized in Fig. 57.

individuals' classifications varied between nights. Intruders tended to move frequently, apparently in search of nests; they rarely gave advertisement calls, but usually produced territorial and encounter signals (Table 10). In contrast, a resident occupied the same basin throughout most of the evening and regularly gave advertisement and territorial calls. A male returning to the same basin two or more consecutive nights clearly was its resident, although he might not have constructed the nest himself. A resident was either isolated from other calling males or a member of a chorus. Chorus residents were involved in more aggressive acts and matings than isolated residents (pp. 140–142). Isolated males did not appear to occupy suboptimal areas, because such locations, even the same nests, frequently were used by chorus residents at other times.

While residents regularly issued advertisement calls from a basin, they often signaled from elevated perches under conditions of low male density or rain and flood. In fact, one of the most conspicuous differences between the high (1977) and low (1978) density years was the degree to which nests were employed as calling stations. Fifty-one males entered 88 nests in 1977 (July 5–August 21; Figs. 29, 48), whereas in 1978 (June 4–July 7, July 9–August 25) 14 males occupied 28 nests (Figs. 30, 51). In 454 sightings of male residents in 1977, individuals were not calling in their nests only 86 times (19%). In 1978, males were outside their nests in 70 of 166 sightings (42%). The

TABLE 10
CLASSIFICATION OF MALE *ROSENBERGI* ACOUSTIC SIGNALS

-
-
- A. Female Intended Recipient
 - 1. High Intensity (advertisement or mating call)
 - 2. Low Intensity (courtship call)

 - B. Male Intended Recipient
 - 1. High Intensity (territorial call)
 - 2. Low Intensity (encounter calls)
 - a. chuckle
 - b. growl¹
 - c. mew¹
 - d. bark
 - e. hiss
-

¹Also issued while being preyed upon.

difference was significant ($G = 32.7$). The low nest use in 1978 might have been a function of the relatively few competing males.

Some males, usually newcomers to the area, gave neither territorial or advertisement calls during the evening, but sat silently 1–2 m above ground. I never observed a male in an uncontested nest that did not vocalize. However, on a few occasions silent males entered nests and remained there for several minutes without evoking an aggressive response from the resident. When the intruder gave any kind of vocal signal he was attacked by the resident. Residents appeared to mistake intruding silent males for females on two occasions in 1977; the resident gave the courtship signal when the intruder entered the nest. Silent resident males rarely, if ever, obtained matings.

The sexual interference strategy (Arnold, 1976) observed in *Rana catesbeiana* (Howard, 1978b) and *Hyla cinerea* (Perrill, et al. 1978) does not apply to *rosenbergi*, because silent males frequently moved during the night, and none was observed trying to intercept a passing female. Forced amplexus was most unlikely in *rosenbergi*, because eggs were deposited in a male's territory (= nest), which the female inspected, and she was capable of escaping if clasped. Also, sexual parasitism, as an explanation for a male's silence, was ruled out for these reasons. Furthermore, I am confident that an intruding male clasping a female would have been attacked by the resident and the pair driven from the nest. Silent males rarely remained near a resident for long, and I doubt they were waiting for a calling site to become available. In any case, a waiting strategy would be a poor one, because oviposition took place in the nest. Resident males usually guarded the nest for two nights, and rapid nest re-use thereafter led to cannibalism. In conclusion, I hypothesize that males were silent because it reduced their chances of being attacked and preyed upon while searching for an unoccupied nest. However, I can not rule out the possibility that males were silent simply because they had no territory to advertise.

VOCALIZATION

Acoustic signaling by male *rosenbergi* was extremely complex, because of the call types (Table 10), existence of intermediate (transitional) sounds, environmental effects, geographic and individual variation, and multiple social contexts. Females were mute, even when preyed upon, although one screamed when toe-clipped. I handled and observed several hundred live *rosenbergi* in the field, but I neither felt or heard either sex issue the release vibrations or calls characteristic of many anurans (Bogert, 1960). The existence of a prolonged breeding season, territoriality and female choice in *rosenbergi* probably provided few situations in which a release vibration or call would be advantageous.

Eight vocalizations made up the male *rosenbergi* acoustic repertoire (Table 10). Classification of the signals was based on the likely recipient of the call (female or male), whether or not it was directed at a specific individual, its intensity (long versus short distance transmission), and the spectral and temporal properties of the sound. It is not exceptional to find so many calls structurally related to the advertisement signal (Pengilley, 1971). Apparently, only *Rana catesbeiana* has more distinct vocalizations than *rosenbergi* (Kolson, 1973).

Advertisement (mating) call: This was the most frequent vocalization given by *rosenbergi*; it formed the nightly chorus between 1800–2200 hr. Most *rosenbergi* males called in small groups, and 2–3 such choruses usually formed each evening. The absence of stationary choruses suggested that breeding sites were not limited. Social factors related to increased probability of mating were a more likely explanation for chorus formation (pp. 140–149). The function of the advertisement call was largely determined by the female's response to tape recordings played in the field. Isolated gravid females always were, and usually quickly, attracted to the sound source, whereas males rarely proceeded in that direction and, when they did so, their movements were much slower and circuitous (pp. 93–95). Mecham (1961) and Pengilley (1971), among others, stated that advertisement calls serve to attract males as well as females. However, such a vocalization is not likely to have evolved as a male attraction signal, from the point of view of the individual emitter, unless unintended male recipients used the calls to locate other sexual competitors and thereby formed choruses to which females were more attracted.

It has been frequently claimed that certain call parameters provide female anurans with cues to the potential mate's size (eg, Licht, 1976; Davies and Halliday, 1977 and 1978; Wilbur et al. 1978). Such claims require two assumptions: (1) the dominant frequencies of the mating call are negatively correlated with male body size, and (2) females have the neurophysiological ability to detect differences in frequencies of conspecific calls. Ryan (1980) summarized the cases

where a frequency-body size correlation has been demonstrated, and the number of examples is small. Also, Zweifel (1968b) noted that the effect of body size may be masked by individual variation in call frequency and variable physical factors (eg, temperature). Such a frequency-size correlation could not be demonstrated in *rosenbergi*. This may not be surprising considering the little range of variation in male size ($ORV_{SVL} = 79.0-88.0$ mm) and the variable conditions under which competitors called (eg, $24.0-26.8^{\circ}$ C air wet-bulb, and vocal sac in contact with water or not).

The advertisement call sounded like someone monotonously beating on a solid piece of wood, and it has been described onomatopoeically as "tonk-tonk-tonk" (Duellman, 1970:256). In the Canal Zone, it consisted of 2-4 notes, rarely one or five, with a mode of three (Fig. 61A; Breder, 1946; Fouquette, 1968). The Costa Rica population (Table 1) had a mode of two, however, Duellman (1970) apparently did not find such a difference in his Costa Rica sample. At the ODSS, the call repetition rate at $24.0-27.0^{\circ}$ C air wet-bulb averaged about 40/min, and the call (with three notes) and individual note duration rates were approx 0.4 and 0.06 sec, respectively. The repetitious nature of the call probably was effective in overcoming a noisy channel (Littlejohn, 1977) and providing good locational cues (Pettigrew et al. 1978; Chung et al. 1978). Each note had two obscure pulses, the call was poorly modulated, monophasic, and with a dominant frequency at approx 400 Hz. The call carried well over 100 m. Gerhardt (1976) indicated that low frequencies are better than high for long distance communication because of their lower attenuation.

The advertisement call was produced with a fully extended vocal sac (Figs. 25-26). It usually was given by a male in a nest or on the ground near a basin. Occasionally, the male called from a perch near a nest, but only rarely from such a height that the frog could not be seen by the investigator or where there was no obvious relationship to an oviposition site. The male's vulnerability to predation no doubt increased when he called from an exposed position such as a nest (Nelson, 1973), and the use of perches may not have reduced a male's chances of mating, at least under low male densities. The pitch and intensity of the advertisement signal in *rosenbergi* were affected by the substrate from which the male called and, in particular, whether or not the vocal sac was in contact with it. A male in deep water seemed to call with slightly lower frequency and much less volume. This difference was most conspicuous when compared to an individual advertising from an open perch above ground.

Two or more males chorusing together usually gave advertisement calls antiphonally; the cadence of the individual calls was irregular at first. Antiphonal behavior between males may have reduced acoustic interference and maximized individual signaling

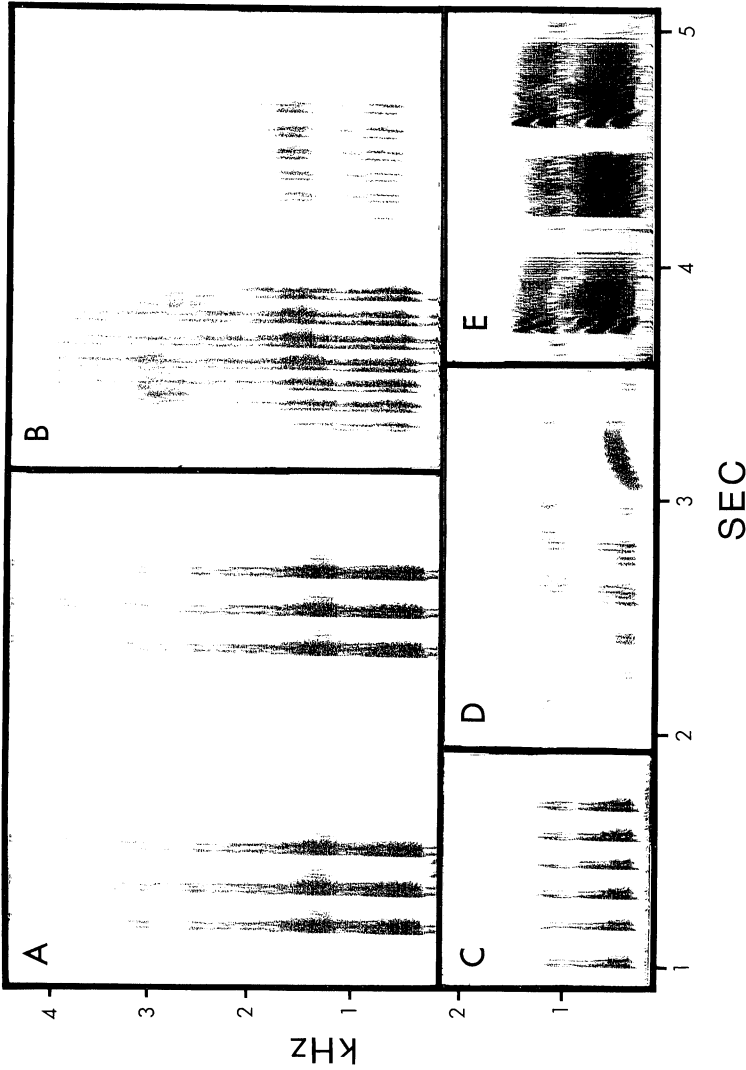


Fig. 61. Representative audiospectrograms of male *rosenbergi* calls (wide band filter 150 Hz). A. Advertisement call issued by male no. 36 from open water on July 22; water temperature 27.0° C. Two successive calls of three notes each are shown. B. Territorial call given by male no. 46 on a perch one meter above ground on July 20; wet bulb air temperature 24.0° C. Male no. 46's call of seven doubly pulsed notes given in rapid succession was answered by an unidentified conspecific several meters away. C. An unusually long, fast and regular series of courtship notes issued by male no. 51 on August 3; nest water temperature 26.0° C. Female no. 36 was inspecting the nest. D. Chuckle and mew encounter calls given by males nos. 36 and 52, on July 25; wet bulb air temperature 25.6° C. These males had finished a wrestling bout, and they were a few centimeters apart when the calls were recorded. The chuckles are the calls with 2-5 notes, the mew the continuous rising sound. E. Three growl encounter calls given by males nos. 31 and 36, on July 18; ground temperature where the fight occurred was 25.8° C. The pair was in a "bear-hug" wrestling position (see Fig. 62) when the growls were recorded; the first and last calls in this sequence were issued by the same male. Note the harmonics.

efficiency (Alexander, 1975; Littlejohn, 1977; Wells, 1977a). Calling in duets, trios, etc. is likely to be found in all species, such as *rosenbergi*, where the signal is a repetitious set of calls and notes. Widely spaced males rarely called antiphonally. Considerable call overlap usually occurred when four or more males sang together. The length of a calling bout varied positively according to the number of males involved, with the exception of some conspicuously long uninterrupted sequences produced by isolated males. Also, bouts usually were shorter early and late in the evening. It was my subjective impression that no particular male in a chorus usually initiated or concluded the bouts. Isolated males were never heard transforming an advertisement signal into a territorial call, however, males in a chorus often did so without pausing, particularly if the other callers were nearby. The transition was made by increasing the frequency, and note and call repetition rates.

Courtship call: The courtship signal (Table 10) was structurally similar to the advertisement call, except for its much reduced intensity and slightly slower rate (Fig. 61C). The number of notes per courtship call was highly variable; two were frequently heard. The vocal sac usually was only partially extended when this call was issued (Fig. 64). A perfect transition, without interruption, to this short-distance vocalization was often heard when a female entered a calling male's nest. A rejected male always gradually shifted to the advertisement call when the female left. In fact, it was the general social context in which these transitions occurred, the unmated female entering or leaving a nest, that indicated so clearly for which sex the advertisement and courtship calls were intended. I know of only one instance where amplexus took place without a courtship signal. Further, the courtship signal's intensity and note repetition rate occasionally varied as the female moved around in the nest or showed signs of leaving, particularly if it was a long period of investigation (Fig. 61C; see also Fig. 60). A transition from a courtship call to either a territorial or a chuckle signal rarely occurred (Table 10).

This contextual information still does not answer the question of function. What information did the courtship call communicate to the female? A male and female in the same nest obviously sensed each other; they usually touched one or more times prior to the "female rub" which initiated amplexus. Heinzmann's (1970) statement that the anuran courtship call is an "excitement" sound begs the question. Did the courtship signal indicate the resident male's lack of aggression and readiness to mate, as Wells suggested (1977a,b; see also Alexander, 1975, and West-Eberhard, 1979), or did it correlate with some aspect of male fitness (eg, size or experience)? These questions remain unanswered, but in any case, the low intensity and usually slower temporal character of the courtship call made it less likely to

be detected and followed by predators and other males (Wells, 1977a). On two occasions, an intruding silent male entered a calling individual's nest, and the resident immediately switched to the courtship signal. Presumably, the resident was fooled by this unusual silent behavior of the intruding male. One intruder left without incidence, but in the other case, the intruder chuckled, and a violent fight ensued.

Territorial call: This vocalization was the second most frequently given by *rosenbergi* (Table 10). Surprisingly, Breder (1946: 425) and Fouquette (1968) did not recognize it as distinct from the advertisement call. A territorial call usually stimulated nearby males to respond with the same sound (as illustrated in Fig. 61B), and nonviolent or violent aggression often followed (Fig. 62). The advertisement call usually did not evoke a territorial vocal response unless males were particularly close (3–4 m). Vocal responses and directed aggression were easily elicited with playback tapes.

The territorial call was nearly always the first *rosenbergi* sound issued each evening (Fig. 57). It was also given sporadically each night after the chorus of advertisement calls and mating ended (Fig. 60). Territorial calls were not always given at these times in immediate response to another male, and their undirected nature suggested some ritualized spacing function. An isolated male rarely used the territorial signal except early and late in the evening. The territorial call was given from almost any location, in a nest, on a nearby perch, near the forest canopy, in a plastic bag, and occasionally even in amplexus. It was the only long distance call given by a male guarding his young.

The territorial call had high intensity and it was not repeated with a regular cadence like the advertisement call (Fig. 61B). There was a certain antiphony to territorial calls, even when large numbers of males were present, because of the stimulus-response nature of the signal. The most conspicuous transition to another call type, although not often heard, involved shifting to the encounter chuckle. These two signals seemed to be the same, except for the much reduced intensity of the chuckle.

Encounter calls: The chuckle, growl, mew, bark and hiss calls (Table 10) given by males during aggressive encounters were distinct vocalizations (Fig. 61D–E), but they were not necessarily given in different social contexts. All five signals were of low intensity and pitch. Usually they elicited a similar sounding response from the antagonist. The chuckle appeared to be a low intensity territorial call and the bark may have been only a pulsed growl. Antiphonal growls were often given by wrestling males (Fig. 61E). The soft bark tended to be made when they broke apart. It was also issued on one occasion by a resident when a female deserted his nest. Encounter call transitions were heard between growl and bark and growl and mew.



Fig. 62. Male *rosenbergi* nos. 128 (below) and 144 (above) wrestling with typical "bear-hug" holds on August 8, 1978. Note the prepollical spine of male no. 128 jabbed into his opponent's eye. The wrestlers were 1.8 m N of nest no. 44 containing the 41 hr old progeny of male no. 128. Male no. 128 repulsed the intruding no. 144 from the vicinity of nest no. 44. See Fig. 67 and text (pp. 116-119) for further explanation.

Why did fighting males give encounter calls, even with low intensity, considering the likelihood that predators were better able to locate the fighters? Wells (1977a) reviewed the extensive literature on encounter calls in hylid frogs. Such vocalizations are common, and he suggested they usually function to warn an intruding male to leave the area. This explanation does not seem to apply to *rosenbergi*, because a fight invariably preceded or followed an encounter call. Female *rosenbergi* solicited fights between adjacent males (pp. 146-147), and perhaps encounter calls signaled a male's aggressiveness to the female and improved his chances of mating.

All four male *rosenbergi* preyed on by *L. annulata* made loud sounds while being attacked. The two recorded distress sounds were similar to the encounter growl and mew (Fig. 61D-E) that were made in male-male aggressive contexts. The prey's distress growl was either a long uninterrupted train of notes or distinctly pulsed, and it was made with the mouth closed. The mew was a transitional extreme of the growl and it was made with the mouth open. The distress growl had the harmonic phase shifted to the end of the call, unlike the aggressive growl (Fig. 61E). The single female prey did not make a sound. However, one female screamed loudly with her mouth closed when I amputated her digit. The simplest explanation for prey sounds is that they startle predators, which allows the prey to escape. Prey sounds also may have a general warning function, although most male *rosenbergi* did not stop calling when a nearby conspecific screamed. Yerkes (1905) showed that lack of auditory reaction in *Rana clamitans* was due to some form of inhibition and not to insensitivity.

AGGRESSION

Gladiator frogs, *faber* and *pardalis*, were claimed to be the most aggressive anurans known (Wells, 1977b:679). However, Breder (1946) did not observe aggression in *rosenbergi* despite extensive field experience with that species. In fact, he (1946:410) implied that none existed, because he reported intruders simply moved away when placed next to a resident calling male. On the contrary, my observations suggest that *rosenbergi* is extremely aggressive in nature, at least under high densities, and, like *faber*, males can kill an opponent. Moreover, reproductively active male *rosenbergi* kept together in large aquaria invariably fought and death usually resulted. Breder's observations on *rosenbergi* appear to have been made at densities sufficiently high where I would predict aggression to have been recorded.

I recognized three levels of aggression in *rosenbergi*: undirected, nonviolent and violent. Undirected aggression consisted of vocalizations not directed toward a particular opponent. These signals

usually included the territorial call and, much more rarely, some of the encounter vocalizations (eg, chuckle and growl). Territorial calls issued by males in the evening from elevated sites near daytime retreats were the best examples of this undirected aggression (Garton and Brandon, 1975; Wells, 1978). The awakening frogs usually were separated by considerable distances, and they were almost certainly out of visual contact with one another. Undirected aggression also was exhibited late at night, after the mating period and the chorusing for females had stopped, when a resident male usually was perched in the vicinity of his nest. Occasionally, he issued a territorial call, but in most instances it was not in response to any other conspecific, whether they were calling or not. Males rarely gave encounter calls when no other *rosenbergi* could be found in their immediate area. It is possible that these encounter calls were given by mistake when one of the numerous smaller species of frogs (Table 8) moved nearby. The fact that the early evening calls were not site-specific suggests they established individual distances (Wells, 1977b). In contrast to the early evening territorial calls, those same undirected signals given after the mating period were usually issued by males close to their nests. No doubt, they generally advertised nest ownership to frequently moving intruders.

The nonviolent form of aggression occurred when males sensed each other, visually and/or auditorially, and yet no physical contact was made. Rapid charges and chases were common on the ground or in vegetation, and occasionally one of the aggressors elevated himself on extended fore- and hindlimbs and walked slowly in this conspicuous fashion toward the other male. Territorial calls, chuckles, mews, barks and hisses were common (Table 10, Fig. 61B, D-E). The fact that these acts took place only when at least one resident was involved, implicates this level of aggression in nest defense.

Violent aggression involved physical contact, including wrestling (Fig. 62) and what I termed "blocking," and wounding frequently occurred. A male blocked by rushing or diving on his opponent and knocking him away. Wrestling and blocking took place on any substrate. Wrestling was more frequent and usually involved a "bear-hug" position (Fig. 62). Occasionally, other holds were assumed, such as around the hindlegs, but I never observed males in an amplexus-like position. Usually wrestling males reached out with their hindlimbs and grabbed vegetation, apparently anchoring themselves in a given area or position. It seemed to make little difference with respect to winning (p. 106) how long one male was on top of the other. Wrestling was accompanied by growls (Fig. 61E), usually given alternately by the males involved. Blocking usually was accompanied by hisses. Violent aggression was always in or near a nest and occurred when the combatants included an intruder and resident or two nearby calling residents, but never two intruders.

Vocal males closer than approx 1.5 m invariably became involved in some form of nonviolent or violent aggression.

Occasionally, an intruder attacked an amplexed pair. In three cases, the intruder uncoupled the pair, and in one instance the intruder mated with the female. There were a few other examples where amplexus was interrupted and a second male was found in the vicinity, but aggression was not actually witnessed. Usually, the attacked pair left the nest, hid nearby in the litter, and returned hours later.

The most distinctive feature of violent aggression in *rosenbergi* was the use of prepollical spines (Figs. 13–15). In the typical wrestling hold (Fig. 62), one or both combatants continuously jabbed and cut the other with their unsheathed spines. Also, these weapons usually were directed at the eyes and ear drums. To impair a frog's sight or hearing should increase the probability of its being preyed upon, and in the case of *rosenbergi* these might be considered critical injuries, because of the high levels of predation often encountered. I found several males with infected eyes, and one male had only a necrotic socket. Punctured ear drums were common, and the recipient of such a wound would almost certainly be unable to locate a sound source, that of a predator, or female or male conspecific (Chung et al. 1978; Pettigrew et al. 1978). Lutz (1960b) noted bleeding from the tympanum of a *faber* that died due to fighting. Thus, violent aggression can result in serious wounds, and two male *rosenbergi* (nos. 10 and 60) apparently died from injuries received in a fight. It is impossible to be certain that either male was killed in or as a result of combat, but the following circumstantial evidence, paraphrased from the field notes, seems overwhelming.

Male no. 10 was involved in a violent fight with no. 5 on July 10, 1977 for at least 19 min, and on the following night he was attacked again, while in amplexus, by another male, no. 33. No. 10's last violent fight, in addition to losing his mate, lasted from 1930–2100 hr, and he was found dead near his nest when I returned the next night.

It was not obvious from my autopsy of the two dead males what the actual causes of death were. Neither frog showed signs of predation, cuts and scratches, or soft tissue damage that might have resulted from envenomation. They had been cut and punctured by prepollical spines.

I never observed a female with a cut that I would attribute to a prepollical spine, even in the neck region where the male clasped the female with his hands (pp. 111–115). This is contrary to Lutz's (1960b:63) finding that female *faber* in prolonged amplexus may be severely wounded by the pollices and perish as a consequence. Cuts almost certainly made by prepollical spines were most easily seen on the dorsal surfaces of the head and neck in males and they were rarely present on the midback region. While difficult to see, occasionally

punctures and cuts were evident on the side of the face, particularly near the eyes and on the ear drums. Cuts, especially those on the dorsal head and body, became emphasized as blackened lines when the animal was preserved in formalin and at times were mistaken for part of the natural color pattern. In fact, the artist who rendered the drawing of *faber* for Wied-Neuwied's (1824) description of that species unknowingly illustrated what were certainly cuts received in combat.

Thirty-eight percent of the males were conspicuously wounded after only a few nights of residency; the proportion of wounded individuals was not significantly different in 1977 and 1978 ($G = 0.24$). No wounds were observed on Chiva Chiva Quarry males. Only two of 92 males exhibited any marks that could be attributed to fighting when first captured. This low frequency of wounding may indicate that most new recruits to the breeding population lacked prior territorial and reproductive experiences. However, wounding and healing rates must be accurately determined before a definitive conclusion is reached.

To quantify nonviolent and violent aggression in *rosenbergi* and to make the most reasonable yearly comparisons, I only used those observations recorded from July 5 to August 21, 1977, and June 4 to July 7 and July 9 to August 25, 1978. Still, the quantitative data are likely to be only crude estimates of reality because of certain sampling biases. For example, the investigator usually was attracted to a fight because of the combatants' vocalizations, their splashing in and out of water, or the general disturbance of vegetation. The initial encounter, at least of the nonviolent kind, could have been relatively noiseless and started before getting the investigator's attention. Nevertheless, I have no reason to believe there existed a bias between years in the relative amounts of aggression observed. Further, the number of observation nights in 1978 exceeded that in 1977 (82 and 48 days, respectively), while the actual amount of time spent transecting the study area was greater in 1977 (approx 182 and 311 hr, respectively). Days and hours were not correlated because most social behavior stopped earlier in the evening in 1978, perhaps because of low density. The actual amounts of aggression sampled in the two years were strikingly different and the general conclusions are not likely to be compromised by unequal sampling times.

In 1977, more than 50% of the males (26/51; Fig. 48) were observed in directed aggression, eight nonviolent, 15 violent, and 13 participated in both. In 1977, there were 27 nonviolent and 21 violent bouts totalling 172 and 887 min, respectively. Aggressive behavior was most frequent at 1900 hr (Fig. 63), only a few minutes after males descended to the ground (Fig. 57). Most aggression disappeared shortly after the amplexus period ended (Fig. 59). The peaks of courtship and aggression were identical. There was more violent than

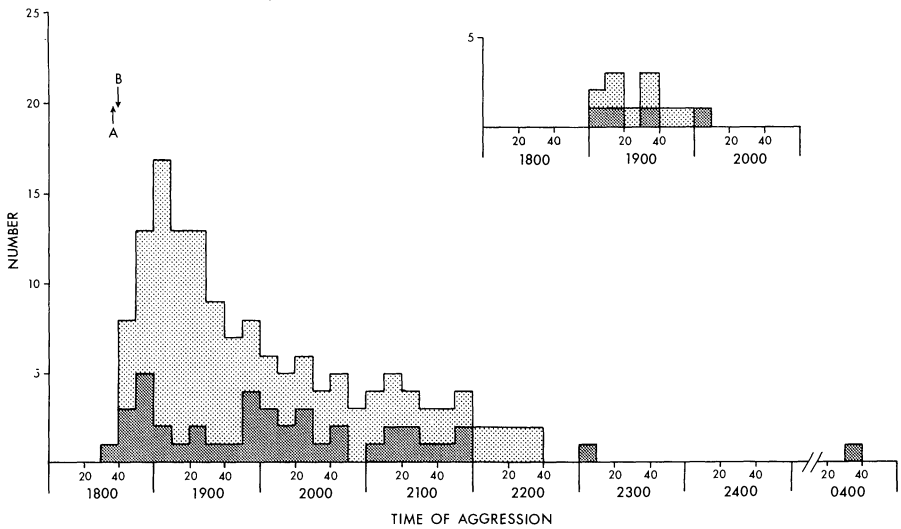


Fig. 63. Temporal distributions of nonviolent (dark) and violent (light) aggression in *rosenbergi* in 1977 and 1978 (inset). The data were collected during July 5–August 21, 1977 and June 4–July 7, July 9–August 25, 1978. A and B arrows refer to the average times when the first territorial calls were given from elevated sites, and the first territorial and/or isolated advertisement calls were issued within or near nests (see Fig. 57). The length of an aggressive bout was rounded to the nearest 10 min interval for purposes of this illustration.

nonviolent aggression in 1977, with the latter occurring throughout the night (Fig. 63). Late night aggression was undersampled because few surveys extended beyond 2400 hr.

In 1978, nine of 14 males (64.3%) visiting the area during the sampling period (Fig. 51) were involved in some form of direct combat, six nonviolent, three violent, and three in both. Nonviolent and violent aggression totalled 26 and 59 min, respectively (see inset, Fig. 63). As in 1977, there was much more violent than nonviolent aggression.

Most of the differences in levels of aggression between years can be explained by differences in male density. The proportion of individuals involved in aggression was not significantly different ($G = 0.79$). The relatively larger number of males involved in aggression in 1978 probably was due to the longer survey period and the longer average residency of individuals (Fig. 56). Size appeared to have little influence on success in fights, but residency was important, particularly when violence was expressed (Table 11).

Wells (1978) reported *Rana clamitans* males were observed in five hours of wrestling during 1000 hr of observation (18 sec/1 hr). The 1978 rate for violent aggression in *rosenbergi* was nearly identical, 59 min/182 hr (20 sec/1 hr), but the 1977 survey, 887 min/311 hr (171 sec/1 hr), revealed a level of aggression approx 10 times greater. Unfortunately, Wells' data came from a square enclosure in an

TABLE 11
 BINOMIAL TEST OF THE
 IMPORTANCE OF SIZE AND RESIDENCY IN THE
 OUTCOME OF AGGRESSION BETWEEN *ROSENBERGI* MALES
 ON THE OBISPO DIVERSION STUDY SITE IN 1977 AND 1978¹

Contest		N	P
I. SVL			
A. Nonviolent bouts:	8 residents were longer	19	0.65
B. Violent bouts:	4 residents were longer	17	0.05
C. All bouts:	12 residents were longer	36	0.07
II. WT			
A. Nonviolent bouts:	11 residents were heavier	19	0.36
B. Violent bouts:	6 residents were heavier	18	0.24
C. All bouts:	19 residents were heavier	37	1.00
III. SUMMARY OF CONTEST OUTCOME			
A. Nonviolent bouts:	7 residents were displaced	18	0.480
B. Violent bouts:	1 resident was displaced	18	0.002
C. All bouts:	8 residents were displaced	36	0.001

¹P = two tailed test. P = exact probability when $n > 25$; z values were used when < 25 .

artificial pond wherein the densities appear to have been arbitrarily maintained at 21–25 males (see Table 12). It is not clear what are natural densities of male *Rana clamitans*, nor what levels of aggression obtain under these conditions.

Shine (1979) reviewed the literature on size sexual dimorphism in anurans, and he observed (p. 300) that "species in which adult males equal or exceed females in size tend to be those species in which physical combat ("wrestling") between reproductive males has been recorded". In taxonomically more limited surveys, Howard (1978a) and Wells (1978) found larger male *Rana catesbeiana* and *R. clamitans* had distinct advantages over smaller individuals in wrestling bouts, and these authors also made the important observation that territory quality and reproductive success were positively correlated with male size (see also Wells, 1977a). Further, Wells (1978) found male size (relative to female size) and fighting to be correlated in his sample of eight species of North American *Rana*. Thus, most authors have stressed male-male competition as the explanation for the lack of anuran size sexual dimorphism; larger males presumably increase their reproductive success by dominating smaller ones. Not as much credit has been given to alternative explanations, such as female choice (Ryan, 1980), differential mobility (Ghiselin, 1974), different growth rates among the sexes (Wells, 1978), or improved chances of forced amplexus with increased male size (Howard, 1980).

The extremely pugnacious behavior of male *rosenbergi* (Fig. 63)

TABLE 12
NUMBER OF MATINGS PER SEASON
IN VARIOUS SPECIES OF ANURANS¹

Males	0	1	2	3	4	5	6	7	8	10	11
<i>Rana sylvatica</i> ¹	289	54	3								
<i>Bufo bufo</i> ²	58	14	1								
<i>Bufo canorus</i> 1976 ³	302	36	4								
<i>Bufo canorus</i> 1977 ³	112	43	7								
<i>Bufo canorus</i> 1978 ³	137	62	16	1							
<i>Bufo canorus</i> 1979 ³	44	24	7								
<i>Bufo exsul</i> 1977 ³	673	144	17								
<i>Bufo exsul</i> 1978 ³	279	151	21	3							
<i>Bufo typhoni</i> ⁴	98	61	1								
<i>Bufo americanus</i> ⁵	93	33	3								
<i>Hyla versicolor</i> ⁶	26	8	1								
<i>Rana temporaria</i> ⁷	16	15	1	1							
<i>Rana clamitans</i> 1974 ⁸	9	7	4	1							
<i>Rana clamitans</i> 1975 ⁸	12	10	2			1					
<i>Physalaemus pustulosus</i> ⁹	119	43	16	2	4		1				
<i>Rana catesbeiana</i> 1976 ¹⁰	18	15	3	2							
<i>Rana catesbeiana</i> 1977 ¹¹	13	4	4	3	2						
<i>Rana catesbeiana</i> 1978 ¹¹	14	5	5	3			1	1			
<i>Hyla rosenbergi</i> 1977	32	15	12	3	5	1	1				
<i>Hyla rosenbergi</i> 1978	11	9	2	1	2	1	1				
<i>Centrolenella colymbiphyllum</i> ¹²	27	35	22	7	4	3	1	1	1		
<i>Centrolenella fleischmanni</i> ¹³	1	1	1	4	3	1		1		1	1
<i>Centrolenella valerioi</i> ¹²	15	9	9	13	5	4	1				

Females	
<i>Rana sylvatica</i> ¹	3
<i>Bufo bufo</i> ²	4
<i>Bufo canorus</i> 1976 ³	7
<i>Bufo canorus</i> 1977 ³	7
<i>Bufo canorus</i> 1978 ³	4
<i>Bufo canorus</i> 1979 ³	1
<i>Rana temporaria</i> ⁷	3
<i>Rana catesbeiana</i> 1976 ¹⁰	18
<i>Rana catesbeiana</i> 1977 ¹⁰	2
<i>Rana catesbeiana</i> 1978 ¹⁰	8
<i>Hyla rosenbergi</i> 1977	1
	38
	1
	3
	1

¹Howard (1980). ²Davies and Halliday (1979); the four unmated females died during male-male competition, and they were not recorded in the author's Table III. ³Kagarise Sherman (1980). ⁴Wells (1979). ⁵Wells (1977b); ⁶Fellers (1979). ⁷Savage (1962); data incorrectly presented by Wells (1977b:671). Savage's data (pp. 162-163) include four unidentified females which are known to have mated. ⁸Wells (1977c); *R. clamitans* data based on manipulated densities of males and females in artificial enclosure. ⁹Ryan (pers comm). ¹⁰Howard (1979). ¹¹Howard (pers comm). ¹²McDiarmid (pers comm). ¹³Greer and Wells (1980).

and their large size ($\bar{x}_{SVL} = 82.6$ mm) relative to females ($\bar{x}_{SVL} = 85.5$ mm; Table 3) might be interpreted as evidence for the male-male competition hypothesis. However, it appears that while resident males usually were successful in rebuffing intruders, they did not do so because of their larger size (Table 11). Perhaps more revealing, mated males were not significantly larger than unmated individuals either in WT ($U = 985.5$, $N = 95$) or SVL ($U = 1031.5$, $N = 95$). The lack of evidence for different mobilities or growth rates, or improved chance of forced amplexus correlated with increased male size indicates that the alternative explanations provide no better basis for interpreting the evolution of *rosenbergi*'s size sexual dimorphism.

Some of the difficulty in demonstrating a causal basis for size sexual dimorphism in *rosenbergi* might be due to the error term of measurement (Table 2). However, historical and contemporary biological factors are just as likely to be confounding. For example, its not unreasonable to suggest that all of the evolutionary gains in male size occurred in the distant past when the nesting habit originated. Greater similarity of male and female sizes probably evolved rapidly, because the fertilized eggs had to be laid precisely at the surface of the water in the nest if oxygen deprivation was to be avoided. Today, *rosenbergi* appear to attain adulthood in one year and grow little, if any, thereafter, which tends to produce narrow size ranges. Thus, females may not be able to distinguish the largest from the smallest available mate within the limits of the little variation present among males (Fig. 17). Also, minor changes in the position of the female's legs during egg laying (p. 54) might be sufficient to insure maximum fertilization and buoyancy in all cases. In addition, other parameters might compromise a female's choice of a mate, such as his residency, relationship to a chorus and, in most instances, the rather few males from which she has to choose. All things considered, it is not too surprising that the selective basis for the size sexual dimorphism in *rosenbergi* cannot be determined.

Bouts of violent aggression were likely to be costly in *rosenbergi*. Participants increased their chances of being preyed upon because there was extra noise and exposure. Males were often seriously wounded, and they may not have advertised for females (pp. 96-99). Furthermore, Wells (1978) conjectured that a significant energetic cost accompanies fighting. Male *rosenbergi* often left the stream course for the remainder of the evening after a fight, or sat on perches and gave neither mating or territorial calls.

Perhaps not all types of aggression were costly. The relative value of the intruder's subsequent matings may have been increased when he fought and lowered the resident's fitness (the interference component of sexual selection; Arnold, 1976). Furthermore, some field observations indicated that female *rosenbergi* promoted aggression between nearby males before they chose a mate. As described

earlier, females usually were quiet, but sometimes they were conspicuously noisy. In these exceptional cases, they leapt into and out of adjacent males' nests making loud splashing sounds. In all instances, some form of undirected aggression then occurred between the males. A possible adaptive basis for this behavior in females will be considered in the sections on Paternal Care and Mate Choice.

PAIR FORMATION

Behaviors associated with pair formation in *rosenbergi* were stereotyped in both sexes. Males issued the advertisement call from within their nests (Fig. 26). They usually oriented toward the closest or largest number of calling conspecifics. A female approached and entered the nest at a point opposite the resident's back. When she arrived at the rampart, the male either became silent or switched to the courtship call (Table 10). The female's dorsal coloration (yellow and distinctly different from the male's in subdued light) and her silence may have reduced her chances of being confused with an intruding male and attacked by the resident. The courtship signal was hardly audible more than a meter away, and presumably not heard by nearby competing males. The resident became motionless, except for his partially inflated pulsating vocal sac, while the female entered the nest and then swam and dove around the basin and touched the ramparts with her hands (Fig. 64). Only two inspecting females showed evidence of nest renovation behavior before amplexus. These individuals removed leaves and mud from the basin and placed them on the ramparts. Both females subsequently mated with the nest's resident male.

The period of female inspection varied greatly ($\bar{x} = 10.6$ min; Fig. 60). The female usually bumped the resident as she moved around in the nest, sometimes seemingly by accident, and most of the time the male's response to that contact appeared to serve as a basis for the female accepting or rejecting him (pp. 144-146). Bogert (1960:227), presumably reporting from Breder's (1946) unpublished field notes, also recognized this preamplexus contact with males. When the resident male remained in the nest after being touched, the female usually continued her inspection. If she remained in the nest and did not proceed to another caller, she eventually swam to the male's back or side. Then she touched the male's dorsal and/or lateral body surfaces with her hands and chest, and occasionally with her chin. In many instances the female actively massaged the male with her chest with a swimming-like motion and the patting of her hands. Only after this massage did the male turn and mount the female. He clasped the neck at the angle of the jaw with his hands. The prepollical spine was ensheathed and directed away from the female (Fig. 65). The male usually shifted his body, as if obtaining a better

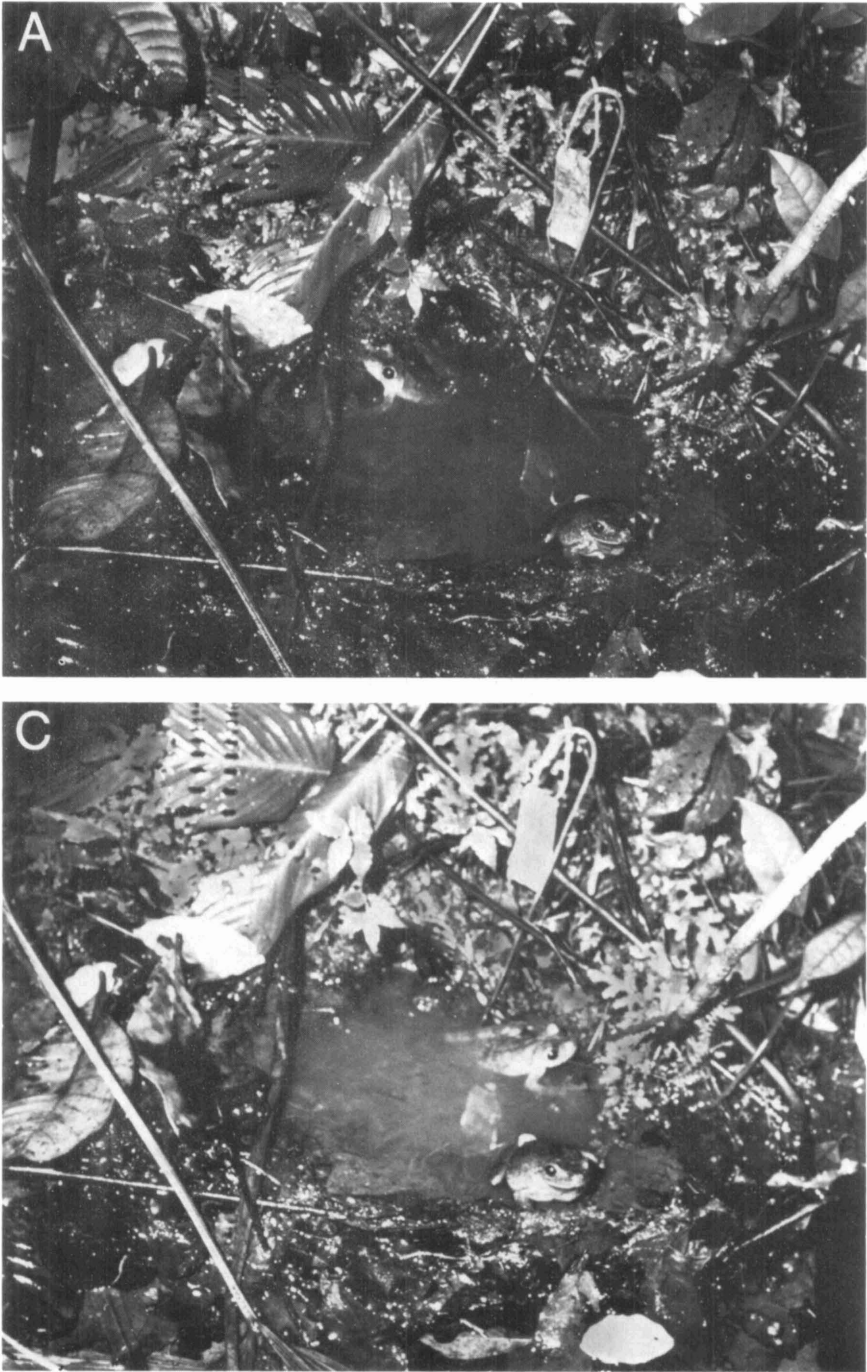


Fig. 64. Male *rosenbergi* no. 144 in the foreground of nest no. 67 on August 13, 1978. Female no. 97 is in the back of the nest. The four pictures (A–D) were taken over a span of approx 15 min during which time the female inspected the basin and ramparts, and rejected the resident



(D); later that evening she chose male no. 128. Note the male's fixed position during the extended period of nest inspection and his partially inflated vocal sac while issuing the soft courtship signal (Table 10). Also note how little the water was muddied by the female's nest inspection.



Fig. 65. Male *rosenbergi* no. 111 in a neck amplexus with female no. 81 in nest no. 45 on June 16, 1978. Note the position of the male's fingers dorsal and posterior to the female's tympanum. Note also the muddy water, which was due to the female's extensive renovation.

purchase, and shortly thereafter the female began her nest renovation behavior (p. 40). Sometimes the male shifted posteriorly into the typical anuran axillary amplexus when the female jumped as the result of an attack by another female, male or predator. The male's more posterior position and the inwardly turned prepollical spine no doubt improved his ability to hang on.

Some males and females may have located each other well before nightly chorusing began. A silent male and female descended together from their diurnal resting sites in four instances. The female had been in or near the male's nest the previous night in two cases, and it seems likely that they retreated to the canopy together.

Forced amplexus appeared to be infrequent in *rosenbergi*. The motionless state of the male probably provided the female with time to inspect his nest and to test him. Should a male clasp an unreceptive female, she probably would kick him off. Some amplexed pairs became uncoupled. However, I can't be certain it was due entirely to the female's action.

Only one male *rosenbergi* forceably clasped a female that had left his nest after a lengthy inspection. Breder (1946) observed a similar situation (see his Plates 52-53). The detailed circumstances under which my observations were made can be visualized from the following paraphrased field notes of August 14, 1977.

At 1855 hr male nos. 56 and 82 began fighting. In addition to a brief bout of wrestling, they hissed, charged and chased each other. They re-entered their nests, which were about one meter apart, wherein they alternated between high and low intensity advertisement and territorial calls (Table 10). It started sprinkling about 2000 hr. Male no. 82 climbed to a perch about one meter above his nest where he gave a territorial call which was answered with the same vocalization by the nearby no. 56. A female, no. 49, jumped from the ground and landed next to male no. 82. He immediately dropped to the ground and landed within 25 mm of his nest, no. 40. He issued a couple of barks and male no. 56 answered with a territorial call. Male no. 82 quickly entered his nest and began a long and continuous bout of advertisement calls. At 2042 hr female no. 49 dropped into male no. 82's nest and landed within 25 mm of the resident's snout. She remained crouched in front of him for about two min. Male no. 82 issued a long courtship call. The female jumped to the back of the nest and began to investigate it. Male no. 56 gave a territorial call and the female immediately moved out of the nest and toward that male. Male no. 82 moved out of his nest and gave a bark in response to another territorial vocalization from male no. 56. The two competing males remained motionless for about two min except for alternating between chuckles and territorial calls. Female no. 49 began to move and male no. 82 amplexed her immediately. The female showed no signs of attempting to reject the male that amplexed her.

It is becoming increasingly popular to refer to all chorusing frogs as exhibiting lek behavior (Wilson, 1975). However, like Wells (1977b) I believe the association must be made more carefully, otherwise the important connotation carried by the term lek can be obscured. According to Emlen and Oring (1977:219), a lek is "a

communal display area where males congregate for the sole purpose of attracting and courting females and to which females come for mating." The essential idea worth preserving here is that the lekking males are not controlling the females directly or some resource useful to females (Halliday, 1978). Ostensibly, females in a lek mating system make their choice on the basis of the males' phenotype or his location. Although, females might preferentially mate with males toward the center of the lek, because this area is "safer" from predators. This could be of proximate benefit to the female.

It is not certain whether female *rosenbergi* based their choice of mate on the male or his nest, or both (see later discussion, pp. 144-149), and it would be premature, if not in error, to apply the term lek to this species. My reservation assumes greater importance when the mating systems of closely related species are considered. Among the gladiator frogs, *crepitans* and *rosenbergi* probably shared a most recent common ancestor (Kluge, 1979). Male *rosenbergi* differentially control nests required by females for oviposition. However, *crepitans* does not build nests, and oviposition almost always takes place away from the place of courtship and amplexus (Kluge, in prep). Thus, *crepitans* better fits the term lek than does *rosenbergi*, and it would obscure the important differences in their mating systems to refer to both as lek species.

PATERNAL CARE

Parental care has been attributed to less than 10% of anuran species (McDiarmid, 1978), and the probable selective advantage of this form of parental investment is unknown in all but one or two (Wells, 1981; Weygoldt, 1980). Male *rosenbergi* continued to defend their nests when offspring were present. Such guarding kept intruding conspecifics, particularly males, from entering the nest and disturbing the surface tension of the egg film. The guarding behavior usually involved a male sitting on a perch each night near or immediately above the freshly laid surface film of eggs he fertilized (Fig. 66). The father tended to face his offspring while on the perch, and the elevated station appeared to provide maximum visibility of the nest and its surroundings. Also, perching probably reduced his chances of being attacked by terrestrial predators, such as *Leptodactylus pentadactylus*. Occasionally, during his nightly vigil, the resident male jumped to the ground and walked around the perimeter of the basin containing his offspring (Fig. 67). Males exhibiting perching and/or patrolling behavior were silent except for infrequent territorial calls (Table 10) usually issued in response to conspecifics calling nearby.

I observed several bouts of nonviolent and violent aggression between a father providing care and an intruding male. The wrestling



Fig. 66. Male *rosenbergi* no. 124 perched above his offspring on July 7, 1978. The guarding behavior exhibited in this photograph followed an advertisement call played from the speaker in the foreground. The eggs were approx 17 hr old.



Fig. 67. Male *rosenbergi* no. 128 (note waist band) at the edge of nest no. 44 on August 8, 1978. Nest no. 44 contained no. 128's offspring which were about 42 hr old. Male no. 128 moved to this guarding position after fighting no. 144. See Fig. 62 and text (pp. 103-104) for further explanation.

males shown in Fig. 62 were a guarding parent and an intruder. Fig. 67 depicts the patrolling behavior of a father immediately after he successfully repulsed an intruder from his nest and offspring. Guarding fathers invariably reacted aggressively toward either taped territorial or advertisement signals played within a radius of a couple of meters of the nest. Occasionally, the father attacked the speaker. Male *rosenbergi* appeared to react equally to their own tape-recorded signals or those of other males. Male parents not present at their nests returned and exhibited parental care behavior when either territorial or advertisement signals were broadcast near their offspring. The degree of responsiveness in playback experiments appeared to depend on time since oviposition and the distance of the male from his offspring. In most instances playback was an effective indirect way to estimate paternity of a freshly laid clutch of eggs.

While it might be reasonable to assume clutches sunk by rain or intruders would not be guarded as frequently as those undisturbed surface films, at least one male gave parental care for two nights after his clutch had been destroyed by rain. Also, all males guarding offspring, like unmated individuals, retreated to high arboreal perches during significant rainfalls.

The frequency of paternal behavior in *rosenbergi* is summarized in Fig. 68. In general, males guarded their young the remainder of the early morning hours following fertilization (night one in Fig. 68) and the two subsequent nights, but never longer. The presence or absence of guarding behavior was scored only for those males actually observed on the study site on a given night, because of the high rates of predation on adult males and the marked effect of rain on breeding activity. Thus, sample sizes differed between nights. The frequency of attendance on the third night was significantly less than on the second in 1977 ($G = 13.72$), but only marginally so in 1978 ($G = 4.29$, $P = .04$). Males were significantly more attentive on the second ($G = 15.05$) and third nights ($G = 7.53$, $P = .006$) in 1977 than 1978.

Parental care in *rosenbergi* was provided during the most vulnerable period of the offsprings' lives, from fertilization to hatching (40–66 hr). Considering the two principal agents of embryo mortality in this species, rain and intruding males, only the latter can be causally related to parental care. In all five cases in which intruding *rosenbergi* were responsible for embryo mortality, the male parent was not guarding his clutch.

Parental care in *rosenbergi* can be considered potentially costly, because males guarding their offspring never advertised for additional females. A male's residency (survivorship?) in the chorus was limited to relatively few nights of possible reproductive activity ($\bar{x}_{1977} = 16.5$; $\bar{x}_{1978} = 23.3$). If the average male obtained 1.2 matings/season (Table 13) and it took an average of about 16 nights of calling to achieve that many matings (Figs. 69–70), then time spent in other

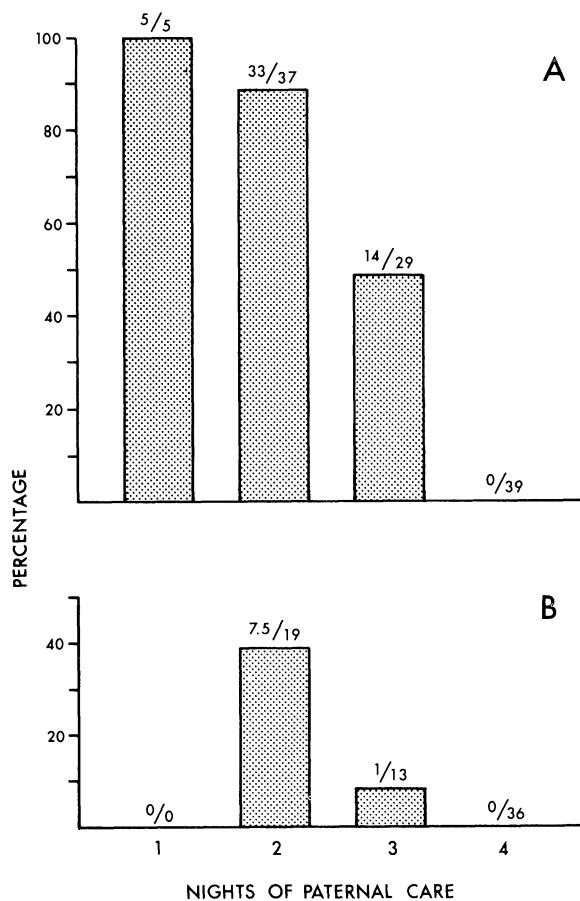


Fig. 68. Male *rosenbergi* parents observed in 1977 (A) and 1978 (B) that guarded their offspring. Night 1 was the morning of the oviposition, two the night following oviposition, etc. The denominator was the number of male parents present, the numerator the number of individuals guarding. The fractional number denotes a male changing his behavior to mate solicitation during the same evening.

activities, such as parental care, were likely to keep the individual from achieving better than the average mating success.

Wells (1981:194) speculated "that parental care should vary as ecological conditions vary, just as social organizations and mating systems vary with changing ecological conditions." This prediction should apply to *rosenbergi*, because of the probable cost in future reproduction. The simple playback experiments described above demonstrated the facultative nature of parental care in *rosenbergi* and how it was related to density of males. The significant difference between 1977 and 1978 in the frequency of attending males was corre-

TABLE 13
SUMMARY OF MATING SUCCESS STATISTICS
IN VARIOUS SPECIES OF ANURANS ¹

Males	N	\bar{x}	s ²	CV ²	Skewness	J
<i>Rana sylvatica</i>	346	0.2	0.161	231.5	2.121	.698
<i>Bufo bufo</i>	73	0.2	0.201	204.7	1.821	.629
<i>Bufo canorus</i> 1976	342	0.1	0.136	286.6	2.895	.632
<i>Bufo canorus</i> 1977	162	0.4	0.316	159.9	1.336	.772
<i>Bufo canorus</i> 1978	216	0.5	0.426	145.3	1.248	.793
<i>Bufo canorus</i> 1979	75	0.5	0.443	131.3	0.946	.780
<i>Bufo exsul</i> 1977	673	0.2	0.209	214.1	2.019	.783
<i>Bufo exsul</i> 1978	279	0.4	0.380	138.5	1.229	.843
<i>Bufo typhonius</i>	160	0.4	0.253	127.7	0.583	.817
<i>Bufo americanus</i>	129	0.3	0.260	168.5	1.384	.738
<i>Hyla versicolor</i>	35	0.3	0.269	181.5	1.572	.609
<i>Rana temporaria</i>	33	0.6	0.496	116.2	1.251	.790
<i>Rana clamitans</i> 1974	21	0.9	0.829	106.2	0.690	.790
<i>Rana clamitans</i> 1975	25	0.8	1.190	143.5	2.454	.740
<i>Physalaemus pustulosus</i>	185	0.6	0.911	171.5	2.413	.779
<i>Rana catesbeiana</i> 1976	38	0.7	0.698	117.6	1.144	.795
<i>Rana catesbeiana</i> 1977	26	1.1	1.866	122.5	0.845	.751
<i>Rana catesbeiana</i> 1978	29	1.3	3.207	140.4	1.779	.741
<i>Hyla rosenbergi</i> 1977	69	1.2	2.067	125.6	1.329	.816
<i>Hyla rosenbergi</i> 1978	26	1.2	2.375	133.6	1.677	.756
<i>Centrolenella colymbiphylum</i>	101	1.5	2.453	104.1	1.702	.899
<i>Centrolenella fleischmanni</i>	14	4.3	9.758 ³	72.9	0.982	.906
<i>Centrolenella valerioi</i>	56	2.0	2.800	83.7	0.376	.898
Females						
<i>Rana sylvatica</i>	63	1.0	0.046	22.5	-4.249	.988
<i>Bufo bufo</i>	66	0.9	0.058	25.6	-3.683	.979
<i>Bufo canorus</i> 1976	55	0.9	0.113	38.5	-2.237	.972
<i>Bufo canorus</i> 1977	63	0.9	0.100	35.6	-2.475	.977
<i>Bufo canorus</i> 1978	100	1.0	0.039	20.5	-4.695	.960
<i>Bufo canorus</i> 1979	46	1.0	0.022	15.1	-6.559	.987
<i>Rana temporaria</i>	23	0.9	0.119	39.6	-2.195	.956
<i>Rana catesbeiana</i> 1976	22	1.2	0.156	33.4	1.650	.979
<i>Rana catesbeiana</i> 1977	27	1.1	0.225	44.2	0.253	.956
<i>Rana catesbeiana</i> 1978	22	1.6	0.242	30.1	-0.567	.990
<i>Hyla rosenbergi</i> 1977	55	1.5	0.882	64.6	2.095	.959

¹The raw data are presented in Table 12. ²The CV values cannot be reproduced exactly from the \bar{x} and s² listed because of their rounding errors. ³I suspect that a large portion of this value is an artifact of small sample size.

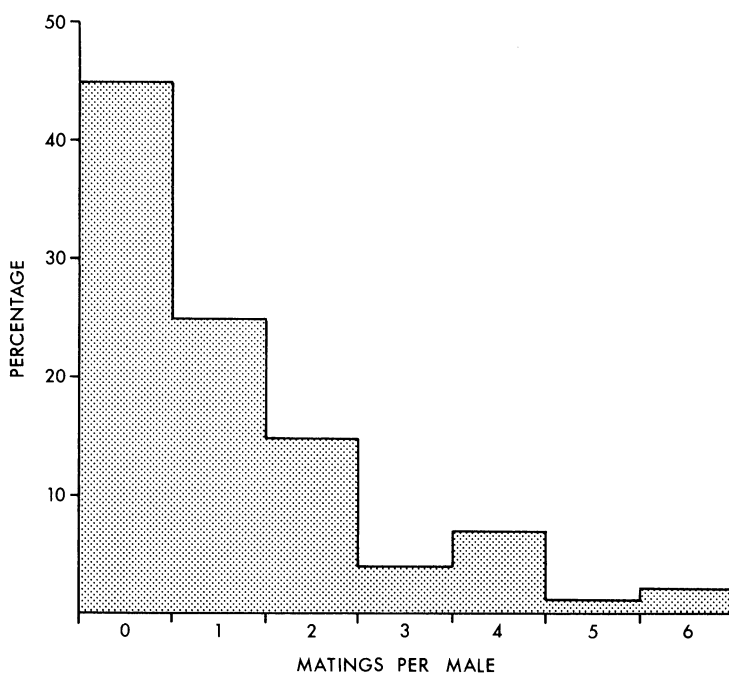


Fig. 69. Matings per male *rosenbergi* ($N = 95$, $\bar{x} = 1.2$; see Tables 12-13).

lated with these experimental findings. When population densities were high, most males guarded their nests against conspecifics. When densities were low, and the probability of intrusion by conspecifics was reduced, males guarded their offspring less frequently. This implies that fluctuating densities probably were a common feature in the evolutionary history of the species.

The following account, paraphrased from the field notes of August 12, 1978, illustrates several important features of parental care in the context of low densities.

At 1840 hr male no. 152 was issuing advertisement calls from nest no. 100. This was a new nest, located approx 80 cm S of nest no. 35 wherein the partially disturbed surface film of male no. 152's mating of August 10 was found. Male no. 128 gave a territorial call from nest no. 125 which was located about 35 cm N of the clutch. In response, male no. 152 mewed and moved 15 cm above and 30 cm S of his clutch. After a long pause, male no. 128 gave a brief territorial call and male no. 152 mewed, dropped to the ground and began to move around as if searching for the intruder. Again, after a brief pause, male no. 128 gave a territorial call from nest no. 125. Then, male no. 152 jumped on the rampart of male no. 128's nest; the two frogs were only 10 cm apart. They remained silent and motionless for a few minutes. Male no. 128 gave a territorial call, and male no. 152 responded by issuing a mew and violently attacking him. Male no. 128 quickly fled. At 1915 hr male no. 152 returned to nest no. 100 and gave advertisement calls.

How did parental care evolve in *rosenbergi*, and why is the male the caring sex? In many vertebrates, certainly in birds and mammals,

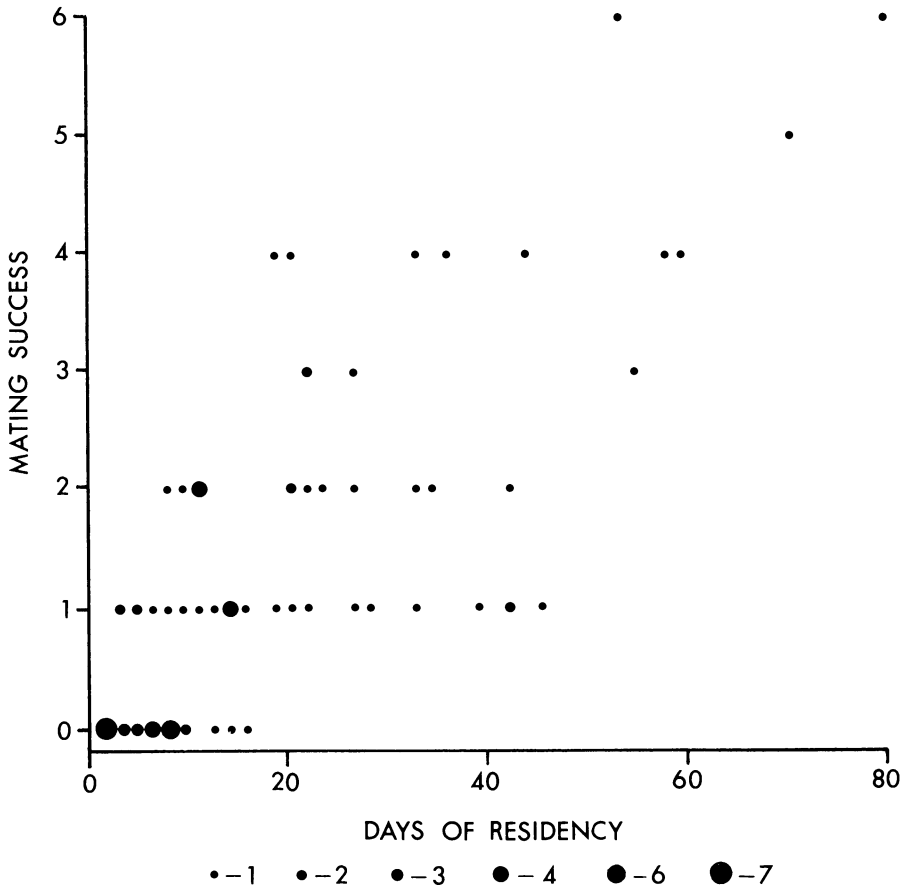


Fig. 70. Male *rosenbergi* matings plotted according to length of male residency. Dot size denotes number of coincident records (N = 80).

maternal care is the rule. On the other hand, in bony fishes most examples of parental care involve males. Four general theories have been tendered to explain the origin of the two kinds of parental care, and I evaluate their relevance to *rosenbergi* in the text to follow.

The first theory emphasizes the probability of genetic relatedness between parent and offspring. Where confidence of paternity is low, the caring parent should be the female. *Rosenbergi* is similar to most species of anurans in employing external fertilization and, except for the improbable situation where more than one male simultaneously clasps the same female, there is certainty of paternity for the individual shedding his sperm on the freshly laid eggs. While Blumer (1979) made a reasonably convincing case for the importance of a high probability of genetic relatedness in explaining the numerous examples of paternal care in bony fishes, this theory is not sufficient to explain the situation in *rosenbergi*.

Wells (1981), in a general review of parental care in anurans, emphasized that males of external fertilizing species are necessarily present when eggs are oviposited and therefore males are immediately available to care for their offspring. This thesis is a necessary precondition for paternal care, but it is an insufficient explanation for most anurans, like *rosenbergi*, because both sexes are present at oviposition.

Dawkins and Carlisle (1976) hypothesized that, in species with external fertilization, females release gametes before males and thus they are able to desert their mates. If parental care exists, then in all likelihood it should involve the male. The desertion hypothesis of Dawkins and Carlisle does not logically apply to *rosenbergi*, nor to many species of anurans with amplexus, because the male does not release the female until he has finished shedding his sperm on the eggs. In fact, in *rosenbergi* it is the male that leaves the site of oviposition first.

Finally, Baylis (1978) developed a complicated argument based on relative rates of gametogenesis and the existence of territoriality. He theorized that philopatry and territorial behavior tend to evolve in external fertilizing species with limited oviposition sites. He claimed that males are likely to be favored as the site-constant sex, because they are able to produce new sets of gametes and remate more frequently than females (see also McDiarmid, 1978). The key assumption in this preliminary argument is whether or not males monopolizing sites will leave more offspring than females controlling those locations for the same period of time. When true, Baylis then goes on to conclude that "parental behavior evolves as a consequence of acts by the male that promote survival of the zygotes at his site" (p. 738). The importance of territoriality, particularly of the oviposition site, also has been emphasized by Alexander and Borgia (1979) and Wells (1981).

Other important considerations in the evolution of parental care might include the physical state of the territorial sex and the relative physiological condition of the parents immediately following oviposition. In *rosenbergi*, the male controlled the oviposition site, and even had females defended the nest from intruding males, they probably would have been less effective, because they almost always were mute and lacked prepollical spines. Furthermore, female *rosenbergi* usually were less active than males after oviposition. Also, females appeared to be preoccupied with shedding their skins shortly after egg laying. Male *rosenbergi* were better equipped to repulse intruders and they may have been better able to expend the energy necessary to guard their young from the time of fertilization.

McDiarmid's (1978) conclusion that reduced clutch size may be a preadaptation for the evolution of parental care does not appear to be relevant to *rosenbergi*. His opinion that predation is important

applies to *rosenbergi* only in so far as the nesting habit probably evolved in response to aquatic predators and exclusive nest use is controlled by resident males.

The following hypothetical scenario illustrates my view of the importance of male territoriality in the evolution of parental care in *rosenbergi*. Initially, *rosenbergi* exhibited no post-fertilization parental investment. Males were territorial and the defended area was the nest. The male sought a new territory following oviposition. Multiple matings in the same nest were disadvantageous, because of the limited food resources in the nest, the cannibalistic nature of the tadpole, and the disruption of the egg film. Any male seeking a new nest in close proximity to his successful one coincidentally included his previous offspring in his territory. Any behavior reducing the chances of an intruding male occupying the old basin and disturbing the surface film of eggs was advantageous. The costs of not guarding eggs in *rosenbergi* appear to be so great they override the reproductive disadvantage of not immediately being able to obtain additional mates. There would be little or no reproductive cost to parental care in species obtaining multiple matings within a territory.

MATING SYSTEM

MATING SUCCESS

The concept of mating systems being either monogamous or polygamous (polygynous or polyandrous) is pre-Darwinian and, with the exception of Emlen and Oring's (1977) application of ecological modifiers, this classification remains unchanged and widely used today. Recently, Payne and Payne (1977) and Daly and Wilson (1978) pointed out many of the problems associated with the traditional classification of mating systems. It is largely typological, because it tends to ignore differences among individuals within local populations, its descriptive states are too few to define all but the grossest differences existing among populations and species, and it does not take into account the variation in mating success often accompanying increasing individual size and age. Most important, no one has been completely successful in demonstrating how the different systems relate to the general theory of evolution. Payne and Payne suggested replacing the traditional classification with one using a statistic summarizing the mating success of all reproductively mature individuals in a local population, and they argued that the sexes should be characterized separately, because of the different bases of sexual selection (intrasexual competition and female mate choice).

The choice of the statistic best describing variation in mating success was considered in some detail by Payne and Payne (1977).

They approached this problem empirically by obtaining mating frequencies for a large number of birds (males: 31 samples of 20 species; females: five samples of four species) representing a wide variety of mating systems (monogamous—polygamous) and calculating four different measures of dispersion for each sample (s^2 , CV, skewness, and the information theoretic index of realized evenness, J). Then the four statistics, each characterizing different parameters of sample variation, were tested for their ability to discriminate between the sexes and among the major kinds of mating systems present. Payne and Payne accepted the theoretical arguments of Fisher (1958), Selander (1972), and Trivers (1972), as well as the empirical findings of Bateman (1948); viz, variation in mating success should be greater in one of the sexes of polygamous but not monogamous species. They claimed the four statistics to be highly correlated with each other, and the authors also concluded that the statistics of mating success were closely related to the different mating systems sampled. The subjects of statistical significance and critical values were not considered by Payne and Payne. However, Payne (1979) used the F-ratio to compare the equality of variances in several samples of blackbird mating success. Unfortunately, a large number of the calculations presented by Payne and Payne (1977: Table 20) are arithmetically incorrect (particularly the CV column). Also, Payne's (1979) approach to comparing equality of variances using the parametric F-statistic is unacceptable, because of small sample sizes and a non-normally distributed mating success variable (Van Valen, 1978). While Payne and Payne focused attention on an important issue, I believe all of the major questions related to it require further discussion. These are: (1) Which statistic best summarizes variability in mating success? (2) How is the null hypothesis of equal variability tested? (3) What form should the new classification of mating systems take? (4) What is the relationship of the chosen statistic to evolutionary theory? I will attempt to seek answers to these questions in the remainder of this section, wherein I compare and contrast variation in mating success in *rosenbergi* to other species of anurans. Also, I compare frogs to birds in order to better understand some of the problems of accurately measuring mating success.

I define mating success as an amplexus that led to oviposition and fertilization. Each *rosenbergi*'s mating history is summarized in Figs. 48–49 and 51–52, and the population estimates, subdivided by year and sex, are presented in Tables 12–13. The 1978 data on females were omitted because of the small sample size and large number of matings that did not take place on the primary section (Fig. 52). Few ovipositions and fertilizations were witnessed during the two years of study, and I assumed a mating success occurred when spawn was found in the resident's nest the next day or when paternal care was exhibited by the resident following amplexus. The amplexus data for

rosenbergi illustrate multiple mating success in both sexes within a breeding season (see also Fig. 22 and pp. 30–32). Few reproductively mature females did not mate, while many males went unmated. If residency data can be interpreted as good estimates of adult survivorship, then we can speak of life-time success in this species. The same male and female *rosenbergi* were never observed mating together more than once.

Table 12 summarizes mating frequencies for 15 species of frogs, including *rosenbergi*, representing five families (see Table 8). There are 34 samples, 11 of which are females, and each is a local population estimate taken during some large part of the species' breeding season. Table 13 summarizes these observations in terms of sample sizes, means, and all measures of dispersion considered by Payne and Payne (1977). The species surveyed represent most of the mating system diversity known in anurans (Wells, 1977b). Both explosive (a few days: *Rana sylvatica*) and prolonged (year long: *Physalaemus pustulosus*) breeders are present. Also included in the list is a wide range of size sexual dimorphism, territoriality, and aggression that probably is related to intrasexual competition for mates and female mate choice (*Hyla versicolor* and *Rana catesbeiana*).

Mating success data probably rarely meet the assumption of a normal distribution. The zero class was largest in all but two of the male anuran samples, whereas one was the biggest class in all but one of the female estimates. Most of the mating frequencies fitted reasonably closely either Poisson or negative binomial models. The latter may be the most appropriate description of these data, because there was a significant correlation between increasing sample means and variances (Tables 13–14; males, $r_s = .983$, $P < .001$; females, $r_s = .554$, $P < .05$) and a wide deviation from the Poisson expectation indicating a tendency toward aggregation. The two male *rosenbergi* case histories fitted the negative binomial (1977: $X^2 = 5.66$, $df = 5$; 1978: $X^2 = 6.06$, $df = 5$), whereas the 1977 female distribution was significantly different from both negative binomial and Poisson. Differences in central tendency among mating success samples were evaluated with the median test, because of the distributions' shapes and presence of many tied observations. For similar reasons, the nonparametric modification of Levene's test was used to assess equality of variances (Levene, 1960; McCauley, 1979). The yearly male *rosenbergi* samples were not significantly different in mean or variance, and the two data sets were graphed together in Fig. 69. The 1977 female sample was significantly different from the males surveyed that year in mean and variance.

What factors were responsible for individual variation in mating success in *rosenbergi*, particularly that observed among males? Aside from chance, the simplest possibility was survivorship or length of residency, viz, the more nights a male advertised the more he

increased his chances of mating. The 1977 and 1978 length of residency data for males, like mating success, were not significantly different according to the median test, and both years were lumped in Fig. 70, where mating success is plotted against residency (untransformed). The correlation between these two variables was significant ($r_s = .749$). The remaining variance in mating success will be considered under the headings of male-male competition and female mate choice.

Payne and Payne (1977) viewed CV as the best descriptor of variation in mating success, and they stated that male/female CV ratios could be used to classify continuous variation in polygamy. Aside from the fact that CV has the desirable property of transforming variances to the same relative scale, it is not clear from Payne and Payne's data analysis and discussion why that statistic was promoted. In fact, none of their measures of sample variation appeared to be particularly good predictors of the mating systems present in birds. The ranges of the values calculated for the three broadly defined kinds of mating systems overlapped considerably. Even the monogamy subset of case histories was not clearly delimited from the polygynous types in s^2 , CV, skewness or J. Perhaps the most disturbing finding was that the samples of mating success for polygynous males were rarely more variable than success of conspecific females, as sexual selection theory predicts. The poor fit between data and theory seems to have little to do with the computational errors present in Payne and Payne's analysis, nor the statistics employed. The observed inconsistencies probably arose from the tendency of ornithologists to underestimate male/female operational sex ratios, because only territorial males were included. The following comparison of the bird and frog case histories reveals the basis for my opinion.

Frogs (Table 13) were much less variable in mating success, in all statistics employed, than birds with a comparable mating system (polygynous species, males only: $s^2 = 10.0$ times, CV = 1.2 times, skewness = 1.2 times, J = 1.5 times). Females showed no consistent pattern of difference ($s^2 = 6.2$ times, CV = 0.8 times, skewness = 0.1 times, J = 9.8 times). There can be little error interpreting male amplexus as successful reproduction in anurans possessing external fertilization. Rarely is a female frog amplexed by more than one male (eg, *Pachymedusa dacnicolor*; Pyburn, 1970) or does internal fertilization occur (eg, *Eleutherodactylus coqui*; *Nectophrynoides*, Grandison, 1978), and therefore paternity is certain when oviposition is observed. Usually, one cannot be sure each mounting, or even a copulation, results in reproduction in internal fertilizing species, such as birds and mammals. Only in a few internal fertilizing species, eg, the colubrid snake genus *Thamnophis*, does the female copulate once for each brood; hence, mating success is unambiguous (S. J. Arnold, pers comm). Also, if the system of sperm precedence is known, mating

success can be inferred (Wade and Arnold, 1980). Birdsall and Nash (1973) found that female mammals received multiple inseminations and not all were equally effective in reproduction. Further, reproductive success in birds inferred from circumstantial evidence such as territorial behavior (Bray et al. 1975) and pair bonding (Beecher and Beecher, 1979) can be erroneous. Payne and Payne (1977) may have scored mountings and copulations that did not lead to reproduction. In fact, much of their lengthy description of how the mating success observations were made in several of their examples supports my contention that the sample distributions represented more than one variable. When compound distributions are present it is reasonable to expect the range of variation among samples to be great (Wright, 1968). It seems inescapable that estimates of male mating success in internal fertilizing species must be verified by studies of genetic similarity between offspring and the putative father if they are to be treated with the same accuracy as data from external fertilizers. All of the anuran examples reported in Tables 12-13 met the prediction of sexual selection theory that mating success is more variable among conspecific males than females. Also, as might be expected, there existed significant rank correlation among my 34 samples in all but one of the pairwise comparisons (s^2 and CV; Table 14). Only CV and J distinguished all male from all female frog case histories.

TABLE 14
RANK ORDER CORRELATION (r_s) AMONG
THE SAMPLE STATISTICS OF ANURAN MATING
SUCCESS SUMMARIZED IN TABLE 13

Statistics	\bar{x}	s^2	CV	Skewness
s^2	+360*			
CV	-.682***	+324		
Skewness	-.322	+441*	+790***	
J	+580***	-.384*	-.916***	-.713***

* $<.05$; ** $<.01$; *** $<.001$

Either CV or J is the preferred descriptor of mating success variation in frogs, following Payne and Payne's reasoning. However, I advocate CV^2 (Wade and Arnold, 1980), because it has a more obvious theoretical relationship to intensity of selection (Crow, 1958, 1962), and it retains the same statistical virtues of the unsquared term. A simple mating system classification incorporating the concepts of polygyny and polyandry is: (1) $CV^2_{\text{male}} > CV^2_{\text{female}}$, and (2) $CV^2_{\text{male}} < CV^2_{\text{female}}$, respectively. $CV^2_{\text{male}} = CV^2_{\text{female}}$ may not fit our present concept of monogamy in all cases. Frogs appear to fit the polygyny (1) category, but more females must be sampled for a definitive

conclusion. Daly and Wilson's (1978:82) advocacy of male to female variances in reproductive success to classify degrees of polygamy seems unjustified, because that ratio is not a relative measure that can be used across all species, more than mating success is included, and the measure breaks down when the sex ratio departs from 1:1 (see Wade and Arnold, 1980).

INTENSITY OF SEXUAL SELECTION

Bateman's classic paper (1948) clearly established for the first time how mating success is related to the general theory of evolution. Bateman used genetic markers to determine the number of progeny left by individual male and female *Drosophila melanogaster*, and he found the variance in number of offspring sired by males to be greater than that of females. He stated (p. 362) "that the sex difference in variance of fertility, which is itself a sign of intra-masculine selection, is due to the effect of number of mates per fly on fertility. This takes effect in two ways: (a) The higher variance, in males, of the number of mates per fly. This is a *sign* of intra-masculine selection, (b) The stronger correlation, in males, between number of mates and fertility. This is the *cause* of intra-masculine selection." Basically, Bateman's elegant analysis provided the conceptual framework for relating mating success to intensity of selection through variance in reproductive success. Still, two issues remained: (1) the discovery of a general solution for relating variances in reproductive success in males and females, and (2) the impracticality of measuring reproductive success by direct observation in field populations (Howard, 1979). Recent papers by Wade (1979) and Wade and Arnold (1980) derived equations relating variance in reproductive success in males and females, which included the more readily estimated parameters of mating success and fecundity. The relationship of variation in mating success to intensity of selection is briefly described and exemplified in the remainder of this section.

Wade and Arnold (1980; see also Wade, 1979), working from first principles, formulated a relatively simple method of estimating intensity of sexual selection. The first step was based on the relationship between the variances in fitness in each sex, where fitness is defined as number of progeny. Then, given that reproductive success is a major component of fitness, they were able to measure intensity of selection, because of its direct relationship to variance in reproductive success. They employed Crow's (1958) definition of intensity of selection, I , which is equal to the variance in number of offspring per parent divided by the mean number of offspring per parent squared (s^2/\bar{x}^2). According to Crow (1962:64), "if fitness were completely heritable, that is, if each offspring had exactly the average of his

parents' fitnesses, the fitness of the population's next generation would be that of the present generation multiplied by I . A trait or a gene that is genetically correlated with fitness will increase in proportion to this correlation." Of course, in reality, the heritability of fitness remains unknown and the correlation of any trait to it is largely a matter of speculation. Therefore, in the text to follow the term intensity should be taken to mean the "opportunity" for response to selection. Further, it must be emphasized that the Wade-Arnold model assumes that female choice of mating partners is uncorrelated with female fertility, male mortality during the mating season is uncorrelated with mating success, and clutch size does not systematically vary during the breeding season. The latter two assumptions are violated in *rosenbergi* and they will be discussed later. Lastly, it is important to note that the temporal domain of the model is a single season of reproduction.

Most frogs, including *rosenbergi*, are examples of first male paternity, and all relevant parameters of the Wade-Arnold model can be readily estimated from field observations. The following formulation by Arnold and Wade (in prep) applies to species with multiple clutches and therefore it is more generally applicable than their published version (1980). I have replaced the parameter notation of Arnold and Wade (in prep) with the conventional symbols of statistical estimation. Female variance in reproductive success, s_f^2 , is

$$s_f^2 = \bar{x}_c \cdot s_{fc}^2 + \bar{x}_{fc}^2 \cdot s_c^2, \quad (1)$$

where \bar{x}_c is average number of clutches per female, s_{fc}^2 is variance in number of offspring per clutch, \bar{x}_{fc}^2 is average number of offspring per clutch squared, and s_c^2 is variance in number of clutches among females per season. Male variance in reproductive success, s_m^2 , is

$$s_m^2 = \bar{x}_s \cdot s_{fe}^2 + \bar{x}_{fe}^2 \cdot s_s^2, \quad (2)$$

where \bar{x}_s is average number of clutches sired per male, and s_s^2 is variance in number of clutches sired per male. Following Wade and Arnold (1980) and Arnold and Wade (in prep), an index of the total intensity of selection on male reproduction, I_m , is

$$I_m = \frac{s_m^2}{\bar{x}_m^2} = \frac{R \cdot s_{fe}^2}{\bar{x}_c \cdot \bar{x}_{fe}^2} + \frac{s_s^2}{\bar{x}_s^2}, \quad (3)$$

where \bar{x}_m^2 is average number of offspring sired per male $(\bar{x}_s \cdot \bar{x}_{fe})^2$, and R is the sex ratio. The intensity of selection on males due to variance in numbers of mates, viz, pure sexual selection, I_s , is

$$I_s = \frac{s_s^2}{\bar{x}_s^2} . \quad (4)$$

Similarly, the index of the total intensity of natural selection on female reproduction, I_f , is

$$I_f = \frac{s_{fe}^2}{\bar{x}_c \cdot \bar{x}_{fe}^2} + \frac{s_c^2}{\bar{x}_c^2} . \quad (5)$$

The intensity of selection on fecundity of females due to variance in fertility, I_{fe} , is

$$I_{fe} = \frac{s_{fe}^2}{\bar{x}_c \cdot \bar{x}_{fe}^2} , \quad (6)$$

and the intensity of selection on females due to variance in number of clutches per season (selection for iteroparity), I_c , is

$$I_c = \frac{s_c^2}{\bar{x}_c^2} . \quad (7)$$

The intensity of sexual selection term, I_s , is of particular interest in this paper and I used the following values, mostly taken from Table 13, to estimate it for *rosenbergi* in 1977: $s_s^2 = 2.067$, $\bar{x}_s = 1.2$, $s_{fe}^2 = 101,124$ [(= 318.0)²], $\bar{x}_{fe} = 2350.0$, $\bar{x}_c = 1.5$, $s_c^2 = 0.882$. Given these data, $I_s = 1.4$, or stated another way, the sexual selection component was 99% of the total intensity acting on male reproduction (I_s/I_m ; see Table 15). This result suggests that the opportunity for evolution based on intrasexual competition and female mate choice was exceptionally high in *rosenbergi*, and I would expect to find much evidence of both classes of these phenomena in this species. $I_s = 1.7$ for the 1978 male *rosenbergi* sample (Table 13), and the male component remained 99% of the total (Table 15). The same female fecundity measures, s_{fe}^2 and \bar{x}_{fe} , were employed in these calculations and the 1977 and 1978 males were identical in \bar{x}_s . The only difference between the two years was s_s^2 (1977, 2.067; 1978, 2.375). Thus, it seems that small differences in variance in mating success had no affect on intensity of sexual selection.

I have calculated I_s and I_m for most of the other anuran examples in Table 13 (see Table 15). The necessary data on female fecundity (number of zygotes) was obtained from Collins (1975:Table 7), Greer and Wells (1980), Kagarise Sherman (1980), T. R. Halliday (pers

comm)², M. J. Ryan (pers comm)³, and R. W. McDiarmid (pers comm)⁴. The only available fecundity and mating success estimates for the *Bufo americanus*, *Hyla versicolor*, and *Rana temporaria* examples were from different local populations. Howard's (1979) direct estimate of I_m (1.41, or 1.99 when transformed to the comparable CV^2) in *R. catesbeiana* 1976 is close to my indirect measure (1.64). This correspondence indicates that there was little or no covariance ($cov = 0.35$) in male mating success and fertility of mates (cf Wade, 1979). Some interesting conclusions can be reached by comparing all anuran I_s/I_m percentages (Table 15). In spite of the considerable differences in variance in male mating success (0.161–9.758) there was relatively little affect on the proportion of intensity of sexual selection (81–99%). Further, males of some species showed a modest variation between years (*R. catesbeiana* 87–95%) whereas others exhibited none (*rosenbergi* 99%). The most unexpected conclusion concerns how little the proportion of the intensity of sexual selection varied among these diverse species. Perhaps this is not too surprising, because of the little maximum variance in mating success possible among anurans that was realized (0.3–9.1%). The maximum variance possible was determined for each sample in Table 12 by assuming that one male obtained all of the observed matings, all other individuals received none; see equivalent, more convenient expression in Table 15. The realized variances are listed in Table 13, the proportions of the maximum are summarized in Table 15. Further study of maximum variance estimation is required, because average mating success, total number of observed matings and number of males were significantly correlated ($P < .01$).

The estimates of intense sexual selection characterizing the more explosive breeders probably were due to highly skewed sex ratios that made it impossible for most males to mate (Wells, 1977b). For example, females are relatively rare in *Rana sylvatica*, because it takes most two years to reach sexual maturity, but males only one (Collins, 1975). No doubt the range of I_s values will increase with studies of a wider variety of frogs, in particular dendrobatids where sex-role reversal may occur (eg, *Colostethus trinitatis*, Wells, 1980). Perhaps a more realistic appraisal of the degree to which the anuran estimates reflect reality will come from comparisons with monogamous species of other kinds of organisms, such as claimed for various mammals and birds. The estimates of male mating success in taxa with internal

²The clutch size data for *Bufo bufo* are $N = 41$, $\bar{x} = 1333.6$, $s = 569.6$. Those data for *Rana temporaria* are $N = 55$, $\bar{x} = 828.5$, $s = 367.6$.

³The clutch size data for *Physalaemus pustulosus* are $N = 32$, $\bar{x} = 278.8$, $s = 123.80$.

⁴The clutch size data for *Centrolenella colymbiphylum* are $N = 53$, $\bar{x} = 50.4$, $s = 7.38$. Those data for *C. valerioi* are $N = 52$, $\bar{x} = 28.9$, $s = 4.61$.

TABLE 15
SUMMARY OF SEXUAL SELECTION VARIABLES
FOR VARIOUS SPECIES OF ANURANS¹

SPECIES	I_m	I_s	I_f	I_c	I_y/I_m	I_m/I_f	I_c/I_f	$s^2_{f_{max}}$	$s^2/s^2_{f_{max}}$
<i>Rana sylvatica</i>	4.6	4.0	.16	.05	.87	28.3	.28	10.435	.015
<i>Bufo bufo</i>	5.9	5.0	.27	.07	.85	21.7	.26	3.507	.057
<i>Bufo canorus</i> 1976	14.2	13.6	.21	.14	.96	68.3	.67	5.677	.024
<i>Bufo canorus</i> 1977	2.1	2.0	.19	.12	.93	11.2	.64	20.180	.016
<i>Bufo canorus</i> 1978	1.8	1.7	.10	.04	.93	18.3	.39	43.763	.010
<i>Bufo canorus</i> 1979	1.9	1.8	.08	.02	.94	22.8	.27	19.513	.023
<i>Bufo exsul</i> 1977	5.8	5.2			.90			47.149	.004
<i>Bufo exsul</i> 1978	2.7	2.4			.90			146.777	.003
<i>Bufo typhonius</i>								24.962	.010
<i>Bufo americanus</i>	3.3	2.9			.88			11.883	.022
<i>Hyla versicolor</i>	3.4	3.0			.89			2.941	.091
<i>Rana temporaria</i>	1.7	1.4	.37	.15	.81	4.7	.40	12.500	.040
<i>Rana clamitans</i> 1974								16.198	.051
<i>Rana clamitans</i> 1975								15.041	.079
<i>Physalaemus pustulosus</i>	2.9	2.5			.89			57.658	.016
<i>Rana catesbeiana</i> 1976	1.6	1.4	.24	.11	.87	7.0	.46	19.702	.035
<i>Rana catesbeiana</i> 1977	1.7	1.5	.32		.92	5.2		33.638	.055
<i>Rana catesbeiana</i> 1978	2.0	1.9	.19		.95	10.6		48.891	.066
<i>Hyla rosenbergi</i> 1977	1.5	1.4	.40	.39	.99	3.6	.97	91.779	.023
<i>Hyla rosenbergi</i> 1978	1.7	1.7			.99			35.998	.066
<i>Centrolenella colymbiophyllum</i>	1.1	1.1			.99			231.040	.011
<i>Centrolenella fleischmanni</i>	0.5	0.5			.99			276.821	.035
<i>Centrolenella valerioi</i>	0.7	0.7			.98			228.071	.012

¹ I_y/I_m = proportion of the sexual selection component of the total intensity acting on male reproduction. I_m/I_f = relative severity of selection on the sexes. I_c/I_f = opportunity for selection for iteroparity. $s^2_{f_{max}} = (x^2_{f_{max}} - (\bar{x}^2_{f_{max}} / N_m)) / N_m - 1$, where $x_{f_{max}}$ = total number of observed matings or clutches sired, \bar{x}_s = avg mating success, and N_m = number of males.

fertilization will have to be particularly carefully evaluated in terms of apportionment of paternity (Wade and Arnold, 1980). Wade and Arnold (1980) determined I_s/I_m values of 59–81% for a population of red-winged blackbirds (*Agelaius phoeniceus*). However, these estimates probably are inflated, because of the likelihood of unobserved stolen copulations.

I_m/I_f , the relative severity of selection on the sexes, is another potentially useful ratio that can be derived from the Wade-Arnold model (Table 15). Most of these values are much higher than those calculated by Wade and Arnold (1980) for red-winged blackbirds (*Agelaius phoeniceus*), 4.5–9.1. The exceptional values for anurans may be due to highly skewed sex ratios.

One of the most unrealistic assumptions of the Wade-Arnold model (1980) is that clutch size does not vary within a breeding season. Until recently, it was thought that only tropical species of anurans were iteroparous and that clutch size does not vary systematically with time (Turner, 1962; Salthe and Duellman, 1973; Salthe and Mecham, 1974). However, recent mark-recapture studies suggest that multiple clutches are the rule, and systematic seasonal variation in clutch size exists (Table 12; Wells, 1976). The common trend appears to be a reduction in clutch size, and *rosenbergi* provides evidence for an even more complicated temporal pattern (Fig. 24). The assumption may be unrealistic even in semelparous species, if smaller females breed later.

The opportunity for selection for iteroparity, I_c , among anurans was estimated from the data presented in Tables 12–13 under the assumption that there was no systematic change in the size of successive clutches, and the relative I_c/I_f measure is listed in Table 15. As might be expected, the intensity of selection for multiple clutches varied greatly (26–97%) relative to I_s , although the magnitude of the range of CV in mating success was much less than that of conspecific males (0.3 times).

Another assumption of the Wade-Arnold model that most organisms fail to meet is the absence of correlation between male mating success and mortality. A significant positive correlation between length of residency and mating success occurred in *rosenbergi* (Fig. 70), and residency probably was a measure of survivorship in this species (pp. 86–88). The exact effect of the failure to meet this assumption is unknown. However, in qualitative terms, a positive correlation should produce inflated values of I_s (Wade and Arnold, 1980).

NIGHTLY SEX RATIOS

Emlen and Oring (1977) emphasized the importance of the operational sex ratio. They defined this dimensionless variable (p. 216) “as the average ratio of fertilizable females to sexually active

males at any given time" (see also Emlen, 1976 for an example). It was promoted as an empirical measure of the degree to which one sex affects the other's mating. Emlen and Oring claimed (p. 216) that "The greater the degree of imbalance in the [operational sex ratio], the greater the expected variance in reproductive success among members of the limited sex and the greater the degree of polygamy. Where the [operational sex ratio] is skewed toward males [the limited sex], polygyny is expected." These authors did not consider what is the most realistic sampling period, nor the many ambiguities associated with determining "sexually active." Also, they did not offer advice on how to treat some well-known statistical problems of ratios. Should samples be instantaneous or taken over some longer time, such as a night or week? What constitutes a sexually active male? Should male *rosenbergi* calling from nests be distinguished from those calling elsewhere (eg, males without any obvious relationship to a basin)? Should silent males and those providing parental care be considered sexually active? Occasionally they mate. There seems to be no general rule to follow in answering these questions and, in the analysis to follow, I arbitrarily treated all male *rosenbergi* observed in or near any oviposition site as sexually active, regardless of their behavior. No doubt, my interpretation produced slightly inflated estimates of the number of sexually competing males. My method probably will not affect the intraspecific comparisons made in this paper, nor those made with species with similar life histories. However, when my operational sex ratio values are compared to those of different species, eg, without paternal care, they must be considered over-estimates. I chose nightly estimates because this period of time seemed to suffer least from sampling bias and it was the most reasonable with respect to proximate factors.

The existence of zero data, which was frequent in *rosenbergi*, is an even more troublesome issue when calculating the operational sex ratio. When males were absent on a given evening, so were females, and it is reasonable to ignore these matched zero records. However, females were often absent when sexually active male(s) were present. Some number divided by zero does not produce a realistic value, and what would a zero quotient mean if the number of females (absent) were treated as the numerator? Does one ignore those nights when males are present but females are not when calculating operational sex ratios over some long period of time, eg, an entire breeding season? It might be argued that males are not going to alter their competitive sexual-aggressive behavior on any night that there is a reasonably high probability of a female entering the chorus. Emlen (1976) avoided many of these issues by lumping his nightly observations of *Rana catesbeiana* into six day intervals, which removed all zero observations. No doubt such treatment will yield a poor estimator when there is considerable variance in the nightly samples. It

would be useful, if not essential, in species as variable as *rosenbergi* to estimate both central tendency and dispersion. However, there appears to be no reasonable way of presenting the variance of a ratio (Atchley, Gaskins and Anderson, 1976; Atchley and Anderson, 1978, Atchley, 1978). Regression analysis applied to numbers of males and females per some unit time (eg, a night) might provide a solution to operational sex ratio estimation. Zero values, where numerous, probably should be truncated, because they tend to fix the intercept at a biologically uninteresting point. Other statistical problems with regression analysis include whether the data fit model I or II conditions (Sokal and Rohlf, 1969) and the variates are normally distributed. The *rosenbergi* variables were not normally distributed and it is doubtful that they fit a model I. Given the several unresolved difficulties with ratios and regression analysis I plotted the raw *rosenbergi* data, the numbers of males and females observed each night during the breeding season (Fig. 71), and evaluated them qualitatively.

In 1977 (Fig. 71A), the number of competing males gradually increased, reaching a high of 17/night (July 13), numbers dropped to an average of about 9–10 individuals in the following two weeks, then rapidly rose to 18, and finally slowly declined to the end of the breeding season. There were several precipitous crashes even during the height of the breeding season (July–August; Fig. 11), and the numbers of males present was inversely correlated with the amount of rain (Fig. 10). Rarely during the 1977 mating season were no males seen or heard during a nightly survey. However, there were many instances when no females appeared. The two main peaks of male abundance in July and August were correlated with number of available females, the latter reaching a maximum of five/night (August 6 and October 16). The late season rise in number of females, 4–5 on October 15 and 16, may be evidence for that sex being able to “anticipate” the end of the breeding season. Females probably avoided carrying an unlaidd clutch of eggs into the dry season (pp. 32–35), and a sudden rush of activity near the end of the breeding season is expected. The operational sex ratio varied from a high of 16 males:zero females (August 10) to three males:five females (October 16) in 1977. The average nightly estimate ($N = 71$; only those nights were omitted where both sexes were absent) was 8.5 males and 1.2 females, and their ratio was 6.9:1.

In 1978, males were never more abundant than seven/night (August 14) and females did not exceed two (June 14 and August 23). There were no obvious peaks of abundance of either sex. The average nightly estimate ($N = 129$) was 2.7 males and 0.3 females, and their ratio was 9.3:1.

The between-year differences discovered in so many other variables may not be evident in the average operational sex ratio because

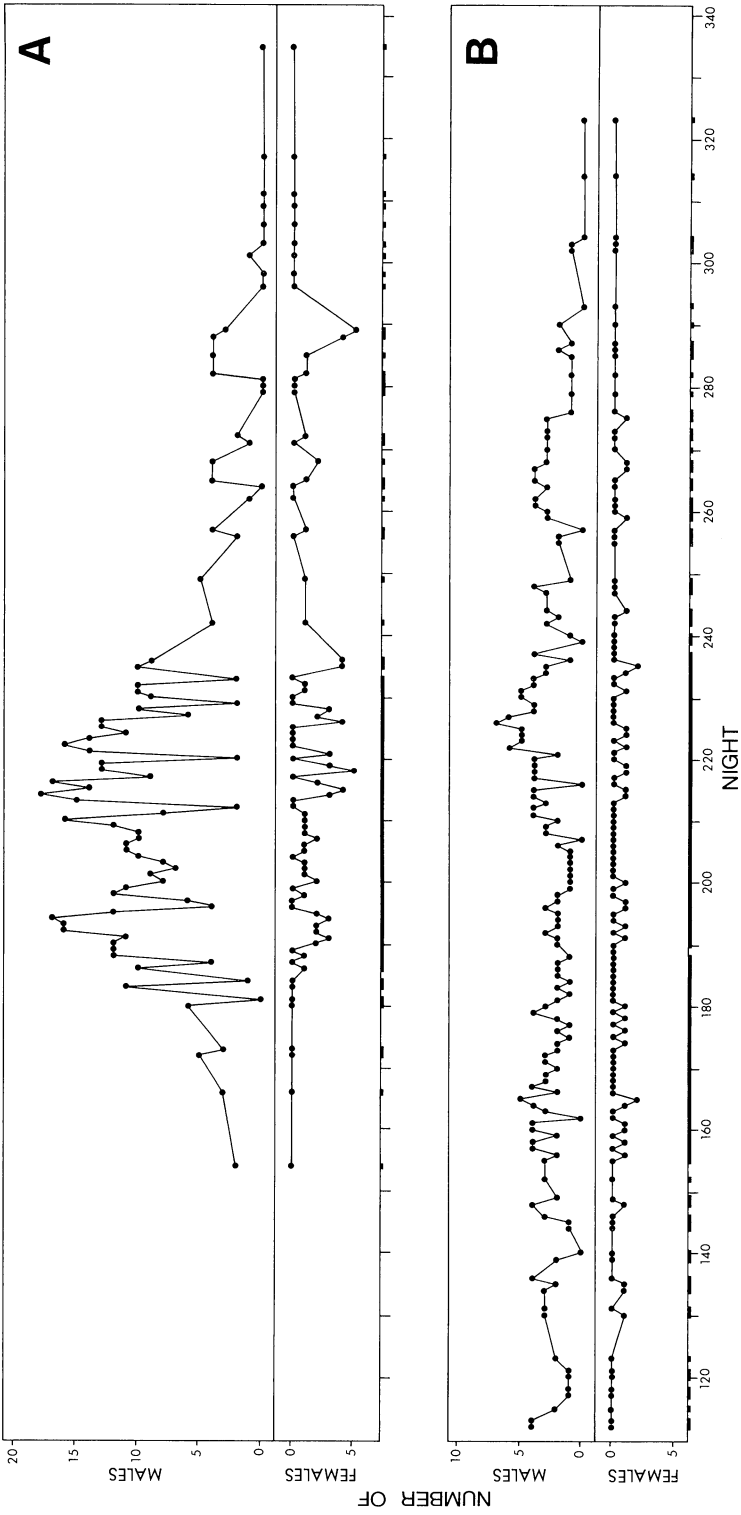


Fig. 71. Numbers of male and female *rosenbergi* present each night in 1977 (A) and 1978 (B). Estimates include all individuals, even those heard but not observed, and the values are slightly larger than those graphed in Fig. 10. The thickened portions of the horizontal axis were nights one or more investigators surveyed the primary section.

of the way it was calculated. There were many more males ($G = 118.77$, $df = 17$, $N = 200$) and females ($G = 46.63$, $df = 5$, $N = 200$) per night in 1977. However, the proportions of the two sexes over the entire two seasons were not significantly different ($G = 1.97$, $N = 1075$). While the operational sex ratio was somewhat higher in 1978 (9.3:1) than in 1977 (6.9:1), the difference was not statistically significant. This is consistent with male mating success variances not being significantly different in 1977 and 1978.

What factor(s) produced the operational sex ratio found in *rosenbergi*, and what predictions can be made knowing males outnumbered females almost every night of the breeding season and male mating success was not random? The temporally asynchronous distribution of fertilizable females was the most obvious factor responsible for the polygynous mating system. The breeding season was long (Fig. 5), the recruitment phase extended (Figs. 50, 53), and a moderate rate of vitellogenesis existed (Fig. 22). Once males entered the breeding population they were rarely absent (Fig. 54). Was the mating system affected by certain males controlling access to females by monopolizing critical resources (Emlen and Oring, 1977)? Nests were important to embryo survivorship, and well-renovated depressions might have been limiting to females, because they would have had to expend considerable energy building a basin or improving one unattended by a male. However, nest sites did not appear to be in short supply; usually there were more renovated basins available than males. Still, the male's high degree of competition for nests within a chorus might be interpreted to mean they were locally limited. Even at this level, it did not appear to be nests per se that were important to mating success, but rather the close spatial relationship of the competing males (pp. 147-153). Thus, resource dominance does not appear to be as important as male dominance (sensu Emlen and Oring, 1977:217). If the local distribution of males was the important factor in the evolution of the *rosenbergi* mating system, then the arbitrary way in which I scored the number of sexual competitors probably made my operational sex ratio estimates of little predictive value.

In contrast to the general prediction made by Emlen and Oring (1977), *rosenbergi* females were the limiting sex, but males exhibited parental care. Paternal care was performed only over a few days in *rosenbergi*, and it might be argued that males lost little opportunity to exploit the "polygamy potential." Still, considering the apparent short-lived nature of the species, any time lost in non-breeding activities must be viewed as relatively costly.

In summary, I do not believe the operational sex ratio provided a unique, or any better, insight into the intensity of sexual selection and the type of mating system found in *rosenbergi* than did the estimates of individual reproductive success and its variance. The

identical values (99%) for the proportion of the total intensity of selection due to sexual selection in males in 1977 and 1978 suggests that operational sex ratio differences were poor descriptors of the underlying processes. It may be that it was the use of ratios that obscured the real issues involved.

INTRASEXUAL COMPETITION FOR MATES

Fisher (1930, 1958), recapitulating Darwin (1871), stated that in general two processes may be involved in sexual selection, intrasexual competition and female mate choice. Given two sexes there exist four possible sources: male-male and female-female competition and male and female choices. There appeared to be no evidence for exploitative competition in male *rosenbergi*. The infrequently observed silent males were not considered sexual parasites, because they never mated when adopting that behavior. Further, the opportunistic strategy, involving random movement, ascribed to many explosive breeding anurans (Wells, 1977b) did not apply. No *rosenbergi* issuing the advertisement call moved frequently, let alone randomly, during a night. In fact, males exhibited exceptionally strong nest-oviposition site fidelity (pp. 82-86). This is predicted for species where the territory is the oviposition site.

The most conspicuous form of sexual interference in male *rosenbergi* was the aggressive behavior displayed when procuring and defending a nest. All directed aggression in *rosenbergi* was density dependent and invariably associated with nest ownership. Eggs rarely were laid outside a nest, most females oviposited in the basin occupied by the chosen male, and there existed considerable variation in nest-oviposition success (Fig. 37). If this form of sexual interference was effective I predict a significant correlation between aggression and mating success. The correlation would breakdown if males successfully controlling nests exhibited high levels of aggression and intruders contested with less "vigorous" residents.

To investigate the existence of the statistical relationship between aggression and mating success, males were separated into groups depending on whether they were involved in aggression or not. Mating success differences between years within the same behavioral class of males were not significantly different, and therefore I grouped the temporal samples together (Fig. 72). Aggressive males received significantly more matings than did the nonaggressive sample ($U = 458.5$; $P = .001$) in the lumped data.

The correlation between mating success of aggressive males and number of nonviolent and violent acts in which they were involved was used to investigate the significance of interference competition in greater detail. The number of acts was subdivided according to whether the male was a resident or intruder. The 1978 data were ex-

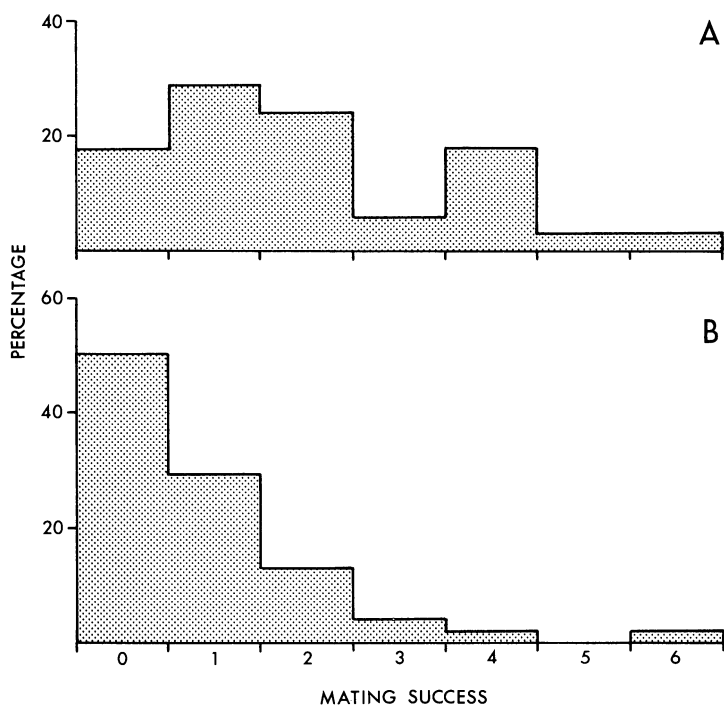


Fig. 72. Mating success of male *rosenbergi*. A. Individuals observed in nonviolent or violent acts (n = 34). B. Individuals exhibiting no form of non-ritualized aggression (n = 48).

cluded, because so little aggression was exhibited (Fig. 63) and the likelihood of significant sampling error was great. Over 25 males displayed considerable aggression in 1977. However, mating success was not significantly correlated with any of the aggression variables scored (number of nonviolent or violent aggressive acts as an intruder or resident, total number of nonviolent or violent acts, and total number of aggressive acts).

If a cause and effect relationship existed between level of aggression and mating success, as suggested by the significant correlation observed initially, why didn't it hold when considered by degree? There is always the possibility of poor sampling. Large numbers of males were not always available, and I am reasonably sure that not all aggression was observed, even during the early part of the evening when most matings took place. Some bouts of aggression were brief and not accompanied by much noise, at least sufficient to attract the investigator's attention. The best evidence for this comes from the fact that males not seen fighting were cut nevertheless by prepollical spines. Also, it may have been the case that the more individuals fought (the more frequent were the acts or the longer each one was) the more it cost them in energy and time, and ultimately in matings.

The longer, more vigorous bouts of aggression ended with one or both contestants perched silently above ground for a long time, often for the remainder of the evening; these silent periods probably were reproductively costly. Wells (1978) stated that vigorous and extended fighting in anurans probably depends more heavily on anaerobic than aerobic metabolism. Anaerobic metabolism requires much greater energy expenditure, particularly if the build-up of lactic acid is excreted. Also, vigorous bouts of activity require extended periods to repay the oxygen debt (Bennett and Licht, 1973, 1974; Bennett, Dawson and Bartholomew, 1975). However, Feder and Olsen (1978) recently indicated that lactate concentration alone may not explain fatigue and recovery.

In addition to male *rosenbergi* contesting for nests, sexual interference existed in the form of one male attacking an amplexed pair. All of the five unmistakable cases of such behavior were observed in 1977. The amplexed male and female became uncoupled in two of the five attacks, and the intruding male got the mating in one of those. The following paraphrased field notes describe male no. 33 (SVL = 84.0 mm, WT = 27.6 gr) attacking an amplexed pair, male no. 10 (SVL = 81.0 mm, WT = 25.8 gr) and female no. 9 (SVL = 85.0 mm, WT = 27.7 gr with eggs), on July 11. This sequence illustrates typical behavior.

Male no. 10 began issuing the advertisement call from his nest (no. 20) of the past few nights, about 1855 hr. Male no. 10 and female no. 9 were found in amplexus in nest no. 20 at 1930 hr. Male no. 33 was about 20 cm away from nest no. 20. The intruding male was silent and in full view of the nest occupants. The intruder approached the edge of the basin and one or both members of the pair responded by kicking the water vigorously and growling. Male no. 33 called briefly at the edge of the occupied nest. At 1950 hr the intruder jumped into nest no. 20 and the pair kicked toward him. They probably made contact. Male no. 10 mewed and the female jumped just (5 cm) beyond the edge of the nest. Male no. 33 briefly called from the nest. At 1958 hr the female, including the amplexed male, jumped about 75 cm farther from nest no. 20, and the attacker followed. The pair returned to within 30 cm of their nest and male no. 33 moved to within 15 cm of them. At 2005 hr male no. 33 called and turned away from the pair who were hidden from his view among vegetation. At 2055, male no. 10 was located alone giving the advertisement call in nest no. 61, which was about 1.5 m from nest no. 20, wherein I found male no. 33. The latter male also actively gave the advertisement signal. Female no. 9 was observed 1.5 m up in a bush and approx halfway between the competing males. Male no. 10 had a fresh cut across the top of his head. Later, he was found dead. At 2200 hr, female no. 9 was observed in amplexus with male no. 7 (SVL = 79.0 mm, WT = 25.8 gr) in nest no. 23. Nest no. 23 was 1.7 m and 5.9 m from nests nos. 21 and 61, respectively.

Female *rosenbergi* rarely exhibited mate competition. However, the behavior involved was so explicit in one case as to deserve description.

On August 3, 1977, male no. 38 (SVL = 82.5 mm, WT = 28.9 gr) amplexed female no. 8 (SVL = 88.0 mm, WT = 30.3 gr with eggs) in nest no. 32 by 1925

hr. At 1955 hr I was attracted to the vicinity of the amplexed pair by loud splashing. This sound can be imitated by rapidly moving a narrow stiff object, such as the side of one's hand, back and forth through the water. As I approached the noise, female no. 10 (SVL = 81.0 mm, WT = 28.2 gr with eggs) was crouched against the ground about 5 cm from the nest wherein the amplexed male no. 38 and female no. 8 were located. After 3–5 min in this position one or both members of the amplexed pair vigorously splashed the water with their hindlegs—they floated on the surface and kicked backward rapidly. The water was not obviously directed at the intruding female. The amplexed female appeared to be responsible for the kicking, although the action was so rapid and the water turbid that I couldn't be certain. Female no. 10 jumped into the nest and more vigorous kicking occurred. After a few seconds, female no. 10 leapt about 30 cm S of the nest while the pair remained in the basin. After approx five min, female no. 10 rose on all four limbs and quickly walked to the nest in an uncharacteristic frog manner. She paused, jumped into the nest and vigorous kicking and loud sounds followed. The amplexed pair bounded from their nest and remained motionless on the ground about 30 cm W of it. Female no. 10 began to swim slowly around the basin. She paused, put her hand on the rampart and then continued to swim. The swimming lasted about five min and most of it was confined to the perimeter of the basin. The pair jumped over the nest and landed loudly about 45 cm E of it in shallow water. Apparently in response to the pair's movement, female no. 10 leapt from the nest, and she perched on a horizontal branch of a small bush about 45 cm W and faced the basin. Shortly after this action (2033 hr), the pair moved westward where they remained motionless for a long time. At 2155 hr female no. 10 jumped into the empty nest making a loud splash. Again she swam haltingly around its perimeter and touched the rampart with her hands. She dove below the surface at least once. Male no. 38, still in amplexus, gave a chuckle type of encounter call and female no. 10 instantly turned toward him, climbed out of the nest, paused, and then returned to the basin. At 2215 hr the amplexed male no. 38 and female no. 8 moved into the nest and the paired female kicked vigorously in the direction of the intruder. Female no. 10 was kicked but not moved. At 2222 hr the pair shifted to another part of the nest and the amplexed female no. 8 faced away from the intruder and kicked her several times. Female no. 10 was rarely separated from the pair by more than 4 cm. Male no. 38 chuckled softly and female no. 10 placed her hand on his back and briefly massaged it in a manner identical to the females' action in normal courtship behavior. An extended period of kicking by female no. 8 followed female no. 10's contact, and then the pair moved on to the rampart. Female no. 10 slowly advanced toward the pair, whereupon they left the nest. Immediately outside the basin additional kicking occurred, but only leaves moved, and it was clear that the amplexed female no. 8 was responsible for all of this activity. Male no. 38 was in a typical neck amplexus throughout this interaction with female no. 10. At 2238 hr a large *Leptodactylus pentadactylus* moved toward the pair and they jumped farther from the nest. At 2253 hr female no. 10 left the basin and disappeared from the general area, while much later that night the amplexed male no. 38 and female no. 8 returned to nest no. 32. A fertilized clutch was present in nest no. 32 the following day. The intruding female no. 10 was not obviously aggressive in her behavior while female no. 8 was clearly so. Female no. 10 appeared repeatedly to attempt to get the male to release the amplexed female by using the key massage stimulus of normal courtship.

I interpreted the intruder's behavior in the above example as a form of female seduction, and if her behavior represented an evolved strategy, it is surprising because female *rosenbergi* would not ordi-

narily be considered the limited sex. Female no. 10 reappeared the night after her unsuccessful seduction, and she mated with male no. 63 (SVL = 81.2 mm; WT = 27.5 gr). The operational sex ratio on August 3 was 14 males:four females, and there were five actively calling males, including male no. 63, within 16 m of the attempted seduction. During 1977, males no. 38 and 63 mated two and five times, respectively. All of the other males in this area reproduced at least once and two obtained four and six matings. Nest no. 32 received only one oviposition in 1977 and it was not reused in 1978. The point of these remarks is that male no. 38 and nest no. 32 did not appear to be exceptional, at least insofar as their mating successes might indicate. Other calling males with considerably greater mating success were immediately available. An additional example of this form of female competition may have occurred on August 24, 1977, and in that situation the intruder obtained the mating. The behavioral details were not observed. So few cases do not form a pattern that demands further interpretation. However, these data serve as a caution not to dismiss the possibility of mate competition by the "limiting" sex.

MATE CHOICE

No behavioral data suggest male *rosenbergi* chose among females. The highly skewed operational sex ratios imply that most males would not have gotten a second chance if a female had been rejected. Further, the little variation in female size (Fig. 17), its apparent lack of correlation with clutch size (Fig. 23) and the complicated pattern of temporal variation in individual clutch size (Fig. 24) provided the male with little physical evidence relating to fecundity on which to base a choice. No male readily released his amplexed mate, even in the context of another female (pp. 142-144). Several pairs became uncoupled, but it usually appeared to result from an attack by a predator or conspecific male.

The most compelling evidence for the existence of mate choice in *rosenbergi* involved female behavior that I believe can only be interpreted as rejection (see also Breder, 1925a, 1946). I define rejection as a gravid female exiting from a nest, leaving an unmated resident behind, and without interruption from predators or significant rain, achieving amplexus with another male. As defined, rejection was observed on five of 23 occasions in 1977 and nine of 17 in 1978. The proportion of rejections was significantly greater in 1978 ($G = 4.20$, $P = .04$). I view these unambiguous acts of rejection as good evidence of female choice and that it occurred rather frequently. Furthermore, I will argue below from a larger body of evidence, but of a more circumstantial nature, that many females exercised a choice before entering a nest. While the two types of female rejection, outside

and within the nest, were based on different criteria, the tendency was to select the same kind of male. The variance in number of rejections might be used as an index to the intensity of selection on female choice. However, no general model has been developed for this purpose. Rejection would affect female reproductive success insofar as it altered encounter rate.

Characteristics of the nest and male were the two most obvious obvious sources of information on which females might have based their choice. Figs. 60 and 64 illustrate that a female inspected a prospective mate's nest. As previously described, she took as long as 48 min, $\bar{x} = 10.6$ min, and her behavior involved swimming slowly in circles, diving to the bottom, and climbing on the rampart and touching it with her hands. It was not obvious what information the female obtained during her inspection. However, it may be recalled that the female invariably renovated the nest of the male she mated with (Fig. 65) and this behavior implied to me that the nest need meet only some minimum standard. That nest quality may not have been important was also suggested by the fact that there was no significant relationship between the numbers of clutches laid in the same nest in 1977 and 1978 (Fig. 39). There appeared to be few local habitat changes between years. In most places the mud shelves were not obviously different in extent or slope in 1978, and occasionally the local vegetation consisted of the same plants (eg, an individual *Heliconia* stock). If nest quality (at least location) had been important, I would have expected a correlation between nest mating success from one year to the next.

One might hypothesize that female *rosenbergi* chose the largest (older, more experienced) males, because they were more aggressive, more likely to be successful in fights, or not as likely to be frightened in territorial contests. This hypothesis was addressed with WT and SVL data; the 1977 and 1978 samples were lumped in the absence of significant between-year differences. The differences in size ($U_{WT} = 985.0$; $U_{SVL} = 1031.5$) between mated ($N = 52$) and unmated males ($N = 43$) were not significant. This finding is consistent with my earlier conclusion that larger males did not win more fights than smaller individuals (Table 11).

Also, it is reasonable to hypothesize that a female *rosenbergi* selected a male on the basis of his size in relation to hers. Given the delicate nature of the surface film and the fact that the male and female cloacae must be brought together exactly at the surface of the water at the time of oviposition in order to realize successful reproduction, I predicted that the SVL of the male and the female in amplexus would be highly correlated. An analysis of 112 mated pairs ($N_{1977} = 79$; $N_{1978} = 34$) rejected that hypothesis ($r = .141$). Further, there was no significant correlation with respect to WT ($r = .172$). The female bending her back downward at the time of oviposition

and the male shifting more anteriorly as the result of his neck amplexus may be sufficient behavioral adjustments to avoid unsuccessful fertilizations and placement of the eggs below the surface of the water.

The female usually bumped the male during nest inspection, seemingly by accident at times, but often deliberately. This contact must not to be confused with her final courtship stimulus, the "female rub" described previously (pp. 111-115), which invariably caused the male to turn and clasp her (Bogert, 1960; Breder, 1946). The two kinds of female contact require further study because they were not always obviously different. I interpreted a deliberate bump as one where the female moved quickly and directly across the basin to the male and struck him with such force that he rocked back and forth from his otherwise immovable position. Sixty-five percent of the females observed in full view from the time they entered a nest more or less deliberately bumped the resident calling male. The between-year proportions (10/17, 1977; 7/9, 1978) were not significantly different ($G = 0.97$). The higher percentage in the low density/low aggression year, 1978, corroborated my thesis (p. 114) that females exercised some mate selection before entering the nest, and that it was based on aggressive behavior observed and heard at a distance. The less opportunity the female had to evaluate males at a distance, the more she was likely to do so in the nest. In all four cases where the resident male bolted from his nest upon being bumped (one in 1977, three in 1978), the female quickly exited from the basin and mated that evening with another individual. Males leaving the nest under such circumstances did not appear to be out of sight of the female, and in any case all rapidly returned and attempted to recall the female. One case history of rejection is particularly revealing.

An unmarked female entered the nest of male no. 115 about 1950 hr on June 14, 1978. She touched the resident. In response, he jumped from his nest, whereupon she left and did not reappear. Male no. 115 returned in less than five min, and another female, no. 80, entered his basin. She bumped him, he remained motionless and, after further nest inspection, she rubbed him and he clasped her at 2001 hr.

I hypothesize that female *rosenbergi's* bumping behavior tested how easily the prospective mate could be frightened from his territory (see pp. 148-149). The fact that only one female rejected a male that did not jump from his nest when bumped may be viewed as evidence that the resident's quality was more important to the female than was his nest's.

Occasionally, a female *rosenbergi* advertised her presence at some distance to available males, and I believe these individuals evaluated their prospective mates according to their subsequent intrasexual interactions. Four gravid females splashed back and forth between nearby competing males. In one case, a female jumped noisily into

and out of adjacent nests in full view of both resident calling males. This female behavior was conspicuously different from that ordinarily exhibited. Usually the female moved slowly and noiselessly into a resident's nest at a point opposite his back. Some form of aggression between the competing males followed in all cases where a female appeared to advertise her presence. The advertising female always mated with one of the two aggressively interacting males.

It became apparent after only a few nights of fieldwork in 1977 that many calling males concentrated in relatively small areas, while few individuals were conspicuously isolated. On a nightly basis there existed as many as three "mini-choruses," wherein membership varied from 2-6 individuals (Fig. 73). As expected, there were frequent bouts of aggression among the residents of these groups. Isolated males were never observed physically defending their nests against the other residents present. Further, intruding males never competed for an isolated resident's nest. However, they were responsible for many of the bouts of aggression involving "mini-chorus" residents. A median test revealed that 1977 and 1978 (Fig. 73) were significantly different years in terms of the numbers of calling males present in both groups or isolated. Moreover, in 1977 a significant inverse correlation existed between the total number of males calling per night and the percentage that were isolated. In 1977, $r_s = -.776$ ($N = 51$), and in 1978, $r_s = -.365$ ($N = 40$, $P > .05$). This distribution of calling males was not related to the availability of nesting areas, because much of the shore-line remained unused on those nights with the highest male densities. More importantly, these unused areas were not of low quality, because they were successful calling stations on other nights.

If females were really testing a male's fright response and aggressive tendencies, as the behavioral observations discussed above suggest, then a relatively low mating success among isolated males might be expected. The number of mated and unmated isolated or grouped individuals were examined to test this hypothesis. There were 27 nights in 1977 and four in 1978 where at least one mating took place and where both grouped and isolated calling males were present. Table 16 summarizes the data, and the hypothesis that there is no relationship between location and mating success among males was rejected ($G = 6.33$, $P = .01$). This means that the probability of a male mating was improved by his calling from a group. Both isolated and groups of calling males certainly were within hearing distance of females when they descended from the canopy, and therefore the supposition that larger choruses might attract mates from greater distances would not apply to *rosenbergi*. It seems that we are left with the conclusion that female *rosenbergi* perceived males in groups as better mates (Alexander, 1975), and I hypothesize that "better" means more successful at holding territories. The female's own behavioral

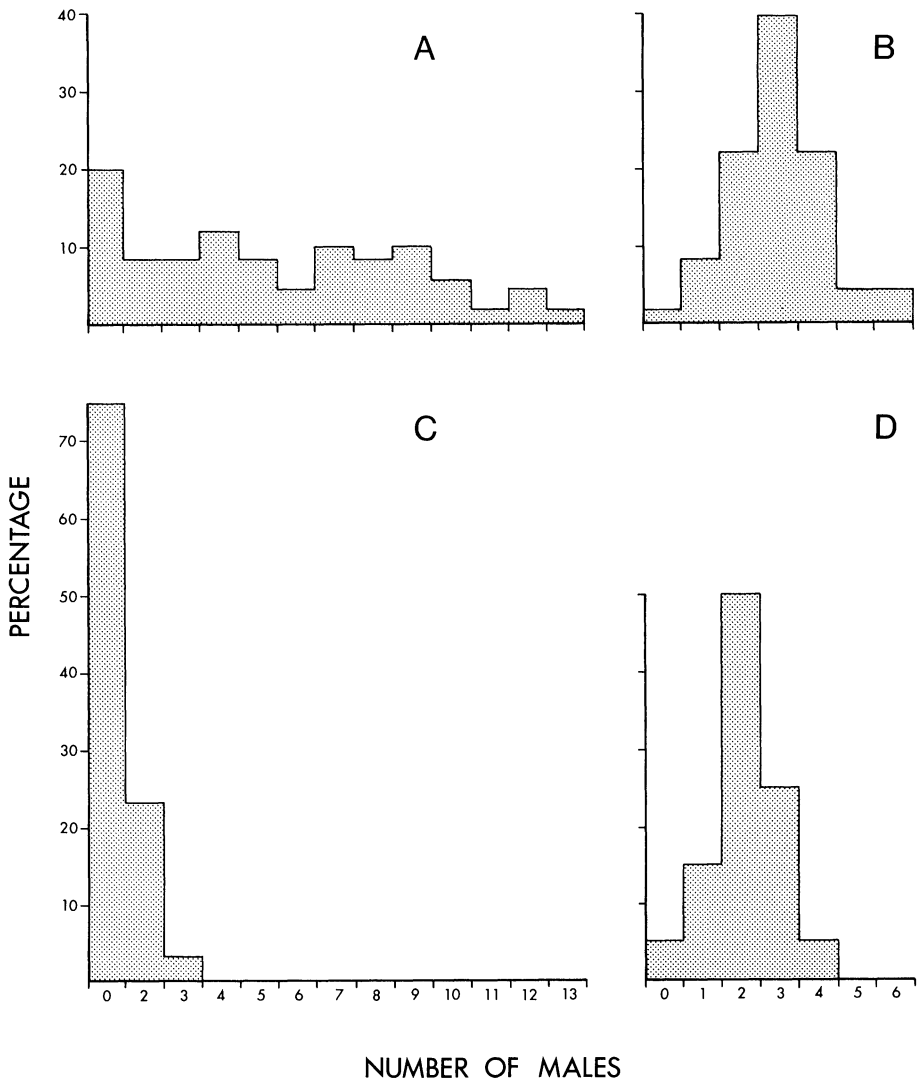


Fig. 73. Number of male *rosenbergi* calling each night in groups (A, C) or isolated (B, D) in 1977 (A, B) and 1978 (C, D). $N_{1977} = 51$; $N_{1978} = 40$.

actions support this prediction; bumping a resident calling male and rejecting him if he is "frightened" from his territory, and the solicitation of aggression between nearby competing males. Thus in summary, mini-choruses of *rosenbergi* were not resource-based, but were favored by males because females preferred their residents as mates (Wells, 1977b).

How was the female's reproductive success increased by preference for a more territorially tested and aggressive mate? I predict that such males were more likely to provide effective parental care. A male not frightened from his territory and that would attack an intruding

TABLE 16
 TEST OF ASSOCIATION
 BETWEEN MALE *ROSENBERGI*
 CALLING STATIONS AND MATING SUCCESS

Mating Success	Location Of Calling Males	
	Grouped	Isolated
Yes	45	9
No	143	72

$G = 6.33; P = .012$

conspecific is likely to increase embryo survivorship and thus the female parent's fitness.

The evolution of aggression in male *rosenbergi* may be the result of what Fisher (1958) called "runaway selection." This species is exceptionally aggressive, and such behavior must have been strongly selected for in the context of male-male competition (territoriality). If the female's preference for more aggressive males as mates is added to that, then the selective force is compounded. Like Fisher, I believe such an example is unlikely to be unlimited, and thus to be truly runaway (pp. 150-153).

Female choice experiments were used to test the conclusion that female *rosenbergi* preferred mates in a chorus (Table 16; see also pp. 6-8 for further technical details of the experimental design and equipment). The tests were carried out in the field in 1978 from June 29 to August 17. Each of 11 gravid females was given the opportunity to move toward an advertisement call given by a single male and that same signal repeated four times asynchronously in the same interval. Continuous tape loops were employed, and the four-male chorus was created by first recording simultaneously two identical loops of the one male's call played asynchronously and then rerecording simultaneously two such products played asynchronously. The one- and four-male tapes were alternated between sound systems (tape recorder and speaker), and each female was tested twice after approx 10 min of tape recorder silence.

The 11 females tested showed no significant preference for the four-male chorus as was expected; the results were nearly random. I believe it would be worthwhile to repeat the tests, but under more ideal circumstances than were available in 1978. For example, the experiments were far from perfectly controlled and the most important variable that must be reconsidered is the condition of the female (Gerhardt and Mudry, 1980). Nineteen hundred and seventy-eight was a low density year, and in order to generate a reasonably large sample size all possible females were used in the experiments. Unfortunately ,

some individuals were taken out of amplexus, while others were captured before they entered the chorus, while still others were taken well before they heard any *rosenbergi* calling naturally that evening. In addition to using unexposed females, I think the experiments should be carried out in a controlled laboratory environment. Unpredictable gusts of wind and rain, and sticky tape loops due to humidity may have confounded the 1978 results. Perhaps most important, the method of measuring equal volumes of the two speakers at the point of the female's release is questionable (pp. 6-7). A sensitive sound level meter must be employed in future studies.

If there was a strong mating preference for male *rosenbergi* in a group, then how does one explain the existence of isolated individuals? If fitness and calling site preference are heritable one would not expect to continue to find isolated calling males. In the most general terms, three possible explanations for the apparent polymorphism exist: chance, some form of heterozygous advantage, or frequency (density) dependent selection. Some isolated individuals are expected by chance alone considering the following hypothetical scenario. Three males form a mini-chorus on a given night. One is preyed on and one mates. The following night, one of the surviving males provides parental care while the other individual advertises alone for females. Several such examples were observed, particularly in 1977. Further, it is possible for a male regularly calling from an isolated position to attract one or two newly recruited males to his immediate area, because no choruses are present. This situation was rarely observed and it appeared to happen only when densities were low. In spite of these overriding complexities, a few males were never observed in a chorus. Fig. 74 summarizes the number of nights in 1977 that 45 calling males were isolated (A) or in a group (B). The discontinuity (absence of records) in the distribution corroborates my opinion that there were two kinds of males present (A and B). The relationship between location of calling males and their mating success in these data was significantly different ($G = 6.14$; $P = .01$), as it was for the combined two years of data shown in Table 16. The hypothesis that more frequently isolated individuals did not obtain fewer matings was rejected for the A assemblage treated alone ($G = 3.70$; $P = .05$) but not for the B group ($G = 1.23$; $P = .27$). I interpret these findings to mean that there were few males in group B with the inherent predisposition to be isolated. The continued existence of the isolated male phenotype in the population could be maintained if those males lived longer. This is a reasonable expectation, because predators concentrated on the more frequent callers, however, my limited quantitative data do not support that contention (pp. 86-88). Another possible explanation involves higher embryo survivorship to hatching. Here too, the hypothesis seems reasonable, because fewer

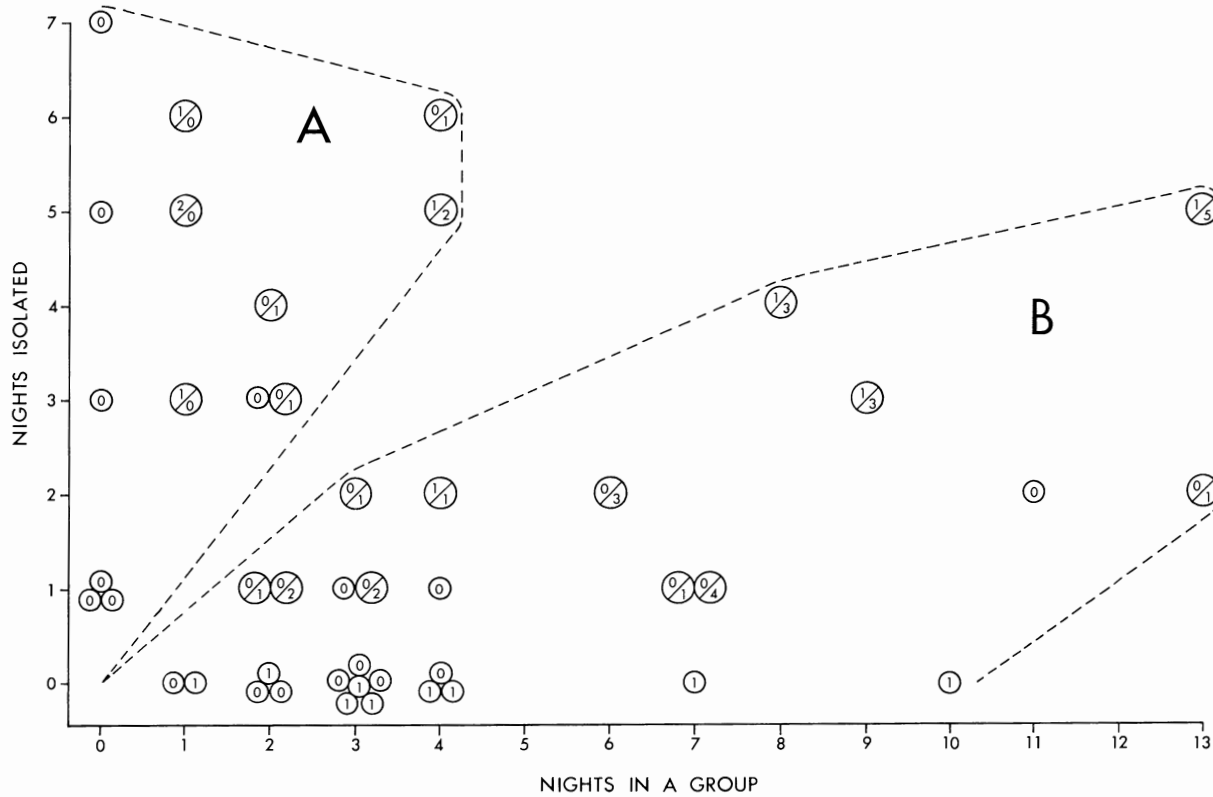


Fig. 74. Number of nights 45 male *rosenbergi* spent calling in groups or isolated from other competing males in 1977. Each circle represents one male, and the numbers therein were the mating success when isolated (above the diagonal) and in a group (below the diagonal). No matings were obtained or the male was only in a group when no diagonal is present. The large dashed inclosures emphasize the discontinuity between predominantly isolated (A) and grouped (B) sets of males.

males were observed intruding upon isolated males. If intruders affected early embryo survivorship, as argued earlier, then survivorship should be higher. The data are inadequate to test this thesis.

Most *rosenbergi* males sought membership in "mini-choruses" in 1977, the high density year, whereas relatively far more isolated than grouped individuals characterized the low density breeding season of 1978 (Table 17). Earlier, I stated that this difference could not be explained by the nesting area in the first year being so limited that clumping of males under their higher densities necessarily had to be greater. Consider the fact that under the highest densities there was a large excess of nests; the maximum number of males calling from nests per night in 1977 was less than 18 (Fig. 71) and the actual or potential number of nests available was well over 100 (Fig. 29). Most males seemed to switch to the "isolated" mating strategy in 1978, in spite of the increased mating success that came from group membership.

TABLE 17
TEST OF ASSOCIATION
BETWEEN MALE *ROSENBERGI*
CALLING STATIONS AND YEAR OF STUDY

Year	Location Of Calling Males	
	Grouped	Isolated
1977	262	152
1978	21	84

G = 65.80

I propose the following explanation for this male behavior. When male densities increased, the probability of a mini-chorus forming by chance alone increased. In this regard, one must remember that suitable nesting areas, shallow mud banks, were not uniformly present along the ODSS. Whenever males began to form groups, even the smallest ones, females tended to differentially select their mates from among the grouped individuals, and thus when a cluster formed, it had a contagious affect on the behavior of many other males.

In summary, I suggest that isolated males had several advantages that could have increased their mating success. These are: (1) The probability of surviving was higher, because predators had greater difficulty locating isolated males. (2) There was less opportunity for being fatally wounded in territorial encounters (levels of aggression were lower). (3) Paternal care duties were relaxed, because of the lower probability of one's nest and offspring being intruded upon by a competing male, and this time was spent advertising for additional

mates. In spite of the probable benefits accompanying isolation, calling in a chorus often occurred in *rosenbergi*, at least under high densities. The presence of alternative mating strategies indicated the existence and power of female choice in this species.

SUMMARY

Territoriality in the nest-building gladiator frog *Hyla rosenbergi* was studied in the Canal Zone, Panama, mostly along the Obispo Diversion in relatively dry (1977) and wet (1978) years. Complete summary statistics and levels of significance may be found in the text. Differences are not emphasized in the following text when $P < .05$.

Breeding began on May 25, 1977 and April 20, 1978. Its origin was correlated with an amount of accumulated rainfall (25 cm) necessary to raise the water table to a favorable nest-building and flooding environment. Rainfall and number of males were negatively correlated. The minimum daily rainfall keeping all males from descending to their nests was 17.8 mm. Rainfalls of this or a greater amount occurred at average intervals of 6.5 days and they were highly unpredictable. Breeding activity stopped in late October-early November before the rainy season ended and the stream dried. The local population of adults probably was much reduced, if not eliminated altogether, by predation and death due to fighting before the favorable breeding environment disappeared.

Males possess a bony spine on the medial aspect of each hand. Frequently, these weapons were used in intrasexual combat. The spines are not likely to have originated as weapons. The females' yellower coloration may have kept them from being attacked by territorial males.

Considerable geographic variation in adult size was observed. Females were slightly longer than males, but they weighed significantly more or less depending on whether or not they had recently oviposited. Males and females had the following average size characteristics: $SVL_{\text{male}} = 82.6$ mm, $SVL_{\text{female}} = 85.5$ mm, $WT_{\text{male}} = 27.7$ gr, $WT_{\text{female}} = 31.9$ gr, $WT_{\text{female wo/eggs}} = 24.6$ gr. The average clutch was 7.2 gr and it accounted for 22.7% of the female's weight. Lack of correlation between egg weight and female size probably was due to an individual's seasonal variation in clutch size. Body size did not appear to vary with time of recruitment, and males and females exhibited no growth after entering the breeding population. Males fed on arthropods (mostly orthopterans) that are found within 3 m of the ground. The absence of growth does not appear to be due to low food availability. Insect abundance is high during the wet season.

Males probably utilized considerable energy for daily maintenance, calling for mates, building nests and behaving territorially, while females converted most of their food into eggs at an average rate of 0.3 gr/day.

Ninety percent of the gravid females amplexed on the night they appeared, none took longer than three nights to select a mate. The average female oviposited a clutch every 24.7 days with an average size of 2350 eggs. The entire clutch was oviposited at one time. Clutch size was not correlated with either female SVL or WT at first breeding or date of oviposition. An individual's seasonal variation could have masked the correlation. Second and third clutches were nearly always smaller than the first, while clutches 4-6 were invariably larger. More frequent smaller clutches may be an adaptation to the unpredictable rains that often inflicted heavy mortality prior to hatching. Larger late season clutches may have two advantages. Fewer larger clutches might increase the female's life expectancy by avoiding the increasingly numerous terrestrial predators. Also, fewer larger clutches might result in greater lifetime reproductive success, because the breeding season ends unpredictably, either in disappearance of males or change of environment.

Average ovum diameter between clutches, 1.6-2.1 mm, was not correlated with day of oviposition, number of eggs per clutch, clutch weight or female size (WT or SVL). No significant differences were observed between years or first and second clutches. Ovulation appeared to occur well after amplexus was established; this timing probably evolved because preferred matings were often interrupted.

The water-filled nest was the resident male's territory and place of oviposition. He usually issued advertisement calls while in the basin. Only males initiated nests. Most nests were started in extant depressions, even boot-prints and vacated egg chambers built by the predatory *Leptodactylus pentadactylus*. No male advertised for mates and constructed a new nest at the same time. The substantial reproductive and energetic costs associated with nest construction probably were responsible for intruders competing aggressively with residents for their nests. Nests deteriorated rapidly and nightly renovation by the resident male was common. Females inspected the nest prior to amplexus, but they never renovated it until clasped by the resident. Substrate condition markedly affected nest size, shape and composition. The optimum volume of water for embryo development probably was extremely difficult for females to predict during nest inspection, because of the considerable temporal variation in the water table and varied nest shapes. Miniature canopies immediately above nests protected freshly oviposited surface films of eggs from rain. However, there was no evidence that nests were preferentially constructed beneath broadleaf vegetation. The unpredictable variation in stream-side vegetation may be responsible for this lack of

correlation. Nests were concentrated in small areas on shallow mud banks, and not all banks were used. One hundred and six nests were present in 1977, 43 in 1978; 17 were used in both years. The maximum rate of new nest addition in 1977 was 3.4/day, whereas it was only 0.7/day in 1978. Nests were infrequently occupied by any male ($\bar{x} = 4.1$ nights), and their little use was due to heavy rain, the shifting nature of choruses and avoidance of nests containing embryos. Most nests (64.3%) were used by different males. Availability of nests probably was the result of low adult life expectancy and the shifting nature of choruses. Multiple residency was not due to intruding males evicting territory holders. Rarely were nests occupied the same night by different males ($\bar{x} = 0.2$). The 1978 average distance between nearest calling males was nearly twice that in 1977 (13.6 m versus 7.0 m). The mini-choruses formed less frequently in 1978, probably because fewer males were present and they switched to an alternate mating strategy. The number of clutches laid in a nest averaged 0.97 per season (ORV = 1-5) and it was correlated with frequency of occupancy ($r_s = .663$), number of multiple male occupancies per night ($r_s = .223$), and number of days between first and last occupancies ($r_s = .675$). It could not be related to time between nest origin and first mating. The average time between successive ovipositions in the same nest was 32.5 days, and the absence of overlap probably was an evolved response to cannibalism. Males rarely (11/582) reoccupied a nest they mated in, and only two were successful in mating a second time. No female oviposited more than once in the same nest. These observations suggest that nest quality had little effect on male mating success. Moreover, there was no positive between-year correlation in a nest's mating success, as might be predicted if site quality were important. Mating success in those nests used in both 1977 and 1978 was significantly correlated with frequency of male residency ($r_s = .727$). The skewed distribution of nest/oviposition success appeared to be explained just as well by male-male competition as it did by variation in nest quality.

Oviposition took place in the early morning hours of the night during which amplexus occurred ($\bar{x} = 0301$ hr). Two factors may have contributed to the long period of amplexus: (1) a female's long period of nest renovation, and (2) increased egg survivorship, because most of the intruding males that disturbed surface films had retreated to the canopy by time of oviposition.

Amplexus involved the male holding the female's neck with his hands, the ensheathed prepollical spines were directed away from his mate. The soles of his hindfeet rested on the anterior surface of the female's thighs. In this position, the amplexed pair's cloacae were brought together, which no doubt accounted for the efficient fertilization observed. The female, while on extended fore- and hindlimbs, maintained her cloaca at the water surface during the brief period of

oviposition (approx 10 min). Ovipositions usually occurred in well-shaded environments, and the dark egg pigmentation may be cryptic. Eggs were laid singly and each was surrounded by two clear membranes. The stickiness of the outer-most capsule and the surface tension of the water were responsible for the monolayer of eggs that rested on top of the water.

A marked increase in between-sample variance in embryo size began about 150 hr postfertilization, and some cohorts of nest-bound larvae did not grow nor mature for an additional 300 hr. Hatching occurred from stage 17–19, 40–66 hr postfertilization. Average nest oxygen ($\bar{x} = 1.3$ ppm) was significantly lower than that of open water ($\bar{x} = 2.3$ ppm). The large filamentous gills present at stages 19–23 probably are a respiratory adaptation for a period of exceptionally rapid growth. Stage 25, reached in 150–165 hr postfertilization, was characterized by an exogenously feeding and free swimming tadpole. All larvae at stage 25, or older, left their nest when it flooded. Rate of growth to stage 25 was closely correlated with the average interval between rains that caused most nests to flood (151–163 hr). Rate of growth and maturation beyond stage 25 in broods confined to unflooded nests was correlated with tadpole density (negatively) and amount of organics in the basin (positively). Cannibals had an increased growth rate. Nest water temperature was lower ($\bar{x} = 25.4^\circ\text{C}$) than that outside the basin ($\bar{x} = 25.8^\circ\text{C}$), and the hypothesis that the nesting habit evolved because of an increased rate of development due to warmer water proved false.

Metamorphosis occurred about 21.0 mm SVL, approx 40 days postfertilization. Postmetamorphic froglets grew at an average daily rate of 0.21 mm SVL. Pre- and postmetamorphic growth rate data indicated adult size can be achieved in one year.

Subadult survivorship appeared to be low. Only 24% of clutches in the nest suffered little or no mortality and all embryos died in 22%. Most death occurred when eggs sank to the bottom of the nest. Only rain and intruding males disrupted the delicate egg film resting on the water's surface. Field observations and laboratory experiments implicated oxygen deprivation as the proximate cause of mortality. Embryos were particularly sensitive prior to neural tube formation (stage 14), within 20–30 hr postfertilization. The increased embryo mortality in 1977 probably was a function of higher adult densities. Tadpoles of *Leptodactylus pentadactylus*, *Physalaemus pustulosus* and *rosenbergi* were the most conspicuous predators of eggs and early larvae. The predators exhibited no obvious morphological adaptations for carnivory. Of the three predatory species, *rosenbergi* tadpoles were the most frequently encountered in nests and they often outnumbered their prey. The predatory efficiency of *L. pentadactylus* tadpoles increased as a function of prey density, and smaller prey were consumed more quickly. Temporary lack of rain and nest desiccation

accounted for less than 8% of the premetamorphosis mortality. The nesting habit probably evolved in response to cannibalism, and that pressure must be viewed as considerable, because of the several disadvantages accompanying nesting.

One hundred and five adult males were marked in 1977 and 73 in 1978. Local density was lower the second year, because more breeding environments were available as the result of greater rainfall. Considerably fewer males moved to different areas than would be expected by chance, and a greater proportion of moves per male occurred in 1978. These data suggest that once an individual entered a chorus he rarely moved to another, and that moves were more likely as number of local breeding environments increased. When a male moved he sought lower density choruses, which implies males became exhausted from intrasexual competition for mates.

Seventy-three adult females were marked in 1977 and 36 in 1978. The proportion of males to females did not differ significantly between years in spite of density differences. Females and males did not differ in their predisposition to move to a new area. A transplant experiment indicated that site familiarity was extremely important, which no doubt was a major reason for *rosenbergi's* infrequent emigration.

The seasonal sex ratio did not deviate significantly from 1:1 in 1977 and 1978. This finding was consistent with the similar survivorships and growth rates for males and females.

Recruitment of adults was gradual, rather than pulsed. Individuals probably entered the breeding population about one year after their birth dates. The much lower recruitment rate in 1978 was due to the more widely available breeding environments associated with the wetter season. Female recruitment lagged 10–25 days behind that of males'. The difference probably was caused by the females' greater gamete investment.

Once a male entered a chorus he rarely was absent. Such persistence underscored the importance of acquiring a nest, defending it and ultimately attracting mates. Males returned each night to the same nest, without visiting another basin, 62% of the time. Most of the moves to different nests (33%) followed nights of successful reproduction. Use of more than one basin per night was extremely rare (2/441). The average distance actually moved between nights was less than one meter. The distance moved within a night was significantly longer in 1978 ($\bar{x} = 3.0$ m versus $\bar{x} = 1.0$ m in 1977), which no doubt was related to the lower male densities. The nest occupied by a male after a successful mating was significantly farther in 1978 ($\bar{x} = 3.8$ m versus $\bar{x} = 1.4$ m in 1977). However, the averages of the two years were not different when new territories were established without prior mating success. These findings suggest that males rarely changed locations within the local breeding habitat and moves were

limited to short distances. Site familiarity probably was related to successful territory defense and escape from predators.

No adult male was recaptured in 1978 and only three females returned the second breeding season. Average male residencies were not different between years, and male ($\bar{x} = 18.3$ days) and female ($\bar{x} = 23.2$ days) averages were only marginally significant. Residency data were interpreted as good estimates of survivorship, and the 20.5 day average for the species makes it the shortest-lived anuran known. Individuals have lived several years in laboratory and zoo environments, and high predator densities are the most likely cause of the shorter natural life. Several adult *rosenbergi* were eaten by *Leptodeira annulata* and *Leptodactylus pentadactylus*. Predator abundances seemed to be correlated with that of its prey, both within and between years. Predators probably used *rosenbergi*'s calls as locational cues.

Adults spent the daylight hours in or near the forest canopy. Males issued the first vocalizations of the evening about 1838 hr. Descent to nests was rapid; it was significantly quicker in 1977 ($\bar{x} = 1840.6$ hr versus $\bar{x} = 1853.1$ hr). This difference probably was a function of the lower density of competing males in 1978. A chorus formed shortly after descent in 1977 ($\bar{x} = 1843.6$ hr); the few males present in 1978 rarely produced a recognizable chorus. Females appeared an average of 45 min after males. The females' earlier average appearance in 1978 (1918.8 hr versus 2002.5 hr) may be explained by the fewer males they had to choose among. Females averaged 20 min between first sighting and when they were amplexed; about half that time was spent inspecting the nest. The average time of amplexus was 1937.7 hr, only 54 min after the first males called.

A male can be both an intruder or a resident. A resident usually occupied the same nest several nights and issued advertisement calls. Intruders moved often, usually gave territorial calls and frequently contended with residents for their nests. A resident was either isolated from competing males or geographically close, and thus a chorus member. Chorus residents were involved in more aggression and mated more often than isolated residents. Intruders appeared not to mate. The nests of isolated males could not be considered suboptimal, because they had been, or did become, the territories of chorus residents. Resident males called significantly more often from elevated perches near their nests in 1978 (42% versus 19%). The different nest use may have been a function of generally high terrestrial predator densities and relatively low density of competing males in 1978. A few intruders were silent throughout the night. Their strategy was unlikely to have been one of sexual parasitism and forced copulation. The silence probably reduced their chances of being attacked by conspecifics or predators.

The apparent absence of a release call and body vibration was probably related to the existence of a prolonged breeding season,

territoriality and female mate choice. The eight readily recognized call types in males are the most published for any anuran; many are structurally similar to the advertisement signal. This call type was the most common and it was usually given by chorus residents. Its most obvious function was female attraction; however, it might have been used by intruding males to locate a chorus. Dominant frequency and the caller's size were not correlated. The courtship signal was like the advertisement call except it was slower and much softer. It was issued by the resident male when a female entered his nest. The proximate function of the call was unclear. The territorial call was the second most frequently given signal. It was most evident after 2200 hr when the chorus of advertisement calls stopped for the evening. It was usually given in response to the call of another male, particularly one close to it. It was the only signal given by males guarding their young. Five encounter calls were recognized: chuckle, growl, mew, bark and hiss. They were of low intensity and pitch and they usually elicited a similar sounding response from an antagonist. A unique social context for each was not apparent. Encounter calls probably signaled a male's aggressiveness and it may have improved his chances of attracting a female.

Three levels of aggression were recognized in males: undirected, nonviolent and violent. The first was characterized by territorial and encounter vocalizations that were not directed at a particular individual. The territorial call given late in the evening probably generally advertised nest ownership. The nonviolent form of aggression involved rapid charges and chases, but without physical contact, and territorial and encounter calls directed at a specific antagonist. Violent aggression involved physical contact, usually wrestling, and wounding with prepollical spines was common. Growls and hisses were frequently issued by violent combatants. Nonviolent and violent levels of aggression were never observed between intruders. However, they were frequently seen among an intruder and resident or nearby residents. Residents showed some form of aggression to a calling male closer than 1.5 m. A silent male was never attacked. Occasionally, an amplexed pair was attacked; the intruding male rarely obtained the female. Prepollical spines protruded from their fleshy sheathes during wrestling, and they were usually jabbed at the opponent's eyes and tympana. The wounds received in at least two fights probably caused death. No doubt wounding also increased the likelihood of predation. Thirty-eight percent of the males exhibited wounds after only a few nights of residency. Only 2% of the males had wounds when first encountered. These data suggested that almost all new recruits to the breeding population lacked prior territorial and, perhaps reproductive, experience. More than 50% of the 1977 males were observed in directed aggression, 41% in nonviolent bouts, 35% in violent ones, and 25% in both. There were 27 nonviolent and 21

violent bouts of aggression in 1977, totalling 172 and 887 min, respectively. Most of this aggression occurred at 1900 hr, only a few minutes after males had left their daytime retreats and descended to the ground. Most aggression disappeared shortly after time of amplexus. In 1978, 64% of the males were involved in some form of direct combat, 43% at both nonviolent and violent levels, and 21% participated in both. Nonviolent and violent aggression totaled only 26 and 59 min, respectively. The significant differences in levels of aggression in the two years might be explained by the greater density of males in the dry year, 1977. The number of males involved in the two years was not significantly different. In 1977, approx 10 times more aggression per unit time existed than in 1978. This was also more than 10 times that reported for *Rana clamitans*, another particularly aggressive frog. Size (WT and SVL) had little influence on which male won an aggressive encounter, however, the resident was usually the winner. The adaptive basis for relatively large male size is unclear. It does not appear to have been due to male-male combat. Further, mated males were not significantly larger than unmated individuals. Bouts of aggression may be costly in terms of increased predator exposure and the potential for combat wounding. The direct reproductive cost may be great, because the advertisement signal was not given during a fight. However, some observations suggested females promoted aggression between males before they chose their mates.

The resident became motionless when a female entered the nest opposite his back, and remained so while she swam and dove in the basin and investigated the ramparts. The female usually bumped the resident during her nest investigation. Eventually she rubbed his head and trunk with her hands, chest and chin. Only after this massage did the male turn and mount the female. The male shifted posteriorly into a typical anuran axillary amplexus when the female jumped as the result of an attack by conspecific male, female, or predator. Forced amplexus rarely, if ever, occurred. The motionless state of the resident male probably provided the female with the time necessary to inspect the nest and to test his fright response. Pairs became uncoupled when attacked by predators and conspecifics.

To refer to the *rosenbergi* mating system as a lek seems inappropriate. Males differentially controlled resources (the nest) required by the female for oviposition. However, females appeared to base their choice of a mate more on the male's aggressive behavior. Males guarded their nests the remainder of the early morning hours following fertilization and the two subsequent nights, but never longer. This defense kept intruding conspecific males from entering the basin and disturbing the surface tension of the egg film. Frequency of guarding males declined with each night and males were less attentive in 1978 compared to 1977. The paternal care was

provided during the most vulnerable period of the offspring's pre-adult life, from fertilization to time of hatching (40–66 hr). The male parent was not guarding his offspring in all five cases where intruding males were responsible for egg film disturbance and embryo mortality.

Paternal care affected future reproduction because guarding males never advertised for females. Consider the average male: he survived 18.3 days and took 16 nights of calling to realize 1.2 matings. Therefore, two nights spent guarding offspring reduced the likelihood of the male achieving more than average mating success. The facultative nature of paternal care observed in *rosenbergi* is consistent with this model. When male densities were high, more parents guarded their offspring. Paternal rather than maternal care probably evolved in this species because of the male's territorial behavior and greater ability to defend the nest with calls and prepollical spines. His less exhausted postoviposition condition also may have been important.

Some males and many females mated more than once per season (males: $\bar{x} = 1.2$ in both 1977 and 1978, $s_{1977} = 1.438$, $s_{1978} = 1.541$; females, 1977: $\bar{x} = 1.5$, $s = .939$). Many males did not mate. Males and females never remated together. The yearly samples of male mating success did not differ significantly in either mean or variance, while the female data set was different from the males in both statistics. More than one half of the variation in male mating success was explained by length of residency (survivorship). *Rosenbergi's* mating frequencies were compared to several prolonged and explosive breeding anurans. In general, male frogs were 1.2–10 times less variable in mating success than birds with a comparable mating system (polygynous species). This difference appeared to be due to the difficulty the ornithologist has in equating each mounting with a successful mating. All anuran examples conformed to the prediction of sexual selection theory for polygynous species that mating success is more variable in males. Conformance to theory was not true for the data on birds. All frogs were referred to the polygyny category ($CV^2_{\text{male}} > CV^2_{\text{female}}$) of my mating system classification. Sexual selection was 99% of the total selection intensity acting on male *rosenbergi* reproduction in both 1977 and 1978. Compared to other anurans, *rosenbergi* exhibited the greatest intensity (also shared with *Centrolenella colymbiphylum*); *Rana temporaria* possessed the lowest at 81%. The small between-year difference in variance in male *rosenbergi* reproductive success had no effect on the intensity of sexual selection estimates. There was considerable variation in male mating success variance among anurans (0.136–9.758) but it had relatively little effect on the proportion of sexual selection (81–99%). Some anurans showed modest variation between years in the proportion of intensity of sexual selection (*R. catesbeiana*, 87–95%), whereas

others exhibited none (*rosenbergi*). The surprisingly narrow range in the proportion of intensity of sexual selection in anurans was probably related to how little of the maximum variance in mating success possible was actually observed (0.3–9.1%). The relative severity of selection on the sexes in different species of anurans tended to vary greatly (four in *rosenbergi* to 68 in *Bufo canorus*). The high estimate for *R. sylvatica* (28.3) may be explained by differential survivorships and growth rates. The proportion of intensity of selection for iteroparity varied greatly among anurans (26–97%), with *rosenbergi* possessing the largest estimate.

The operational sex ratio (number of sexually active males: reproductive females) varied considerably within and between years. In 1977, the nightly range was 16:0–3:5, with a seasonal average of 6.9:1. The main peaks of male abundances were correlated with those of females. The late season abundance of females in 1977 suggested they “anticipated” the end of the breeding season. In 1978, the range was 7:0–3:2, with a seasonal average of 9.3:1. There were far more males and females present in 1977 on a per night basis. However, the proportions of the two sexes over the entire two seasons were not different. This finding was consistent with the absence of significant differences in male mating success variance in 1977 and 1978. A long breeding season, extended adult recruitment, and moderate rate of vitellogenesis largely were responsible for the operational sex ratio in *rosenbergi*. The mating system appeared to be more one of male dominance polygyny than resource defense.

There was no evidence for exploitative competition in males. Silent individuals did not mate, and males almost always advertised for mates from fixed positions, usually the nest. Sexual interference in males was density dependent and it involved nest procurement and defense. More aggressive males received more matings than non-aggressive individuals. However, the mating success correlation was not significant when the kind of aggression (nonviolent or violent) and the status of the combatants (intruder or resident) were considered. Small sample sizes and negative feedback involving exhaustion may be responsible for the breakdown in correlation. Sexual interference also involved males attacking amplexed pairs. An intruding male clasped the female in only one case.

Unexpectedly, some females exhibited mate competition. It was inferred when a female entered a basin with an amplexed pair and used the massage stimulus of normal courtship on the coupled male. One such intruding female probably secured a mate by this means.

Strong nest site attachment, rigid position in the presence of a female and little variation in female size that could be correlated with fecundity were probably responsible for the absence of mate choice in males. Mated and unmated males did not differ significantly in size (WT or SVL). This was consistent with the finding that larger males

did not win more fights. Also, there was no evidence of mate choice based on size assortment.

Fifty-five percent of the gravid females that entered a calling male's nest left for another mate that evening, and this form of rejection occurred significantly more frequently in 1978 than 1977. The female almost always inspected the nest, and 65% tested the resident male with a deliberate bump. In all four cases where the resident bolted from the nest upon being hit, the female quickly exited and did not return. Only one female rejected a male that did not jump from his nest when bumped, and this was viewed as evidence that the resident's quality was more important to the female than was his nest's. The female's preliminary harsh contact with the male may have tested how easily the prospective mate could be frightened from his territory. Mate choice also was implied when some females loudly advertised their presence to competing males by splashing and jumping into nests. Male-male aggression always followed and the female always chose one of the two combatants.

Females also appeared to exercise mate choice before entering a nest. Males calling in a group had a higher probability of mating than did isolated individuals. Greater chorus volume, thus more area surveyed for females, did not explain the differential mating success. Nineteen hundred and seventy-seven and 1978 were significantly different in terms of both numbers of calling males present in groups or isolated. The number of isolated individuals was inversely correlated with the total number of males. Limited space or poorer site quality did not explain the correlation. Thus, mini-choruses were not resource-based, but were favored by males, because females preferred their residents as mates. Such males probably were more likely to provide effective paternal care because they were territorially tested.

The isolated male mating strategy may be maintained in spite of lower mating success, because of higher adult and embryo survivorships.

The exceptionally aggressive nature of male *rosenbergi* may be the result of compound selective forces, male-male competition and female choice. The female's choice of a mate appeared to be based more on his aggressive behavior than the nest he occupied. It was within her ability to substantially renovate the nest. Also, a nest's mating success was significantly different from one year to the next, without any obvious changes in the local environment.

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