Checklist of Amphibians and Reptiles of Barro Colorado Island, Panama, With Comments on Faunal Change and Sampling

CHARLES W. MYERS and A. STANLEY RAND

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • 1969 NUMBER 10
Checklist of Amphibians and Reptiles of Barro Colorado Island, Panama, with Comments on Faunal Change and Sampling

SMITHSONIAN INSTITUTION PRESS
CITY OF WASHINGTON
1969
SERIAL PUBLICATIONS OF THE SMITHSONIAN INSTITUTION

The emphasis upon publications as a means of diffusing knowledge was expressed by the first Secretary of the Smithsonian Institution. In his formal plan for the Institution, Joseph Henry articulated a program that included the following statement: "It is proposed to publish a series of reports, giving an account of the new discoveries in science, and of the changes made from year to year in all branches of knowledge not strictly professional." This keynote of basic research has been adhered to over the years in the issuance of thousands of titles in serial publications under the Smithsonian imprint, commencing with *Smithsonian Contributions to Knowledge* in 1848 and continuing with the following active series:

- *Smithsonian Annals of Flight*
- *Smithsonian Contributions to Anthropology*
- *Smithsonian Contributions to Astrophysics*
- *Smithsonian Contributions to Botany*
- *Smithsonian Contributions to the Earth Sciences*
- *Smithsonian Contributions to Paleobiology*
- *Smithsonian Contributions to Zoology*
- *Smithsonian Studies in History and Technology*

In these series, the Institution publishes original articles and monographs dealing with the research and collections of its several museums and offices and of professional colleagues at other institutions of learning. These papers report newly acquired facts, synoptic interpretations of data, or original theory in specialized fields. Each publication is distributed by mailing lists to libraries, laboratories, institutes, and interested specialists throughout the world. Individual copies may be obtained from the Smithsonian Institution Press as long as stocks are available.

S. DILLON RIPLEY

Secretary

Smithsonian Institution

*Official publication date is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, Smithsonian Year.*

UNITED STATES GOVERNMENT PRINTING OFFICE

WASHINGTON : 1969

For sale by the Superintendent of Documents, U.S. Government Printing Office

Washington, D.C. 20402 - Price 25 cents
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.
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 mispellings 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 buforiformis* (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*, *Syrrophus 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 bolivianorum (Cope)
* Hyla phleboidea Stejneger (H. underwoodi)
* Hyla ruifera Stejneger (H. albo-marginata)
† Agalychnis calcarifer (Boulenger) (Phylomedusa calcarifer)
* Agalychnis caldorae (Cope) (Phylomedusa caldorae)
Agalychnis spurrelli (Boulenger) (Agalychnis dacnicolor, Phylomedusa dacnicolor)
† Phrynopus venulosus (Laurenti) (Hyla venulosus)
† 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. pulvoretum)

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. postiguinea)
* Pseudemys scripta ornata (Gray) (P. ornata)

Crocodilia (2)

* Caiman crocodilus fuscus (Cope)
* Crocodylus acutus Cuvier

Sauria (22)

Iguanidae

Anolis auratus Daudin (Norops auratus)
Anolis bipoecurus (Wiegmann) (A. copei)
Anolis capito Peters
* Anolis frenatus Cope (A. longipes, a name that is technically a synonym of A. capito)
* Anolis liomitus Cope
† Anolis lioonotus Cope
Anolis pentaprion Cope
Anolis vittigerus Cope (A. lemurnius, A. sallaei)
* Basiliscus basiliscus (Linnaeus)
Corythophanes cristatus (Merrem)
* Iguana iguana iguana (Linnaeus)
Ploidyurus gutturosus Berthold

Gekkonidae

Thecadactylus rapicauda (Houttuyn)

Phymodationelidae

Gonatodes albovulgaris fuscus (Hallowell)
Lepidoblepharis sanctaemartae fugax Ruthven—type-locality

Phyodactylus 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)

Anomaliidae

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

Boidae

* Boa constrictor imperator Daudin
Corallus annulatus (Cope) KU
Epicrates cenchria maurus Gray
SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY

**COLUMBIDAÉ**

*Amastridium veliferum* Cope

*Chironius carinatus* (Linnaeus) (*Erpetodryas carinatus*)

*Chironius grandisquamis* (Peters) (*C. fuscus, C. melas*)

*Coniophanes fissidens* (Günther) (*C. punctigularis*)

*Dendrophidion percarnatum* (Cope) (*D. dendrophis, Drymobius dendrophis*)

*Dryadophis melanolomus alternatus* (Bocourt) (*Drymobius boddaerti*)

*Drymarchon corais melanurus* (Dumeril, Bibron, and Dumeril) KU

*Enulius flavitorques* (Cope)

*Enulius selateri* (Boulenger) (*Leptocalamus selateri, E. selateri*)

*I. enanto* (Liinaeus)

†*Imantodes gumiata* (Cope) (*I. elegans*)

*Leimadophis epinephalus epinephalus* (Cope) (*Lio- phys epinephalus*)

*Leptodeira annulata rhombifera* Günther

*Leptodeira septentrionalis ornata* (Bocourt) (*L. a. annulata*)

*Leptopis shetulata occidentalis* Günther (*Tha- leropis richardi occidentalis*)

*Ninia maculata maculata* (Peters) AMNH, USNM

*M. nigrocinctus nigrocinctus* (Girard)

*Pseudoboa neuwiedii* (Dumeril, Bibron, and Dumeril) USNM

*Pseustes poecilonotus shropshirei* (Barbour and Amaral) (*Phrynonax poecilonotus*)

*Rhadinaea decorata* (Günther) (*Liophis decoratus*)

*Rhadinaea pachyura julvicps* Cope (Liophis pa- chyurus)

*Siphlophis cervinus girmanatus* (Dumeril, Bibron, and Dumeril)

*S. pullatus pullatus* (Linnaeus)

*Stenorrhina degenerdietii* (Berthold)

†*Tantilla albiceps* Barbour—type-locality

*Trimetopon barbouri* Dunn USNM

*Xenodon radchopephalus* (Wied) (*Opis colubris*)

**ELAPIDAE**

*Micrurus bipartitus* (Duméril, Bibron, and Duméril)

*M. nigrocinctus nigrocinctus* (Girard)

**CROTALIDAE**

*Bothrops atrox asper* (Garman)

*Bothrops schlegeli* (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 seteki* 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 liornotus, 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) doubtless is correlated with the decreasing variety of habitats, as the old clearings change slowly toward mature forest. 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)

1 Enders (1939) describes early changes in levels of mammalian 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.

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
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 caecilians (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 (Geemyda funerea) were added in the second decade, and two additional frogs (Phrynophyas venulosa, Rana palipes) were obtained between 1952 and 1957. Eight snakes \(^3\) were added in the second decade and six others \(^*\) 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.\(^4\)

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, 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

---

\(^*\)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).

\(^\d\)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.

\(^\dd\)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 noteworthy 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.

We are grateful to William E. Duellman, Neal G. Smith, Owen J. Sexton, and Richard G. Zweifel for reading an early draft of the manuscript, and to Graham B. Fairchild and Edward Moll for certain information. Drs. Duellman and Zweifel very kindly permitted us to publish their data on collecting effort.
This paper was prepared while the senior author was on the staff of the University of Kansas Museum of Natural History, Lawrence, and a visiting scientist (1964–1967) at the Gorgias Memorial Laboratory, Panama City, Republic of Panama. The work was supported in part by grant GM 12020 from the National Institutes of Health to the University of Kansas, W. E. Duellman and C. W. Myers co-investigators.

References

Allee, W. C.

Allee, W. C., and Magnhild Torvik

Barbour, Thomas

Duellman, William E., and Linda Trueb
1960. *Thermoregulation in Tropical Amphibians* (abstract). *Year Book of the American Philosophical Society, 1960*, pages 284–287. [Anolis pentaprion and Eleutherodactylus palmatus are recorded from B.C.I. for the “first time,” with voucher specimens deposited in the American Museum of Natural History. The specimens of the former are *A. limifrons*, but in any case *pentaprion* does occur on the island and was listed by Zetek. Specimens called *E. palmatus* are *E. fitzingeri.*]

Dasmann, Raymond F.
1962. Preliminary List of the Reptiles and Amphibians of the Canal Zone and the Provinces of Panama and Colón. *Occasional Papers of the Boston Society of Natural History, 5*: 403–421. [Includes species known at that time from other parts of the Canal Zone and the provinces of Panama and Colón.]

Dunn, Emmett Reid
1931b. The Amphibians of Barro Colorado Island. *Occasional Papers of the Boston Society of Natural History, 5*: 403–421. [Includes species known at that time from other parts of the Canal Zone and the provinces of Panama and Colón.]

Enders, Robert K.

Evans, Howard E.

Gallardo, José M.

Heatwole, Harold, and Owen J. Sexton
1966. Herpetofaunal Comparisons Between Two Climatic Zones in Panama. *American Midland Naturalist, 75*(1): 45–60. [Especially pertinent is the conclusion that some common tropical species have absolute population densities comparable to common temperate forms. On Barro Colorado, *Anolis limifrons* had an estimated mean density of 474 individuals per acre.]

Hilton, William A.
1946. Salamanders from Barro Colorado Island, Canal Zone. *Journal of Entomology and Zoology, 38*(3):37–39. [Salamanders generally are regarded as rare on the island, but this paper indicates that they can be found by special search in the dry season.]

Kenoyer, Leslie A.

Leston, Dennis, and Barry Hughes

Netting, M. Graham

Ortlieb, Edward, and Harold Heatwole
Peters, James A.

Sexton, Owen J.

Sexton, Owen J., and Harold Heatwole

Wake, David B., and Arden H. Brame, Jr.

Woodring, W. P.

Zetek, James
1940. [Number of Genera and Species of Amphibians and Reptiles on Barro Colorado], p. 17 in Anonymous, Sixteenth Annual Report of Barro Colorado Island Biological Laboratory, Panama Canal Zone, National Research Council, 43 pages mimeographed.

1951. Report on the Canal Zone Biological Area. Annual Report of the Smithsonian Institution for 1950, Appendix 10:133-144. [The list of amphibians and reptiles, pp. 138-141, has been the most complete tally to date.]

1953. Report on the Canal Zone Biological Area. Annual Report of the Smithsonian Institution for 1952, Appendix 10:150-157. [Five additions to the 1951 list are given on page 154. Except for Phrynoderma censulata, preserved specimens forming the basis of the records were found recently on Barro Colorado and sent to the United States National Museum.]
Publication in *Smithsonian Contributions to Zoology*

Manuscripts for serial publications are accepted by the Smithsonian Institution Press, subject to substantive review, only through departments of the various Smithsonian museums. Non-Smithsonian authors should address inquiries to the appropriate department. If submission is invited, the following format requirements of the Press will govern the preparation of copy. (An instruction sheet for the preparation of illustrations is available from the Press on request.)

Copy must be typewritten, double-spaced, on one side of standard white bond paper, with 1½" top and left margins, submitted in ribbon copy with a carbon or duplicate, and accompanied by the original artwork. Duplicate copies of all material, including illustrations, should be retained by the author. There may be several paragraphs to a page, but each page should begin with a new paragraph. Number consecutively all pages, including title page, abstract, text, literature cited, legends, and tables. The minimum length is 30 pages of typescript and illustrations.

The title should be complete and clear for easy indexing by abstracting services. Taxonomic titles will carry a final line indicating the higher categories to which the taxon is referable: "(Hymenoptera: Sphecidae)." Include an abstract as an introductory part of the text. Identify the author on the first page of text with an unnumbered footnote that includes his professional mailing address. A table of contents is optional. An index, if required, may be supplied by the author when he returns page proof.

Two headings are used: (1) text heads (boldface in print) for major sections and chapters and (2) paragraph sideheads (caps and small caps in print) for subdivisions. Further headings may be worked out with the editor.

In taxonomic keys, number only the first item of each couplet; if there is only one couplet, omit the number. For easy reference, number also the taxa and their corresponding headings throughout the text; do not incorporates page references in the key.

In synonymy, use the short form (taxon, author, date, page) with a full reference at the end of the paper under "Literature Cited." Begin each taxon at the left margin with subsequent lines indented about three spaces. Within a taxon, use a period-dash (.—) to separate each reference. Enclose with square brackets any annotation in or at the end of the taxon. For references within the text, use the author-date system: "(Jones, 1910)" or "Jones (1910)." If the reference is expanded, abbreviate the data: "Jones (1910, p. 122, pl. 20: fig. 1)."

Simple tabulations in the text (e.g., columns of data) may carry headings or not, but they should not contain rules. Formal tables must be submitted as pages separate from the text, and each table, no matter how large, should be pasted up as a single sheet of copy.

Illustrations (line drawings, maps, photographs, shaded drawings) can be intermixed throughout the printed text. They will be termed Figures and should be numbered consecutively; however, if a group of figures is treated as a single figure, the individual components should be indicated by lowercase italic letters on the illustration, in the legend, and in text references: "Figure 9b." If illustrations (usually tone photographs) are printed separately from the text as full pages on a different stock of paper, they will be termed Plates, and individual components should be lettered (Plate 9b) but may be numbered (Plate 9: Figure 2). Never combine the numbering system of text illustrations with that of plate illustrations. Submit all legends on pages separate from the text and not attached to the artwork.

In the bibliography (usually called "Literature Cited"), spell out book, journal, and article titles, using initial caps with all words except minor terms such as "and, of, the." (For capitalization of titles in foreign languages, follow the national practice of each language.) Underscore (for italics) book and journal titles. Use the colon-parentheses system for volume, number, and page citations: "10(2):5-9." Spell out such words as "figures" and "plates" (or "pages" when used alone).

For free copies of his own paper, a Smithsonian author should indicate his requirements on "Form 36" (submitted to the Press with the manuscript). A non-Smithsonian author will receive 50 free copies; order forms for quantities above this amount with instructions for payment will be supplied when page proof is forwarded.