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Synopsis of the Biology of the  
Middle American Highland Frog  
*Rana maculata* Brocchi

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**Synopsis of the Biology of the  
Middle American Highland Frog  
*Rana maculata* Brocchi\***

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**Abstract.**—The ranid frog *Rana maculata* Brocchi is common at high elevations (usually 800-2400 m) from southeastern Mexico to Nicaragua. Tadpoles reported from Belize, because of differences in tooth formulae, oral disc, and caudal pigmentation, may represent a different species (no adults are available). *Rana maculata* is always associated with clear, swift-flowing mountain streams and, in Nicaragua, may be the dominant non-arboreal frog there. Although reproduction appears to take place throughout the year in some localities, in Nicaragua *R. maculata* is the only frog breeding exclusively in the dry season; possible reasons for this curious reproductive pattern are given. Egg masses are laid at night attached to rocks or vegetation in the streams. Masses collected in slower parts of streams contained more eggs than those from faster ones. The developmental stage at hatching varies similarly, with "early hatchers" (Gosner's Stage 17) in slower, and "late hatchers" (20-21) in faster streams. The reasons behind this variation are given, as well as details on the development and size of egg clutches, embryos, tadpoles and recently-metamorphosed individuals. An interspecific association, of still uncertain nature, was found involving egg masses and the planarian *Dugesia* (*Girardia*) sp. (Platyhelminthes: Turbellaria). The carnivorous planariae did not feed on the embryos of *R. maculata*.

\* \* \*

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*Rana maculata* is a moderate-sized ranid frog inhabiting the high elevations in northern Middle America. Although often locally abundant, little has been published about its biology. At San José de la Montaña, Departamento de Matagalpa, Nicaragua, *R. maculata* is the most common land amphibian, and its tendency to leap into the water makes it the most conspicuous frog there.

Villa (1972) reported some observations on Nicaraguan *R. maculata*. Additional observations were made, especially during 1974-77, in connection with another study (Villa, 1977, 1978). These, complemented with the available literature reports, are summarized below.

### Distribution

*Rana maculata* is found in southeastern México (Chiapas), central and southern Guatemala, Honduras, El Salvador, and Central Nicaragua. The southernmost locality is the Cerro Masigüe (ca. 30 km E of Boaco, Nicaragua). Records from Belize (Henderson and Hoevers, 1975; Lee, 1976) require further consideration.

Throughout its range *R. maculata* is found at elevations of 800-2400 m. Individuals from lower elevations are believed to have been washed down by flood waters (Stuart, 1948) or usually inhabit hilly areas with swift-flowing waters similar to highland streams. The distributional maps presented by Villa (1972) and Lee (1976) depict two lowland localities (near Lakes Managua and Nicaragua). Examination of the specimens on which these records were based revealed that they are juveniles, not in good condition, and apparently represent *R. palmipes*. Both species are difficult to distinguish as juveniles and adults (Stuart, 1948), although the tadpoles are easily differentiated (Volpe and Harvey, 1958).

I have also examined all Belizean specimens assigned to *R. maculata*. Two small specimens (MPM 7672, 10777), although resembling *R. maculata*, are too immature (the largest one is 27.0 mm SV) to permit a positive identification. A third specimen (KU 157161), the basis for Henderson and Hoevers' (1975) and Lee's (1976) record, is also a juvenile (29.5 mm SV). The tadpoles, although similar to those of *R. maculata*, have differences in caudal pigmentation and tooth formulae (Lee, 1976). Another difference not mentioned by Lee but clearly visible in his illustration (Lee, 1976, Fig. 3) and documented in his description, is the emargination of the oral disc. In *R. maculata* the disc lacks this emargination (Volpe and Harvey, 1958, Fig. 4B). The lack of this emargination, resulting in a more complete oral disc, was noted in Nicaraguan *R. maculata* and *R. warschewitschii* (both highland forms) and considered to be an adaptation to swift mountain streams (Villa, 1972). Tadpoles of *R. sierramadrensis*, another highland form (Zweifel, 1968; Webb, 1978), also lack the disc emargination (Webb



and Korky, 1977; Webb, 1978). Since the Belizean specimens inhabit "a clear, narrow and swift stream" at ca. 450 m elevation (Lee, 1976) the emarginated oral disc is significant since it may indicate a different phylogenetic line and not an environmental adaptation. Because of the striking structural and pigmentary differences when compared with *R. maculata* tadpoles from elsewhere in Central America, and because of the geographic isolation of the Belizean specimens, it is possible that they represent a different (perhaps undescribed) taxon related to *R. maculata*. Therefore, examination of adult specimens is necessary to verify the status of the Belizean populations.

In spite of the "slight but constant" differences between adults, Stuart (1948) stated that *R. maculata* (as *macroglossa*) "appears to be an upland form of *palmipes*", and Volpe and Harvey (1958) suggested that *maculata* is a highland ecotype of *palmipes*. I preferred to consider both as separate species on the basis of the morphological differences (of larvae and adults) and the sympatry of some populations in Nicaragua (Villa, 1972). I now have doubts regarding the identity of the specimens supposedly found sympatrically, but these were destroyed in the 1972 Managua earthquake. Thus, the three remaining populations in which sympatry was apparent (see Villa, 1972, Fig. 49) should be sampled and re-identified to clarify the taxonomic relationship of *palmipes* and *maculata*. The distinctness of their tadpoles could easily be attributed to lentic versus lotic habitats (Volpe and Harvey, 1958; Villa, 1972).

### Habitat and Habits

*Rana maculata* is usually found in clear, swift mountain streams throughout its range. I have rarely found individuals on the forest floor far from streams. They are either hidden in vegetation bordering a stream, or partially or totally submerged (Villa, 1972), sometimes concealed in the mud. If crevices in the rocks or stream banks are available, they are frequently used during the day, but I have not determined if the frogs actually dig them in the banks. The frogs seem to be active (or at least alert) during the day, although their calls are more frequently heard at night.

Stuart (1948) noted the habitat separation of *R. macroglossa* [= *maculata*], *pipiens* and *palmipes* in Alta Verapaz, Guatemala; *palmipes* is restricted to the quiet waters of the lowlands, *maculata* to the highland waters, and *pipiens* inhabits both. When sympatric, *R. pipiens* was in the slower, and *R. maculata* in the faster, parts of the streams. Only *R. pipiens* was present in water holes and ponded waters. A similar habitat separation occurs in Nicaragua (Villa, 1972) except that in Matagalpa *R. maculata* is often found in artificial impoundments, although I never observed it breeding in these situations.

As with many ranids, individuals of *R. maculata* leap into the water when frightened (Mertens, 1952; Villa, 1972), and either seek shelter among the rocks (or silt, when present) on the bottom, or swim erratically—skimming over the bottom and partly walking underwater—to the other side of the stream, where they remain motionless and partly concealed among rocks or marginal vegetation. The swiftly-moving water makes it very difficult to follow these frogs visually after they leap into a stream. In Matagalpa some stream segments have rocky walls more than 10-15 m high. Individuals of *R. maculata* can frequently be found perched on the rocks or hidden among the scant vegetation covering them, and often make spectacular leaps to the stream below. The habitat near Matagalpa is depicted by Villa (1972:frontispiece).

#### Food

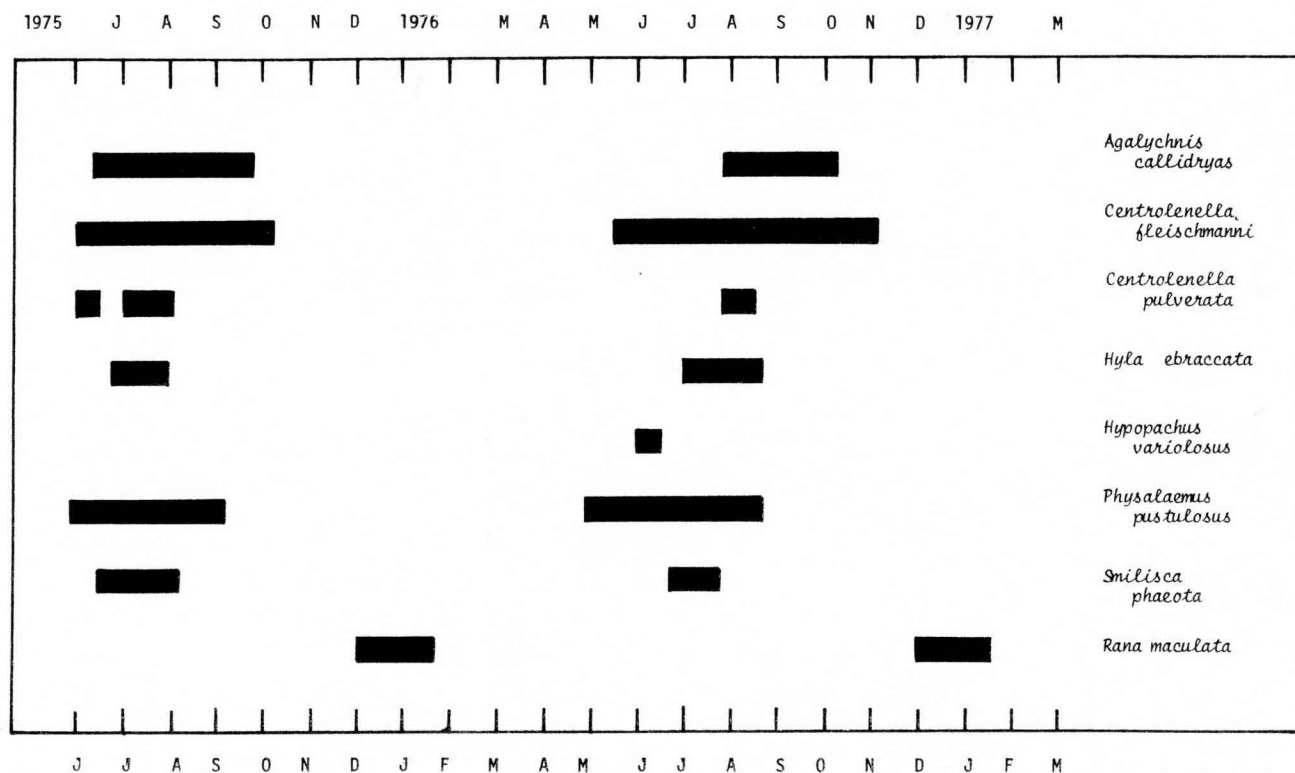
Food items were not analyzed in detail, but cursory examination of stomach contents and fecal droppings were made from time to time. No single food item clearly predominated, but nymphal dragonflies and larval Lepidoptera, adult Coleoptera, crickets, grasshoppers, and cockroaches, were especially abundant in the samples examined. Tadpoles and recently-metamorphosed conspecifics were sometimes eaten. No earthworms were found in the stomachs although they were readily taken in captivity. The distribution of food items suggests that *R. maculata* is a non-selective carnivore, feeding on whatever is available at the time. One stomach contained solely 8 nymphal dragonflies, and another solely 10 larval Lepidoptera.

Captive specimens are known to eat lizards (*Anolis*) and other frogs (*Eleutherodactylus*) (Villa, 1972). *Anolis*, *Eleutherodactylus* and *Centrolenella fleischmanni* were not uncommon in the Matagalpa stomach samples studied.

#### Reproduction

Stuart (1951:53) noted that on the Guatemalan Plateau "an extended breeding season is indicated for this species since tadpoles in various stages of development may be found the year round in mountain streams." In El Salvador (Santa Tecla: Finca El Paraiso) Mertens (1952:32) found recently-laid clutches and large tadpoles at the same time, and concluded that reproduction in *R. maculata* "is certainly extended over the greatest part of the year, at least during the rainy season." He observed several amplexing pairs on September 15 (height of the rainy season) and found egg clutches the following day.

An entirely different situation occurs in central Nicaragua. During 1975-76, and part of 1977, I made periodic surveys of the breeding activity of the amphibians at the Matagalpa locality (Fig. 1). Only rarely were amplexing pairs of *R. maculata* (or their egg masses) found before late No-



**Figure 1.** Breeding activity (black bars) of eight species of frogs at Finca "San Jose de La Montaña" (Matagalpa, Nicaragua) 1975-77. Species were considered to be breeding if eggs or amplexing pairs were found, except in *Centrolenella pulverata*, where breeding was assumed to be taking place when calls were heard (the species apparently oviposits most frequently in the higher vegetational strata).

vember. During December and the first half of January they were very abundant, but were rare again after that time, although non-breeding individuals were commonly seen year round. *R. maculata* was the only frog I found breeding exclusively during the dry season (November to May). Sporadic observations made at nearby Ciudad Jinotega, where *R. maculata* is also abundant, seem to indicate a similar breeding period. Official climatological data are not available for the Matagalpa site; my records indicate that water temperatures were 23-26°C in the rainy season and 15-18°C during the dry season.

The following points are of interest in considering the breeding strategy of this species:

- 1) Few other species of frogs breed in the same streams as *R. maculata*. The most common frogs are centrolenids, mainly *Centrolenella fleischmanni*. Their tadpoles are probably fossorial (Villa, 1978), digging into the stream-bank mud and feeding there. Another stream breeder is the hyliid *Ptychohyla spinipollex*. Very little information is available on the habits of its tadpoles (Duellman, 1970). In central Nicaragua they are less abundant than *R. maculata* tadpoles where they are sympatric; they are also almost half as large and, judging from the structure of the oral region, probably have different feeding habits. Therefore, *R. maculata* tadpoles appear to have no competition for space or food from other sympatric tadpole species, and thus there seems to be no selective pressure for *R. maculata* to avoid competition by breeding during a restricted time of the year.

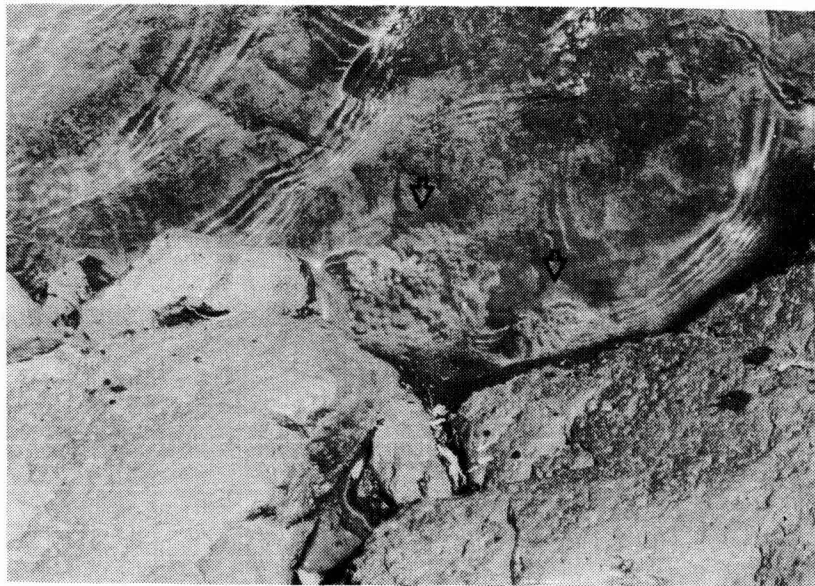
- 2) The high relative humidity at the Matagalpa site also does not seem to favor breeding at any specific time of the year. My records indicate that the relative humidity in December and January (when *R. maculata* breeds) usually exceeds 85% at night (when breeding occurs), and is even higher near waterfalls because of the water spray. Thus even in the dry season frogs are able to search for potential mates and proceed with amplexus without risking dehydration.

- 3) In the central Nicaraguan localities increased rainfall during the first half of the rainy season often produces, by September, intensive flooding in the streams *R. maculata* inhabits. The flooding is usually violent and carried rocks, logs and vegetation downstream. Although *R. maculata* tadpoles clearly are stream-adapted, their early development (1-2 months) would probably not be optimal under such conditions. Since the streams are permanent it would be more adaptive to delay breeding until the rainy season—or at least the flooding—is over. By October or November streams have receded to normal flow levels and their water is no longer turbid. Detritus, carried by the rains, has settled on the bottom under rocks, and especially in slower parts of the streams, and is available as food to *R. maculata* tadpoles.

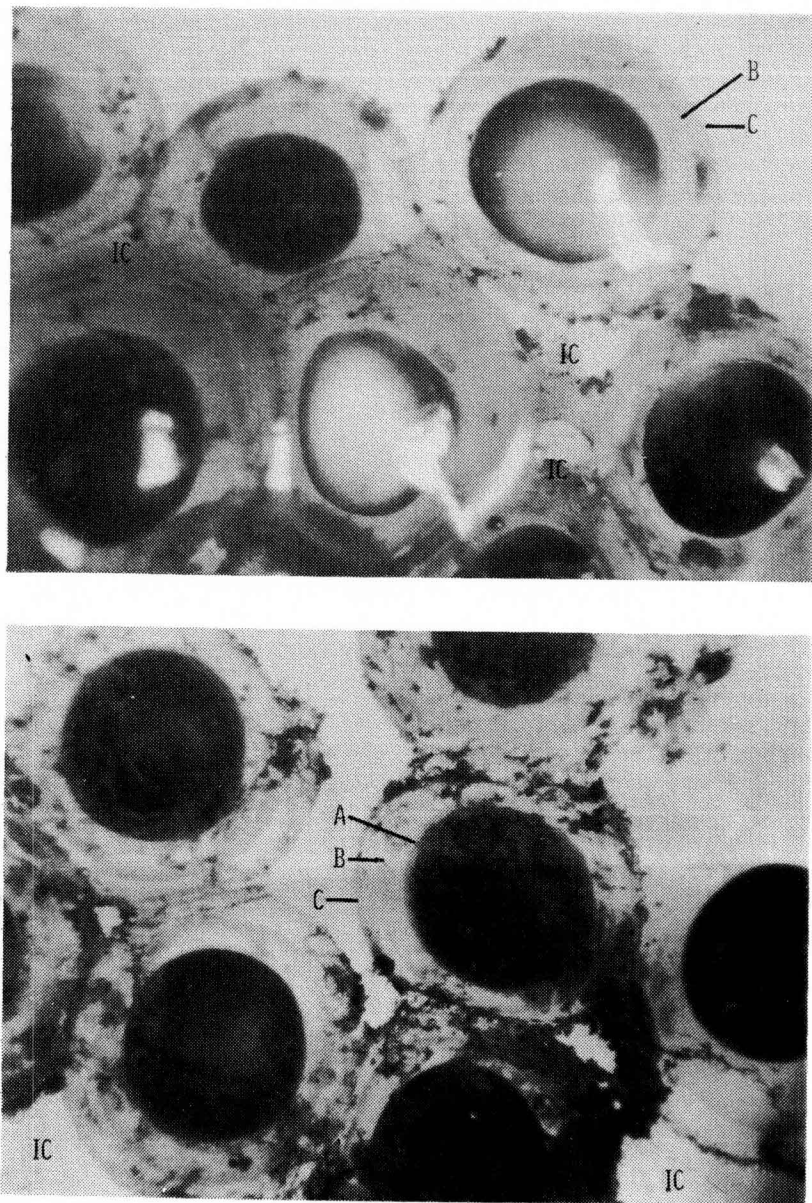


When the following rainy season arrives (usually in May), tadpoles hatched in December have developed for six months and are probably ready to metamorphose any time after the onset of the rainy season, or may develop for 18 months, and metamorphose during the first part of the following rainy season. No data are available on the duration of the entire larval period of this species. However, metamorphosing individuals are most frequently found at the beginning of the rainy season; this allows them to leave the streams before they are flooded, and at the time when relative humidity is highest. Thus, the dry-season breeding period (December-January) seems to be an adaptation to avoid flooded conditions.

*Oviposition Sites.* Mertens (1952) found amplexing pairs of *R. maculata* in a large swimming basin in El Salvador but did not actually observe oviposition. Floating egg clumps were found on the following day. I have never found *R. maculata* egg masses in ponded water—although amplexing pairs are sometimes found there—only in swift streams. The frogs usually choose a site with minimum water movement, often in nooks and crannies where egg masses are at least partially protected from the strong current (Fig. 2). Masses are always totally submerged and attached to some hard substrate, such as rocks or vegetation. I have never seen floating egg



**Figure 2.** An oviposition site of *Rana maculata*. Egg masses (arrows) are typically deposited in a sheltered spot of the stream margin where water current is minimal; nevertheless they are subjected to continuous movement, as can be seen by the ripples in the photograph.



**Figure 3.** Developing embryos of *Rana maculata*. A: embryos in stage 9. Two egg capsules (B, C) can be seen, as well as the intercapsular canals (IC). B: same clutch in late stage 14. The vitelline membrane (A) has begun to separate from the embryo. Note, in both cases, the detritus attached to the capsules.

**Table 1.** Measurements of the living embryos and capsules of *Rana maculata* in pond water. The means  $\pm$  a standard deviation are given below the range (in millimeters).

Developmental Stage	Embryo	Vitelline Capsule	Second Capsule	Outer Capsule	Number Measured
8	2.1-2.6 2.33 $\pm$ 0.16	Adherent	2.7-3.7 3.27 $\pm$ 0.24	3.9-4.8 4.39 $\pm$ 0.25	15
11	2.6-2.8 2.67 $\pm$ 0.07	Adherent	3.3-3.9 3.56 $\pm$ 0.19	3.9-4.2 4.09 $\pm$ 0.11	7
14	2.3-2.7 2.47 $\pm$ 0.12	Adherent	3.1-3.7 3.40 $\pm$ 0.19	3.9-4.4 4.23 $\pm$ 0.23	8
16	2.5-2.9 2.74 $\pm$ 0.16	2.6-3.1 2.74 $\pm$ 0.15	3.5-3.9 3.61 $\pm$ 0.15	4.0-4.6 4.17 $\pm$ 0.29	7

masses of this species, although it is conceivable that if laid in ponded water, where there would be no obvious need for attachment, floating clutches may be produced. Those examined in Matagalpa, however, did not float but sank when experimentally detached.

*The Egg Clutch.* Oviposition usually occurs at night. Although I did not observe the actual moment of oviposition, combined field and laboratory observations indicate that the female produces a string of eggs which is attached to a substrate every 16-20 cm, eventually forming a loop 8-10 cm in diameter. The loops fuse where they touch, but only at the edges of the spherical outer capsules; thus the egg mass is not solid but has abundant intercapsular canals (Fig. 3). in *R. t. temporaria* (Savage, 1961) these canals allow circulation of water around nearly every egg, so that gas exchange and waste diffusion can take place within a few mm of each embryo, even in those located in the center of the clutch. In the ponds where *R. t. temporaria* oviposits there is usually enough water movement to produce a gentle circulation of water through the canals. In *R. maculata* egg masses are vigorously aerated by the strong stream current.

Live clutches were examined and measured at various developmental stages (of Gosner, 1960). Measurements are presented in Table 1. The animal pole is dark brown or black, and the vegetal pole varies between light cream and white. Until stage 15 the vitelline membrane is adherent to the zygote, and scarcely visible, but it separates as rotation begins. Two additional capsules are present. The outer one remains sticky, and dirt and detritus soon attach to the jelly (Figs. 3-4), hiding the mass from view.

The ova of Salvadorian *R. maculata* (Mertens, 1952) are 2.6-2.8 mm in diameter. Although Mertens gave no developmental stage, his measurements fall within the range of the Nicaraguan *R. maculata* eggs (Table 1).

The size of 10 recently-laid and apparently intact masses was estimated by volumetry. One of the masses was also counted to determine the difference between real and estimated clutch size; the estimated size was 3% smaller. Estimated clutch sizes were 738-1288 ( $\bar{x}$  = 977) when laid in relatively slow-flowing water and 328-930 ( $\bar{x}$  = 654) in faster waters (5 clutches were counted in each case). I could not determine if the size difference was due to (i) more eggs being laid in slower water or (ii) parts of the mass breaking off because of the current. I did not estimate the number of ovarian eggs.

*Embryonic Development and Hatching.* A few of the clutches brought to my Matagalpa field station were examined at irregular intervals to follow their development (water temperature: 15.5-18°C). Table 2 summarizes these observations.

Hatching presumably is aided by the production of a jelly-dissolving



enzyme, as in *R. dalmatina*, *R. t. temporaria* and probably other ranids (Savage, 1961) although this is not yet substantiated. It is certain that in *R. maculata* hatching is not effected by movements of the embryo or by an "egg tooth." The stage of development at hatching appears to vary. Recently-laid clutches brought to the field station normally hatched at stage

**Table 2.** Time required by *Rana maculata* embryos to advance from one developmental stage (of Gosner, 1960) to another.

Stage Change	Time Taken (hr) (Means in Parentheses)	Number of Clutches	Water Temperature (°C)
0- 8	12-16 (14)*	3	16.6-18
0-10	13-15 (14)*	2	16.6
8-20	152	1	18
10-11	9	1	18
10-15	20.5	1	18
11-12	10.5	1	18
12-15	25	1	18
15-16	9-20 (14.5)	2	18
15-18	95	1	18
16-17	23-35.5 (29.5)	2	18
17-18	51	1	18
20-21	62*	1	16.6

\*Estimated

17, and some even earlier, as many pond-breeders do. In the field, however, tadpoles did not hatch until at least stage 20 (Fig. 4), a few days later. Clutches collected at stage 15 or later were also "late hatchers." I made no attempt to keep the water moving in the laboratory or to stop it in the field so as to experimentally determine if this would affect the hatching stage. However, it appears that the degree of development required before hatching is environmentally determined. Tadpoles hatching in faster waters are more likely to be swept away by the current if they hatch in stage 17 (not yet capable of movement) than in stage 20 or 21, when their tail muscles, fins and muscular coordination are better developed. In ponded water tadpole mobility does not seem as critical, therefore hatching may occur earlier. Thus, by leaving their egg capsules earlier, slow-water tadpoles come in direct contact with their environment, and gas exchange and waste diffusion may become more efficient. In swift mountain streams,

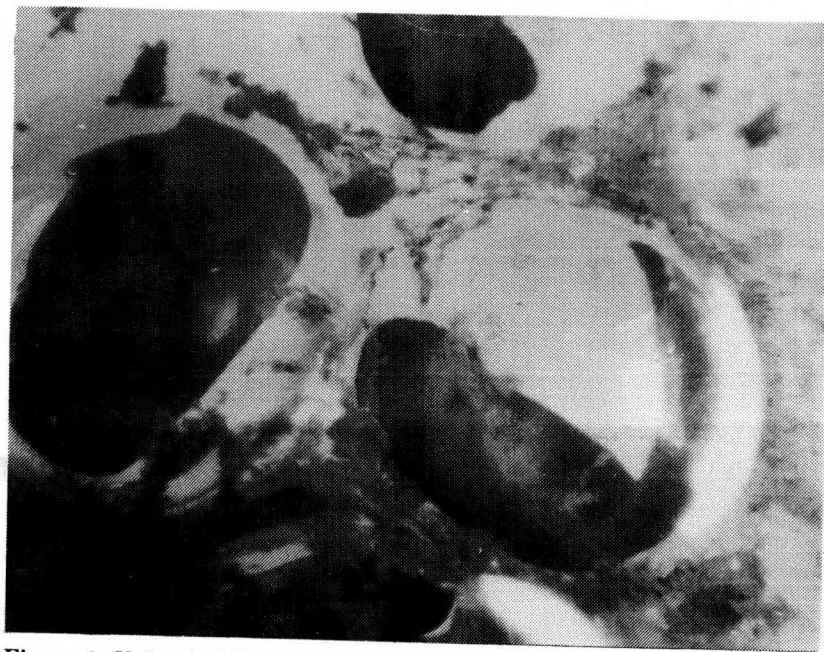


Figure 4. Unhatched *Rana maculata* embryos in stage 21.

however, oxygen tension and water circulation are greater, thus the embryo does not need to be in direct contact with its environment and may remain longer inside the jelly.

Both "early" and "late" hatching tadpoles remain attached to the jelly mass—or to the neighboring substrate—by their oral suckers until they

become more active, in stage 22 or 23. Later—perhaps 2-3 days later—they begin to disperse throughout the stream. No data are available on the duration of post-hatching stages because they were raised for other purposes and were not kept long enough to metamorphose. Under natural conditions tadpoles are most frequently found on the stream bottom, feeding upon the algae growing on the rocks and on accumulated detritus. *R. maculata* tadpoles are found also in artificially ponded sections of streams, where they frequently surface, apparently gulping air. They also may remain motionless, attached to the pond's sides or walls, or to floating leaves and twigs.

Two sets of recently-metamorphosed froglets from near Cerro Masigüe (Boaco: 30 km E Boaco, KU 17366-78) had the following SV measurements (in mm): set 1 (4 specimens) 26.0-27.0 ( $\bar{x}$  = 26.5  $\pm$  0.125); set 2 (5 specimens) 30.0-35.5 ( $\bar{x}$  = 32.0  $\pm$  2.15).

### Interspecific Associations

#### Predators

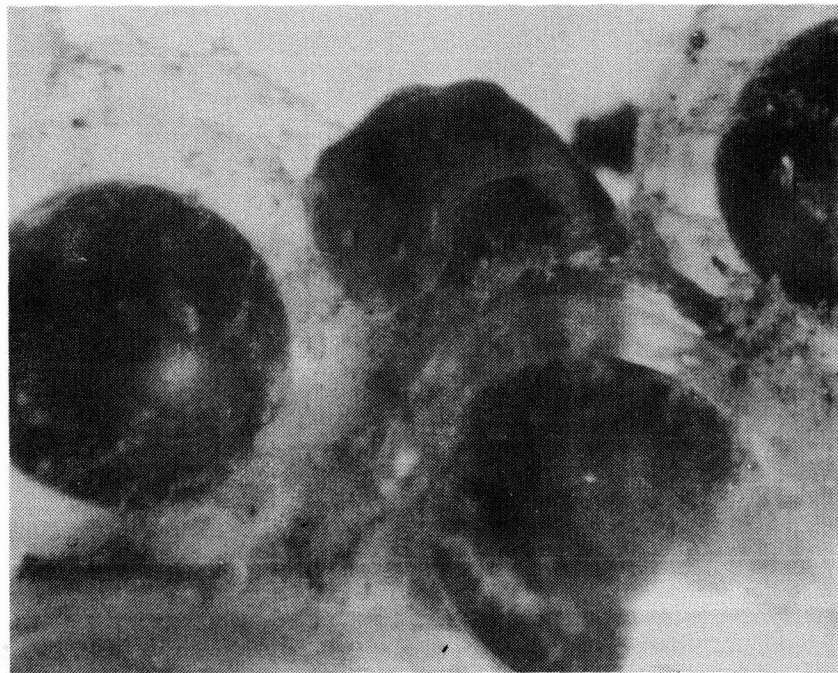
Predation is very difficult to observe in nature, even in species which, like *Rana temporaria*, have been under careful study for many years (Savage, 1961). Dragonfly nymphs (Odonata: Anisoptera) occasionally were seen eating *R. maculata* tadpoles, but actual attacks were not observed. Tadpoles were often found in stomachs of *Thamnophis proximus rutiloris*, a semiaquatic colubrid snake common in the Matagalpa area; recently-metamorphosed *R. maculata* appeared to be taken rarely, probably due to their large size. *Drymobius margaritiferus* (Colubridae), though less commonly found, more frequently contained *R. maculata* froglets. It is likely that other snakes, as well as other reptiles, birds and mammals, prey upon *R. maculata* (larvae and adults) but no evidence is available.

Water bugs (Belostomatidae) were common. A very large species (measuring about 7 cm) was twice seen feeding on the body of an adult *R. maculata* but, again, predation was not observed.

#### Planariae

An interesting case of interspecific association, still to be resolved in detail, involves planariae (*Dugesia* [*Girardia*] sp.). They often were collected among the *R. maculata* clutches in November-December 1976. Because more than one *R. maculata* egg mass usually was collected and brought to the laboratory in the same container, the number of planariae found in most of the clutches was not determined. However, at least 21-33 could be found in a single egg mass collected during the day. Considerably fewer appeared to be present in masses collected at night, although no supportive data are available.

Since planariae are carnivorous the possibility of their feeding upon embryos or recently-hatched tadpoles was immediately considered. However, no evidence of predation was obtained; no planariae were observed feeding upon *R. maculata* embryos or tadpoles in several hours of observation. They were observed feeding on dead *Hyla ebraccata* and *Agalychnis callidryas* tadpoles, but it was not clear whether these were killed by the planariae, or died from other causes.



**Figure 5.** Planaria emerging from the interior of the clutch, moving among the *Rana maculata* egg capsules.

An experiment was designed to determine if predation would occur. Ten planariae were placed in Petri dishes, each containing either (a) five *R. maculata* embryos in stage 10 or earlier, or (b) five stage 17 (hatched) tadpoles, (c) five empty egg envelopes, or (d) a 3 cm strand of *Elodea*. All dishes were half-filled with stream water, and five replicates were made of each category. Planariae were observed in or near the egg envelopes, whether empty or not, as they were in the *Elodea* cutting. No embryos or tadpoles were consumed or harmed during the first week of the experiment. Five additional embryos in stage 10 were then supplied to the probably-starving planariae but they also were not harmed during the following week. At the



end of the second week the experiment was terminated. In all cases, considerable shrinkage was evident in the planariae, but no cannibalism was noted and no tadpoles were attacked. Since the same planariae later fed readily on bits of meat and small tadpole bits of other species, it seems that *R. maculata* tadpoles have an effective means of discouraging planarian predation.

The planariae seem to be using *R. maculata* egg cases as a substrate, as they would use submerged roots or aquatic plants (i.e., as hiding places during the day). No attempt was made to determine if they were using the egg masses preferentially over other available substrates, but this appeared to be the case. Although not observed, it is possible that planariae feed on the small insect larvae or crustaceans that are often associated with the clutches.

### Resumen

La rana *Rana maculata* Brocchi (familia Ranidae) es común en las regiones altas (generalmente de 800 a 2400 m) desde el sureste de México a Nicaragua central. Los renacuajos antes reportados de Belize, debido a diferencias en la fórmula dental, disco oral y pigmentación caudal, posiblemente pertenezcan a otra especie afín a *R. maculata*, pero se necesitarán ejemplares adultos para comprobarlo. *R. maculata* siempre se encuentra en las aguas rápidas y cristalinas de arroyos montañosos, y aunque su reproducción parece ocurrir durante todo el año en ciertos lugares, en Nicaragua central es la única especie cuya reproducción está restringida a la época seca ("verano", Diciembre a Enero). Se discuten algunas razones que parecen explicar esta peculiaridad reproductiva.

Las masas de huevos son puestas, durante la noche, sumergidas en arroyos rápidos y adheridas a las rocas o la vegetación. Aquellas obtenidas en arroyos relativamente lentos contenían mas huevos que las encontradas en los mas rápidos. La etapa de desarrollo embrionario requerida para eclosionar varía de forma semejante; en los arroyos mas lentos los renacuajos eclosionan mas temprano (etapa 17 de Gosner) que en los mas rápidos (20-21). Se discuten las razones que parecen explicar esta variación. También se ofrecen datos sobre el número y tamaño de los huevos, la duración del desarrollo embrionario, y el tamaño de renacuajos y de individuos inmediatamente después de la metamorfosis.

Se encontró una relación interespecífica, de tipo aun incierto, entre las masas ovíferas de *R. maculata* y la planaria *Dugesia (Girardia)* sp. (Platyhelminthes: Turbellaria). Las planarias, a pesar de ser carnívoras, no se alimentaron de los huevos, embriones o ranacuajos, de *R. maculata*, aunque sí de los otras ranas.

### Acknowledgements

Most of the observations for this and other studies were made in Finca "San José de la Montaña", Matagalpa (Nicaragua) and environs. They would not have been possible without the generous hospitality of the Finca's owner, General J. Rigoberto Reyes, G.N. (Ret.) and his family Mauricio and Gloria Reyes. They allowed me to set up a field station on their property and to use it for almost two years. Several people aided me in the field, especially my former assistants Alejandro Cajina, Richard Cittar, Allen Porter and Miguel Torres.

Roman Kenk (National Museum of Natural History) identified the planariae; William E. Duellman, University of Kansas Museum of Natural History (KU), Robert W. Henderson, Milwaukee Public Museum (MPM) and Julian C. Lee, University of Miami, allowed me to examine specimens under their care and provided additional information about them and related topics. Edward J. Greeding, R. W. Henderson, J. C. Lee, and Richard G. Zweifel, offered constructive criticism in reviewing the typescript. Roberta Aldrich and Alma Hill typed the manuscript.

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