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

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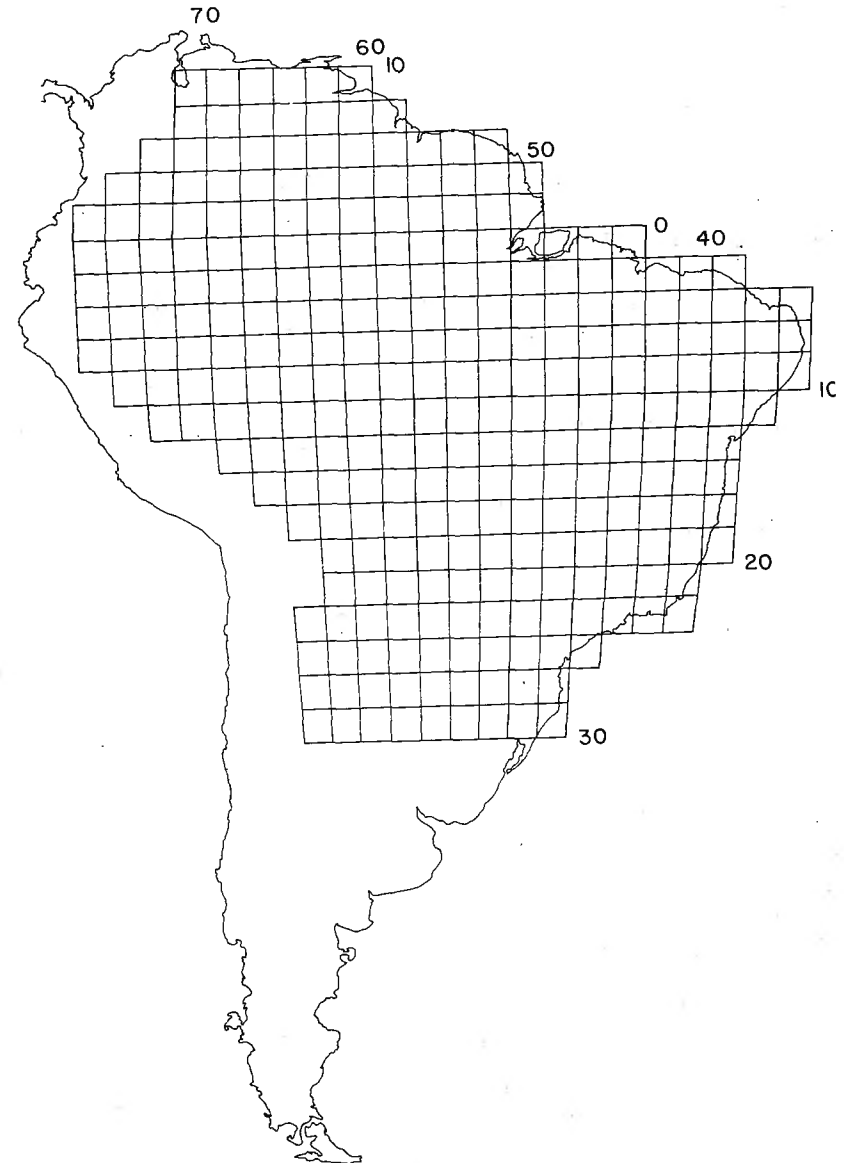
Figure 1. Grid system used to plot species group occurrences.

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
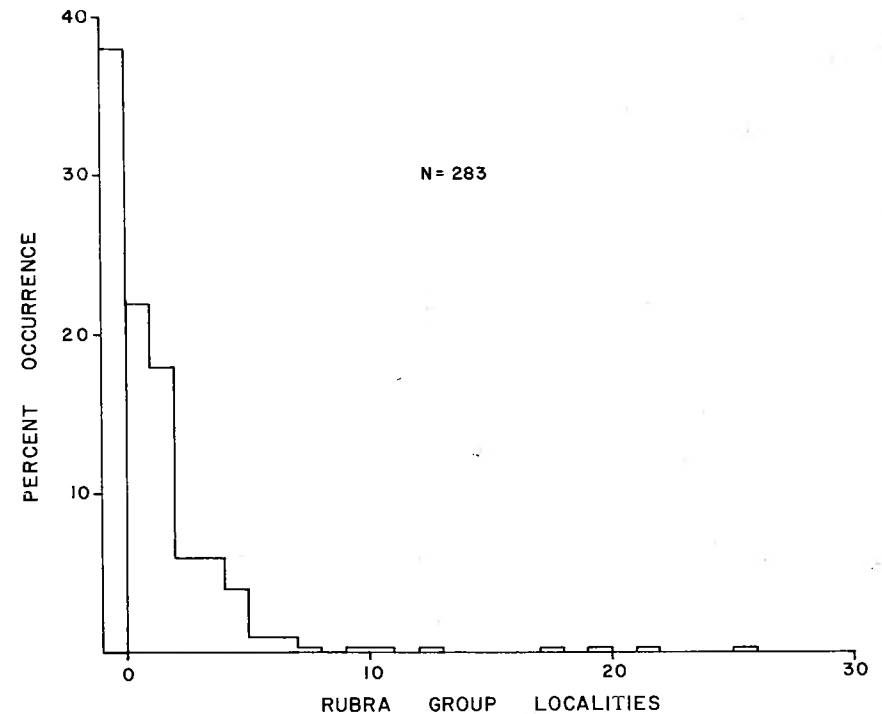

Figure 2. Percent occurrence of *Ololygon rubra* localities among grid quadrilaterals.
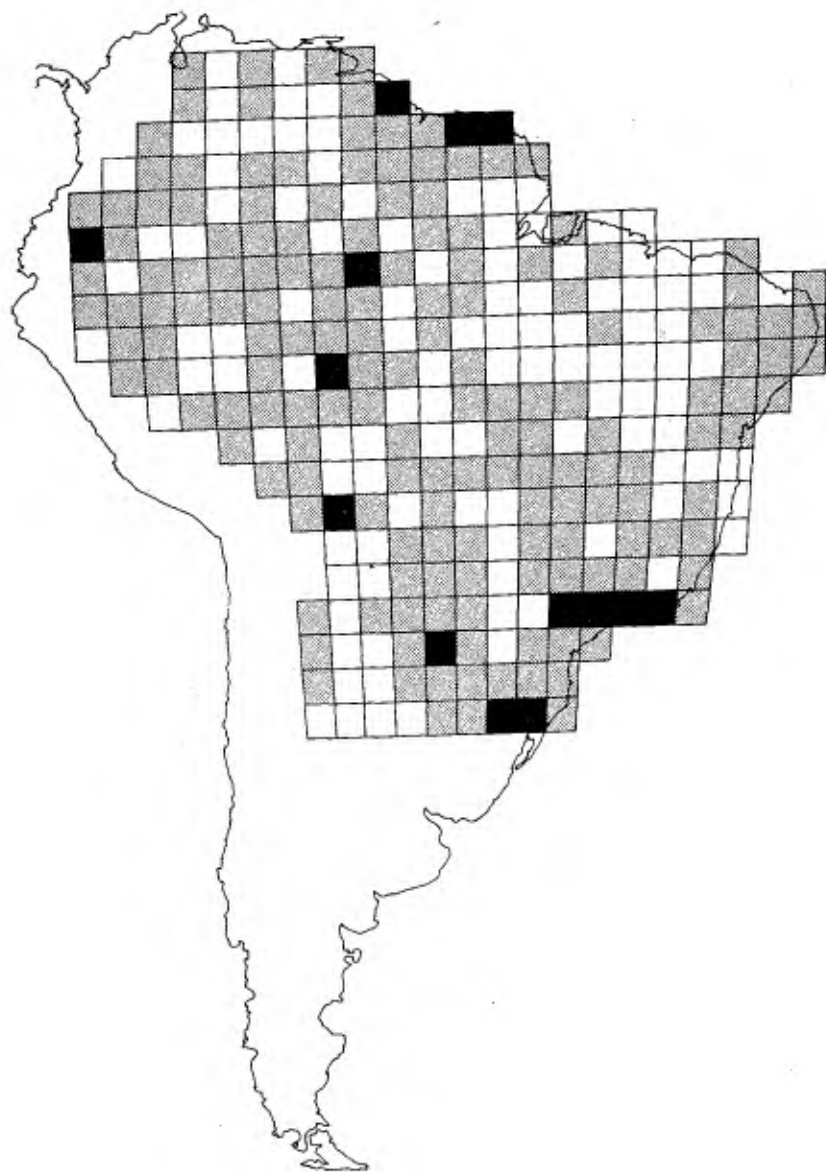
number of localities for any grid quadrilateral is 26. The number of localities per grid quadrilateral with the highest frequency of occurrence (38%) is zero. The geographic distribution of numbers of *O. rubra* group localities shows that the best geographic samples are from the Guianas; southeast Brasil; 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 3. Density of collecting localities for the *Ololygon rubra* group. Blank = no localities, stipple = 1-5 localities, black = 6-26 localities per quadrilateral.
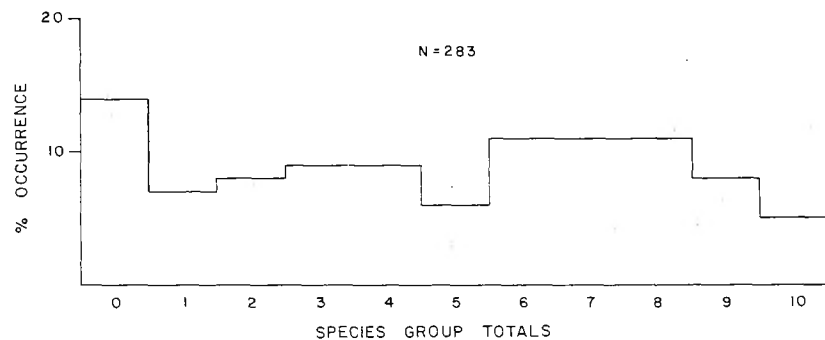

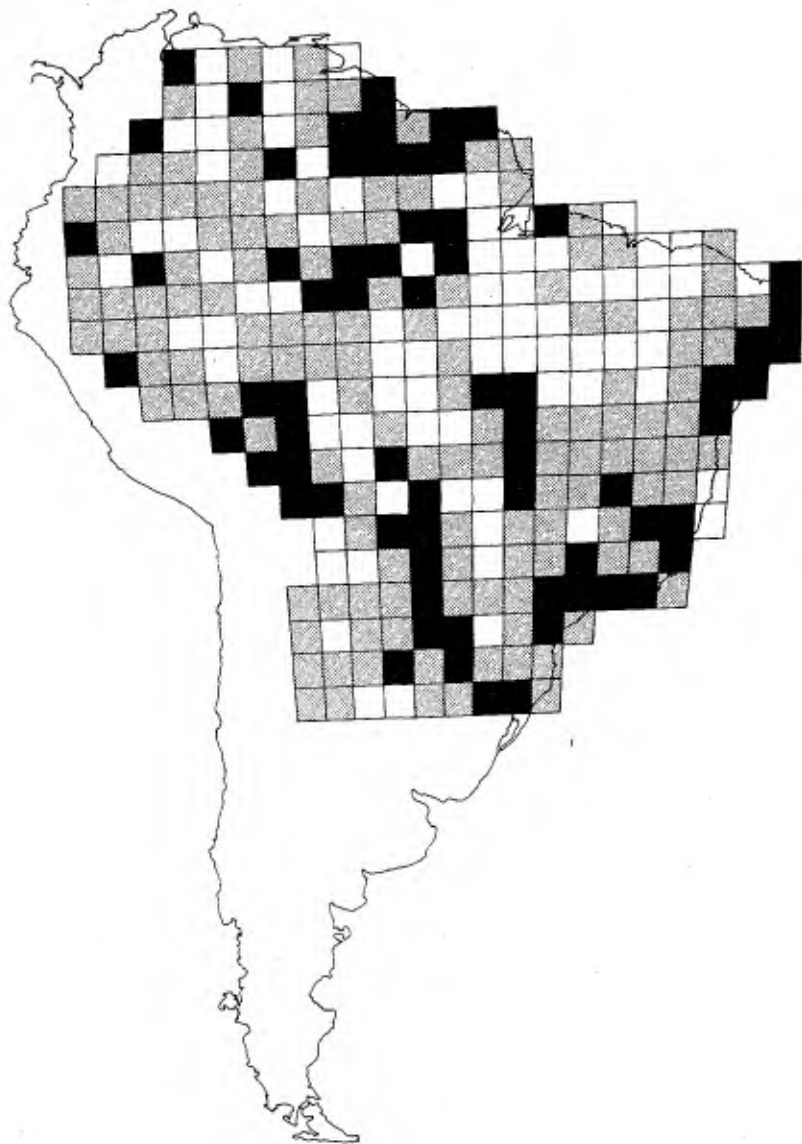Figure 4. Percent distribution of number of species groups occurring within grid quadrilaterals.

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).
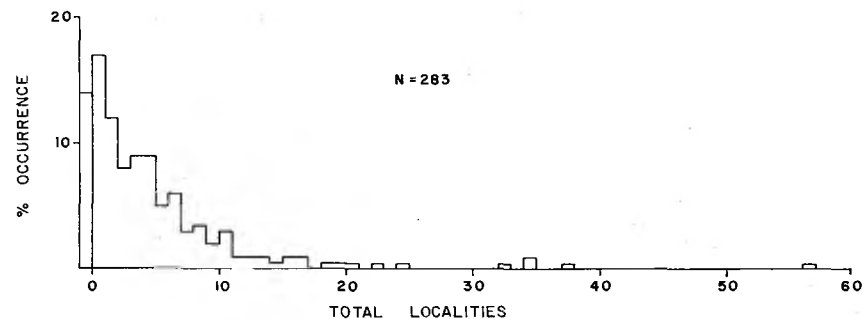

Figure 6. Percent distribution of total number of localities among grid quadrilaterals.

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
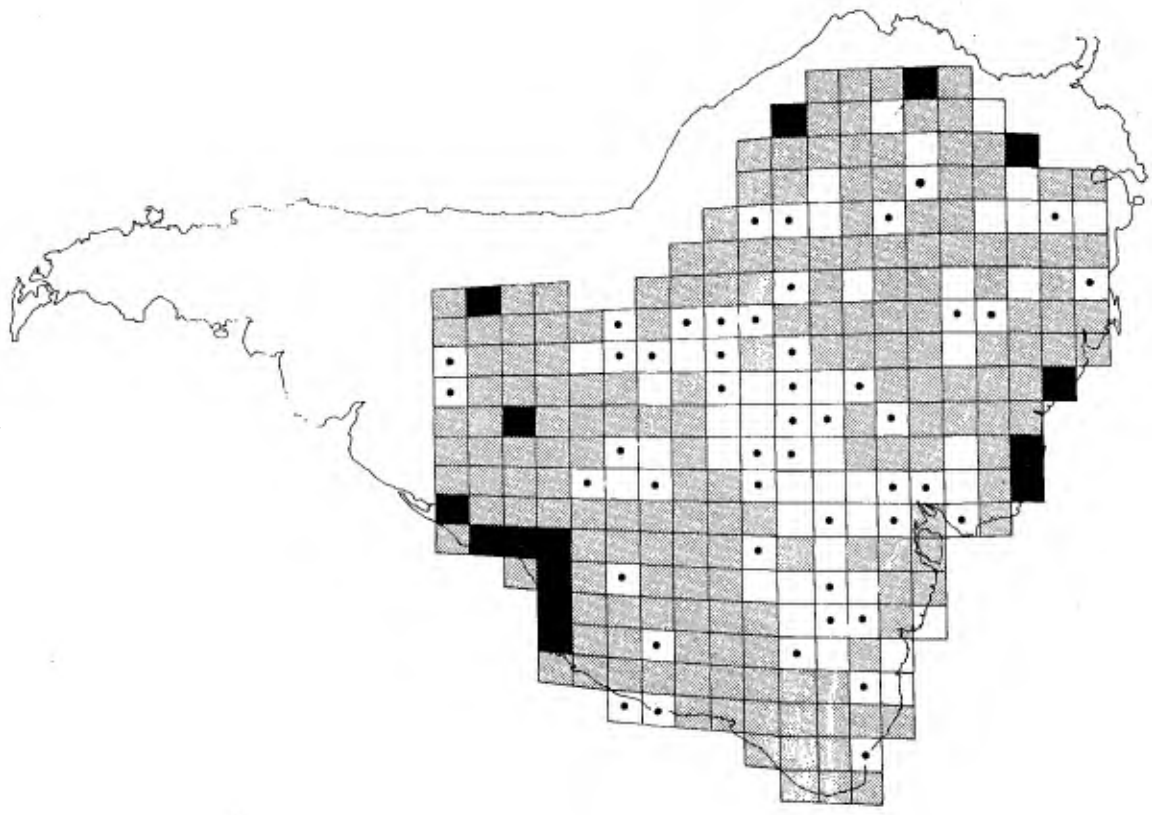
Figure 7. Geographic distribution of numbers of collecting localities per quadrilateral. Blank = 0 localities, dot = 1 locality, stipple = 2-14 localities, black = 15-57 localities.
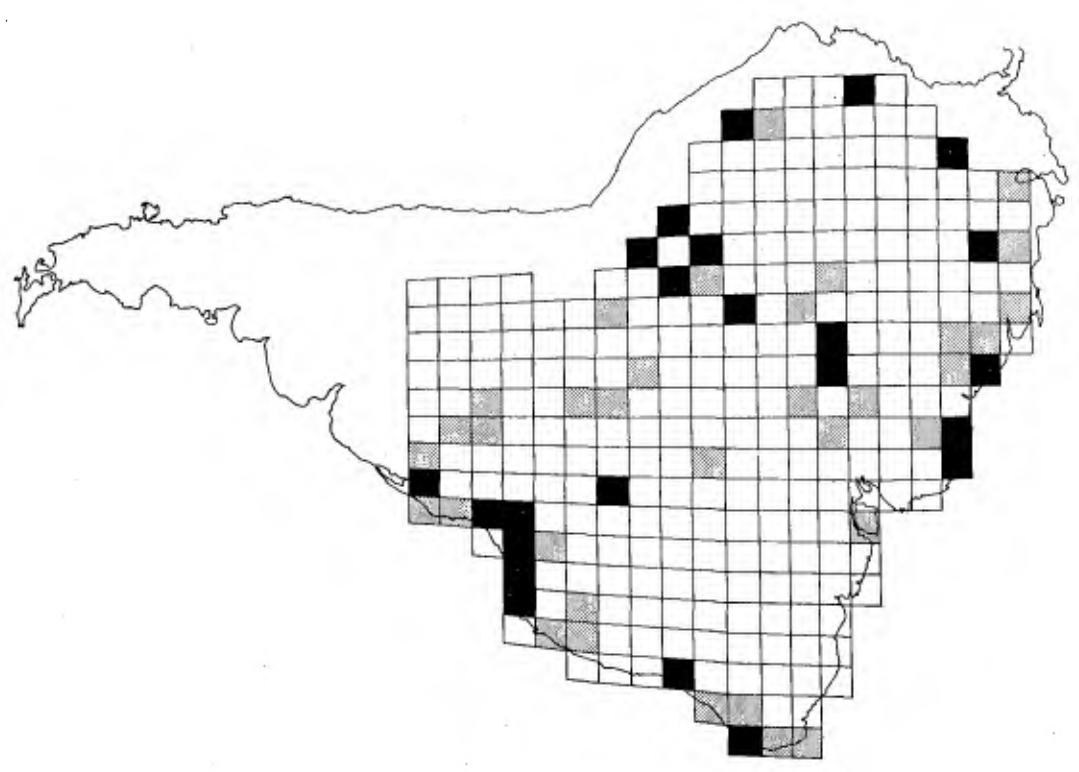
Figure 8. Confidence map of distributional data base. Blank = no confidence, stipple = reasonable confidence, black = best confidence that negative data can be trusted.

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.
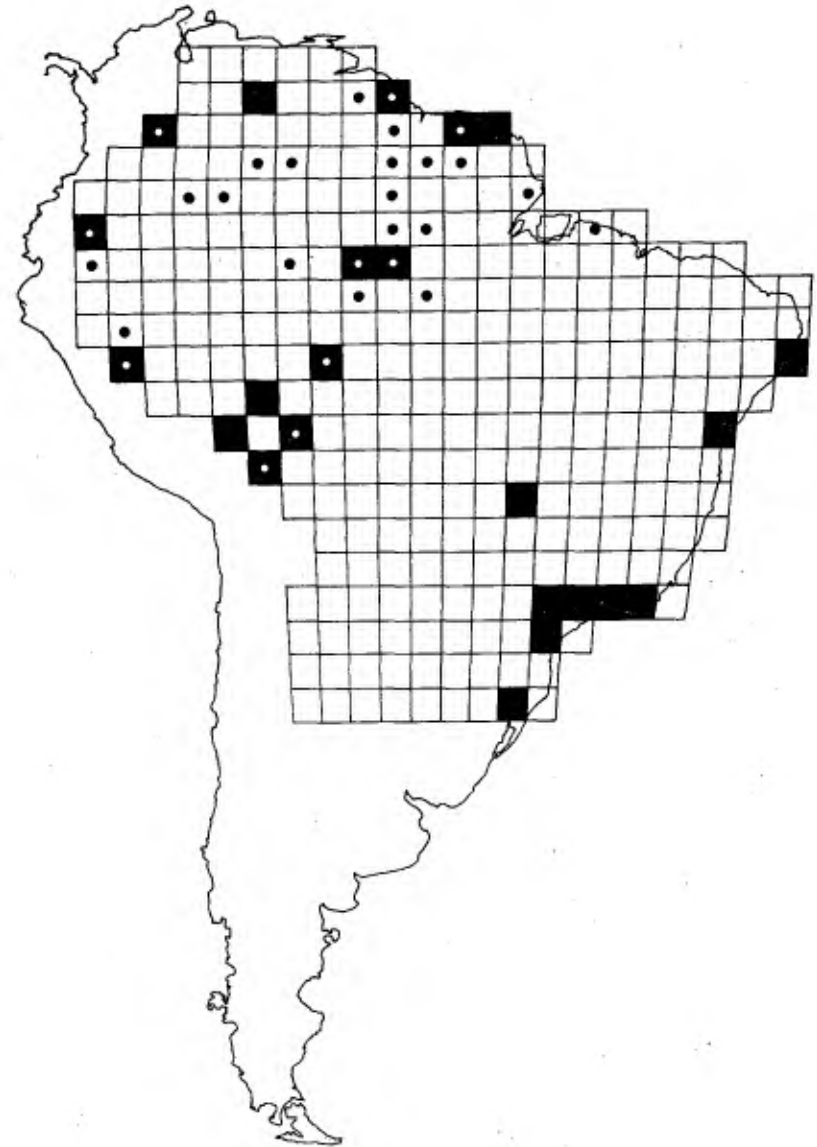

Figure 9. Distribution of *Leptodactylus knudseni* (circles and dots) within grid superimposed on best collected quadrilaterals (from Figure 8).
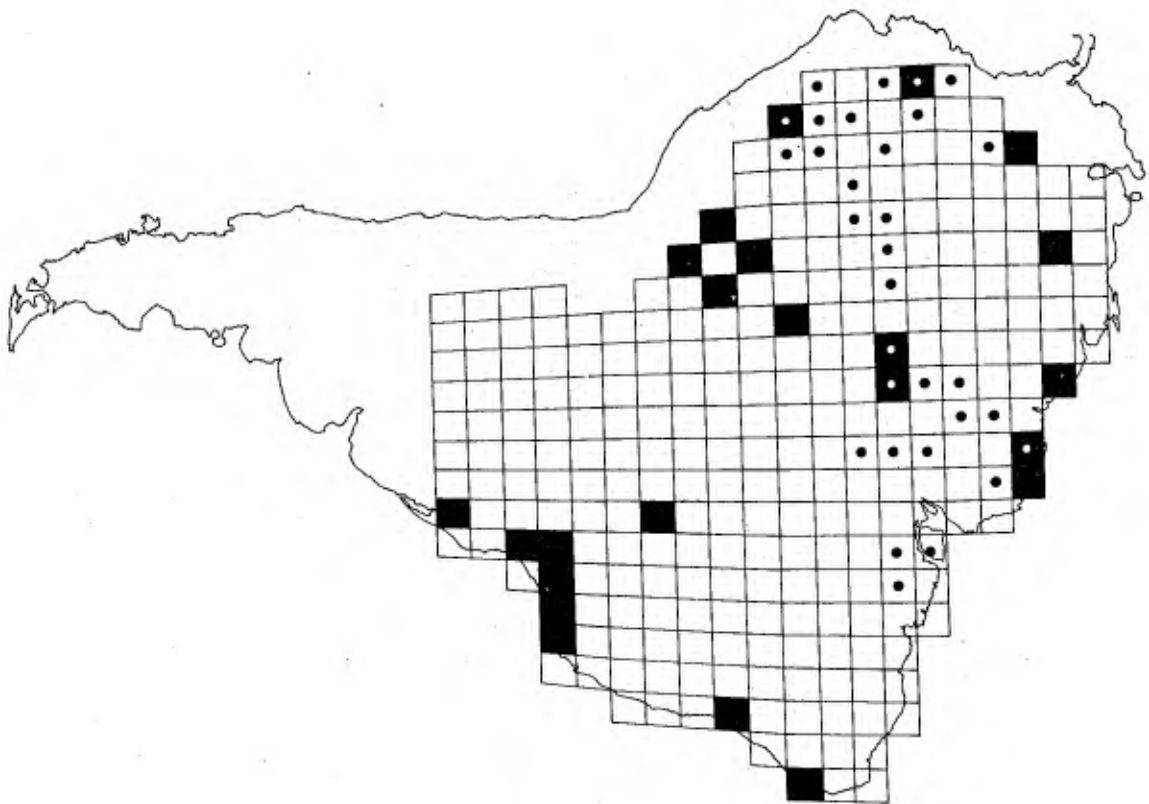
Figure 10. Distribution of *Leptodactylus pentadactylus* (circles and dots) within grid superimposed on best collected quadrilaterals (from Figure 8).
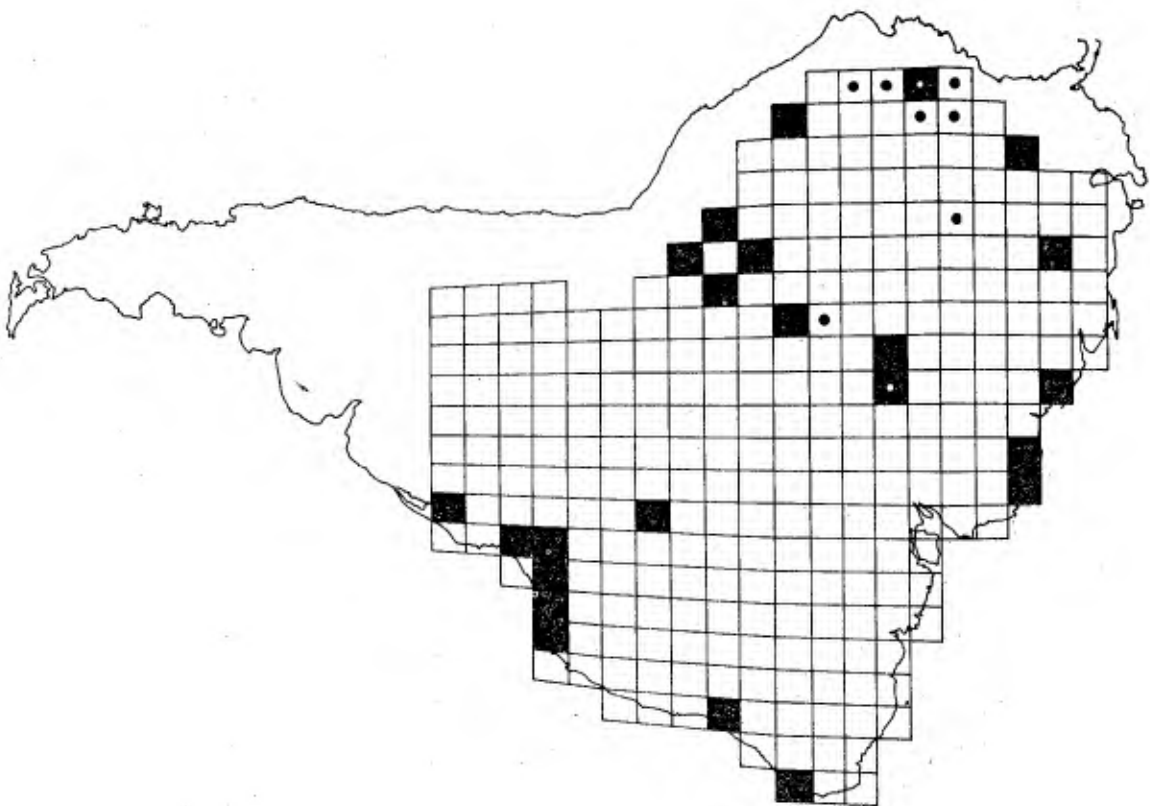
Figure 11. Distribution of *Leptodactylus stenodema* (circles and dots) within grid superimposed on best collected quadrilaterals (from Figure 8).

HOW ADEQUATE ARE THE DISTRIBUTIONAL DATA FOR THE BEST COLLECTED GRID QUADRILATERAL?

The best collected quadrilateral in terms of total localities is that in the State of São Paulo bounded by 22-24° latitude and 46-48° longitude with a total of 57 localities. In a recent revision of the genus *Cycloramphys* (Heyer, 1983; Heyer and Maxson, 1983), predictive areas of occurrence were mapped based on areas of sharp relief likely containing small streams within the boundaries of the Atlantic Forest Morphoclimatic Domain. The known distribution of *Cycloramphus* within the best collected grid quadrilateral (Figure 12) all occur in only one of the predicted areas. From this example (the only meaningful one I know of), it would
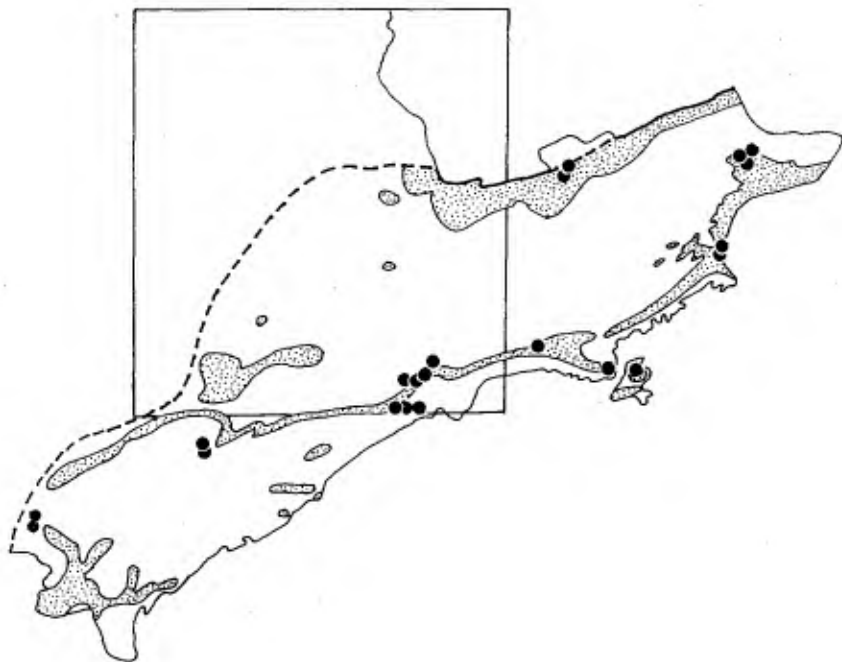

Figure 12. Best collected quadrilateral (outline) in context of predicted areas where *Cycloramphus* species should occur within the State of São Paulo. Heavy line = limit of Atlantic Forest Morphoclimatic Domain (dashed line) or coincidental limit of Domain and State boundary (solid line). Stippled areas are predicted areas of *Cycloramphus* occurrence. Dots are all known *Cycloramphus* localities for State of São Paulo.

appear that anyone studying contact zones between closely related species had better collect the data from the field rather than rely on museum collections.

WHAT PUBLISHED FROG DISTRIBUTION PATTERNS CAN BE EVAULATED FOR CREDIBILITY?

For distribution patterns published within the last year or so, and at least for another year or so, the maps of Figures 5, 8, and 9 can be compared with the proposed patterns to evaluate the effect of collecting bias. The frog data base has been improving due to new collections, especially those associated with the MZUSP. There is some information that suggests that distributions published within only the last few years are based on much better distributional data than previously published distributions.

Frogs of the *Leptodactylus melanonotus* group were revised in 1968-69 (Heyer, 1970). In that revision, distributions of members of *L. podicipinus* and *wagneri* were based on 189 locality records from the MZUSP collections. Together, these two species range throughout the area of the grid of this paper, so Brasilian localities are critical to understanding the distributional limits of these two species. Now, there are 303 MZUSP localities for these two species, including new records from five Brasilian states not available previously. This 160% increase in Brasilian locality data obviously represents a marked improvement in understanding the distributions of the species involved. The reasons for this dramatic increase are two-fold. First, although I had access to the MZUSP collections in the late 1960's, many specimens of this group were identified to genus only and for practical purposes, not available. Due to an intensive curation effort, the MZUSP frog collections are now among the most usable collections in the world. The second reason is that there has, in fact, been a considerable inflow of newly collected specimens since the late 1960's.

Duellman published a revision of the *Hyla geographica* group (1973) in which he made the following point on the distribution of *Hyla fasciata*: "all localities are at elevations between 300 and 1000 m near the Andean front." Since that revision, *Hyla fasciata* has been collected or identified from one locality in the State of Acre, Brasil, four localities in Rondônia, Brasil, eleven localities in Amazonas, and even one locality from the State of Pará. Thus, rather than being a western amazonian
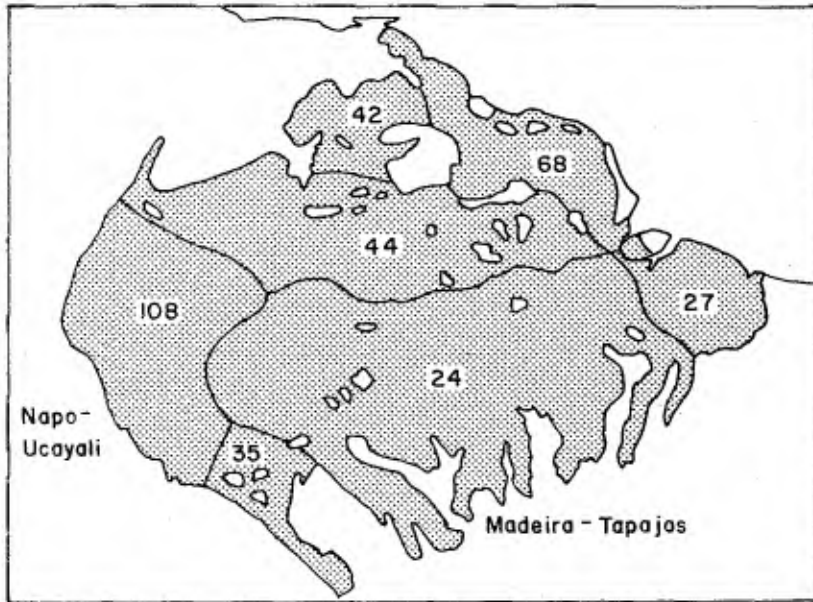
Figure 13. Species density distribution map modified from Duellman (1982). Note that Napo-Ucayali area was reported to have 108 species of frogs and the adjacent Madeira-Tapajos area a total of 24 species of frogs.

endemic, *Hyla fasciata* has a widespread amazonian distribution pattern.

Duellman (1982, Fig. 21.7, simplified here as Figure 13), modifying a distribution pattern map proposed by Lynch (1979), contrasted a Napo-Ucayali unit with a high diversity of frogs (108 species) with many endemics (65) with the adjacent Madeira-Tapajós unit of low diversity (24) with few endemics (3). Duellman apparently overlooked the published results (Heyer, 1977) of expeditions made on the Rio Purus and Rio Madeira, in which 74 species were reported from the Madeira-Tapajós unit. These Purus-Madeira data clearly significantly modify the distributional models proposed by Lynch (1979) and Duellman (1982).

Thus, for practical purposes the current state of knowledge (Figures 5, 8, 9) should only be compared with distribution patterns published since about 1980 that include data from the MZUSP collections.

AN ASIDE — COMPARISON WITH OTHER DATA SETS

The frog distributional data invite comparison with other groups, such as whether frogs are better or more poorly collected than lizards. To my knowledge, there are no exactly comparable data sets to contrast with the frog data. I would not be surprised if lizards were better known and snakes less well known geographically due to the relative diversities and abundances of the groups involved. One impression that several researchers share is that birds and butterflies are reasonably well collected. The bird gazetteers produced by Paynter and associates include maps of localities for all the countries represented by the grid of Figure 1 except for Bolivia and Brasil. By counting locality dots for the bird data from the same quadrilaterals for which frog data are available (Figure 14), two conclusions can be drawn: (1) birds in fact seem to be known
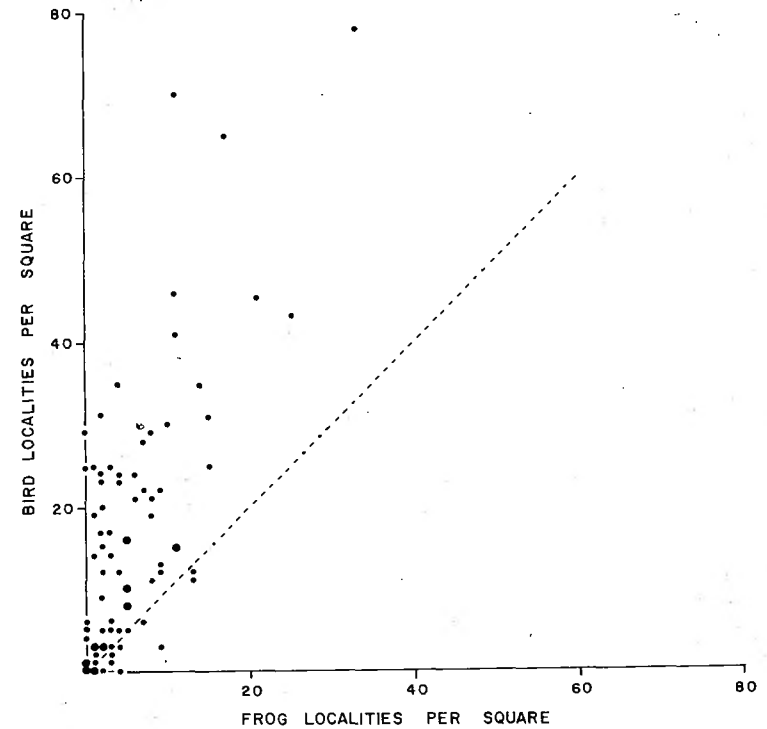

Figure 14. Number of birds localities plotted against frog localities for the same quadrilaterals.

from more localities than frogs (even assuming the frog data based on 10 species groups comprises only 70% of all known frog localities); and (2) there are still enough grid quadrilaterals with 0-5 bird localities (10 bird grid quadrilaterals with no localities) that even bird distributions are not completely known in the area under study (it is clear from the bird locality maps that much more collecting effort has been expended in the montane and mountain slope regions of South America than in the lowlands).

SUMMARY OF FROG DISTRIBUTIONAL DATA

The grid analysis of the most commonly collected frogs is quite coarse-grained. Even at this coarse-grained level, the deficiences of the frog distributional data base are apparent. The following conclusions seem appropriate for 1987, when this analysis was completed.

1) Frog distributional data east of the Andes are not adequate to distinguish between alternate distributional patterns. For example, whether amazonian frog distributions correlate better with the distribution of tropical lowland forests as mapped by Hueck and Seibert (1972) or with the Equatorial Amazonian Domain as mapped by Ab'Sáber (1977) can not be appropriately evaluated with the present data. Nor can patterns currently proposed as restricted to the andean slope regions of the amazonian lowlands be unequivocally accepted as not having broader distributions including the central amazonian regions.

2) Published frog distributions can be consistently relied upon only for presence data; the data base is not yet adequate to generally rely on it for negative data, although the data base is approaching usefulness to evaluate negative data.

3) Current frog distributional data are about an order of magnitude better now than they were even 10 years ago. Distribution patterns published prior to 1980 should be believed more on the basis of faith and intuition than data.

4) Even in the best collected regions east of the Andes, currently available distributional data are probably not adequate for fine scale analysis and understanding.

DISTRIBUTIONAL SPECULATIONS AND QUESTIONS

Distribution patterns can be proposed on the basis of sketchy data and be correct. What is lacking at this stage is sufficient distributional data to meaningfully evaluate competing distributional hypotheses for frog distributions east of the Andes. For example, Duellman's (1982) use of Pleistocene forest refuges to explain the diversity of amazonian frogs next to the Guiana highlands and Andes and Heyer's (1973) use of forest refuges to explain distributions of *Adenomera* species can neither be supported or refuted by the available distributional data base. The following represent my current thoughts on distributional patterns and open questions. These observations, like all others currently, are presently untestable hypotheses or questions.

FROG DISTRIBUTIONS CORRELATE WELL WITH MORPHOCLIMATIC DOMAINS

Certains species groups and genera appear to have distributions restricted within or concordant with the morphoclimatic domains as defined and mapped by Ab'Sáber (1977) (Figure 15) (*Leptodactylus fuscus* group, Heyer, 1978; *Leptodactylus pentadactylus* group, Heyer, 1979; *Cycloramphus*, Heyer, 1983a, Heyer and Maxson, 1983; *Eleutherodactylus guentheri* group, Heyer, 1984). There are two problems areas concerning the correlation of frog distributions with morphoclimatic domains, however. First, the morphoclimatic domains themselves are heterogeneous. For example, within the Equatorial Amazonian Domain, the regions around Altamira, Pará and Manaus, Amazonas differ noticeably in terms of vegetation and types of streams and there is a marked gradient of rainfall and temperature regimes within the Atlantic Forest Domain from north to south. We do not know the degree to which frogs respond in a distributional sense to differences found within morphoclimatic domains. Second, one of the critical areas to determine whether frog distributions are best understood in the context of morphoclimatic domains is the area of transition between the Equatorial Amazonian Domain on one border and the Caatinga and Cerrado Domains on the other border. This is exactly the region we have the poorest locality data from (Figure 8). 1 nevertheless think that morphoclimatic domains provide a better context for understanding frog distributions east of the Andes than either vegetation maps (such as that of Hueck and Seibert, 1972) or Holdridgean Life Zones (e.g. Tosi, 1960 for Peru).

Figure 15. Morphoclimatic Domains (Ab'Sáber, 1977) east of the Andes important to understanding frog distributions. Stipple = Equatorial Amazonian Domain; outlined domains from left below to right above = Central Chaco Domain, Cerrados Domain (including two small isolates), Caatingas Domain; black = Atlantic Forest Domain.

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FOREST AND OPEN-FORMATION DISTINCTIONS ARE IMPORTANT

Most species of frogs appear to form two major ecological groupings at any tropical forest locality: the largest group of species is restricted to within the closed-canopied forests themselves and a smaller group of species is restricted to open formations. Open formations include naturally occurring vegetations with open canopies as characteristic of entire Domains (such as the Caatinga, Cerrado, Chaco Domains), along flood plains of tropical rivers with closed-canopied forest domains, as well as man modified habitats such as pastures or farms. Very few species commonly occur in both forest and open formation habitats (Heyer, 1976; Heyer et al., in press). Making this primary distinction does lead to better resolution of distribution patterns. For example, it is the forest delimited species at Boracéia that have restricted distributions while the open formation delimited species at Boracéia have much more widespread distributions (Heyer et al., in press). Unfortunately, most specimens in museum collections lack these data and no such data are available to determine whether geographic differences obtain in habitat fidelity or whether there are seasonal shifts of habitat use within localities. These kinds of data are needed in order to understand the origin and dispersal of the frogs east of the Andes. For example, we do not know whether forest associated species have ever invaded open formations, or whether invasions from open habitats to forests has been a one way process.

SMALL AND LARGE DISTRIBUTIONS

As proposed above, it does appear that in general, open formation delimited species have larger distributional ranges than forest delimited species. There also appears to be a noticeable difference in the relative geographic extent of forest delimited species within the Equatorial Amazonian Domain and the Atlantic Forest Domain. Forest delimited species with geographic ranges much smaller than the entire Domain dominate the Atlantic Forest Domain (e.g., *Cycloramphus*, Heyer, 1983a, Heyer and Maxson, 1983); there appear to be very few, if any, forest delimited species that occur throughout the Atlantic Forest Domain. On the other hand, there does appear to be a considerable component of the amazonian frog fauna that is distributed throughout the Equatorial Amazonian Domain (e.g. *Adenomera andreae*, Heyer, 1973; *Leptodactylus knudseni* and *rhodomystax*, Heyer, 1979). The rela-

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tive number of forest delimited species with distributions restricted to areas within the Equatorial Amazonian Domain and the nature of their patterns is unknown at present.

From what is known about population differentiation of amphibians and relative ages of frog species, the general pattern of forest delimited species having small geographic ranges that result in a north to south change in species assemblages along coastal Brasil is not surprising. The few data available indicate that most species of Neotropical frogs date from the Paleocene to Pliocene, with relatively few species arising in the Pleistocene (Heyer and Maxson, 1983; Maxson and Heyer, in press) and that there is considerable genetic differentiation among local demes of amphibians (Larson, 1984). These factors, when put in combination with a latitudinal gradient of temperature and rainfall in the topographically complex region of coastal Brasil can account for the high degree of endemicity characteristic of the Atlantic Forest Domain. What seems mildly surprising is that these same factors have not led to greater species restrictions within the Equatorial Amazonian Domain than seems to be the case. This is one question that requires further study.

FROGS OF THE CAATINGAS AND CERRADOS

The distribution of species group totals by Morphoclimatic Domains (Figure 16) indicates that the Cerrado and Caatinga Domains are more poorly sampled than the Equatorial Amazonian Domain and Atlantic Forest Domain and that the Domain best sampled is the Atlantic Forest Domain.

Our knowledge of frogs of the caatingas and cerrados is so rudimentary that even basic questions regarding their distributions are unanswerable at present. For instance, we do not know: (1) whether the caatingas and cerrados share a common frog fauna or whether the faunas are distinct; (2) whether the frog faunas of the caatingas and cerrados are part of a general open formation domain fauna that includes the central Chaco Domain or whether the caatinga and cerrado fauna is derived from the Chaco fauna, or *vice versa*; (3) to what degree the caatinga and cerrado fauna has invaded the open formations of the Equatorial Amazonian and Atlantic Forest Domains or conversely, to what degree the open formation species of the Amazonian Equatorial and Atlantic Forest Domains have evolved in situ (at least some species appear to demonstrate this last pattern, e.g. *Leptodactylus mystaceus, notoaktites, spixi,* Heyer 1978 for patterns and 1983b for taxonomic
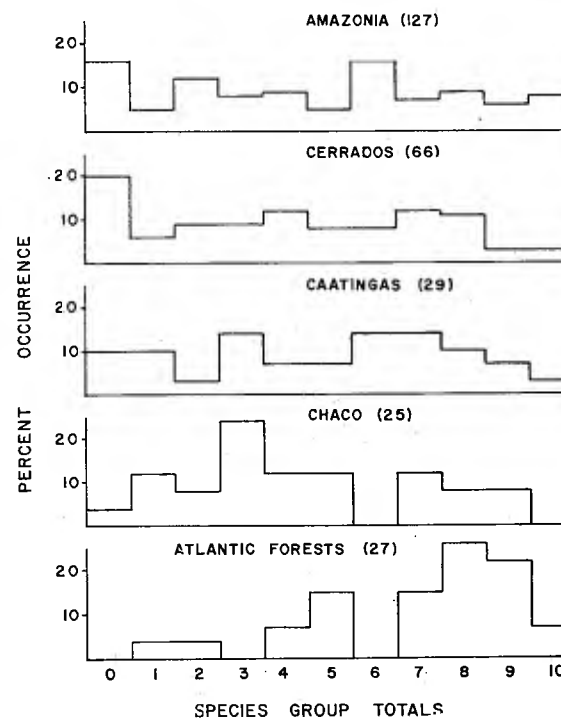
Figure 16. Species group total distributions among grid quadrilaterals by Morphoclimatic Domains.

clarification). In order to understand the historical interplay of the Equatorial Amazonian and Atlantic Forest Domains (they were connected at times in the Pleistocene), we have to have a better understanding of the frog faunas of the caatingas and cerrados.

PRACTICAL CONSEQUENCES AND SUGGESTIONS

WHY SHOULD THE DATA BASE BE IMPROVED?

Because of the efforts needed to amass the data to really understand the frog distribution patterns east of the Andes, why should resources be put into improving the frog data base and not used to improve a better

existing data base, such as exists for birds? There are valid reasons for improving distributional data bases for several distinct groups of organisms. Frogs provide a good distributional perspective because: (1) the frog assemblages east of the Andes are very diverse both in terms of species and life history patterns; (2) frogs apparently show a general pattern of genetic differentiation at the local deme level which contrasts with birds and mammals in general (matched only in such fossorial mammals as *Thomomys* (Patton and Yang, 1977)); (3) frogs are relatively collectable both in terms of relative abundance (in contrast to snakes, for example) and persistence of at least a significant component of assemblages in patches of forest isolated by clearing; (4) most species limits can be determined accurately without recourse to biochemical analyses, as the advertisement calls of frogs are overwhelmingly species specific. Study of any one group of organisms in the complex area east of the Andes will give but one perspective to an understanding of the entire biogeography of the region because the differences among groups are such that they have not interacted in the same way with the environmental diversity and fluctuations of the area east of the Andes. We need to build adequate distributional data bases for several groups occurring east of the Andes — frogs should be among them.

HOW MUCH COLLECTING EFFORT IS NEEDED IN ANY UNKNOWN REGION?

Even the wettest regions east of the Andes have seasonal rainfall patterns. The greatest number of frog individuals and species can be collected at the beginning of the rainy season. Data available for the amazonian regions indicate that about one half of the frog fauna at any site is collected with 30 days of effort, and about two thirds of local faunas collected with 50 days of effort (Heyer, 1976). Due to the dynamic nature of frog assemblages, some complete local faunas are likely unknown even after 30 years of collection effort (e.g., the frog fauna of Boracéia, Heyer et al., in press). Thus, to get a reasonable first approximation of the frog fauna from any area within the amazonian or Atlantic Forest regions, a minimum of 30 days should be planned for the area involved. The sporadic and unpredictable nature of rainfalls that initiate frog activities in the caatingas and cerrados are such that the frog faunas of these regions can best be sampled by resident biologists, who should be encouraged to do so. However, if a person is at the right place at the right time in the caatingas and cerrados, it is likely that a good sample of the frog fauna could be taken with no more than a week of effort.

HOW TO IMPROVE THE DATA BASE

Two kinds of programs need to be initiated that will operate simultaneously. First, all presently collected data should be made available. For example, in this paper, data were not used from the collections in Leiden, Netherlands, or natural history collections in Colombia, Venezuela, Peru, Argentina (in part), the Museu Goeldi, or Museu Nacional in Rio de Janeiro. All of these collections (and others, as well) contain important distributional data that can often be obtained only by visiting the collections involved. Efforts need to be made to make these distributional data more accessible. The second program is the obvious one of making new collections. The map of Figure 7 gives one good indication of where new collections should be targeted that would have the most impact in improving the data base — but even well known regions should be collected if the opportunities present themselves. The most rational approach for new collections would be to identify 20-30 sites for in-depth surveys, choosing the sites within and outside of morphoclimatic domains so absence of species from those sites would have meaning.

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