CHARLES W. MYERS
and A. STANLEY RAND

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ABSTRACT

One hundred species of amphibians (32) and reptiles (68) are estimated to occur on Barro Colorado Island, on the basis of approximately 47 years of collecting. The island is a seasonally wet, tropical forest locality in man-made Gatun Lake, central Panama. The faunal composition has not been static since the island's formation in 1912–1914. Some species have disappeared from the island whereas some others seem to be recent arrivals. Faunal change is at least partly correlated with vegetational succession, as old clearings change toward mature forest. The extirpation of certain "edge" species and their failure to have recolonized the laboratory clearing indicates that it is easier for a resident population to become extinct than for new colonization to occur. The sampling of such a complex, tropical herpetofauna is shown to be not so difficult as might be expected. Man-hours of collecting are plotted against percent of the herpetofauna for several collections, indicating that nearly one-half of the species can be collected in a few weeks of intensive effort in the rainy season. Approximately 80 percent of the species recorded from the island had been collected by 1931, after only about a decade of sporadic, unsystematic collecting by various persons. The generalization that tropical species have lower population densities than temperate species may not be valid for such groups as frogs and lizards but does seem true of snake faunas in low, humid forest regions. Snakes also are more difficult to collect in the tropics because of shifts in habits. There is a great expansion of tropical snakes into arboreal situations and a general avoidance (by all vertebrates) of rock and log microhabitats, which are frequently occupied by large arachnids. Small terrestrial snakes of lowland tropical forests tend either to be fossorial or to inhabit the leaf litter, where they are difficult to detect. Seasonal aggregations of snakes are rare in the wet tropics.

Recent years have brought a greatly increased use of Barro Colorado Island by ecologists, physiologists, and other nontaxonomists, thus creating a need for lists of the currently accepted names of local animals. The present checklist of amphibians and reptiles brings up to date the nomenclature and included species of earlier lists (Dunn, 1931a, 1931b, 1949; Zetek, 1951), and also indicates departures in nomenclature from other papers, including Allee (1926), Allee and Torvik (1927), and Netting (1936).

One hundred species of amphibians and reptiles are estimated to occur in this forested area of less than six square miles. This count probably is the most complete available of the herpetofauna of any humid locality on a tropical mainland, and is the result of collecting efforts of a number of persons over several decades. By reason of its relative completeness, the present list should be useful as a means of comparing the amphibian and reptile faunas of other areas less well known. In concluding paragraphs, we comment briefly on faunal changes and abundance and demonstrate that a fauna even as large and complex as this one can be effectively sampled within reasonable time limits.

Barro Colorado (9° 10′ North Latitude) is a former hilltop and the largest island in Gatun Lake, which was formed by the dredging of the Panama Canal and the damming of the Chagres River in 1912. The island is approximately 3600 acres in area (about 14.5 square kilometers), hilly, and has a maximum elevation of 452 feet above Gatun Lake, or 537 feet (164 meters) above sea level. Surface drainage is by small, clear-water streams with rocky beds that dry to isolated pools

Charles W. Myers, Department of Herpetology, The American Museum of Natural History, New York, New York 10024. A. Stanley Rand, Smithsonian Tropical Research Institute, Box 2072, Balboa, Canal Zone.

near the end of most dry seasons. There is a small, upland swampy area near the center of the island. Except for two small, maintained clearings, the island is covered by forest stands of various ages, the youngest and least extensive being of about 25 years and the oldest of unknown age but still showing traces of disturbance by the human animal. The forest can be classified broadly according to any of several systems, i.e., tropical monsoon forest (Köppen's climatic classification), tropical moist forest (Holdridge's life zone classification), or intermediate between evergreen and semievergreen seasonal forests (Beard's climax classification). The annual rainfall averages 106.91 inches (76.57–143.42 inches, 1925–1965). A well-differentiated dry season occurs from about the end of December into April; average rainfall during the period January–April is 8.22 inches (1.20–26.64 inches) and two months each average less than 2 inches. A map showing physiognomic aspects of the vegetation is found in Bennett (1963), and various photographs of the forest are given in Kenoyer's account of vegetational succession (1929). A view of the laboratory clearing and surrounding forest is appended to Woodring's geological reconnaissance of the island (1958, pl. 2).

In the list that follows, an asterisk (*) before a name means that in our experience, the species is relatively common in the proper habitat. A dagger (†) denotes a species thought to be unusually rare, but there are certainly other rare species, especially snakes, not so indicated. The phrase "type-locality" after a name means that the name is based on a specimen (the holotype) collected on Barro Colorado Island. Except for the frog *Phrynohyas* (q.v.), those species added since the publication of Zetek's list (1951) are represented by specimens in the American Museum of Natural History (AMNH), the United States National Museum (USNM), or the University of Kansas Museum of Natural History (KU); the depository is noted by the initials following the name of the species. Barbour (1925, p. 11) foresaw that, "It will be years before the herpetological possibilities of the island are adequately investigated, and much strictly systematic work will be necessary before students of life histories will be certain of the species which they are observing." In the course of progress toward taxonomic stability (an illusive goal save in the relative sense) it is natural that many names in the literature of Barro Colorado are different from those presently used; such names may be synonyms, misidentifications, or misspellings and, if substantially different, are shown in parentheses behind names now considered valid. We have not been completely consistent in our treatment of subspecies, omitting available trinomials in some cases where intraspecific variation is not or only poorly known, but other times inserting them for no other reason than that the name is well established in the Panamanian literature. We consider the designation of subspecies to be of dubious value and a frequent hindrance to thorough variational analysis.

Amphibia (32)

Gymnophiona (1)

Oscaecilia ochrocephala (Cope) (*Caecilia ochrocephala*)

Caudata (2)

Oedipina complex (Dunn) (*Oedipus complex, O. simplex, Oedopinola complex*)

Oedipina parvipes (Peters) (*Oedipus parvipes, Oedopinola parvipes*)

Salientia (29)

LEPTODACTYLIDAE

Eleutherodactylus biporcatus (Peters)

**Eleutherodactylus bufoniformis* (Boulenger) (? *E. rugulosa*)

Eleutherodactylus cruentus (Peters)—application of name uncertain

**Eleutherodactylus diastema* (Cope)

**Eleutherodactylus fitzingeri* (Schmidt) (*E. fleischmanni, E. palmatus*)

†*Eleutherodactylus gaigeae* (Dunn) (*Lithodytes gaigei*)

Eleutherodactylus longirostris (Boulenger)

Eleutherodactylus molinoi (Barbour)—type-locality; (*E. lutosus molinoi, Syrrhopus molinoi*)

**Eleutherodactylus ockendeni* (Boulenger)—application of name uncertain

**Engystomops pustulosus* (Cope) (*E. ruthveni*)

Leptodactylus insularum Barbour (*L. bolivianus*)

**Leptodactylus pentadactylus* (Laurenti)

BUFONIDAE

**Bufo marinus* (Linnaeus)

**Bufo typhonius alatus* Thominot

DENDROBATIDAE

**Dendrobates auratus* (Girard) (*D. tinctorius*)
**Colostethus nubicola flotator* (Dunn)—type-locality; (*Phyllobates* "near *latinasus* and *talamancae*," *P. flotator, P. nubicola flotator*)

HYLIDAE

**Hyla boulengeri* (Cope)
**Hyla phlebodes* Stejneger (*H. underwoodi*)
**Hyla rufitela* Fouquette—type-locality; (*H. albomarginata*)
†Agalychnis calcarifer (Boulenger) (*Phyllomedusa calcarifer*)
**Agalychnis callidryas* (Cope) (*Phyllomedusa callidryas*)
Agalychnis spurrelli (Boulenger) (*Agalychnis dacnicolor, Phyllomedusa dacnicolor*)
†Phrynohyas venulosa (Laurenti) (*Hyla venulosa*)
†Smilisca phaeota (Cope) (*Hyla phaeota*)
**Smilisca sila* Duellman and Trueb (*Hyla gabbii, H. sordida*)

CENTROLENIDAE

**Centrolenella fleischmanni* (Boettger) (*Centrolene fleischmanni*)
Centrolenella prosoblepon (Boettger) (*Centrolene prosoblepon*)
Centrolenella spinosa Taylor (*Centrolene parambae, C. pulveratum*)

RANIDAE

Rana palmipes Spix AMNH, KU

Reptilia (68)

Testudines (5)

†Chelydra acutirostris Peters
Geoemyda annulata (Gray) (*Rhinoclemmys gabbii*)
†Geoemyda funerea (Cope)
Kinosternon leucostomum (Duméril and Bibron) (*K. postinguinale*)
**Pseudemys scripta ornata* (Gray) (*P. ornata*)

Crocodilia (2)

**Caiman crocodilus fuscus* (Cope)
**Crocodylus acutus* Cuvier

Sauria (22)

IGUANIDAE

Anolis auratus Daudin (*Norops auratus*)
Anolis biporcatus (Wiegmann) (*A. copei*)
Anolis capito Peters
**Anolis frenatus* Cope (*A. longipes*, a name that is technically a synonym of *A. capito*)
**Anolis limifrons* Cope
†Anolis lionotus Cope
Anolis pentaprion Cope
Anolis vittigerus Cope (*A. lemurinus, A. sallaei*)
**Basiliscus basiliscus* (Linnaeus)
Corythophanes cristatus (Merrem)
**Iguana iguana iguana* (Linnaeus)
Polychrus gutturosus Berthold

GEKKONIDAE

Thecadactylus rapicauda (Houttuyn)

SPHAERODACTYLIDAE

Gonatodes albogularis fuscus (Hallowell)
Lepidoblepharis sanctaemartae fugax Ruthven—type-locality
Sphaerodactylus lineolatus Lichtenstein and von Martens

XANTUSIIDAE

Lepidophyma flavomaculatum obscurum Barbour

TEIIDAE

**Ameiva festiva* (Lichtenstein and von Martens)
**Ameiva leptophrys* Cope (*A. ameiva, A. undulata*)
†Leposoma southi Ruthven and Gaige

SCINCIDAE

**Mabuya mabouya* (Lacépède)—application of name uncertain; (*M. agilis*)

AMPHISBAENIDAE

Amphisbaena fuliginosa Linnaeus

Serpentes (39)

ANOMALIPIDIDAE

Anomalepis dentata Taylor—type-locality; (*A. mexicanus*)
Liotyphlops albirostris (Peters) USNM

BOIDAE

**Boa constrictor imperator* Daudin
Corallus annulatus (Cope) KU
Epicrates cenchria maurus Gray

COLUBRIDAE

Amastridium veliferum Cope
Chironius carinatus (Linnaeus) (*Erpetodryas carinatus*)
Chironius grandisquamis (Peters) (*C. fuscus, C. melas*)
**Coniophanes fissidens* (Günther) (C. *punctigularis*)
**Dendrophidion percarinatus* (Cope) (*D. dendrophis, Drymobius dendrophys*)
**Dryadophis melanolomus alternatus* (Bocourt) (*Drymobius boddaertii*)
Drymarchon corais melanurus (Duméril, Bibron, and Duméril) KU
Enulius flavitorques (Cope)
Enulius sclateri (Boulenger) (*Leptocalamus sclateri, E. slateri*)
**Imantodes cenchoa* (Linnaeus)
†*Imantodes gemmistratus* (Cope) (*I. elegans*)
**Leimadophis epinephalus epinephalus* (Cope) (*Liophis epinephelus*)
Leptodeira annulata rhombifera Günther
Leptodeira septentrionalis ornata (Bocourt) (*L. a. annulata*)
Leptophis ahaetulla occidentalis (Günther) (*Thalerophis richardi occidentalis*)
Ninia maculata maculata (Peters) AMNH, USNM
**Oxybelis aeneus aeneus* (Wagler) (*O. acuminatus*)
Oxyrhopus petola sebae Duméril, Bibron, and Duméril
Pliocercus euryzonus dimidiatus Cope (*Urotheca dimidiata*)
Pseudoboa neuwiedii (Duméril, Bibron, and Duméril) USNM
Pseustes poecilonotus shropshirei (Barbour and Amaral) (*Phrynonax poecilonotus*)
Rhadinaea decorata (Günther) (*Liophis decoratus*)
Rhadinaea pachyura fulviceps Cope (*Liophis pachyurus*)
Siphlophis cervinus geminatus (Duméril, Bibron, and Duméril)
Spilotes pullatus pullatus (Linnaeus)
Stenorrhina degenhardtii (Berthold)
†*Tantilla albiceps* Barbour—type-locality
**Tantilla armillata* Cope (*T. ruficeps*)
Trimetopon barbouri Dunn USNM
Xenodon rabdocephalus (Wied) (*Ophis colubrinus*)

ELAPIDAE

Micrurus mipartitus (Duméril, Bibron, and Duméril)
**Micrurus nigrocinctus nigrocinctus* (Girard)

CROTALIDAE

Bothrops atrox asper (Garman)
Bothrops schlegelii (Berthold)

Species Erroneously Recorded

Some literature records that incorrectly add a species to the fauna are considered below. Not discussed are names known to have been wrongly applied to species definitely occurring on the island; such names are among those parenthesized in the list preceding.

AMPHIBIANS

Bolitoglossa schizodactyla Wake and Brame: Rand caught one of these salamanders near the laboratory, and the record was cited by Wake and Brame (1966) in their original description of the species. There seems a probability that the specimen was one captured on Cerro Campana (about 55 km SW Panama City) several months earlier and which may have escaped on the island. Individuals of this species are conspicuously active on vegetation by night and probably would not have remained undetected for so long if naturally present on the island; the finding of the specimen close to the laboratory buildings makes the record doubly suspect. Myers recently ascertained that *schizodactyla* is common in the Atlantic coastal plain of Veraguas and eastern Bocas del Toro provinces in western Panama, but there are no acceptable records below 200 m in central Panama where most stations are closer to 800 m.

Eleutherodactylus caryophyllaceus (Barbour): This distinctive little frog was listed by Dunn (1931a), but inasmuch as it is not mentioned in his later paper (1931b), nor reported by any subsequent worker, it is assumed that a mistake was made. The species is found the length of Panama, especially in wet, subtropical forest, where it sits conspicuously on leaves at night.

REPTILES

Anolis tropidogaster Hallowell: This species is recorded from the island under the synonymous name *A. stigmosus,* by Dunn (1931a). However, it is not present on other lists nor in the old card catalog from which the lists were drawn (Dunn seems to have revised the amphibian and reptile section of the file during his visits to Barro Colorado). The

early presence of *"stigmosus"* on the island would not be any more surprising than that of such open-country inhabitants as *Bufo granulosus, Anolis auratus,* or *Imantodes gemmistratus,* but no definite confirmation seems available. Rand recently found it in disturbed areas at Frijoles, just across the lake from the laboratory clearing.

Ctenosaura similis (Gray): One gathers from Barbour's curious note (1932) that *Ctenosaura* was observed on the island, "next the quarters of Mr. James Zetek, the resident custodian of the Barro Colorado Island Laboratory." However, Dr. G. B. Fairchild (verbal communication) informs us that Zetek's residence was in Balboa, Canal Zone, not far from the Bay of Panama. In Panama, the rock or black iguana is confined closely to the vicinity of Pacific-side beaches.

Ameiva ameiva praesignis (Baird and Girard): Dunn (1931a) lists this species (as *A. praesignis*) from Barro Colorado, but later (1940) states that it has not been taken on the island. Allee's (1926) use of the name *A. ameiva* almost certainly refers to *A. leptophrys. A. ameiva* is the largest of the four species of Panamanian ameivas and it shuns forest, unlike the other two species (*festiva* and *leptophrys*) that are found in central Panama. It has long been known to occur at Frijoles and would not be overlooked if it were on the island.

Dipsas variegata nicholsi (Dunn): This snake was reported by Peters (1960, pp. 138–139) on the basis of information supplied by E. R. Dunn on two specimens. One of these (no. 7157, a head) is in the Barro Colorado laboratory in a jar of mixed species labelled "not known from B.C.I." Both specimens are from the old Panamanian snake census and, hence, probably never had specific data (other than a general region). Furthermore, as a wildlife preserve, Barro Colorado was not included in the scope of the census and Dunn (1949, table 7), who reported on the census, did not denote the species (by asterisk) among those which he knew to occur on the island. But it would not be surprising if *D. variegata* eventually reached Barro Colorado, as it does occur in the Chagres drainage and is not uncommon in lowland Madden Forest Preserve, about 24 km to the southeastward. It is curious that although several dipsadines occur in the region, none has been found on Barro Colorado Island.

Extirpated Species

AMPHIBIANS

Bufo granulosus humboldti Gallardo: This toad occurs on the Pacific side of the Isthmus, mostly in the savanna areas east and west of the Canal Zone region of moist forest, and there are no recent records of it from the vicinity of Gatun Lake. The Barro Colorado record is based solely on AMNH 22830 (Gallardo, 1965; Zetek, 1951), which was collected by J. A. Weber on 10 August 1928.

Denrobates minutus minutus Shreve: type-locality (*Phyllobates lugubris, P. truncatus*). Although seemingly no longer on the island, this very small frog is locally common in hill areas to either side of the Canal Zone and occurs also in the Atlantic lowlands southwest of Colón. Specimens from Cerro Campana (Pacific side, west of Canal Zone), the type-locality of *D. shrevei* Dunn, exhibit no important differences from ones collected in the low ridges above Puerto Pilón (Atlantic side, east of Canal Zone), and *shrevei* is here considered a synonym of *minutus*. The dorsal light areas are golden (sometimes tinged with orange) rather than red as given in the type-description of *shrevei*.

Rana warschewitschii zeteki Barbour: type-locality. Allee and Torvik (1927) indicate this forest frog as being common in 1924, and Dunn (1931b) says that it was "not rare" when he worked on the island in 1928–1930.

REPTILES

Anolis auratus Daudin: This is a grassland lizard that apparently was eliminated on the island by vegetational succession. However, since it was purposely re-introduced to the laboratory clearing in 1966, it is retained in the preceding list.

Gonatodes albogularis fuscus (Hallowell): We agree with Heatwole and Sexton (1966, p. 59) that successional changes in the forest probably caused the disappearance of this diurnal gecko. *Gonatodes* is not commonly found in dense forest in the Canal Zone region, where it occurs mostly about human habitations and in opened, disturbed forest. Like *Anolis auratus,* it was experimentally re-introduced to the laboratory clearing in 1966, and, for that reason, is retained in the checklist.

There probably are a few other species that have been extirpated from the fauna, but the above are the only ones of which we are reasonably certain at this time. Some additional possibilities include the frog *Smilisca phaeota,* the turtles *Geoemyda funerea* and *Chelydra acutirostris,* the stream-side lizard *Anolis lionotus,* and the snakes *Tantilla albiceps* and *Imantodes gemmistratus,* none of which has been seen on the island in recent years.

General Considerations

The faunal composition of Barro Colorado is not static. The trend is towards an ecologically more uniform herpetofauna. The extinction or rarity of savanna and open forest species (*Bufo granulosus, Anolis auratus, Gonatodes albogularis, Imantodes gemmistratus*) doubtlessly is correlated with the decreasing variety of habitats, as the old clearings change slowly toward mature forest.[1] Although the frog *Smilisca phaeota* has a lowland forest distribution (Duellman and Trueb, 1966, p. 313), possibly it does not find its optimal conditions within uniformly heavy forest. Of 33 museum specimens listed from Barro Colorado by Duellman and Trueb, 27 were collected in 1924–1928, five in 1939–1940, and one in 1954; we have been unable to find this usually conspicuous Panamanian frog on the island (except for three males released near the laboratory by a visitor). The tiny *Dendrobates minutus* is a forest frog that is most common at slightly higher elevations; perhaps it was never more than a fringe population at Barro Colorado, supported by repeated immigration before the lake was formed. The same may be true of *Rana warschewitschii,* although the extirpation of this species might have been due to the arrival of a competitor (*R. palmipes,* see below). *Geoemyda funerea* (and perhaps *Chelydra* as well) probably was only a refugee from lowland swamps and sluggish rivers and seems not to have colonized the island—at least not with much success—as have other semiaquatic reptiles (*Crocodylus, Pseudemys*) that now are intimately associated with the lake margin but which presumably came from the Chagres River, originally a mile away.[2]

Of eight species added to Zetek's 1951 list (six snakes and two frogs, see page 8), the snakes *Liotyphlops* and *Pseudoboa* are probably remnants of the Pacific-side faunal influence that is disappearing as the forest matures. Of the remaining six species, a few snakes (especially *Corallus annulatus* and *Drymarchon corais*) may be recent arrivals, but only a frog (*Rana palmipes*) is assuredly too conspicuous to have been overlooked during all the early years of faunal exploration. *Rana palmipes* is a lowland forest species and has been on the island at least since 1957, but we do not know whether its arrival coincided with the local extinction of *R. warschewitschii.* Certainly these two frogs are not precise ecological replacements, but both include forest streams among the habitats utilized.

The list now totals 100 species, excluding ones erroneously recorded or no longer found on the island. Although Barro Colorado is a young island and close to the mainland, there is a real insular effect on the fauna. During the course of vegetation change and because of the water barrier, it seems easier for a resident population to become extinct than for new colonization to occur. This is especially evident in an ecological assemblage of lizards that live in disturbed areas about Gatun Lake and colonize clearings, and which probably occurred on what is now Barro Colorado Island during the 1890s when the forest was disturbed and extensively cut during the French attempt at building a canal. Without a water barrier it is probable that *Gonatodes albogularis, Ameiva ameiva, Anolis auratus, Anolis tropidogaster,* and *Gymnophthalmus speciosus* would have recolonized the laboratory clearing. *Anolis auratus* and *Gonatodes albogularis* are definitely known to have occurred on the island and have been purposely reintroduced. *Mabuya* is the only member of this group that has maintained a population in the clearing, possibly because it is adapted also to maintain low population levels in forest. Although some species of amphibians and reptiles presently on the list have

[1] Enders (1939) describes early changes in levels of mammal populations. He attributes to poaching a decrease in large herbivores and carnivores, with a corresponding increase in other, smaller species, including paca and agouti (which, however, are favorite foods of humans and easily hunted or trapped). Poaching probably is not the only factor, as it seems certain that vegetational succession must affect the mammals as well as the herpetofauna. Relative inaccessibility of protein in forest with decreasing edge (Dasmann, 1964, pp. 65–66, 69) might be especially effective in limiting the larger terrestrial herbivores and, consequently, their predators. Also, although range-size requirements are poorly known for tropical mammals, it seems possible that a lack of space eventually was a contributing factor in some cases.

[2] Several other successful reptiles (*Kinosternon, Caiman, Basiliscus*) utilize streams as well as the lake margin, and may have occurred here even before the Chagres was dammed.

probably disappeared from the fauna, it is conceivable that a few additional species still remain to be found. And a number of forest species of the region might eventually reach the island under their own powers, as the adjacent mainland is only 400 yards away at the closest point; examples are *Corallus hortulanus, Clelia clelia,* and *Lachesis muta* (bushmaster), to name a few presumably strong swimmers known to occur in the Chagres drainage. Whatever extinctions or colonizations might come to light in the near future, we suggest that the actual tally of 100 species is also a reasonable estimate of the present herpetofauna of Barro Colorado Island and probably accurate to less than 10 percent error one way or the other.

Based on general observation in a variety of habitats, and also on frog vocalizations, about a third of the species in this fauna are common (starred in the list), in the sense that they are seen or heard not infrequently, and about a tenth of the species are actually abundant. This might seem to differ from an observation by Heatwole and Sexton (1966, p. 54) that, "Of the 15 species of reptiles and amphibians captured in fenced quadrats at Barro Colorado, all were rare (represented by a total of only one or two individuals from the 8 plots), except for one species, *Anolis limifrons.*" But the difference is only one of approach. Heatwole and Sexton were studying a restricted habitat, in the region of the forest floor, and basing their concept of abundance on a lizard having (at that time) an extremely high population density. They were not considering arboreal species, lake margin, creek or ravine species. This, incidentally, is the reason they did not see *Colostethus nubicola* (op. cit., pp. 58–59), a common little frog along some streams in wooded ravines.

We are less certain about estimating the number of actually rare species. The few species marked by daggers in the list are mostly those that would be conspicuous if they were present in numbers. Some species must be very rare or at least highly localized in this region, as for example *Tantilla albiceps,* which is known to science only from the holotype that was caught on Barro Colorado in 1925. Possibly it would take a major portion of one's lifetime to collect all the species in a herpetofauna of a moist, tropical lowland, even on such a limited area as Barro Colorado Island. But as a matter of interest to anyone concerned with the sampling of faunal assemblages, one can make a reasonable sampling in a few weeks by utilizing varied but standard collecting techniques. This claim is justified by the following examples of collecting success on Barro Colorado, using the estimate of 100 species as a standard. During the wet season in July 1962, Richard G. Zweifel sampled 32 percent of the species in 36 hours of actual collecting. William E. Duellman and the senior author got 43 percent of the species in 91 man-hours in June 1963. As might be expected, collecting in the dry season is not so productive: William E. Duellman and Charles J. Cole took 27 percent of the species in 54 man-hours in January 1964; the Nettings obtained 39 percent of the species (22 of frogs, 17 of reptiles) in 26 days in March 1934 (Netting, 1936). Pertinent facts concerning these collections (except Netting's) are set down in Table 1 and Figure 1.

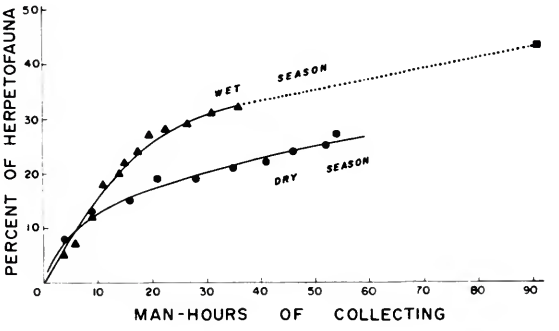

FIGURE 1.—Collecting success versus effort on Barro Colorado Island. Percent of species is equivalent to number of species since N=100 (i.e. the number estimated as occuring on the island at present).

The wet season curve is based on data supplied by R. G. Zweifel for July 1962 (triangles), with an extension to a single point (square) signifying the effort of W. E. Duellman and C. W. Myers in June 1963. Dry season data (circles) are from W. E. Duellman and C. J. Cole, January 1964.

In some years more effort probably would have to be expended to obtain results comparable to those mentioned above. Populations of some common forest species on the island have declined since 1964, possibly due to the combined effects of more arid than normal dry seasons in 1964 (2.98 inches of rainfall below average) and 1965 (3.88 inches below average). These figures are for the January-April periods, but that the dry seasons were also prolonged is shown by December rainfall deficiencies in excess of 7 inches for both 1963 and 1964 (December average is 10.52 inches in 41 years of record). Such climatic fluctuations appear to influence animal populations (and hence collecting success) in the tropics just as in higher latitudes. *Anolis limifrons* underwent a particularly noticeable

TABLE 1.—*Comparisons of the total herpetofauna of Barro Colorado Island with the number of species collected within given time limits*

Group	Number species occurring	Number species collected*		
		A	B	C
Caecilians	1	0	0	0
Salamanders	2	0	0	0
Frogs and Toads	29	15	17	10
Turtles	5	0	2	2
Crocodilians	2	1	1	0
Lizards	22	9	12	9
Snakes	39	7	11	6
Totals:				
Amphibians	33	15	17	10
Reptiles	67	17	26	17
Grand Totals	100	32	43	27
Man-Hours of Collecting	–	36	91	54

*Collections: A=R. G. Zweifel, 9–21 July 1962 (wet season); B=W. E. Duellman and C. W. Myers, 1–9 June 1963 (57 hours day, 34 hours night, wet season); C=W. E. Duellman and C. J. Cole, 12–18 January 1964 (36 hours day, 18 hours night, dry season).

population decline in 1964–1966, which is documented in part by Sexton (1967).

With respect to faunal sampling, it also is instructive to plot the number of species as they have been collected within the last five decades (Figure 2). For this purpose we arbitrarily choose 1920 as a starting date for collecting on the island, which was formed about 1914 and was made a wildlife preserve and research station in 1923. A glance at Figure 2 shows that 83 of the 103 recorded species were obtained by the end of the first decade. All the salamanders and caecilian (3 species), crocodilians (2), and virtually all of the anurans (28 of 32), turtles (4 of 5), and lizards (21 of 22) had been obtained. Two frogs (*Eleutherodactylus cruentus, E. gaigeae*), one lizard (*Anolis pentaprion*), and one turtle (*Geoemyda funerea*) were added in the second decade, and two additional frogs (*Phrynohyas venulosa, Rana palmipes*) were obtained between 1952 and 1957. Eight snakes [3] were added in the second decade and six others [4] within the last two decades. (No species of any group was added during the 1940s, for obvious reasons.) Thus, only 20 species have been added to the known fauna since the first decade of collecting (circa 1920–1930) of which 70 percent has been snakes.[5]

There probably has been as much or more work on the island since 1951 as in the early years, but only eight species have been recently added and at least some of these are new elements in the fauna. These data speak well of the energy of the early collectors,

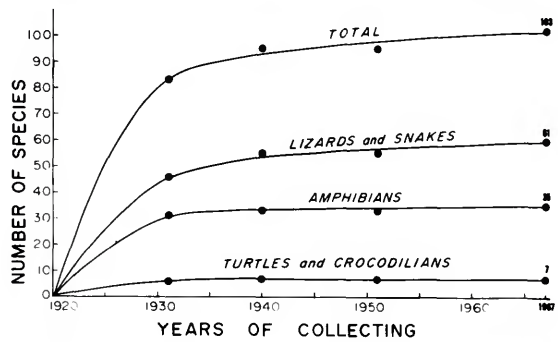

FIGURE 2.—Cumulative totals of species of amphibians and reptiles collected on Barro Colorado Island. Sources: Dunn (1931a), excluding four names erroneously listed (*Eleutherodactylus caryophyllaceus, Phyllomedusa dacnicolor, Ameiva praesignis, Anolis stigmosus*) but adding one (*Bufo granulosus*, collected in 1928); Zetek (1940), less one species of amphibian (probably *P. dacnicolor*, based on a misidentification by Dunn, 1931a); Zetek (1951); present list (including extirpated species).

whose intermittent efforts in the first decade were most concentrated in the last several years of that period, as indicated by perusal of the Barro Colorado annual reports. It seems possible that results similar to those of the first decade could be duplicated in comparable forest by a party of several people working intensively for a month or two in one wet season plus a week or so in

[3] *Enulius flavitorques, Imantodes gemmistratus, Leimadophis epinephalus, Leptodeira* (probably *septentrionalis*), *Oxyrhopus petola, Pliocercus euryzonus, Siphlophis cervinus*, and *Micrurus mipartitus*.

[4] *Liotyphlops albirostris, Corallus annulatus, Drymarchon corais, Ninia maculata, Pseudoboa neuwiedii*, and *Trimetopon barbouri*.

[5] Species added in the second decade were determined by comparing Dunn's 1931a list (=end first decade) with Zetek's 1951 list, inasmuch as the number of names in the latter did not add to the simple counts of species given by Zetek in 1940 (=end second decade). *Bufo granulosus*, collected in 1928, was not listed by Dunn (1931a, b) for the island but is here added to his figures. The recent additions are given in Zetek (1953) and the present list. Due consideration has been given nomenclatorial changes in these comparisons of several lists.

Species erroneously recorded by Dunn and by Zetek and omitted from present calculations are listed in the legend under Figure 2.

one dry season. One of us was part of a party that obtained 85 species in 26 days (July, but unusually dry) in evergreen seasonal forest of eastern Panama; most of the species were collected about a lowland camp (130 m) although several came only from a higher elevation (740 m).

As most experienced field workers will testify, and as indicated in Table 1 and preceding discussion, snakes form a large herpetofaunal segment that is difficult to adequately sample. Snakes, especially those attaining lengths in excess of 30 cm, are mostly predators of vertebrates and this position in the food web results in their having lower population densities than most amphibians and other reptiles, which generally prey on the abundant invertebrate life and even, in some cases, on vegetation. Snakes also are behaviorally and structurally well adapted to avoid discovery, especially in lush tropical vegetation and in the dimness of tropical forests. However, the relative scarcity of snakes is especially noticeable in lowland tropical regions, where many species occur, and is the result of still additional factors. There is a widespread belief that whereas there are more plant and animal species in the tropics than in higher latitudes, all of the individual tropical species are comprised of fewer individuals. But this generalization does not pertain to the frogs and lizards, in which there are some very abundant species, and it probably is not true of many other groups. It does hold for tree species in regions of rain forest, although there are notable exceptions (as in some swamp forests). Extensive field work leads us to suspect that the generalization is likewise valid for snakes; snake species of comparable size seem more likely to have lower biomasses in wet (and dry?) tropical regions than in temperate ones. Unfortunately, the quantitative data needed to test this statement are not available. In any case, there certainly is a latitudinal shift in the habits of snakes that either (a) superimposes apparent scarcity on the real rarity of individuals suggested above, or (b) causes only the illusion of rarity. The most obvious point in this connection is the development in wet tropical forests of a highly arboreal snake fauna. Even fairly large species that forage on the ground are apt to be arboreal when not active, or to spend part of their time foraging above ground. Many species are completely arboreal. The small and strictly terrestrial snakes are more difficult to find than their extratropical counterparts. More are fossorial for one thing, and those that live on the surface are most likely to be inhabitants of ground litter, where they are hard to detect even when they are actively foraging. The rock and rotting log microhabitats, so well occupied by amphibians and reptiles in temperate regions, are comparatively devoid of vertebrates in lowland Panama, where the space is taken over by several kinds of quite large spiders, scorpions, and other arachnids. Aggregations of snakes, seasonal or otherwise, are decidedly uncommon. It would be no great surprise to find a dozen snakes under one rock in Kansas or in a single pine log in Florida, but in several years of collecting in Panama, neither of us has caught more than twelve snakes in any 24-hour period spent in lowland forest. In Panama, at least, the semiaquatic niche filled by *Natrix* in the United States is unoccupied, at least by a reptile, although there are a few small, bottom-feeding "mud snakes"; but whether the absence of *Natrix*-like snakes has an ecological-evolutionary basis, or a primarily zoogeographic one, we are not prepared to say.

There are 39 species of snakes in the present list and it seems significant that Leston and Hughes (1968) consider 40 species as "probably the upper limit for a forest locality." These authors base their conclusion on the census of 3.5 square kilometers of a disturbed, semideciduous forest situation in tropical West Africa; the climatic pattern is similar to, but drier than, that on Barro Colorado. The present paper had gone to press when the Leston and Hughes publication appeared, so detailed comparison of our results must wait until later. It will be exceedingly interesting when comparable censuses become available for some small plots of lowland tropical rain forest, which is characterized by lack of a dry season but which has a vegetational physiognomy much like the forest of Barro Colorado.

Acknowledgments

Present-day investigators on Barro Colorado owe particular gratitude to those earlier workers who outlined the extent of the fauna and provided the taxonomic basis for further study. In herpetology, Emmett Reid Dunn and James Zetek (a general biologist) deserve special mention.

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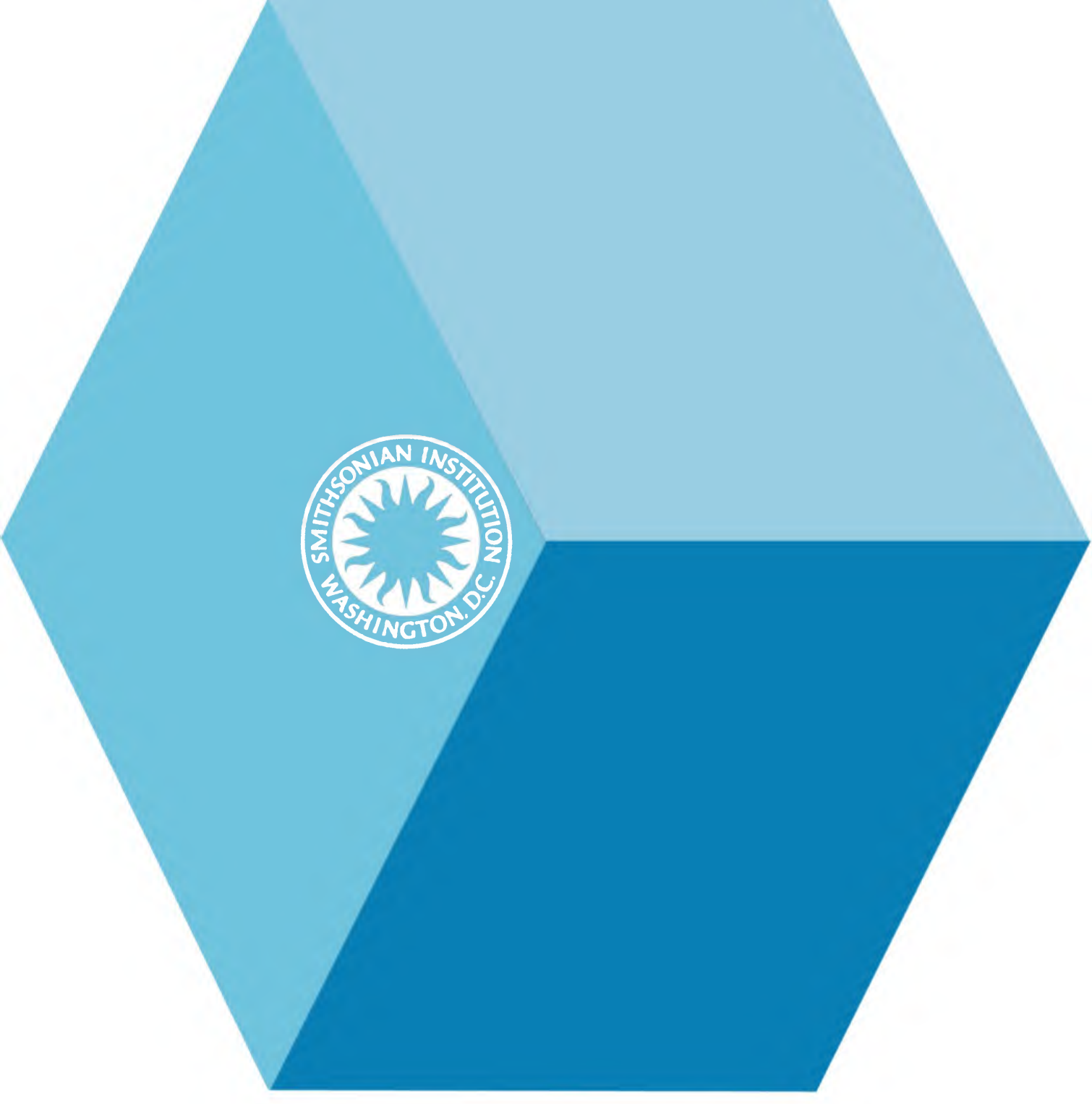
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