

The Herpetological Contributions of William Beebe: Naturalist, Explorer, and Father of Neotropical Ecology

Few metropolitan regions of the world have produced as rich a legacy of zoo herpetologists as New York City. Together with academic institutions such as the American Museum of Natural

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History and the city's numerous colleges and universities, zoological parks in New York have played a key role in shaping North American herpetology. Many celebrated herpetologists of the 20th century began their careers with, or became employed mid-career by at least one of New York's six zoological parks, although none of these institutions have supported as a great a lineage of productive herpetologists as the Bronx Zoo (Adler 1989; Brazaitis and Abene 2008; Card and Murphy 2000; Murphy 2007).

For more than a century, reptile curators at the Bronx Zoo (formerly the New York Zoological Park) have made significant

contributions to the study of reptiles and amphibians through a variety of research activities and publications (see Murphy 2007). Unfortunately, their works have often overshadowed significant contributions made concurrently by staff members of the zoo's parent organization, the New York Zoological Society (now the Wildlife Conservation Society). For example, Charles Haskins Townsend published several important articles on reptiles, particularly Galapagos tortoises, during his tenure as the director of the New York Aquarium between 1902 and 1937, and had several species of reptiles named in his honor (see Grant 1947). William Beebe, the New York Zoological Park's original bird curator and founding director of the society's Department of Tropical Research, was also responsible for many important contributions to herpetology. As colleagues of Raymond Ditmars, the zoological park's original, and perhaps most celebrated reptile curator, Townsend's and Beebe's important work with reptiles and amphibians is often overlooked in part due to Ditmars' many publications and widespread popularity as the chief herpetologist of the society during its early history (e.g., Adler 1989; Murphy 2007; Wood 1962).

Although not a strict herpetologist given his background in ornithology and broad interests in ecology and natural history, William Beebe's important contributions to the study of reptiles and amphibians rivaled those of many professional herpetologists of the period. Yet surprisingly, despite authoring numerous articles and book chapters on the ecology and behavior of reptiles and amphibians and collecting thousands of herpetological voucher specimens, Beebe has seldom been recognized in works on herpetological history (e.g., Murphy 2007, 2008). This is not to say, however, that his name is unfamiliar among herpetologists, as Beebe is perhaps best known as one of America's greatest naturalists and explorers, and for his pioneering work in the fields of ecology, marine biology, and wildlife conservation (Gould 2004; Welker 1975). Here, I highlight the impressive career and herpetological contributions of William Beebe, the father of neotropical ecology. Readers interested in more detailed accounts of his life, travels, and career should refer to the important works of several biographers and historians (Berra 1977; Bridges 1974; Gould 2004; Welker 1975).

LIFE AND CAREER

Charles William Beebe was born in Brooklyn, New York in 1877. Growing up in rural New Jersey, he developed a strong interest in natural history, and amassed an impressive personal collection of zoological specimens, especially birds (Welker 1975). At Columbia University, he studied within the Department of Zoology from 1896 to 1898, but left before graduating for a position with the newly formed New York Zoological Society (NYZS) (Welker 1975). Although he would eventually receive honorary doctorates from both Colgate University (LL.D) and Tufts College (Sc.D) in 1928 (Berra 1977; Crandall 1964) and was identified as "Dr." in many of his later written works and by peers, Beebe never officially completed a baccalaureate degree. Nevertheless, the lack of a traditional academic background would not hinder his career or literary success, or the scope and magnitude of his scientific achievements.

Beebe was hired by the NYZS in 1899 as the assistant curator of ornithology at its newly established zoological park in the Bronx. During his first few years with the society, he assembled a sizeable collection of live birds and oversaw the design and construction of several new buildings and aviaries, and in 1902

was promoted to curator of birds (Bridges 1974). In 1903, Beebe departed on the first of more than 50 scientific expeditions that he would lead during his career with the NYZS, a self-funded trip to Mexico with his wife to study, identify, and collect birds for the zoological park (Beebe 1905a). This trip was followed by collecting trips to Trinidad, Venezuela, and British Guiana (now Guyana) in the following years (Beebe and Beebe 1910), and in late 1909, he embarked on an extensive year-and-a-half-long expedition to the Far East to study pheasants, which eventually culminated in his monumental and perhaps most celebrated publication, "*A Monograph of the Pheasants*" (Beebe 1918–1922).

Beyond his curatorial duties at the zoological park and his increasing research and collecting activities in the field, Beebe was also interested in paleontology, particularly the ancestry of birds and the evolution of flight (e.g., Beebe 1938a, 1942a). In 1915, he authored a theoretical paper that predicted the existence of an intermediate four-winged, or "Tetraapteryx" stage in the evolution of flighted dinosaurs (Beebe 1915) that preceded *Archaeopteryx*. His ideas were largely dismissed or forgotten for 85 years until the discovery of *Microraptor* (Xu et al. 2000), a small, four-winged theropod whose features nearly mirror those of his original "Tetraapteryx" illustration (Beebe 1915). Since 2000, several species of *Microraptor* have been discovered (e.g., Gong et al. 2012; Xu et al. 2003), and his original idea of avian flight evolving from a four-winged ancestor continues to gain support as additional fossil material is located (e.g., Zheng et al. 2013).

In 1915, he traveled to Brazil to arrange a shipment of birds for the zoological park in New York, and it was during this trip that his research interests began to change (Welker 1975). Stopping to investigate and inventory the organisms found around a large jungle tree (Beebe 1916a,b,c), this study marked a departure from his widespread ornithological collecting to more refined and intimate investigations on the ecology of tropical forest ecosystems (e.g., Beebe 1925b).

"AGAIN AND AGAIN WE HAVE PROVED THE VALUE OF LIMITED, CONCENTRATED INVESTIGATIONS OVER WIDER-RANGING, THINNER EXPLORATION."

—WILLIAM BEEBE, HIGH JUNGLE, 1949:187

With assistance and support from former US President Theodore Roosevelt, a close friend and founding chairman of the NYZS, Beebe established Kalacoon, an ecological research station located in northeastern Guyana in 1916 (Beebe 1919; Beebe et al. 1917; Gould 2004). Impressed by his research and collecting activities abroad, the NYZS founded the Department of Tropical Research in 1916 and appointed Beebe as its directing curator (Welker 1975). This appointment officially relieved him of all curatorial duties at the zoological park and enabled him to focus chiefly on his fieldwork and writings (Bridges 1974). Over the next four decades, he led numerous expeditions with the department to poorly surveyed terrestrial and marine environments of the neotropics and established field stations at various locations in South America (Beebe 1925b, 1949a,b, 1952; Beebe and Crane 1947). Staffed by naturalists, hunters, artists, and taxidermists, the Department of Tropical Research under Beebe's direction procured tens of thousands of zoological voucher specimens, photographs, artwork, and film footage depicting wildlife encountered through its expeditions. Hundreds of scholarly articles, notes, and reports were produced by the department, and covered a broad range of topics including, but not limited to, taxonomy, ecology, ethology, and marine biology.



FIG. 1. William Beebe in collecting mode, Guyana, 1917.

Returning to Guyana in 1919, the department established Kartabo, a field research station located just upriver from the former site of Kalacoon (Welker 1975). There, over several seasons, Beebe and his staff intensively studied the ecology of a small tract of jungle roughly 65 ha in size (e.g., Beebe 1925b).

Aside from his interests in tropical forest ecology, Beebe had long been fascinated by marine environments and even experimented with underwater diving equipment (e.g., Beebe 1926, 1934) more than a decade before famed oceanographer Jacques Cousteau. During the late 1920s and throughout the 1930s, Beebe focused the Department of Tropical Research's expeditions heavily on oceanographic exploration. These included expeditions to survey and study the marine life of the Galapagos Islands (Beebe 1926), Haiti (Beebe 1928), Bermuda (Beebe 1932), and the Gulf of California (Beebe 1938b), as well as Beebe's unprecedented and record-setting half-mile (ca. 805 m) descent inside a steel bathysphere in 1934 (Beebe 1934). At this depth in waters off of Bermuda, he became the first biologist to observe deep sea life in situ, including bioluminescent organisms and many species unknown to science (Beebe 1934).

In 1941, Beebe and his department returned to studying terrestrial ecosystems, carrying out ecological investigations in Caripito, Venezuela (Gould 2004), and then later establishing Rancho Grande, a field station headquartered inside the former jungle palace of Venezuelan dictator Juan Vicente Gómez, in 1945. There, the department studied the ecology of the surrounding cloud forest over a period of three years (Beebe 1949a). In 1949, Beebe purchased Simla, an estate located in the Arima Valley of Trinidad's Northern Range, which he established as a tropical research station and later gifted to the NYZS (Gould 2004).

Beebe officially retired in 1952 as Director Emeritus of the Department of Tropical Research after more than 50 years of service with the NYZS, but remained active in field research up until his death in Trinidad in 1962 (Bridges 1974; Gould 2004; Welker 1975).

PUBLICATIONS HISTORY

"NO AMERICAN NATURALIST OF RECENT TIMES HAS GIVEN US SO COPIOUS AND DETAILED A RECORD OF HIS WORK, HIS TRAVELS, THE CHALLENGES HE FACED AND HIS RESPONSE TO THEM. THESE BOOKS WERE NOT MERELY OF SCIENTIFIC REPORTAGE, BUT OF SCIENTIFIC ADVENTURE; MORE IMPORTANT, THEY WERE CREATIVE WORKS, INFORMED BY AN INTELLIGENCE OF EXTRAORDINARY RANGE AND A STYLE AND CONSCIOUSNESS HIGHLY LITERARY."

—ROBERT H. WELKER, *NATURAL MAN: THE LIFE OF WILLIAM BEEBE*, 1975:XII

Beebe was a gifted and prolific writer, authoring 24 books and more than 800 articles, reviews, and reports over the span of his career (Berra 1977). Many of his technical works, which numbered in the hundreds (Crandall 1964), were published in *Zoologica*, the official research journal of the NYZS which was initially founded in 1907 as a publishing outlet for Beebe's research (Bridges 1974), and included taxonomic treatises (including the descriptions of some 87 species of fishes and one bird) as well as studies on the ecology and behavior of birds, mammals, amphibians, reptiles, fishes, and arthropods (Berra 1977). Many additional biological accounts and notes on the husbandry of birds at the zoological park were published in the *Bulletin of the New York Zoological Society*, which became *Animal Kingdom* in 1942.

Most of Beebe's books and popular articles shared extensive details of his travels and experiences abroad, gaining him widespread popularity and celebrity status, to the extent where his personal affairs became fodder for headlines in major US newspapers (Gould 2004; Welker 1975). He regularly contributed to several high profile magazines including *Atlantic Monthly*, *Harpers*, and *Ladies Home Journal*, among others, where he popularized science, natural history, and exploration. Many of these works were later republished as chapters in his books.

HERPETOLOGICAL CONTRIBUTIONS

The vast majority of William Beebe's herpetological contributions stem from his field investigations and collecting activities in Guyana, Venezuela, Trinidad, and the Galapagos Islands, although some additional accounts briefly described the natural history, occurrence, or behavior of herpetofauna encountered during trips to Asia (Beebe 1927), the Caribbean (Beebe 1918), Mexico (Beebe 1905a,b 1938b), and Central America (Beebe 1942b).

Collections.—As depicted by the iconic 1917 photograph taken of him in Guyana with butterfly net and rifle in hand (Fig. 1), Beebe was a prolific collector of zoological specimens, and made no exceptions for reptiles and amphibians. Inventories of herpetofauna collected by Beebe and his staff during expeditions to South America are vast, and appear in several publications (e.g., Beebe 1919a, 1925b, 1944a,b, 1945, 1946a, 1952). Because his knowledge of reptile and amphibian taxonomy was limited, he frequently sought assistance from G. K. Noble and Charles Bogert at the American Museum of Natural History (AMNH), and

Karl Schmidt at the Field Museum of Natural History, in identifying specimens collected in South America (e.g., Beebe 1944a,b, 1945, 1946a; Myers 2000). Despite tensions arising between Beebe and AMNH staff over the identification of some of his herpetological specimens, most of his collections were eventually gifted to the museum's herpetology department (Myers 2000). In fact, Myers (2000) noted that Beebe's 50-plus years of collections with the NYZS represent the best example of material deposited in the museum's herpetology section by non-AMNH led expeditions. Major collections from Beebe deposited in the AMNH include those from Guyana (>1100 specimens), Venezuela (700 specimens), and Trinidad (>150 specimens) (Myers 2000). Additional voucher material was deposited in several other American museums and institutions abroad including the Georgetown Museum in Guyana (e.g., Beebe 1945). At least ten holotypes were collected by Beebe (Table 1).

In recognition of his contributions, at least five species of herpetofauna have been named after Beebe, although most now represent junior synonyms (Table 2). *Plasmodium beebei*, a protozoal lizard parasite of the gekkonid genus *Gonatodes*, was also named in his honor (Telford 1978).

Besides voucher material, Beebe also collected many specimens that were delivered alive to the New York Zoological Park for display in its reptile house. Noteworthy specimens included *Amblyrhynchus cristatus*, *Conolophus subcristatus*, and *Tropidurus* spp. (now *Microlophus*) from the Galapagos Islands (Beebe 1923a, 1924), and *Platemys platycephala*, *Chelus fimbriatus*, *Testudo tabulata* (now *Chelonoidis denticulata*), *Caiman sclerops* (now *C. crocodilus*), *Polychrus marmoratus*, *Boa constrictor* (including a 3.8-m long individual), *Bothrops atrox*, *Chironius carinatus*, *Corallus cooki*, *Crotalus durissus*, *Eunectes murinus*, *Helicops angulata* (now *H. angulatus*), *Lachesis muta*, *Pseustes sulphureus*, *Siphlophis cervinus*, *Spilotes pullatus*, and *Gastrotheca ovifera* from Guyana and Venezuela (Beebe 1918a, 1923c, 1925b, 1946a, 1949a; Beebe and Beebe 1910). From Southeast Asia, he collected and sent back live specimens of gliding reptiles including *Draco volans*, *Ptychozoon* sp., and *Chrysopelea ornata* (Gould 2004).

Field investigations:

Anurans

"THE HUMBLE POLLIWOG IN ITS DEVELOPMENT IS SIGNIFICANT OF FAR MORE MARVELOUS FACTS THAN THE CATERPILLAR CHANGING INTO THE BUTTERFLY, EMBODYING AS IT DOES THE DEEPEST POETRY AND ROMANCE OF EVOLUTION."

—WILLIAM BEEBE, THE LOG OF THE SUN, 1906:112

Beebe showed a particular fondness for frogs, especially their development, courtship behaviors, and calls, and devoted several articles and book chapters to these subjects (Beebe 1906, 1921a,b, 1946b, 1947a, 1953). In Guyana, he described the nesting habits and larval emergence of *Phyllomedusa bicolor* from leaves overhanging water (Beebe 1921a), provided information on the ecology of *Leptodactylus caliginosus* (now *L. latrans*) including its behavior and defensive call, described the call of *Hyla maxima* (now *Hypsiboas boans*) (Beebe 1922, 1925a), and provided details on the predator-prey relationships and stomach contents of 36 frog species from the region (Beebe 1925b). In Venezuela, he documented the call, courtship behaviors, and

TABLE 1. Holotypes collected by William Beebe in the collection of the American Museum of Natural History (AMNH). Current taxonomic conventions for amphibians and reptiles are based on Frost (2013) and Uetz (2013), respectively.

Family	Holotype	AMNH voucher #	Current taxonomy	Locality
Aromobatidae	<i>Hyalaxalus beebei</i> Noble, 1923	A18683	<i>Anomaloglossus beebei</i> (Noble, 1923)	Guyana
Craugastoridae	<i>Eleutherodactylus riveroi</i> Lynch & La Marca, 1993	A70599	<i>Pristimantis riveroi</i> (Lynch & La Marca, 1993)	Venezuela
Hylidae	<i>Hyla ornaticissima</i> Noble, 1923	A13491	<i>Hypsiboas ornaticissimus</i> (Noble, 1923)	Guyana
Leptodactylidae	<i>Leptodactylus minutus</i> Noble, 1923	A13495	<i>Adenomera hylaedactyla</i> (Cope, 1868)	Guyana
Colubridae	<i>Chironius multivenitris septentrionalis</i> Dixon, Wiest & Cei, 1993	R98228	<i>Chironius septentrionalis</i> Dixon, Wiest & Cei, 1993	Venezuela
Dipsadidae	<i>Hypsigena ochrorhynchus unaocularis</i> Tanner, 1944	R62756	<i>Hypsigena ochrorhynchus unaocularis</i> Tanner, 1944	Mexico
Elapidae	<i>Micrurus bogerti</i> Roze, 1967	R96952	<i>Micrurus bogerti</i> Roze, 1967	Mexico
Gymnophthalmidae	<i>Leposoma taeniata</i> Noble, 1923	R21266	<i>Leposoma percarinatum</i> (Müller, 1923)	Guyana
Leptotyphlopidae	<i>Leptotyphlops tenellus</i> Klauber, 1939	R14269	<i>Epictia tenella</i> (Klauber, 1939)	Guyana
Sphaerodactylidae	<i>Gonatodes beebei</i> Noble, 1923	R21251	<i>Gonatodes annularis</i> Boulenger, 1887	Guyana

TABLE 2. Reptile and amphibian taxa named after William Beebe. Current taxonomic conventions for amphibians and reptiles are based on Frost (2013) and Uetz (2013), respectively.

Order	Family	Taxon named after Beebe	Current taxonomy
Anura	Eleutherodactylidae	<i>Eleutherodactylus beebei</i> Chochran, 1956	<i>Eleutherodactylus inoptatus</i> (Barbour, 1914)
	Bufonidae	<i>Bufo beebei</i> Gallardo, 1965	<i>Rhinella humboldti</i> (Gallardo, 1965)
	Aromobatidae	<i>Hyloxalus beebei</i> Noble, 1923	<i>Anomaloglossus beebei</i> (Noble, 1923)
Squamata	Gekkonidae	<i>Gehyra beebei</i> De Rooij, 1915	<i>Gehyra mutilata</i> (Wiegmann, 1834)
	Sphaerodactylidae	<i>Gonatodes beebei</i> Noble, 1923	<i>Gonatodes annularis</i> Boulenger, 1887

tadpole carrying behavior of *Prostherapis trinitatis* (now *Manophryne trinitatis*), as well as the anatomy, defensive behavior, and reproductive biology of *Gastrotheca ovifera* (Beebe 1949a).

In Guyana, Beebe was the first to discover a population of a smaller-sized *Pipa*, which was later identified as a new species, *P. aspera* Müller 1924 (Beebe 1925b).

Saurians

“BOUND TO THE GROUND BY THEIR SHORT SCALES AND FOUR LIMBS, THESE SMALL LIZARDS ARE YET REMARKABLY BIRDLIKE IN THEIR VIVACITY AND THEIR ENTHUSIASTIC PLAYING OF THEIR LITTLE GAME OF LIFE.”

—WILLIAM BEEBE, JUNGLE PEACE, 1918:43

Lizards are prominently featured in Beebe's writings on herpetology and appear to have been his most extensively studied group. In his book, *Jungle Peace*, he recalled first being taught how to noose lizards by a 12-year-old girl on the island of St. Thomas, thereby enabling him to more closely study members of this group (Beebe 1918a). In the Gulf of California, he documented the color variation and behaviors of insular lizard populations (Beebe 1938b), and recorded observations on the coloration, activity, and defensive behaviors of *Ctenosaura acanthura* in Mexico (Beebe 1905a, b). In 1919, he described in detail the geographic variation and ontogenetic color changes in lizards of the genus *Ameiva*, and discussed their relevance to Barbour and Noble's (1915) recent taxonomic revision of the genus (Beebe 1919b).

During a brief visit to the Galapagos Islands in 1923, Beebe studied many aspects of the ecology and behavior of the archipelago's lizard fauna (Beebe 1924). He described the differences in coloration between island populations of *Tropidurus* (now *Microlophus*), and discussed the possibility that insular populations of these animals within the archipelago could have originated through rafting on debris (Beebe 1923a). Captivated by the languid behavior and tameness of *Amblyrhynchus cristatus*, he carried out several crude behavioral experiments to study their lack of fear towards humans:

“TO TEST THE ACQUISITION OF FEAR, I CAUGHT AN IGUANA OF MEDIUM SIZE, JERKED HIM INTO THE AIR, PLAYED WITH HIM FOR A FEW MINUTES AND THEN LOOSENED THE NOOSE AND SET HIM FREE. HE RAN OFF A FEW FEET, TURNED AND LOOKED AT ME AND OFFERED NO RESISTANCE TO BEING AGAIN CAUGHT AND SWUNG THROUGH SPACE. SIX TIMES I REPEATED THIS, AND IF ANYTHING HE WAS TAMER AFTER THE ROUGH TREATMENT THAN BEFORE, IN THE FACE OF A SERIES OF EXPERIENCES WHICH WOULD HAVE DRIVEN ANY ORDINARY WILD CREATURE INSANE WITH FRIGHT.”

—WILLIAM BEEBE, GALAPAGOS: WORLD'S END, 1924:119

In addition to recording information on the diet, activity, and behavior of *A. cristatus*, Beebe also documented parasitism in the species, including the mutualistic removal of ticks by the Scarlet Rock Crab, *Grapsus grapsus* (Beebe 1924). He studied various aspects of the ecology of *Conolophus subcristatus* on Baltra Island, and observed mockingbirds removing ticks from its skin, which were later determined to be a new species (Beebe 1924).

Beebe's most important scientific works on lizards were a series of technical articles that provided extensive ecological data for 41 species collected in Guyana and Venezuela (Beebe 1944a, b, 1945). Particularly noteworthy from these reports were detailed descriptions, measurements, and line drawings of eye and hyoid morphologies for many of the species discussed, as well as a discussion on the termitaria-nesting habits of *Tupinambis*. In an earlier report, he provided detailed information on the ecology of 31 species in Guyana, including a comparison of the stomach contents of *Ameiva* and *Cnemidophorus* (Beebe 1925b).

Serpentes

“BUT THEIR MOVEMENTS ARE SLOW, AND RATHER THAN PURSUE THEIR PREY, THEIR FORTE IN LIFE IS WAITING, WITH ALL THE PATIENCE IN THE WORLD, FOR SOME SMALL CREATURE TO CROSS THE SPOT WHICH THEY HAVE RENDERED MORE DEADLY THAN ANY PITFALL OR TRAP OF HUMAN DEVISING.”

—WILLIAM BEEBE, NOOSING A BUSHMASTER, 1916:1375

Intrigued by bushmasters, Beebe described close encounters with *Lachesis muta* as well as their capture, and provided general information on the natural history and habits of the species (Beebe 1916c, 1918a). Of particular interest, he noted that *L. muta* emitted a delicate, but noticeable odor when alarmed or disturbed (Beebe 1925b), and even asserted his ability to detect the presence of the species by smell while blindfolded (Beebe 1949a)!

In 1925, he provided detailed information on the ecology of 52 snake species collected from a small section of forest in Guyana (Beebe 1925b). A follow-up study that included data from both Guyana and Venezuela yielded extensive data on the ecology of 54 species (Beebe 1946a). Among this information, Beebe (1946a) described a peculiar liana-mimicking behavior and defensive behavior in *Pseustes poecilonotus*. In the Galapagos Islands, he studied the stomach contents, reproductive biology, and geographical variation of *Dromicus* spp. (now *Pseudalsophis*) (Beebe 1924), and in Costa Rica, he recorded notes on the behavior and natural history of *Pelamis platurus* (Beebe 1942b).

As a collector of many snake specimens, Beebe (1947b) became frustrated by the loss of scale coloration through fixation and preservation, particularly with coral snakes of the genus

Micrurus. This prompted him to develop a novel method of preserving and mounting snake skins so that their colors remained vivid as in life (Beebe 1947b).

In 1952, Beebe produced an inventory of snakes native to the Arima Valley of Trinidad, reporting a total of 27 species (Beebe 1952). Many decades later, Boos (2001) noted some mistakes in Beebe's (1952) list, such as his inclusion of *Oxybelis fulgidus* as an inhabitant of Trinidad. As that species has never been collected in Trinidad, Boos (2001) suspected that this error represented a mistaken locality for nearby Patos Island.

Testudines

"I HAVE SEEN THESE TURTLES IN BOTH HEMISPHERES AND ALONG THE SHORES OF FOUR CONTINENTS, BUT NOT UNTIL MY WEEK ON CLARION ISLAND DID GREEN TURTLES LEAVE THE REALM OF EXCLAMATORY RECOGNITION AND BECOME EXCITING INDIVIDUALS, OBJECTS OF INTENSE INTEREST AND WONDER."

—WILLIAM BEEBE, ZACA VENTURE, 1938: 276

Over the course of his many oceanic voyages with the Department of Tropical Research, Beebe had the opportunity to observe many sea turtles, particularly *Chelonia mydas*. During an excursion to Clarion Island, off the west coast of Baja California, he made extensive observations on *C. mydas*, and described in detail the stomach contents and nesting biology of the species, reviewed earlier accounts of its biology, and clarified anthropomorphic misconceptions regarding its reproduction (Beebe 1938b).

In his book, *Galapagos: World's End*, Beebe (1924) offered an extensive review of historical accounts dating back to 1684 that described encounters with Galapagos tortoises and their exploitation, as well as scientific expeditions that had collected individuals from the archipelago. On Pinzón Island, his crew located and secured a single tortoise, whose behavior and climbing abilities up steep, rocky slopes were studied by Beebe (1924).

Interestingly, Beebe rejected the idea that the terrestrial fauna of the Galapagos Islands had originated by overwater emigration from mainland South America; insisting instead that there must have once been a land bridge connection (Beebe 1924). This position appears to have been reinforced by a crude experiment carried out aboard his ship, whereby the tortoise collected from Pinzón was tossed into open water to see if it could float. Much to Beebe's surprise, the tortoise not only floated upright, but was also capable of controlled swimming as it attempted to climb back aboard a rowboat. Its death aboard the ship one week later, which Beebe attributed to congestion in the lungs caused by the inhalation of sea water while swimming, led him to the conclusion that:

"THIS WOULD NEGATIVE ANY POSSIBILITY OF THE TORTOISES BEING ABLE TO MAKE THEIR WAY OVER WIDE EXPANSES OF WATER, EITHER FROM THE MAINLAND OR FROM ISLAND TO ISLAND, IN SPITE OF THEIR UNUSUAL SWIMMING ABILITY."

—WILLIAM BEEBE, GALAPAGOS: WORLD'S END, 1924:228

In Guyana, Beebe et al. (1917) described the nesting habits and ecology of several species of freshwater turtles, but provided only local names for the species, complicating their identification. Beebe (1925b) collected basic ecological data on eight turtle

species in Guyana, and on Trinidad, he recorded the occurrence of two species from the Arima Valley (Beebe 1952).

Crocodylians

"COMMON IN MANY PLACES AND ACTUALLY ABUNDANT IN A FEW, THESE GREAT SAURIANS ARE FAR LESS CONSPICUOUS THAN THEIR INFINITELY SMALLER RELATIVES- THE LIZARDS WHICH EVERYWHERE SCAMPER UP TREE-TRUNKS OR BARGE CLUMSILY THROUGH THE FALLEN LEAVES."

—WILLIAM BEEBE ET AL., THE ALLIGATORS OF GUIANA, 1917:283

Although he had observed them in both eastern and western hemispheres, and even collected specimens for museums, Beebe's writings on crocodylians appear to be limited to encounters with caimans in Guyana. There, he and others reported on the ecology and anthropogenic threats to caiman (probably *C. crocodilus*) living in the vicinity of Georgetown (Beebe 1917; Beebe et al. 1917), and briefly described the stomach contents of a young *C. sclerops* (now *C. crocodilus*) (Beebe 1925b). Beebe et al. (1917) reviewed local accounts of attacks on Guyanese villagers by *C. niger* (now *Melanosuchus niger*).

Captivity-based investigations

To supplement their field investigations, Beebe and his staff regularly maintained live reptiles and amphibians in their field station laboratories. In addition to providing opportunities for observing cryptic behaviors and developmental processes, maintaining specimens in the laboratory also served as a way of keeping them alive and healthy in preparation for their delivery to the zoological park in New York.

Frogs were frequently kept subjects, and led to the discovery of many fascinating behaviors and developmental processes that had not been seen or documented before. For example, Beebe (1946b; 1947a, 1949a) was the first to describe the "birth" or emergence of newly metamorphosed froglets from the dorsal pocket of the marsupial frog, *Gastrotheca ovifera*, and described larval development and metamorphosis in *Phyllomedusa bicolor* (Beebe 1921a,b). Several additional frog species were maintained in the laboratory, including *Leptodactylus caliginosus* (now *L. latrans*), *Phylllobates inguinalis* (now *Colostethus inguinalis*) (Beebe 1921a), *Prostherapis trinitatis* (now *Mannophryne trinitatis*), *Bufo marinus* (now *Rhinella marina*), *Atelopus cruciger*, and *Hyla rubra* (now *Scinax ruber*) (Beebe 1925b; 1949a).

Snakes were also regularly kept in terraria. On one occasion, Beebe (1949a) recalled tripping over an escaped coral snake (*Micrurus* sp.) while walking through a dark laboratory at night. A large *Bothrops asper* that was thought to have recently consumed a large meal was captured in the hallways of Rancho Grande and temporarily housed in a terrarium (Beebe 1949a). Several days after its capture, it unexpectedly gave birth to 28 live offspring, yielding important details about the reproductive biology of the species, and possibly representing the first birth of the species in captivity. Additional snake species kept included *Boa constrictor*, *B. canina* (now *Corallus caninus*), *Chironius carinatus*, *Pseustes sulphureus*, and *Tantilla melanocephala* (Beebe 1946a).

Many lizards including *Anolis nitens* (now *A. chrysolepis*), *A. sagrei*, *Cnemidophorus lemniscatus*, *Gonatodes annularis*, *Mabuya mabouya*, *Plica umbra*, *Polychrus marmoratus*, and *Uranoscondon superciliosus* (now *U. superciliosus*) were kept and studied in the laboratory, with eggs from several species laid in

captivity (Beebe 1944a,b, 1945). Although most eggs were dissected to study their development, some were artificially incubated and left to hatch in the lab. For example, Beebe (1945) described the successful captive hatching of *Tupinambis nigropunctatus* (now *T. teguixin*) and documented, perhaps for the first time, that disturbances to the surface of the eggshells prompted the pipping and rapid emergence of hatchlings (1925a). Today, this technique is often used by herpetoculturists to trigger hatching in tegu eggs. *Gonatodes annularis* was also successfully hatched in the laboratory (Beebe 1944a), and neonatal *M. mabouya* (now *Varzea bistriata*) were born to captive females (Beebe 1945).

On the voyage back to New York from the Galapagos Islands, a large group of *C. subscristatus* destined for the zoological park was maintained aboard the ship and fed a diet of lettuce and cabbage (Beebe 1923a). A group of *A. cristatus* was also brought back to New York on the same trip, but not on board the ship. Instead, they were housed for the duration of the two-month journey inside a floating wire cage that was pulled by the ship (Beebe 1923a, 1924). Although the animals survived the trip, they could not be encouraged to feed on any of the seaweed or vegetable matter offered to them (Beebe 1923a).

Miscellany.—Several of Beebe's published works on herpetology were accompanied by skillful illustrations painted by Department of Tropical Research artist Isabel Cooper. These included both color and black-and-white illustrations of *Conolophus subscristatus*, *Tropidurus albemarlensis* (now *Microlophus albemarlensis*), and *Amblyrhynchus cristatus* in Beebe's (1924) book, *Galapagos: World's End*, as well as nearly 100 black-and-white illustrations accompanying his technical articles on the ecology of lizards and snakes from Guyana and Venezuela (Beebe 1944a,b, 1945, 1946a).

Beebe authored the foreword to Curran and Kauffeld's (1937) popular book, *Snakes and their Ways*, and prepared the introduction to Tweedie's (1956) article on flying lizards of the genus *Draco*. Popular accounts on the etymology of reptile and amphibian common names were also given (Beebe, 1905a, 1906).

CLOSING REMARKS

In retrospect, William Beebe's impact on the field of herpetology extends far beyond the observable contributions hitherto discussed. Together with his important fieldwork in other disciplines, including ornithology, ichthyology, and entomology, Beebe's herpetological investigations have helped stress the importance of studying not only the animals, but their ecological roles and relationships with other organisms. His pioneering fieldwork in the neotropics was critical in paving the way for future researchers and studies in the emerging fields of ecology and conservation biology.

Beebe's impressive career demonstrated that an academic background was not necessarily a prerequisite for carrying out important scientific investigations or becoming a leading contributor to a particular field. Indeed, the breadth and extent of his lifetime scientific achievements surpassed those of most of his academic contemporaries.

It is impossible to discuss the impacts of Beebe's contributions on the fields of ecology, conservation biology, or herpetology without noting his critical role in the history and development of the New York Zoological Society. It was largely Beebe's pioneering fieldwork and oversight of the Department of Tropical Research that prompted the society's outward growth from an

organization established upon zoological park management to a driving force in wildlife research and conservation. Concerned about the welfare of his zoological park, if founding NYZS director William Hornaday had gotten his way, Beebe would not have been permitted to take such extensive stints away from his curatorial duties at the zoo (Bridges 1974); this would have limited or even prohibited his collecting and research activities in the field. Fortunately, seeing the importance of his fieldwork, influential members of the society's executive committee disagreed with Hornaday's position and fully encouraged and supported Beebe's research endeavors (Bridges 1974). Without Beebe's dedication and investment of his personal finances towards fieldwork abroad (Gould 2004), it is unlikely that the Department of Tropical Research would have been founded and sustained. Without the important work carried out by the department under his direction, it is doubtful that the society would have followed the same trajectory towards becoming the Wildlife Conservation Society (WCS), the world's largest wildlife conservation organization. Today, the WCS supports and manages hundreds of field-based conservation initiatives throughout the world, including many which focus on conserving reptile and amphibian populations and their habitats.

Finally, of the many formal and informal roles that Beebe assumed during his lifetime, perhaps the most important was his popularization of science, nature, and exploration. His writings invited readers of a broad audience to relive his remarkable experiences as a naturalist traveling the world in search of wildlife and wild places, and have been attributed to inspiring and launching the careers of many renowned naturalists, ecologists, and conservation biologists, including Ernst Mayr, E. O. Wilson, Roger Tory Peterson, Rachel Carson, and Sylvia Earle (Gould 2004; Welker 1975; Wilson 1994), as well as many professional and amateur herpetologists (e.g., Bartlett 1988). Beebe's far-reaching influence continues to this day, as reprints and older copies of his books continue to be purchased and read by the next generation of naturalists and conservationists.

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