THE PANAMIC BIOTA:
SOME OBSERVATIONS
PRIOR TO A SEA-LEVEL CANAL

A Symposium Sponsored by
The Biological Society of Washington
The Conservation Foundation
The National Museum of Natural History
The Smithsonian Institution

MEREDITH L. JONES, Editor
THE STATUS OF HERPETOLOGY IN PANAMA

BY CHARLES W. MYERS

American Museum of Natural History
New York, New York

Few regions in the world support such a diversity of terrestrial life in such a small area as the Isthmus of Panamá, illustrated, for example, by my estimate that 4 per cent of the world's living species of amphibians and reptiles occur there. The principal reasons for this diversity now seem evident, even though the details are complex and incompletely understood. There is, of course, the deceptively simple fact that humid tropical mainlands seem almost inherently to have great numbers of species; and there is the historical closing of the Tertiary seaways, with the subsequent mixing of biotas that had evolved in long isolation. Two additional factors, which only recently have begun to be fully appreciated, are the alternation, in Pleistocene and post-Pleistocene time, of wet and dry climatic periods that allowed different biotic assemblages access to the region at different times, and, finally, the maintenance in present-day Panamá of markedly different types of climates and habitats, thus permitting preservation of the diverse historical elements and encouraging the evolution of new forms through isolation (Haffer, 1967, 1970; Myers, 1969). The present report briefly considers the state of knowledge of the Panamanian herpetofauna, and emphasizes the correlation between habitat diversity and faunal size. A few guidelines are then presented

1 Based on work initiated at the Geotag Memorial Laboratory in Panama City, with support from National Institutes of Health Grant No. GM-12020 and, subsequently, from National Science Foundation Grant No. GB-8139 (W. E. Duellman and C. W. Myers, co-investigators).

2 For comparison, only about 5 per cent of the living species occur in the vastly greater area of the United States.

for estimating the effort that must be put into a sampling program on an interoceanic canal route.

Several hundred publications relate more or less directly to the amphibians and reptiles of Panamá, with the vast majority being taxonomically oriented. Nonetheless, it is a rare paper that can be used by a nonspecialist to identify specimens, and then usually only for a single group, and few papers contain any attempt at synthesis. All of the combined literature proved inadequate for the purpose of drawing up a faunal list that was reasonably complete and which did not record the same species under more than one name. This is a statement of fact and not a disparagement of past work, which provides an essential base and which was by necessity limited to single collections or restricted geographic areas. Some important geographic regions have only recently been sampled, and a few areas are biologically unexplored, even at this time. But, even though the taxonomic base has not yet attained the desired firmness, the Panamanian fauna has stimulated other kinds of work that enrich the biological literature. Thus, there are preliminary studies of tropical amphibians and reptiles in relation to human health (Craighead, et al., 1962; Kourany, et al., 1970); analyses of anuran skin toxins that are of protective value to the amphibian and of potential importance in biomedical research (Daly and Myers, 1967; Daly, et al., 1969; Fuhrman, et al., 1969; Shindelman, et al., 1969); discussions of the influence of the human population on faunal distributions (Bennett, 1968; Heatwole, 1966); demonstrations that populations of some tropical species can be as large as populations of common temperate-zone species, and can fluctuate just as much (Heatwole and Sexton, 1966; Sexton, 1967; Sexton, et al., 1963); estimates of the relative abundance of different kinds of snakes, based on the extraordinary snake census made by the Gorgas Memorial Laboratory (Dunn, 1947, 1949, 1954; Dunn and Allendoerfer, 1949); and a growing number of other ecological, life history, behavioral, and evolutionary studies (e.g., Ballinger, et al., 1970; Breder, 1946; Davidson and Hough, 1969; Duellman, 1965a, 1966b; Fouquette, 1960; Myers, 1966, 1969; Myers and Rand, 1969; Rand, 1968; Rand and Marx, 1967; Rubinoff and Kropach, 1970; Sexton, et al., 1964; Sexton and

A survey of the amphibians and reptiles of Panamá was initiated in 1964 by Professor William E. Duellman and me; full-time collecting was carried out for a period of three years, especially in remote areas of the republic, and continues on an intermittent basis. Various taxonomic problems remain to be solved, and new species to be described, before the objective of an exhaustive catalogue can be attained, but it is now possible to make a reasonable estimate of the number of species actually occurring in the Republic of Panamá (Table 1). Of the total of 357 species, 40 per cent are amphibians and 60 per cent are reptiles. The anurans comprise 80 per cent of the amphibians, and 32 per cent of the total fauna. The major order of reptiles is the Squamata, of which the snakes make up 36 per cent of the total herpetofauna and, the lizards 19 per cent. Therefore, an overwhelming 87 per cent of the herpetofauna is comprised of snakes, frogs, and lizards. Allowing for the probability that Savage's (1966, p. 719) estimate of 625 species for all of Central America (Guatemala through Panamá) is conservative, it would seem that over half of the entire Central American herpetofauna occurs in Panamá.

Of course, not all of the amphibian and reptile fauna of Panamá occurs in any one part of the republic, but a surprisingly large 28 per cent can exist in an area as small as Barro Colorado Island (Table 2). The Barro Colorado figures probably are the most complete count available of the herpetofauna of a humid, tropical mainland locality, and the relative numbers of species in the different groups are indicative of the kind of ecological diversity to be expected in most humid, lowland forests in Panamá. However, the actual tally of species can be geographically altered within amazingly short distances, both horizontally and vertically. Thus, there is an important faunal change in the wet Atlantic-side forest between the Bocas del Toro region and the present Canal Zone, and then a discernible change between the Atlantic and Pacific sides of the Zone itself; these changes are correlated with a seasonal shift in rainfall distribution that seems to be reflected more noticeably in the actual biota than in the physiognomy of the
Table 1. Number of Amphibians and Reptiles in Panamá.

<table>
<thead>
<tr>
<th>Group</th>
<th>Families</th>
<th>Genera</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caecilians</td>
<td>1</td>
<td>4</td>
<td>11</td>
</tr>
<tr>
<td>Salamanders</td>
<td>1</td>
<td>2</td>
<td>17</td>
</tr>
<tr>
<td>Frogs and Toads</td>
<td>9</td>
<td>26</td>
<td>115</td>
</tr>
<tr>
<td>Turtles</td>
<td>6</td>
<td>10</td>
<td>14</td>
</tr>
<tr>
<td>Crocodilians</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Amphisbaenians</td>
<td>1</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>Lizards</td>
<td>7</td>
<td>29</td>
<td>67</td>
</tr>
<tr>
<td>Snakes</td>
<td>6</td>
<td>55</td>
<td>128</td>
</tr>
<tr>
<td>Totals:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amphibians</td>
<td>11</td>
<td>32</td>
<td>143</td>
</tr>
<tr>
<td>Reptiles</td>
<td>22</td>
<td>97</td>
<td>214</td>
</tr>
<tr>
<td>Grand Totals</td>
<td>33</td>
<td>129</td>
<td>357</td>
</tr>
</tbody>
</table>

*These figures include species (both named and unnamed) not formally reported from the country; the several marine species also are included. The species estimates are, nonetheless, conservative and eventually will have to be revised upward, but probably not to such an extent as to greatly alter conclusions based on present figures.

Forest. Areas of tropical “savanna” climate on parts of the Pacific side of the isthmus support a fauna that is notable in being not only distinct from that of the moist forests but also in having a particularly strong South American aspect. Such species as *Leptodactylus fuscus* (*L. sibilatrix*, auct.), *Pleurodeema brachyops*, *Dryadophis pleei*, *Lygophis lineatus*, and others, occur in the Pacific-side savannas as relicts that are widely separated from conspecific populations in the dry country of northeastern South America. Dunn (1940) pointed out this peculiarity of Panamanian zoogeography, where part of the Pacific-side fauna is allied to that of the Atlantic lowlands of northern South America and the Atlantic-side fauna to that of the Pacific lowlands of northwestern South America; but it bears emphasizing that the “Panamanian X” is a broken one and is the result of present-day climatic diversity as well as historical factors. In the eastern half of Panamá, the situation is complicated by the concurrent increase of humid-forest amphibians and reptiles from South America, and striking physiognomic changes in the lowland forests; here, on the nearly base-leveled plains of the Chucunaque and Tuira rivers, we find extensive river-swamp forests and large expanses of
monsoon rain forest that is peculiar in being dominated by a single species of tree (Myers, 1969, p. 7). Panamá is a mountainous country, and the effects of the highlands on moisture-laden air partly accounts for the diverse lowland habitats. The montane habitats are also varied, and the several disjunct highland regions, with their different histories, add many species to the faunal list that do not occur in the lowlands.

The preceding remarks hint at the variety of environments on the Isthmus of Panamá and suggest a partial explanation as to why the terrestrial fauna is so diverse. But diversity implies more than mere numbers of species. We scarcely have any knowledge at all of the dynamic aspects of tropical diversity, and we have only begun to acknowledge the existence of rapid temporal changes in populations of tropical amphibians and reptiles (Sexton, 1967; Myers and Rand, 1969). Even in tropical rain forest there is more short-term environmental variation, and biological response to that variation, than some writers have led us to believe.

Thus, even though the approximate numbers and kinds of species in Panamá are becoming fairly well known, the extent of our ignorance also is more evident. The Panamanian fauna

---

TABLE 2. Number of Amphibians and Reptiles on Barro Colorado Island.*

<table>
<thead>
<tr>
<th>Group</th>
<th>No. species on island</th>
<th>As a per cent of Panamanian fauna</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caecilians</td>
<td>1</td>
<td>9</td>
</tr>
<tr>
<td>Salamanders</td>
<td>2</td>
<td>12</td>
</tr>
<tr>
<td>Frogs and Toads</td>
<td>29</td>
<td>25</td>
</tr>
<tr>
<td>Turtles</td>
<td>5</td>
<td>56</td>
</tr>
<tr>
<td>Crocodilians</td>
<td>2</td>
<td>100</td>
</tr>
<tr>
<td>Amphibiansenians</td>
<td>1</td>
<td>33</td>
</tr>
<tr>
<td>Lizards</td>
<td>21</td>
<td>31</td>
</tr>
<tr>
<td>Snakes</td>
<td>39</td>
<td>31</td>
</tr>
<tr>
<td><strong>Totals:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amphibians</td>
<td>32</td>
<td>22</td>
</tr>
<tr>
<td>Reptiles</td>
<td>68</td>
<td>33</td>
</tr>
<tr>
<td><strong>Grand Totals:</strong></td>
<td><strong>100</strong></td>
<td><strong>28</strong></td>
</tr>
</tbody>
</table>

* Based on Myers and Rand (1969), and on Table 1.
  The marine turtles and the sea snake are excluded from these calculations.
varies in a complex manner, both geographically and in time; we lack the information needed to do more than very generally predict the changing composition of the herpetofauna in any given transect across the isthmus. Any biotic survey of a new canal route should certainly provide for adequate sampling of the amphibians and reptiles, many of which are sensitive indicators of ecological conditions and zoogeographic events and some of which are of potential significance in the area of public health.

A great potentiality for evolutionary studies might seem almost inherent with the creation of a new sea barrier across the Panamanian isthmus, but such potential was largely nullified by the Canal Study Commission’s choice (announced late in 1970) of “route 10,” which is situated only about 10 miles west of the present canal. The existing fresh-water canal, as well as ecological disturbance on either side, already provides a barrier of variable effectiveness to most wingless terrestrial animals. For example, Myers and Rand (1969, p. 6) note the increasing insular effect on the fauna of Barro Colorado, a 60-year-old island formed in Gatun Lake by construction of the present canal, and observed that it seems easier for a resident population to become extinct than for overwater colonization to occur. A number of isthmian species have a distributional break in the region of the Canal Zone, and a similar gap also separates a few pairs of closely related species. Although few of these discontinuities are well studied, many seem correlated with topographic features and probably are the result of climatic fluctuations that antedate the present canal, but the circumstances are complex and some significant distributional breaks possibly have occurred in this century. It is unlikely that we shall ever be able positively to ascribe a cause and effect in the majority of such cases; thus, the appearance of a salt-water strait will reinforce an already existing barrier whose effects cannot be determined because of the inadequacy of precanal data. I do not mean to imply that there will be no chance at all of gathering new data that are relevant to evolutionary zoogeography, particularly in the case of non-forest and “edge” species, but the situation is a distressing example of what opportunities can be lost by the failure to conduct
thorough surveys of a biota threatened with major disturbance. Most biologists would be genuinely shocked at how little we really know about the biota of the present Canal Zone, and, surely, an informed scientist could not have been responsible for the statement (Commission, 1971, p. 59) that the "... total effects [of a new canal] upon land ecology can also be estimated with confidence ..."! The complexity of tropical ecosystems was scarcely appreciated when construction was started on the present canal, and the "Biological Survey" of 1911–1912 was, in retrospect, woefully deficient; it is fervently to be hoped that the mistake will not be made a second time.

An assessment of herpetology in relation to a sea-level canal would be incomplete without mention of *Pelamis platurus*, the sea snake, which is being ably studied by Dr. Ira Rubinoff and his associates at the Smithsonian Tropical Research Institute. The possibility of sea snakes migrating to the Atlantic Ocean through a sea-level canal is a subject of frequent concern (e.g., *The New York Times*, December 13, 1970, p. E-12; *Congressional Record, House*, January 21, 1971, pp. 22-26). Because of tidal differences, a freely floating object would take only about two and a half days to transit an unobstructed canal from the Pacific side to the Atlantic (Commission, 1971, p. V-96), and, if the object were a sea snake, it probably would find favorable habitats off the Atlantic coast, although predation from native Atlantic predators initially might be high (Rubinoff and Kropach, 1970). That sea snakes would indeed enter the canal is indicated by the pertinent fact that they sometimes even occur in Panamanian rivers—I found two specimens that were actively swimming in the Río Jaqué (Darién), about 2 kilometers above its mouth, where the snakes presumably had been carried by tidal currents. The possible consequences of migration of sea turtles should also be considered, particularly in light of their economic importance and endangered status.

A basis for estimating the effort required in a terrestrial sampling program is given in Figure 1, in which collecting success is plotted against the time expended in building up a faunal list. Myers and Rand (1969, pp. 8, 9) concluded that at least 80 per cent of the herpetofauna of a lowland, humid forest locality could be determined by ". . . a party of several
people working intensively for a month or two in one wet season plus a week or so in one dry season.” Such a program, of course, would have to be repeated in each major physiographic and vegetational region and in different parts of any climatic gradient. At the same time, an attempt should be made to determine relative abundance of species and, if possible, the actual population densities of those species sufficiently abundant for such a task. The mistake should not be made, however, in thinking that sampling techniques required for determining population densities will be adequate for censusing the entire fauna. For determining the variety of species present, there is no substitute for hours of patient “cruising,” during which many microhabitats are explored both by day and night; however, quadrat sampling (e.g., Heatwole and Sexton, 1966, p. 50, fig. 2) and utilization of such devices as open trenches and turtle traps are likely to add some secretive species that might not otherwise be seen. The rate at which species are discovered in different habitats, and the relative abundance of species and comparison of their ecological roles, might provide some solid data on the relationship between environmental carrying capacity, biomass, and that aspect of diversity reflected by
numbers of species. Indeed, a systematic sampling program on any transect across the isthmus could usefully contribute a variety of data to the study of biological diversity in a tropical region. This is a field in which formulation of theory has outdistanced factual evaluation, which would be all right—except, that, given the rate at which tropical environments are being altered, we may soon be left with only the theories.

LITERATURE CITED


