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LEPTODACTYLUS (AMPHIBIA, LEPTODACTYLIDAE)
FROM ECUADOR

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LEPTODACTYLUS (AMPHIBIA, LEPTODACTYLIDAE)
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ABSTRACT: Ecological data were gathered on five sympatric species of *Leptodactylus* over a two month period from a study site in Amazonian Ecuador: *L. discodactylus*, *L. knudseni*, *L. mystaceus*, *L. pentadactylus*, and *L. wagneri*. Three species have broad niches (*L. knudseni*, *L. mystaceus*, and *L. wagneri*); two have narrower niches (*L. pentadactylus*, *L. discodactylus*). *L. wagneri* apparently is a broad-niched species over much of the Amazon Basin, indicating that the species is well adapted to changing environments and is probably an excellent colonizer species. *L. discodactylus* has relatively low niche overlap with all the other species; *L. pentadactylus* has moderate overlap with *L. knudseni*, *L. mystaceus*, and *wagneri*; *L. wagneri*, *mystaceus*, and *knudseni* have broadly overlapping niches. The latter three species each belong to different species groups within the genus. Male *L. mystaceus* and *wagneri* call from different microhabitats within the same general habitat (clearings), male *L. discodactylus* call from a distinct habitat (stream seepages). Two distinct call strategies are employed. The first is a loud call used to attract females from some distances; males call each night during the breeding season, larval success is relatively independent of individual rainshowers. *Leptodactylus mystaceus* utilizes this strategy. The second strategy, used by *L. discodactylus* and *L. wagneri*, is characterized by a weak call used to attract females over a short distance; calling correlates with heavy rains and larval success is greater if mating correlates with heavy rain activity. Neither male *L. mystaceus* or *wagneri* demonstrated any chorus structure. Female *L. mystaceus* have relatively small clutches of large, unpigmented eggs, *L. discodactylus* have large clutches of small, unpigmented eggs, and *L. wagneri* have very large clutches of small, pigmented eggs. No differences in female temporal reproductive patterns were evident over the study period. *Leptodactylus wagneri* larvae occur in dense, extremely active schools. Individual *L. wagneri* larvae apparently are not distasteful to aquatic insect predators.

A two month field study which had the main objective of studying members of the frog genus *Leptodactylus* was conducted in Amazonian Ecuador. This report adds to our ecological understanding of sympatric members of the genus *Leptodactylus*. The following aspects are discussed: niche breadth, niche overlap, male calling sites

and patterns, clutch size and female reproductive patterns, larval behavior, and results of a larval-predator experiment.

The study site of Limoncocha, Napo Province, Ecuador, 0°24'S, 76°37'W, 260 m elevation, lies in the upper Amazon basin, near the equator, in a Tropical Moist Bioclimate (Holdridge, 1964).

MATERIALS AND METHODS

Three types of data were taken from 5 June to 5 August 1971 on five species of *Leptodactylus*: (1) observational data, (2) experimental data, and (3) locality data, including microhabitats. Locality data were recorded for each individual frog for three major habitat categories: vegetation, horizontal position, and vertical position. Four vegetation categories were recognized at the study site: (1) primary forest, (2) secondary growth, immature or regenerating forest, (3) primary-secondary forest mixture, and (4) clearings, including the camp area and a pasture area. The following horizontal positions were recorded for the frogs (more categories were recognized for both horizontal and vertical position, but the following are the ones utilized by *Leptodactylus*): on a stream bank; away from any running water; in the water of a pond; on the bank of a pond; on vegetation above a stream. The following vertical positions were recorded: under the surface of the soil; under leaves or bark; under tree roots; under logs or boards; in decaying logs; on the surface of the soil; on dead leaves; on logs; on a plant less than 1 m high; on a shrub or young sapling 1-7 m high; in grass.

The five species of *Leptodactylus* are: *L. discodactylus*, *knudseni*, *mystaceus*, *pentadactylus*, and *wagneri*. Specimens of *L. knudseni* are in the collections of the Los Angeles County Museum of Natural History, where the other study material will also be deposited.

NICHE BREADTH

Niche breadth scores were calculated from the formula suggested by Levins (1968), where p_{ij} is the proportion of occurrences of species j in plot i , niche breadth of species j (B_j) equals:

$$1/B_j = \sum_i p_{ij}^2$$

The proportion of species occurrence was calculated using the locality data as described above. Proportions were calculated

for each of the three major habitat categories, thus the maximum niche breadth index for this study is 3. The niche breadth values (from highest to lowest) followed by the number of individuals (in parentheses) used in the analysis are: *L. knudseni*, 2.54 (33); *L. wagneri*, 2.53 (208); *L. mystaceus*, 2.36 (65); *L. pentadactylus*, 1.44 (3); *L. discodactylus*, 1.29 (16). Three species groups are represented: (1) the primitive Melanonotus group including *L. discodactylus* and *L. wagneri*; (2) the relatively more advanced Pentadactylus group by *L. knudseni* and *L. pentadactylus*; and (3) the advanced Fuscus group by *L. mystaceus*. One member of each of these groups has a broad niche, which Levins (1968) argued is characteristic of species adapted to unstable habitats. Levins further suggested that species with broad niches are excellent colonizers. This would appear to be especially true for *L. wagneri*. In the only comparable study, Crump (1971) analyzed the entire amphibian and reptilian fauna around Belém, Brasil. In that study, *L. wagneri* had the broadest niche of the frog species studied. These results indicate that *L. wagneri* probably is an excellent colonizer. Excellent colonizer species are characterized by having broad niches and occurring in marginal and/or modified habitats. *L. wagneri* was abundant in the man modified environments at Limoncocha. Further, because *L. wagneri* was found in a variety of habitats at Belém and Limoncocha, it is certainly well adapted to the environments at both areas. Apparently the broad niche of *L. mystaceus* at Limoncocha indicates that the species is adapted to the varying environments at Limoncocha but the niche is not broad enough to successfully include the range of environments around Belém. The same is true for *L. marmoratus* from Belém, that is, it has a broad niche at Belém, but was not collected from Limoncocha even though the species occurs in the vicinity of Limoncocha. The species in common at the two sites are *L. mystaceus*, *L. pentadactylus*, and *L. wagneri*.

TABLE 1.—Niche overlap values for five species of *Leptodactylus*. Number of specimens in parentheses.

	<i>L. discodactylus</i>	<i>L. knudseni</i>	<i>L. mystaceus</i>	<i>L. pentadactylus</i>	<i>L. wagneri</i>
<i>L. discodactylus</i>	(16)	.2559	.2551	.2740	.2577
<i>L. knudseni</i>		(33)	.9946	.6337	.9967
<i>L. mystaceus</i>			(65)	.6787	.9929
<i>L. pentadactylus</i>				(3)	.6400
<i>L. wagneri</i>					(208)

NICHE OVERLAP

Niche overlap values were obtained from the formula suggested by Horn (1966); p_{ij} is the proportion of occurrences of species j in microhabitat i . Overlap of species j and k (α_{jk}) is estimated by:

$$\alpha_{jk} = 2 \sum_i p_{ij} p_{ik} / (\sum_i p_{ij}^2 + \sum_i p_{ik}^2)$$

The index is from 0.0 (no overlap) to 1.0 (complete overlap). The overlaps among the species fall into three categories, low, moderate, and high (Table 1). *L. discodactylus* overlaps very little with the other species, due in part to the distinctive male calling sites (see below). *L. pentadactylus* shows moderate overlap with *L. mystaceus*, *L. wagneri*, and *L. knudseni*. These overlaps are suspect, however, because of the small sample size of *L. pentadactylus* collected. *L. mystaceus*, *L. wagneri*, and *L. knudseni* all have high overlap values in all combinations among the three species. It is interesting that each species belongs to a different species group. This may indicate that fundamental biological differences associated with each of the groups may be more meaningful with respect to niche differentiation and overlap than habitat differences. Two species pairs involving species from the same groups involve low or moderate overlap: *L. knudseni*, *L. pentadactylus*; *L. discodactylus* and *L. wagneri*.

MALE CALLING SITES AND PATTERNS

Three species were heard calling during the field work. The sonograms of the calls will be reported on separately. Our Quichua guide indicated that *L. pentadactylus* breed during December and Jan-

uary at Limoncocha and that the foam nests are abundant at that time of the year. We only collected juveniles of *L. knudseni*; since they are members of the *Pentadactylus* group, they may well breed at the same time *L. pentadactylus* breed.

Male *L. mystaceus* and *wagneri* called from our camp area and in the pasture. The *L. wagneri* males call at the edges of small grassy ponds in camp and in the pasture. Individual calling males are very difficult to capture. *L. mystaceus* males were calling from underground chambers, that were under logs or other types of debris. On the night of 19 June 1971, Heyer sat in the pasture to determine any social structure among calling males. *L. mystaceus* were actively calling and a few *L. wagneri* were calling. At 1715 hr the first *L. mystaceus* was heard, but calling was sporadic for the next hour. At 1811 hr (still light), many *L. mystaceus* were heard in the distance, but few close by. The calling seemed to be coming from an area of heavier ground cover and the calling sites may have become darker earlier than in the open pasture. At 1813 hr, the first *L. wagneri* was heard calling. At 1820 hr, the *L. mystaceus* were in full calling activity. At 1830 hr it was almost dark, both species were calling as actively as either did the remainder of the observation period. At 1845 hr it was completely dark. Calling patterns were recorded until 2130 hr and may be summarized as follows for *L. mystaceus*. (1) The number of calls in a call group is variable. One individual gave the following series of calls per call group: 2,5,5,19,9,4,9,12,8,14,14. The highest number of calls per call group recorded was 43. (2) Individual males call for a few minutes then stop, then resume call-

ing, etc. A few males were not heard for 10-min periods between calling activity; one individual was quiet for a half hour and another for an hour. (3) There was no apparent chorus structure. Some individuals called at the same time, but call groups were initiated by different individuals. Three different individuals did most of the calling, each at different time spans throughout the evening.

Since few *L. wagneri* were heard on the night of 19 June, Heyer recorded their call patterns on the night of 11 July in a roadside ditch puddle. Observations were made from 2000–2040 hr. Four individual males were calling, the closest two were 1.5 m apart. The frogs did not appear to move during the observation period. There was a shift in dominance (loudness and frequency of calling) from the number 3 male to the number 2 male during the observation period. Individuals appeared to call at random; there was no order of calling. Thus, it appears that males of both *L. wagneri* and *mystaceus* call at random, not in an organized chorus. The two species do have very distinctive call strategies, however. The call of *L. mystaceus* is loud and males called every night regardless of the rainfall pattern. The call of *L. wagneri* is weak; males called actively day and night after a heavy rain. If there was no rainfall for a period of 2 or 3 days, *L. wagneri* ceased calling. Apparently, the two species are using the mating calls in different ways. In *L. mystaceus*, the call is used to attract a female over a considerable distance to the calling site of the male. As the eggs undergo considerable development in the incubating chamber (Heyer, 1969), egg laying can be independent of individual rain storms. In *L. wagneri*, apparently the weak call is used to attract a nearby female to an individual male. *L. wagneri* appears to be a riparian species, and both males and females are usually found at or near grassy pond margins. Since the foam nest of *L. wagneri* is laid on top of the water and the hatchlings drop into the water a couple of days after

fertilization, larval survival is increased if the adults reproduce during or immediately following rainstorms.

Male *L. discodactylus* were calling next to a stream seepage in a forested area. The seepage area was 2–3 m wide, about 15 m long, and the water was 1–2 cm deep. The males were calling along the edges of the seep, under roots or leaves at the water's edge. The males were hidden, calling from naturally-occurring chambers. *L. discodactylus* appeared to use the same call strategy as *L. wagneri*. The calls were relatively weak; males called day and night after heavy rains, they did not call during rainless periods or periods of weak rain.

CLUTCH SIZE AND FEMALE REPRODUCTIVE PATTERNS

Two female *L. discodactylus* had 226 unpigmented eggs 1.5 mm in diameter and 1177 unpigmented eggs 1.0 mm in diameter. Five foam nests of *L. mystaceus* with unpigmented eggs or larvae were collected and contained the following: (1) 77 eggs 2.5 mm in diameter, (2) 156 eggs 2.5 mm in diameter, (3) 246 stage 18 (Gosner, 1960) larvae, (4) 233 stage 25 larvae, and (5) 240 stage 27 larvae. In addition, 2 female *L. mystaceus* each had 285 and 266 unpigmented eggs 2.0 mm in diameter. Five female *L. wagneri* had the following pigmented eggs: (1) 2793 eggs 1.0 mm in diameter, (2) 3483 eggs 1.0 mm in diameter, (3) 3375 eggs 1.0–1.25 mm in diameter, (4) 3602 eggs 1.0–1.25 mm in diameter, and (5) 2813 eggs 1.0–1.5 mm in diameter.

Eighteen female *L. mystaceus* and 103 female *L. wagneri* were examined for egg development. The data were organized into two week intervals and by size of ova within time intervals to determine whether any differential reproductive patterns could be discerned over the study period (Table 2). *L. mystaceus* has the same pattern expected if all stages of egg development were equally represented throughout the total observation period ($\chi^2 = 2.50, P > .05$). The data for *L. wagneri* indicate that dur-

ing the latter three biweekly periods, more females had the .75–1.25 mm category egg than expected (when expected values are figured as equal representation among categories for each 2 week period, $\chi^2 = 19.706$, $P < .05$). The limited data indicate that both *L. mystaceus* and *L. wagneri* populations were breeding throughout the entire study period and there were no temporal differences in reproductive patterns.

LARVAL BEHAVIOR AND PREDATION EXPERIMENT

During the morning of 27 July 1971, Heyer observed *L. wagneri* tadpoles in a 3 × 20 m grassy pond in the pasture. The larvae were associated in tight schools. At the beginning of the observation period, four schools were present. Each school was marked with a stake and movements were recorded. The larvae within a school were extremely active, so much so, that a school could be seen from a considerable distance because of the boiling water and black mass of tadpoles. On close inspection, the larvae were moving their mouthparts extremely rapidly. Some larvae were also scraping blades of grass in a frantic manner. In the roiling school, detritus was stirred up in the water. The individual schools appeared ameboid, usually the whole school would slowly shift position in the pond. In 20 min, one school moved 1.5 m. Some of the schools fragmented and one time during the observation period, two schools fused.

Wassersug (1972) defined two modes of schooling in tadpoles and commented on a third. One of the modes he termed the *Bufo* mode, in which large numbers of conspicuous, bad-tasting larvae are in close physical contact. *Bufo* schools are usually quiet, but still very obvious due to the contrast of the aggregated black bodies against a lighter background. Wassersug argues that the schools can be obvious because predators have learned to avoid the bad-tasting larvae. Schools of *Bufo* and *L. wagneri* are similar in that the individuals are in contact and the larvae

TABLE 2.—Occurrence of egg sizes in female *Leptodactylus* by two week periods in 1971.

Date	Egg size (mm)	Females
	<i>L. mystaceus</i>	
8/6–21/6	0–1.37	2.5
	1.38–2.5	1.5
22/6–5/7	0–1.37	0
	1.38–2.5	1
6/7–19/7	0–1.37	4
	1.38–2.5	4
20/7–3/8	0–1.37	3.75
	1.38–2.5	1.25
	<i>L. wagneri</i>	
8/6–21/6	0–.75	5
	.75–1.25	4
22/6–5/7	1.25–1.75	3
	0–.75	3
6/7–19/7	.75–1.25	6.5
	1.25–1.75	5
20/7–3/8	0–.75	11
	.75–1.25	19
	1.25–1.75	6
	0–.75	10
	.75–1.25	23
	1.25–1.75	12

are black; they differ, however, in that *Bufo* schools are normally quiet, *L. wagneri* schools hyperactive.

A series of experiments were designed to determine if *L. wagneri* larvae taste bad to natural predators. The purpose of the experiments was to determine if bad taste could account in part for the pattern of obvious schooling in *L. wagneri* larvae. Replicate predator-prey interactions were set up as follows. Three predators were used—dytiscid beetles and belostomatid Hemiptera which have piercing and sucking mouthparts, and dragonfly larvae which manipulate the food items and have chewing mouthparts. The reason for selecting the two predator types was that if the bad taste was due to poison glands in the larval skin, dytiscids and belostomatids might not be deterred, whereas the dragonfly larvae might be expected to react to the skin. A single predator was placed with 2 larvae in a 10 × 16 cm plastic bag with a small portion of water in the bottom with a small bit of grass with algae. Three types of larvae were used, hylids (assumed

to be good tasting), *L. wagneri*, and *Bufo marinus*. Each possible combination of larvae and predator was set up on two different occasions. The first day, 27 July, 3 replicates of tadpole combinations with dragonflies, a single set of tadpole combinations with Hemiptera, and 2 replicates of tadpole combinations with dytiscid beetles were set up. The hylids and *L. wagneri* larvae were of comparable size, but the *Bufo marinus* larvae were much smaller, so that two *B. marinus* larvae were used in place of single individual. The experiment was run for 4 hr. The second day, 28 July, only hylids and *L. wagneri* larvae were used. The same predators were used; the tadpole combinations were reversed. Six replicate tadpole combinations (2 *L. wagneri*, 1 *L. wagneri* and 1 hylid, 2 hylids) were run with dragonflies, 2 replicates with Hemiptera, and 12 sets of 2 *L. wagneri* larvae were run with dytiscids. This experiment was run for 9 hr. The experiments yielded few data, but the data obtained were instructive. On the first day, of the 8 hylids, 8 *L. wagneri* and 16 *Bufo marinus* offered to the dytiscids, only 1 hylid was dead at the end of the experiment. It was intact, suggesting death due to handling during the experiment. On the second day when 24 *L. wagneri* were offered to the same 12 dytiscids, all larvae were living at the end of the experiment. Apparently, the experimental conditions were not conducive for dytiscid feeding. Of the eight *B. marinus* larvae offered to the belostomatids, four were dead at the end of the experiment but appeared as though they had not been fed upon by the hemipterans. Five of the 10 hylids offered to the hemipterans over both days were dead at the end of the experiments. Two of the five appeared untouched, whereas the other three appeared as though the entire head region had been digested, leaving an empty skin bag. Only 2 of the 10 *L. wagneri* offered to the belostomatids over both days were dead at the end of the experiments, but both appeared to have been fed upon by the insects. The only conclusion that may

be drawn with respect to piercing and sucking insect predators is that under experimental conditions, they will feed on both hylid and *L. wagneri* larvae. Six of the 24 *B. marinus* offered to the dragonfly larvae the first day were eaten and 1 was dead at the end of the experiments. These results are no different from results expected if the dragonflies were not discriminating among the three types of larvae [six hylids were eaten (1), or chewed on (5), four *L. wagneri* were entirely eaten during the same experiment, $\chi^2 = 1.50$, $P > .05$]. Two of the 30 hylids offered to the dragonflies over both days were entirely eaten and 10 were chewed on for a total of 12. Nine of the 30 *L. wagneri* offered to the dragonflies over both days were entirely eaten and three were chewed on for a total of 12. It is apparent that dragonfly larvae ingest hylid, *L. wagneri*, and *B. marinus* tadpoles indiscriminately under experimental conditions. As these predators chew the tadpole, they would be expected to react to bad tasting skin. Apparently they do not. Wassersug (1971) has indicated that *B. marinus* larvae taste bad to vertebrate predators. It may be that schooling has been allowed to develop because the larvae taste bad to vertebrate predators rather than aquatic insect predators. The aquatic insects probably pick off weak individuals, and perhaps it makes little difference whether such individuals are alone or part of a school. The interactions of tadpole individuals and schools with vertebrate predators need further study.

DISCUSSION

Leptodactylus discodactylus was previously assigned to the Melanonotus group, based primarily on characteristics of external morphology (Heyer, 1970). Results of this study, primarily based on the male calling sites and nonpigmented eggs suggest that *L. discodactylus* does not belong to the Melanonotus group. Detailed examination of the internal morphology of the recently obtained material is underway to clarify the relationships of *L. discodactylus*.

Results of these studies suggest that *L. discodactylus* is a specialized species both in external morphology and ecology.

Wassersug (1972) suggested that larval *L. melanonotus* might exhibit the *Bufo* mode of schooling. *L. melanonotus* is closely related to *L. wagneri*; both species show similar larval behavior patterns. We think *L. wagneri* larvae exhibit certain traits of Wassersug's proposed *Scaphiopus* mode which is characterized in part by extreme activity. As Wassersug points out, many more basic observations are needed before schooling in tadpoles is well understood.

The two most abundant species which were breeding during the study period, *L. mystaceus* and *L. wagneri*, were reproducing in the most unstable habitats with respect to temporary pond availability. Ponds in the pasture and in camp where both species were depositing their eggs and larvae often dried up during the study period. In contrast, a large temporary pond in the secondary forest had water during the entire two month period. If the *Leptodactylus* foam nest is an adaptation in response to xeric environments as suggested previously (Heyer, 1970), it is interesting the *L. mystaceus* and *wagneri* are successfully exploiting the most xeric microhabitats represented at Limoncocha.

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