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ON FROG DISTRIBUTION PATTERNS EAST OF THE ANDES

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The frogs of the Tropical and Subtropical lowland forests east of the Andes comprise a diverse assemblage whose basic zoogeographic patterns are just beginning to be understood. Part of the problem in understanding the basic distributions has been the unequal representation of frog collections on a geographical basis. Recently, authors have been proposing some general distribution patterns, especially for the frogs of the Amazonian and Atlantic Forest regions (e.g. Duellman, 1982; Lynch, (1979). One general pattern proposed is that the lowland frog fauna next to the Andes is much more diverse and contains many more endemics than the central Amazonian frog fauna (Duellman, 1982; Lynch, 1979). A second pattern proposed is that the Atlantic Forest frog fauna is characterized by a high local endemicity producing a latitudinal gradient of distribution patterns (e.g. Lynch, 1979). Although almost everyone who discusses Neotropical frog distributions includes a caveat that there is still some question regarding the distributional data-base itself, no one has attempted to assess the adequacy of the data base. In this paper, an attempt is made to assess the adequacy of the distributional data base for the frogs that occur in the tropical forests east of the Andes, emphasizing the Amazonian and Atlantic Forest areas. The first portion of this paper comprises an assessment of whether collecting artifact is cause for concern. The second portion of this paper discusses general patterns, questions, and practical consequences arising from the first section.

METHODS AND MATERIALS

A working base map was prepared as an overlay of a 1:10,700,000 scale map of South America. On this overlay, two degree quadrilaterals

were drawn from 10° latitude North to 30° South and from the Andean lowlands east to the Atlantic Ocean (for configuration of grid used, see Figure 1). A two degree quadrilateral is about one half the size of French Guiana — the grid is coarse.

Ten species groups were chosen to plot as present or absent on the working grid. The species groups were chosen on the basis of: (1) being commonly collected, and (2) having a high likelihood of being distributed throughout the grid area. The species limits are not well understood for all of the species within the species groups. This is not of concern for the purposes of this analysis. Data were used if the only identification was to species group; the assumption is made that the majority of such assignments are correct. The ten species groups and the names associated with them in collections are: (1) *Bufo granulosus* group (*azarai, beebei, dorbignyi, fernadezae, goeldii, granulosus, humboldti, lutzi, major, merianae, minor, mirandaribeiroi, pygmaeus*); (2) *Bufo marinus* group (*arenarum, ictericus, marinus, paracnemis, rufus*); (3) *Hyla boans* group (*boans, circumdata, crepitans, faber, pardalis*); (4) *Hyla microcephala* group (*bivittata, leali, microcephala, minuta, misera, nana, sanborni, walfordii, werneri*); (5) *Ololygon rubra* group (*acuminata, blairi, boesemani, crospedospila, cruentomma, egleri, fuscovaria, hayii, nasica, rubra, x-signata*); (6) *Phrynohyas* (*coriacea, imitatrix, mesophaea, resinifictrix, venulosa*); (7) *Leptodactylus fuscus* group (*bufonius, camaquara, cunicularius, elenae, fragilis, furnarius, fuscus, geminus, gracilis, jolyi, latinasus, longirostris, marambaiae, mystaceus, mystacinus, notoaktites, spixi, tapati, troglodytes*); (8) *Leptodactylys melanonotus* group (*dantasi, podicipinus, pustulatus, wagneri*); (9) *Leptodactylus ocellatus* group (*bolivianus, chaquensis, macrosternum, ocellatus, viridis*); (10) *Leptodactylus pentadactylus* group (*flavopictus, knudseni, labyrinthicus, laticeps, pentadactylus, rhodomystax, rhodonotus, rugosus, stenodema, syphax*). Any collection of frogs from east of the Andes is likely to have representatives among these ten groups. By and large the species in these ten groups are the most common species and most of the species occur in open habitats and are often those found in man-altered habitats.

Data were gathered for the 10 groups from the following sources. Data were taken from publications that dealt with regional distributions (Colombia — Cochran and Goin, 1970; Venezuela — Rivero, 1961; French Guiana — Lescure, 1976; Madeira and Purus rivers, Brasil — Heyer, 1977; Rio Grande do Sul, Brasil — Braun and Braun, 1980), taxonomic revisions or other taxon based works with distributions (*Bufo*

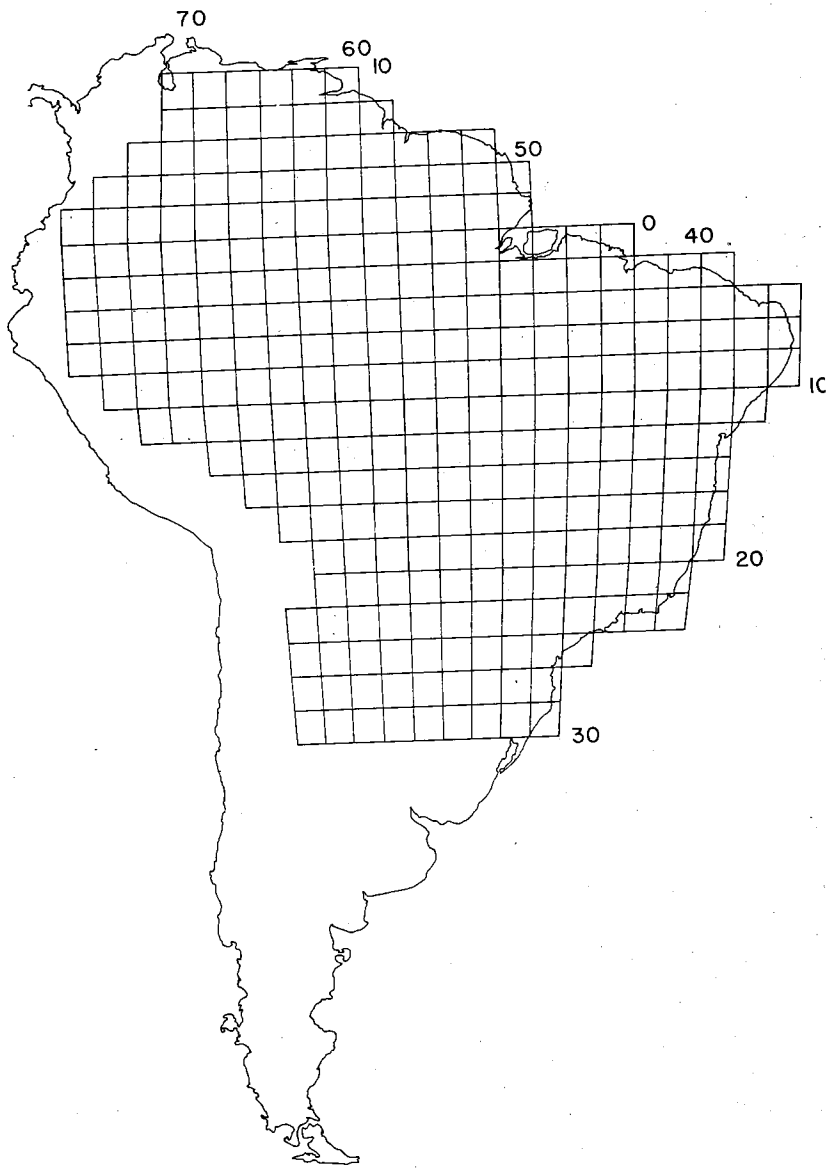

Figure 1. Grid system used to plot species group occurrences.

granulosus group — Gallardo, 1957, 1965; *Bufo marinus* group — Zug and Zug, 1979; *Hyla boans* group — Kluge, 1979; *Phrynohyas* — Duellman, 1971; *Leptodactylus fuscus* group — Heyer, 1978; *Leptodactylus melanonotus* group — Heyer, 1970; *Leptodactylus pentadactylus* group — Heyer, 1979), museum collections (data search complete for Museu de Zoologia, Universidade de São Paulo (MZUSP) and National Museum of Natural History, Smithsonian Institution (USNM), bufonid and hylid species group data (only) from American Museum of Natural History (AMNH), Carnegie Museum (CM), Field Museum of Natural History (FMNH), University of Kansas Museum of Natural History (KU), University of Michigan Museum of Zoology (UMMZ)), and my own locality data base for the *Leptodactylus* species groups built up over the years from collections on a world-wide basis. While the locality data base that results from these sources is not exhaustively complete, it does give a good representation of the distributional data normally available to Neotropical frog specialists.

Each grid quadrilateral was numbered on the overlay grid and a list of localities kept for each grid quadrilateral. Standard resources were used to find the coordinates for localities whose provenance were unknown to me. These standard sources included the series of gazetteers produced by the Office of Geography, U.S. Department of the Interior (available for all countries included in grid) and the series of bird locality gazetteers produced by Raymond Paynter and associates at Harvard (available for all countries except Brasil). Because of the importance of the MZUSP localities, I requested coordinates from Dr. P. E. Vanzolini for MZUSP localities I could not locate. With this level of search, localities for the vast majority of localities were assignable to grids. Again, the level of effort, while not including the final step of inquiring about unplottable localities from the collections involved (with the exception of MZUSP), is that typical of effort put out for locating localities for distributional studies.

The data base used, while not complete, is sufficient for the purposes of this paper. The results of this exercise give an indication of the broad nature of baseline distributional data for the overlay area. Due to the nature of the analysis, a result of all 10 groups being represented in all 283 grid quadrilaterals would not indicate than an adequate knowledge of frog distributions was available. Such a result would indicate that the most common, open-formation species were known from at least one locality in all 283 grid quadrilaterals. Very few forest inhabiting species are represented in the species groups used. Thus, even if we were

confident that an adequate distributional data base was available based on the 10 species group data used herein, there would be no guarantee that the distributional data base for forest inhabiting frogs was adequate.

DISTRIBUTIONAL DATA

The basic data are examined from three perspectives: (1) the distributions of a single species group; (2) the distributions of all ten species groups; and (3) numbers of localities sampled per grid quadrilateral.

Ololygon rubra Group Occurrence and Distribution

Very few grid quadrilaterals have more than five localities where *O. rubra* group members have been collected (Figure 2). The maximum

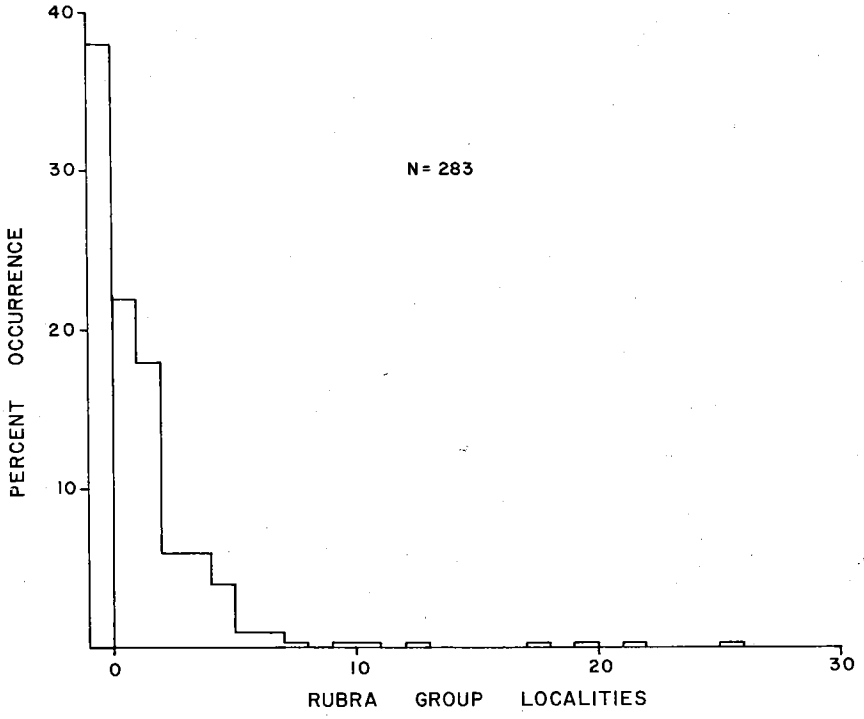

Figure 2. Percent occurrence of *Ololygon rubra* localities among grid quadrilaterals.

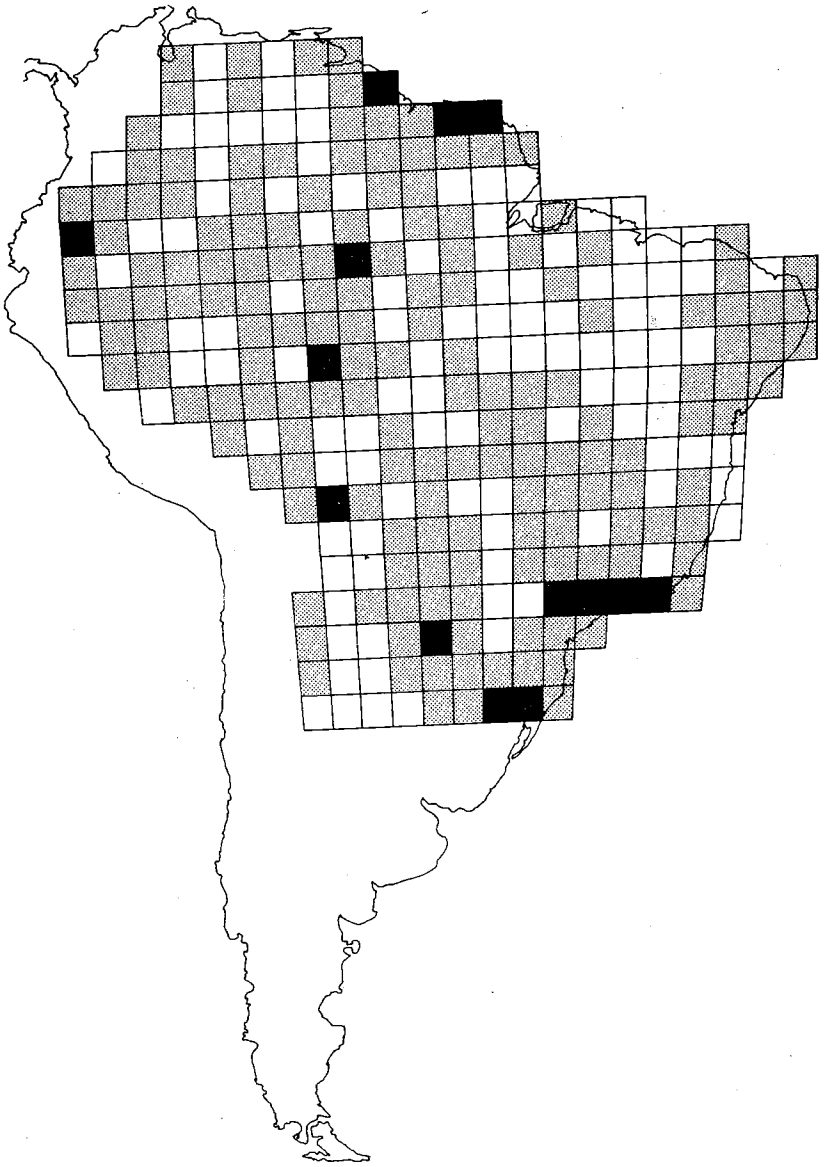

Figure 3. Density of collecting localities for the *Ololygon rubra* group. Blank = no localities, stipple = 1-5 localities, black = 6-26 localities per quadrilateral.

number of localities for any grid quadrilateral is 26. The number of localities per grid quadrilateral with the highest frequency of occurrence (38%) is zero. The geographic distribution of numbers of *O. rubra* group localities shows that the best geographic samples are from the Guianas; southeast Brasil; amazonian Ecuador; around Manaus, Brasil; in Rondônia, Brasil; and a grid quadrilateral each in Bolivia and Paraguay (Figure 3). The geographic distribution of grid quadrilaterals with poor representation of *O. rubra* group localities is a mosaic (Figure 3).

The *O. rubra* group was singled out to examine individually as members of this group are among the most commonly occurring frogs throughout the region under study and known from many localities. The spottiness of the distributional data base is sobering.

TOTAL SPECIES GROUP OCCURRENCES AND DISTRIBUTIONS

When presence/absence data are examined for all 10 species groups by grid quadrilaterals, 14% of the grid quadrilaterals have no species groups represented, 5% have all 10 groups represented, and the other intermediate species group totals have intermediate percentages (Figure 4). The geographic distribution of the data summarized by species groups shows that the grid quadrilaterals with intermediate numbers and the most species group represented do not show any clear patterns (Figure 5). There is an indication that there is a zone from Bolivia to northeast Brasil that is poorly sampled (Figure 5).

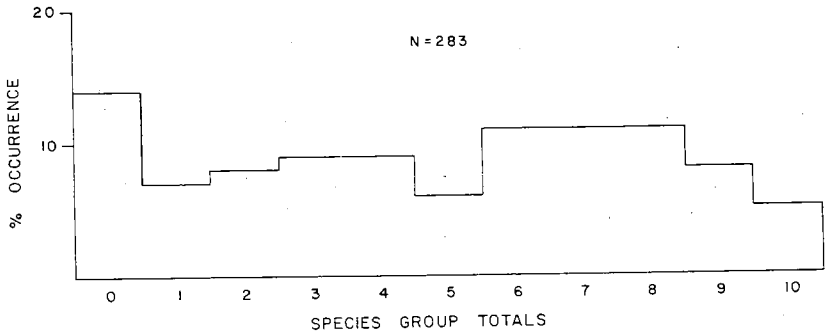

Figure 4. Percent distribution of number of species groups occurring within grid quadrilaterals.

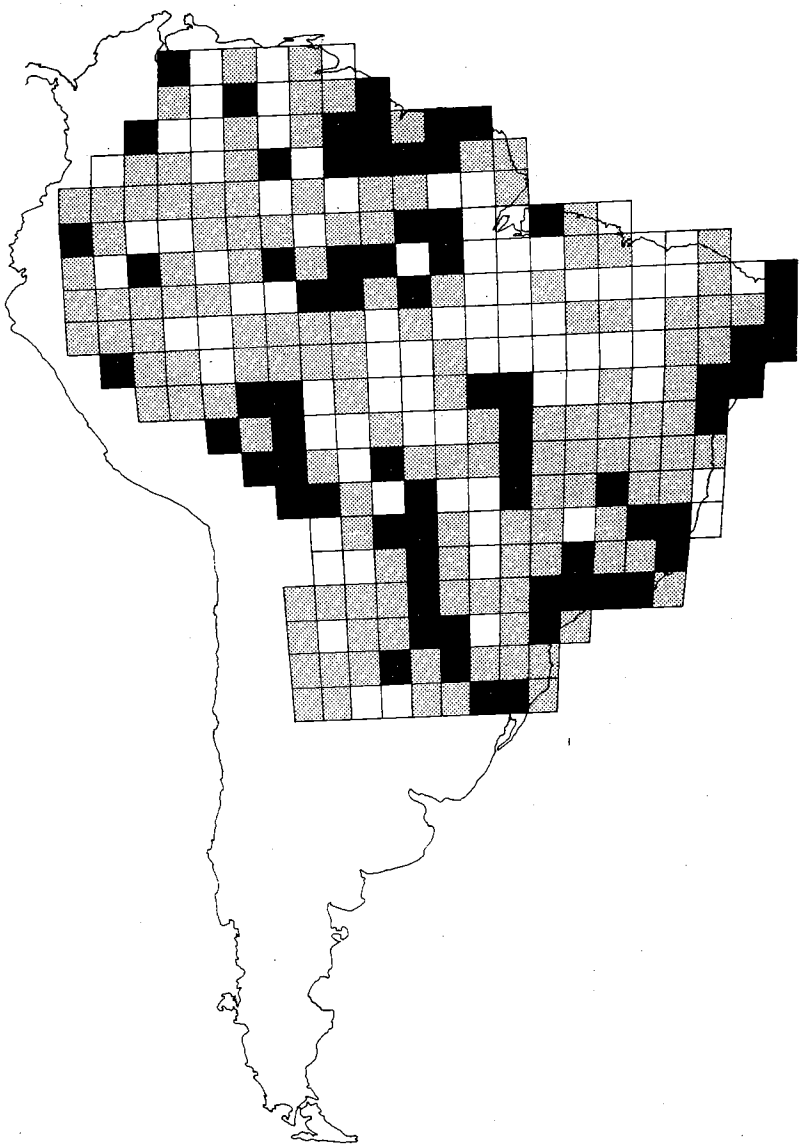

Figure 5. Geographic distribution of numbers of species groups per quadrilateral. Blank = 0-2 species groups, stipple = 3-7 species groups, black = 8-10 species group per quadrilateral.

LOCALITY NUMBER OCCURRENCE AND DISTRIBUTION

As stated in the Methods and Materials, the numbers of localities per grid quadrilateral were recorded. These data also reflect the adequacy of the distributional data base for frogs. These localities represent most of the localities where frogs have been collected within the area under study. Although a precise estimate of how complete these locality records are for all frog localities is not available, one indication is that 83% of the localities collected on MZUSP-USNM expeditions on the Rio Purus and Rio Madeira had frogs from at least one of the 10 species groups analyzed in this paper (Heyer, 1977).

The most localities for any grid quadrilateral was 57, but most grid quadrilaterals had fewer than 10 localities (Figure 6). The number of localities represented by the most grid-quadrilaterals (17%) is one; the second most frequent number of localities among grid quadrilaterals is zero (Figure 6). The geographic distribution of localities by grid quadrilaterals indicates that collecting effort has not been uniform in the area under study. Of particular importance is the large uncollected or undercollected region in central Brasil (Figure 7).

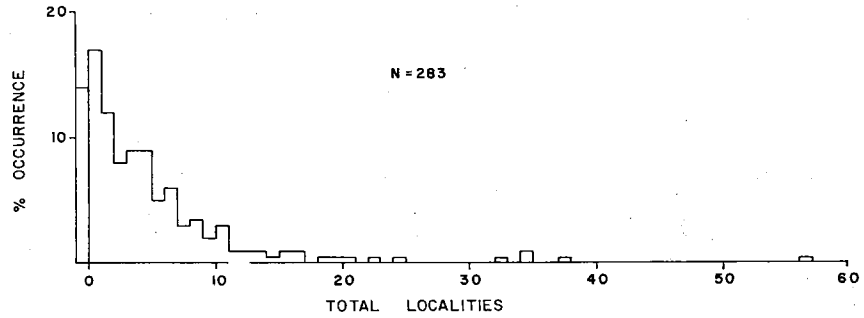

Figure 6. Percent distribution of total number of localities among grid quadrilaterals.

DISTRIBUTIONAL CONFIDENCE MAP

Based on the foregoing data and analyses, each quadrilateral was evaluated based on the question, "If no distributional data were available for frog species x, what confidence would I have that species x really did not occur in that quadrilateral?" No confidence is indicated by a

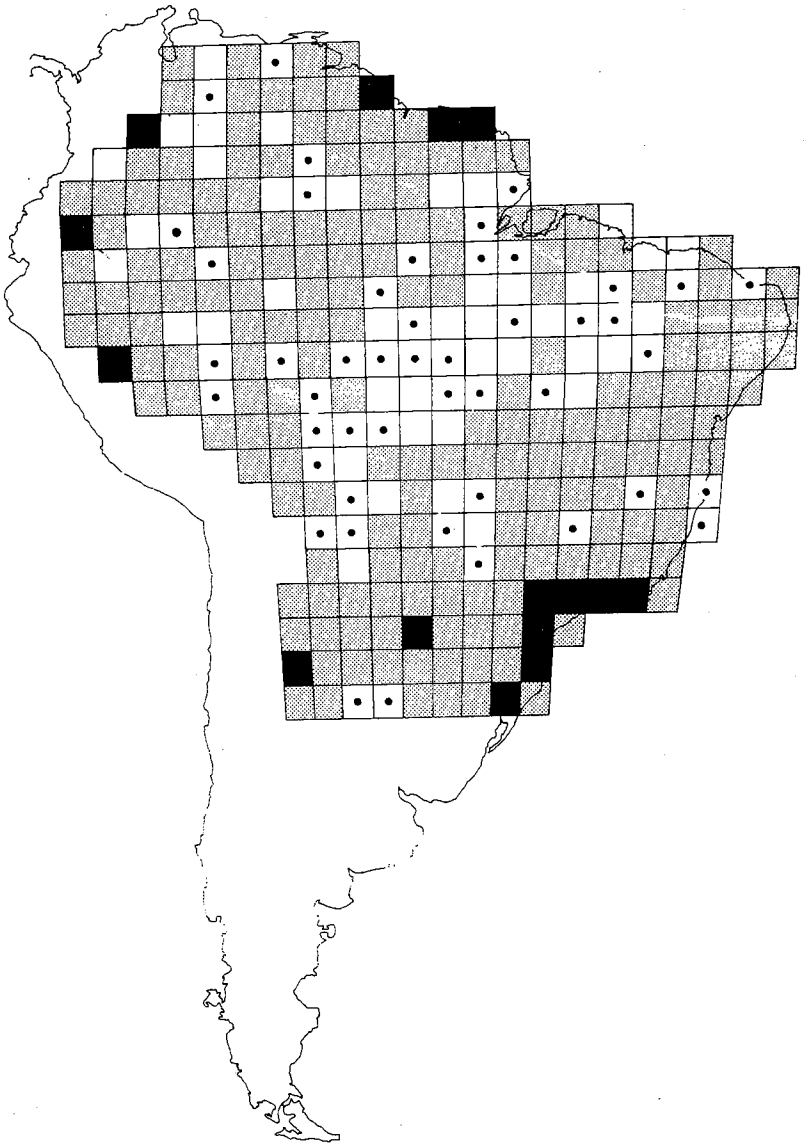

Figure 7. Geographic distribution of numbers of collecting localities per quadrilateral. Blank = 0 localities, dot = 1 locality, stipple = 2-14 localities, black = 15-57 localities.

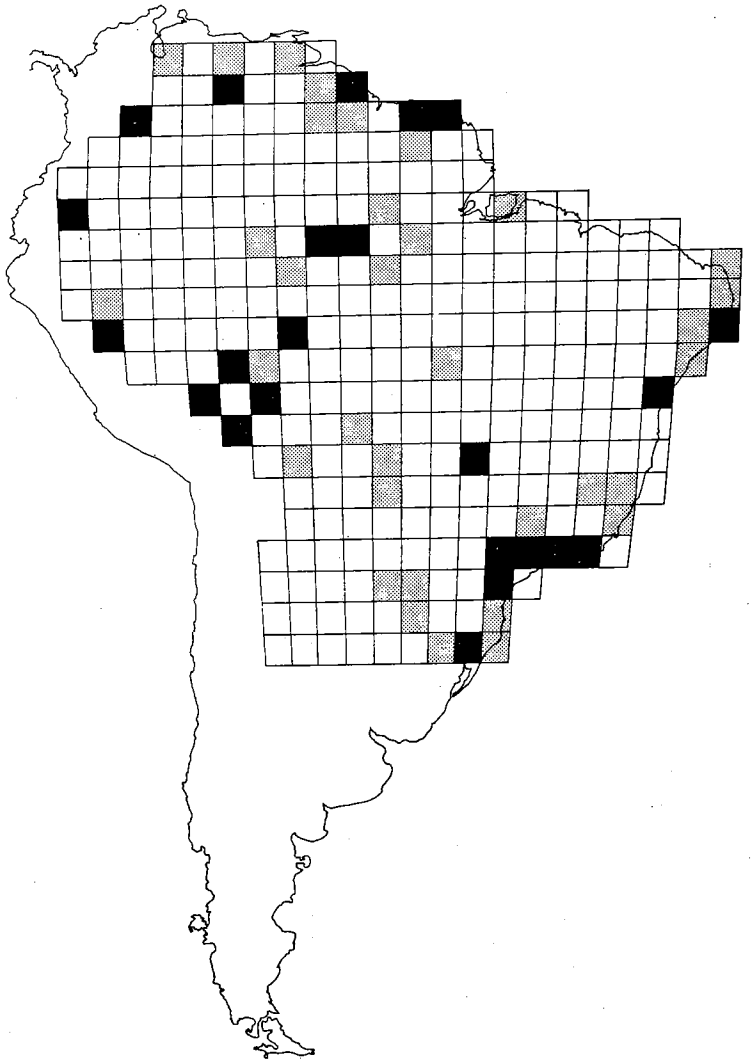

Figure 8. Confidence map of distributional data base. Blank = no confidence, stipple = reasonable confidence, black = best confidence that negative data can be trusted.

blank (that is, further collecting in that quadrilateral could very well document the presence of species x), reasonable confidence by stippling, and the best confidence by black — for most of the area studied, I have no confidence that collecting effort has been adequate to trust negative occurrence data (Figure 8).

THE DATE BASE AND INDIVIDUAL SPECIES DISTRIBUTIONS

The species level systematics of many frogs of the grid area is poorly understood. For example, how many species and what their presently known individual distributions are, are questions that can not be answered with confidence for members of the *Bufo granulosus*, *Bufo marinus*, *Hyla boans*, *Hyla microcephala*, *Ololygon rubra*, *Leptodactylus melanonotus*, and *Leptodactylus ocellatus* groups. Individual species distributions are of interest for two reasons: (1) to determine whether, on the basis of known distributions, there are areas where, although presently unknown, the likelihood is high that they occur there, such that collections would only be an elucidation of the obvious; (2) to see if the present data base can be used to understand individual species distributions. The individual species of the *Leptodactylus pentadactylus* group were plotted on the grid system to evaluate these two aspects.

The known individual species distributions (Figures 9, 10, 11) are generally so spotty that at this point, it would be dangerous to fill in unknown areas rather than assume that the known distribution is correct and relictual.

The data base is verging on being useful to interpret patterns. The distribution of *Leptodactylus knudseni* occurs in several amazonian quadrilaterals (Figure 9, black quadrilaterals from Figure 8). That *L. knudseni* does not occur in the easternmost well collected quadrilaterals in Brasil is not really interesting. The distribution of *Leptodactylus pentadactylus*, when examined against the best collected quadrilaterals, does give an indication that the absence of *L. pentadactylus* from southwest Amazonia may be correct (Figure 10). Similarly, *Leptodactylus stenodema* actually may not occur in the Guianas or southwest Amazonia.

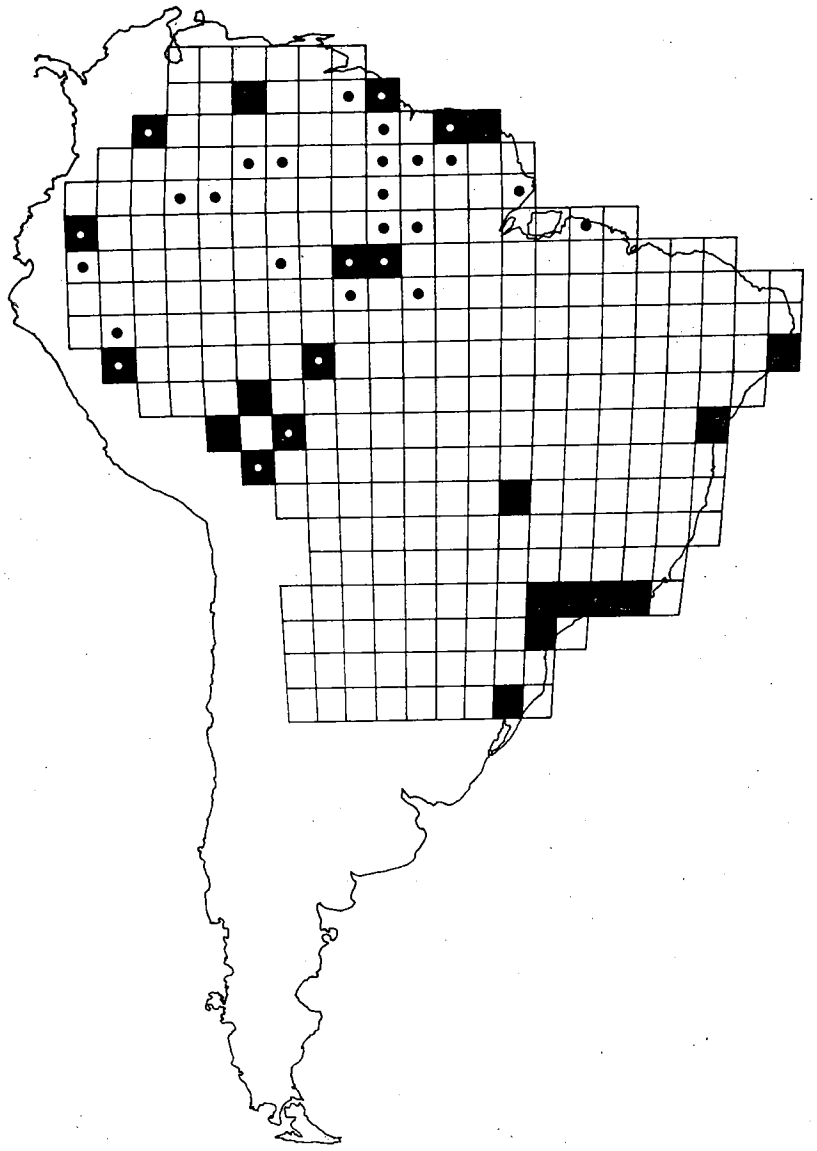

Figure 9. Distribution of *Leptodactylus knudseni* (circles and dots) within grid superimposed on best collected quadrilaterals (from Figure 8).