

Full Length Research Paper

Conservation and historical biogeography: How did the mountain chicken frog get to the Caribbean?

Jay D. King^{1*} and Pamela C. Ashmore²¹Rare Species Conservatory Foundation, Loxahatchee, Florida, United States.²Department of Sociology, Anthropology and Geography, University of Tennessee, Chattanooga, United States.

Received 15 March, 2011; Accepted 3 November, 2014

***Leptodactylus fallax*, commonly known as the mountain chicken frog, is a large terrestrial frog currently found on two islands in the Caribbean. Habitat destruction, overhunting and disease outbreaks have contributed to declining population numbers. In order to identify appropriate conservation strategies, the historic geographic distribution of this frog must first be determined. Because no archeological evidence exists, this was accomplished by reviewing historical documents and inspecting museum collections. Inaccuracies in location and species names were identified in documents as well as in the mislabeling of museum specimens. Two means for natural immigration (dispersal and vicariance) and the artificial introduction by humans were considered. The authors concluded that the Amerindians transported *L. fallax* to eight islands throughout the Lesser Antilles as potential food resources as they colonized this area. The implication that 75% of the historical distribution is currently unoccupied by this species is considered in light of future reintroduction projects.**

Key words: *Leptodactylus fallax*, Amerindians, dispersal, vicariance.

INTRODUCTION

Wildlife biologists, zoo and aquarium personnel, and conservationists are often asked to “save a species” sometimes in a specific location. But should they? Important considerations need to be addressed before answering this question. Is the location part of the historic geographic range? How and when did the species arrive? Is it an endemic or an exotic?

Historical biogeography is the study of the geographic distribution of an organism and how that distribution occurred (Crisci et al., 2003). Understanding the past and present range of a species is necessary to appropriately identify and implement viable conservation strategies. One

species that could benefit from this process is *Leptodactylus fallax*, commonly known as the mountain chicken frog (Figure 1). It is a large terrestrial frog (SNV 121 to 167.2 mm) (Heyer, 1979) with a unique form of reproduction called obligatory oophagy (Gibson and Buley, 2004): a female lays eggs in a foam nest in which tadpole development occurs while the female produces infertile eggs as a source of nutrient for the young.

Currently this species is found on the islands of the Commonwealth of Dominica and Montserrat, but historically may have been found throughout the Lesser Antilles, the southeastern arm of the archipelago of the Caribbean

*Corresponding author. E-mail: leptofallax@yahoo.com. Tel: 314-664-2368. Fax: 314-644-0548.



Figure 1. The mountain chicken frog (*L. fallax*).

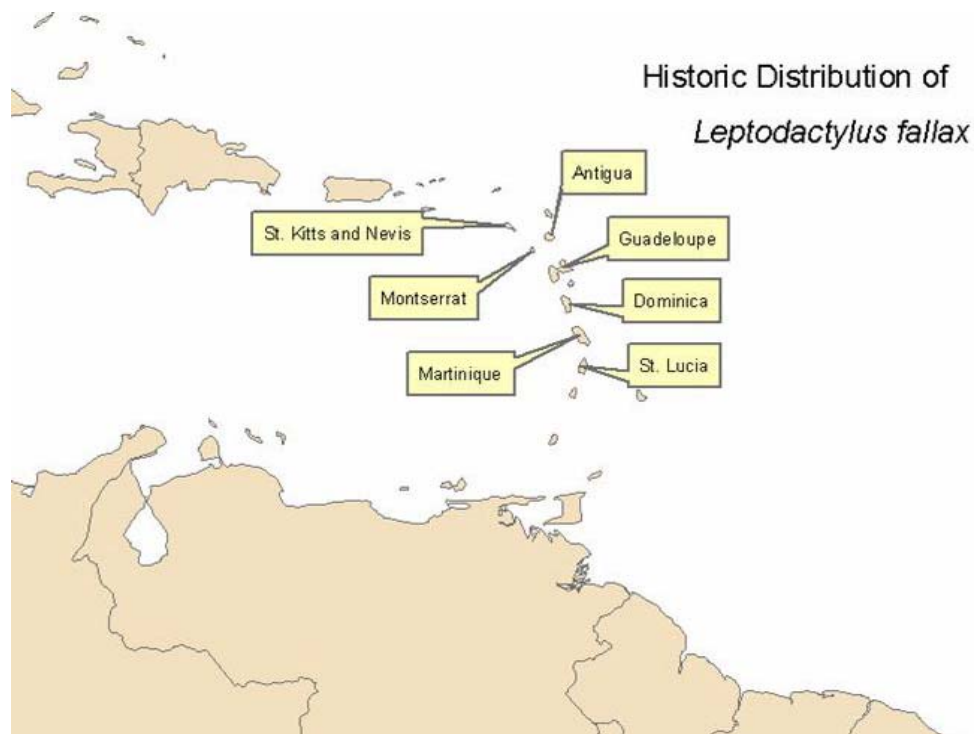


Figure 2. Historic distribution of *Leptodactylus fallax*.

Islands (Figure 2). Conservation organizations have expressed interest in reintroducing this species to several islands in order to re-establish its former range and

create ancillary populations as a “safety net” to catastrophic events: the population inhabiting the island of Montserrat is threatened by volcanic activity and populations found on

this and the island of the Commonwealth of Dominica are being decimated by the pathogenic chytrid fungus, *Batrachochytrium dendrobatidis*. However, it must be determined which islands actually composed the historical range of *L. fallax* before reintroduction should be considered.

A number of factors contribute to the puzzle of reconstructing the historical distribution of *L. fallax*. First, there appears to be no archaeological evidence, such as skeletal remains. As a result, we are forced to rely entirely on the historical literature and preserved specimens. Second, there have been inconsistencies in the taxonomic nomenclature that has been assigned to this species (see "Museum Specimen Search"). Third, preserved specimens have been mislabeled or lost, as will be documented below. And finally, several important historical references describing the geographic distribution of the frog are in French and mistranslations have been done.

METHODOLOGY

Literature search

A comprehensive literature search was conducted for the keywords "*Leptodactylus*" and "*L. fallax*". All relevant literature was obtained and pertinent references found in this literature were also gathered. Often these consisted of field notes from early explorers and many of these accounts were in French. The original French sources were then translated and compared with earlier translations to identify if any inaccuracies existed which are relevant to the geographic distribution of this frog species. The information in these sources was used to piece together the historical biogeography of *L. fallax*.

Museum specimen search

An index to herpetology collections in the United States can be found on the Internet (California Academy of Sciences, 2014). This source lists eight institutions holding specimens of *L. fallax* (Table 1). The web page for each institution was reviewed for information regarding number of individual specimens, location and date collected. In two cases, data were not available on-line and institutional personnel were able to supply collection records. One institution, the University of Kansas, listed ten specimens from the "Republica Dominicana" however there are no historical accounts of this species ever occurring in the Dominican Republic. Consequently, field notes were obtained, the collection was visited, and the specimens examined.

Biogeographical reconstruction

Attempting to reconstruct the historical distribution of *L. fallax* requires consideration of how this species first occurred on islands in the Caribbean. Our own training and field experiences and a review of relevant literature on island immigration enabled us to determine possible means for the arrival of the frog on the islands. Groome (1970) appropriately describes the challenge: "In general, Amphibia are absent on oceanic islands, for their eggs and tadpoles require fresh water and their skins are totally allergic to salt." Similarly, Meyer (1953) identifies the improbability of a natural immigration of the frogs to the islands: "Amphibians as a group are

delicate creatures, extremely susceptible to salt water, to desiccation, and to the heat of the sun, and since they do not possess wings, it is difficult to imagine how they could cross sea barriers."

There are two possible modes of natural immigration: vicariance and dispersal. Vicariance is the process by which one population is divided into two by the formation of a barrier, such as the rising of a mountain range or the flooding of a plain. Dispersal is the process by which members of a population cross a pre-existing barrier, sequentially becoming an isolated population. The arrival of *L. fallax* on islands in the Caribbean was further assessed by investigating known incidents of rafting and studies of ocean currents. In addition, more unusual modes of dispersal were noted in the historical literature.

RESULTS

The historical distribution of *L. fallax* by island in a north to south distribution

This reconstruction is based on accounts from the historical literature, inventories of museum collections, and in some cases a review of the specimens included in the collections.

Jamaica

The Jamaica Journal tells the story of a woman bringing a pair of *L. fallax* to this island and the successful breeding at two different sites (Proctor, 1973). This journal does not have a scientific focus and normally contains essays and poems, so it is likely that this was a fictional account. Additionally, a West Indies herpetologist confirmed no past or present reports of this species in Jamaica (Personal communication – Jay King). It is unlikely that *L. fallax* occurred on this island.

Dominican Republic

Lescure (1979) states that there is a translation error in the word Dominica in the book "*Amphibiens vivants du monde* (World living amphibians)". It states that *L. fallax* was a species found in the Dominican Republic, instead of on the island of the Commonwealth of Dominica. With the exception of a listing of *L. fallax* specimens at the University of Kansas from the Dominican Republic, no other accounts can be found. It was determined that these specimens were actually *L. albilabris* (Personal observation – Jay King). It is unlikely that *L. fallax* occurred on this island.

Puerto Rico

Attempts were made in 1929 and 1932 to introduce *L. fallax* to this island, but both failed. Barbour (1937) states, "The imported population which was taken while calling at night from Dominica, may be males only, according to Major Chapman Grants." Other than the brief unsuccessful attempts to introduce this species, it is unlikely that this

Table 1. Institutions with collections of preserved specimens of *L. fallax*.

Institution	Collection site	Year	No. of specimens
Carnegie Museum of Natural History ^a	Dominica	1969	1
	Dominica	1879	5
Museum of Comparative Zoology Harvard University ^b	St. Kitts / Nevis	1879	2
		?	5
	Dominica	1961	14
		1963	4
	1966	1	
Museum of Natural History University of Kansas ^c	Montserrat	1962	12
		1995	1
	Republica Dominicana*	1963	10
Museum of Vertebrate Zoology University of California ^d	Dominica	1881?	1
Museum of Zoology University of Michigan ^e	Dominica	1930?	1
	Dominica	1929	5
		1930	1
		1964	1
		1964	1
		1965	11
		1966	46
		1967	10
1980	4		
National Museum of Natural History Smithsonian Institution ^f		1996	2
		1980	2
		?	1
	Monserrat		
Natural History Museum of Los Angeles County ^g	Dominica	1963	1
Peabody Museum of Natural History Yale University ^h	Dominica	1890	1
Texas Cooperative Wildlife Collection Texas A&M University ⁱ	Dominica	1991	1
		1997	1

*These specimens were identified as *Leptodactylus albilabris*; ^a<http://www.carnegiemnh.org/>;

^b<http://www.mcz.harvard.edu/>; ^c<http://www.nhm.ku.edu/>; ^d<http://mvz.berkeley.edu/>; ^e<http://www.ummz.lsa.umich.edu/>;

^f<http://www.mnh.si.edu/>; ^g<http://www.nhm.org/>; ^h<http://yale.edu/>; ⁱ<http://wfscnet.tamu.edu/tcwc/tcwc.htm>.

species occurred on this island.

St. Kitts/Christopher

The Harvard Museum of Comparative Zoology contains four specimens collected from St. Kitts in 1879 and 1881 (Harvard, 2008). This represents a confirmed occurrence on this island.

Nevis

The four specimens in the Harvard Museum of Comparative Zoology listed above have “St. Kitts/Nevis” at the top of the record pages, but the identification of the collection location is “St. Kitts”. Since St. Kitts and Nevis are in such close proximity to one another, it is possible that specimens from these two islands were grouped together. *L. fallax* may or may not have occurred on this island.

Antigua

"*Cystiganthus*" was a term historically used to denote a genus of frogs. It is no longer used and frogs that previously were identified with this genus have now been reclassified into 17 other genera in 12 families. For example, Lescure (1979) states, "Dunn (1934) mentions the existence of *L. fallax* in Antigua based on a specimen of the British Museum classified as *Cystiganthus fuscus* by Gunther (1858)." Such name changes have only added to the confusion of the historical distribution of many species. However, Lescure believes the specimen described above may have been from the neighboring island of Montserrat because, "Antigua, originally a coral island, does not seem to offer the biotope conditions in favor of the *L. fallax*," but he offers no additional substantiation of his claim. It is probable that *L. fallax* occurred on Antigua.

Montserrat

L. fallax is currently found on this island (Kaiser, 1994). Amerindian artifacts from Montserrat housed at the National Museum of the American Indian include pottery and stone carvings that depict images of frogs.

Guadeloupe

Historical references are highly contradictory. Lescure (1979) records that Father Du Tertre in 1667 wrote that "None of these frogs can be found on the Guadeloupe," but Barbour (1912) describes this island as "a living environment of the *L. fallax*." *L. fallax* may or may not have occurred on this island.

Commonwealth of Dominica (Dominica)

L. fallax is currently found on this island (Kaiser, 1994). It was first incorrectly identified in 1841 by Dumeril and Bibron as *Cystignathus ocellatus* (Lescure, 1979).

Martinique

In 1776, the naturalist Moreau de Jonnes was the last to report the presence of *L. fallax* on Martinique (Barrau, 1978; Lescure, 1983). A specimen was sent to the Paris Museum but is currently missing from the collection. Barrau (1978) believes the origin of this specimen cannot be confirmed because Moreau de Jonnes also traveled to other islands of the Lesser Antilles including Dominica. Failed attempts to introduce the frog occurred in 1965 and 1966 when a "lot" of frogs from Dominica were reintroduced to Martinique by M. Baly (Lescure, 1983). *L. fallax* did occur on this island but no longer exists.

St. Lucia

Barbour (1912) mentions that *L. pentadactylus* was recorded from this island, but provides no support for this statement. *L. pentadactylus* and *L. fallax* can, however, be easily confused by morphology. Lescure (1979) makes two confusing statements. First, he says, "No *Leptodactylus* specimens from St. Lucia are found in any natural history collections," but then he states, "In the Catalogue of the Museum of Paris, written between 1839 and 1862, someone mentioned the skin of *C. ocellatus* among specimens of reptiles and amphibians sent from St. Lucia by Mur Bonnacour, on January 26, 1850 and on January 1851" (As stated earlier, *C. ocellatus* was inappropriately applied to *L. fallax* in the Commonwealth of Dominica). This specimen no longer exists in the Museum of Paris and, therefore, cannot be examined. Regardless of species, Lescure (1979) questions whether this specimen may have been collected in Dominica and then sent from St. Lucia to Paris. It is probable that *L. fallax* occurred on this island.

Trinidad

Lescure (1979) states, "*L. pentadactylus* can be found in Trinidad. *L. fallax* cannot be found there. The specimen labeled MCZ 8663 which had been identified as *L. fallax* is in fact a *L. pentadactylus*." There was no other occurrence in the literature pertaining to the historical distribution of either species on Trinidad. Another large frog, *L. bolivianus*, does occur on Trinidad and could be easily mistaken for either of these species. It is unlikely that *L. fallax* occurred on this island.

Museum specimen search

As can be seen in Table 1 all known specimens of *L. fallax* in museum collections were originally obtained in the Commonwealth of Dominica, Montserrat, or St. Kitts/Nevis. An interesting exception is the collection at the University of Kansas.

This institution listed ten specimens of *L. fallax* as having been collected in the "Republica Dominicana." Field notes from the collection were obtained which state, "Republica Dominicana: El Seibo: 2.3 mi SE Miches." It was confirmed that this is a location in the Dominican Republic. The collection was visited and specimens examined. All ten frogs in the collection were determined to be *L. albilarbris*. It appears that this error was due to historical name changes.

In 1923, a frog from the Dominican Republic was named *L. dominicensis* (Heyer, 1979). In that same year, a different species from the Commonwealth of Dominica was assigned the same name. It was not until 1926 that this duplication was discovered. In accordance with the principle of priority, the frog from the Commonwealth of

Dominica was renamed *L. fallax* (Heyer, 1979). Later, in 1978, *L. dominicensis* was renamed *L. albilabris*. Apparently, the confusion in the naming and renaming of the species resulted in the incorrect labeling of these ten specimens.

Historical biogeography

In order for vicariance to have occurred there must have been some former land connection between Central or South America and the islands in the Caribbean. The plate tectonic model (Duellman, 1999) proposes that a series of islands were formed in the area of present day Central America but then drifted eastward to form the Greater Antilles. However, the islands on which *L. fallax* likely occurred are part of the Lesser Antilles. These islands were formed by volcanism during the Tertiary Period (1.8 – 65 mya) (Malhotra and Thorpe, 1999). Consequently, there is no evidence to support the past existence of any land bridges connecting the Caribbean islands to either Central or South America thus eliminating the possibility of dispersal due to vicariance.

An alternative explanation is dispersal. Dispersal can occur through various means. Animals may disperse under their own power (e.g., walking, swimming or flying) or be carried. Barbour (1937) speaking of species dispersal in general states, "There has been undoubtedly some dispersal by flotsam and jetsam and some dispersal by winds and some transport by migrating birds and a good many types have been carried by man, both primitive and civilized".

In the literature, the term "floatation" has been applied to active swimming and to the use of rafts (Myers, 1953). This type of dispersal may occur when an individual is randomly "washed" into the water by a storm or when an individual enters the water on its own. Schoener and Schoener (1983) tested the propensity for voluntary dispersal by a lizard, *Anolis sagrei*. In this study, individual lizards were placed on rock outcroppings 1.5 to 3 m from shore. Their behavior was observed and 37% of all trials resulted in individuals leaping into the ocean and swimming or floating to shore. Schoener and Schoener (1983) suggest that, "Results support the hypothesis that lizards will leave islands on their own volition if those islands are inhospitable enough." They also propose that nearly all short-distance dispersals occurred during and immediately after hurricanes when lizards are most likely to be washed into the water (Schoener and Schoener, 1984).

Many evolutionary strategies have developed to aid in floatation. Some pacific species of the lizard family *Gekkonidae* have tubercular or granular scales that form spaces and retain pockets of air that may act as a natural "life jacket" (Schoener and Schoener, 1984). Some lizards have decreased surface tension around the central regions of the body which affects buoyancy thus

keeping their head and upper body above the water level. Yet, other species may gulp air to help them float. Schoener and Schoener (1984) tested the ability of *A. sagrei* to float in saltwater over a 24 h period. All individuals completed a one hour test period. The rate of success of floating decreased linearly with increasing time, with 30% being able to complete 24 h of floating. Therefore, a lizard jumping into the sea could conceivably reach an island, if currents were pulling in the right direction (Schoener and Schoener, 1983).

Although floating in seawater may be a possible option for the dispersal of lizards, this would not be a viable means of dispersal for frogs. In the case of frogs, floatation would necessitate the use of rafts.

During heavy rains animals often seek refuge in vegetation. As rivers rise and vegetation is torn away from the banks of rivers, rafts are created that may contain and then sweep animals downstream (Figure 3). King (1962) observed "rafts" floating pass a given point in the Rio Tortugero in Costa Rica. The amount of material ranged from 0.15 to 305 m² of vegetation per minute. King (1962) states, "If the whole year is considered similar to the seven weeks of observation, and if the total number of rivers entering the Caribbean from Central and South America is considered, the square feet of rafting material entering the Caribbean each year must be impressive."

Many rafts were torn apart by waves and eddies as they entered the mouth of a river. However, if the surf was low or if there was an off shore wind to blow a raft through the surf, rafts would float out to sea. Once in the open ocean, water hyacinth rafts would last two to three days and hyacinth/grass rafts would last an additional several days.

Heatwole and Levin (1972) provide data on the frequency of finding individual organisms on rafts. Of 59 pieces of flotsam (floating debris) picked up at sea, 25% contained live terrestrial animals, 21% had two species, 6% had three or more, and one contained 12 species. In 22% of flotsam a number of conspecific individuals occurred on the same drift item. Termites, ants, lizards, snakes, toads, mammals and a crocodile have been found on flotsam.

Henderson and Powell (1999) propose that all species that successfully colonized the islands of the Caribbean originated in "coastal habitats, forest edges, and other open situations making them more tolerant of high ambient temperatures and sun-drenched habitats than, for example, forest-dwelling species." Such an increased tolerance would facilitate the ability to survive a prolonged over-the-water journey. For example, some species of Puerto Rican anoles appear to have a high tolerance to saltwater, with a body impermeable to water (Schoener and Schoener, 1984). In addition, if rafting occurred during heavy rains, the possibility of desiccation and predation by birds may be greatly reduced.

Although no comprehensive study addressing the rate



Figure 3. Water hyacinth raft, Costa Rica.

of success of rafting from one island to another was found, there are accounts of successful rafting. In 1828, a boa constrictor, drifted to St. Vincent on the trunk of a cedar tree (Guilding, 1828). Apparently it rafted 250 miles from the Orinoco River. In another case, an alligator was carried on a tree trunk from South America to Barbados in 1886 (Fielden, 1889).

Another report lends credibility to the possibility of natural dispersion via rafting (Censky et al., 1998). In 1995, at least 15 green iguanas (*Iguana iguana*), males and females, were observed arriving on Anguilla after floating ashore on a mat of logs and uprooted trees. Iguanas were also found on Scrub Island (off Anguilla) and Barbuda. This occurred after Hurricanes Luis and Marilyn crossed the eastern Caribbean. This species had previously never been identified on any of these islands and is believed to have originated on Guadeloupe.

Myers (1953) describes another means of dispersal: "Except by the hand of man, two methods are available, flotation and wind-dispersal. Wind dispersal is available only to smaller animals which may be borne aloft by the wind or blown by the storm winds of high velocity, often in pieces of vegetation." Despite the fact that it seems improbable that frogs would be dispersed by winds, there have been reports of such events throughout history. McAfee (1917) wrote, "The idea of organic matter and particularly of living things raining down from the sky, on first thought, is hard to entertain. There have been recorded in all periods of historic time, however, showers of one kind or another of animals and plants or their products: showers of hay, of grain, or manna, of blood, of fishes, of frogs, and even of rats."

Two spectacular accounts involving flying or raining frogs can be found in the historical literature (McAfee, 1917): "During the storm that raged with considerable fury in Birmingham (England) on Wednesday morning, June 30 (1892), a shower of frogs fell in the suburb of Moseley. They were found scattered about several gardens. Almost white in color, they had evidently been absorbed in a small waterspout that was driven over Birmingham

by the tempest." And: "In Paeonia and Dardania [Greece] (200 AD), it has, they say, before now rained frogs, and so great has been the number of these frogs that the houses and the roads have been full with them; and shutting up their houses endured the pest; but when they did no good, but found that all their vessels were filled with them, and the frogs were found to be boiled up and roasted with everything they ate, and when besides all this they could not make use of any water, nor put their feet on the ground for the heaps of frogs that were everywhere, and were annoyed also by the smell of those that died, they fled the country."

One last possible means for the dispersal of frogs in the Caribbean is artificial dispersal (or transport) by humans. Pre-Columbian Amerindians traveled maritime routes throughout the Caribbean. Amerindians from the Orinoco region of South America reached the Lesser Antilles as early as 2000 BC and continued their expansion into the Greater Antilles (Steadman et al., 1984). At the time of Columbus' arrival the Taino, Hatabey and Carib cultures were established throughout the Caribbean. As observed in the carvings and pottery of Amerindians, frogs were of symbolic value to the cultures of the Amerindians (Rouse, 1992).

Honeychurch (2002) investigated the role of the frog in traditional Carib culture. "The Carib, like their other Amerindian ancestors who lived on the islands before them, divided the year into two. One half of the year was male. The other half of the year was female. The male was dry. The female was wet. The man was represented by the bat. The woman by the frog, the dry season was the time of the Bat Man. The wet season was the time of the Frog Woman. June 21, is the time of the Frog Woman. The wet season is beginning and frogs come out when it rains. They produce many eggs and the Frog Woman represents fertility.....Under the spirit of the Frog Woman it is the task of the female to plant the crops."

Images of frogs commonly occur in Pre-Columbian art. Lesure (2000) assessed clay figures and effigies from the Mazatán area of Mesoamerica dated between 1400 and 1000 BC. He compared the kinds of reptiles and amphibians represented in art to the frequencies of the same animals occurring in faunal remains. "Toads" were found in 72% of effigies but were completely absent from faunal remains.

Images of frogs were carved into rocks in the form of petroglyphs, depictions are found on pottery, and in jewelry (Figures 4 and 5). Images of the Frog Woman, the Tainos refer to her as Atabey or Attabeira, can be found throughout the Caribbean, Central America, and South America. The Kalinago people and other Caribs crafted her in stone, bone, shell and clay as half frog and half woman (Figure 6). "Her hands and feet are webbed like a frog. She faces us with her anus and legs wide apart like the limbs of a frog. Her navel is prominent at the centre of every image made of her. Her vagina is exposed. She is ready for sex (Honeychurch, 2002)".

A variety of frogs provided an essential food source for



Figure 4. Toad effigy vessel – earthenware – Veracruz culture – 1st century.



Figure 6. Stone carving depicting the Frog Woman.



Figure 5. Frog pendant – cast gold – Costa Rica – 11th to 16th century.

the people who brought them to the Caribbean. Paintings and carvings found in South America show frogs being sold in markets (Figure 7). It is known that frogs were consumed by the Aztec, Inca and Maya. The Maya ate a frog called the *uo* (*Leptodactylus* spp.), which was a source of fat, and the Aztec, not only ate adult frogs, but the tadpoles (Coe, 1994). They are considered a delicacy and *L. fallax* was the national dish of Dominica.



Figure 7. Ceramic vase. Pre-Columbian. Woman holding frog.

Historical literature depicts a strategy used by early maritime travelers of transporting a variety of animals to islands to establish ready food supplies. Portuguese sailors released rabbits, pigs, sheep and monkeys (*Macaca fascicularis*) on the island of Mauritius around 1528 (Sussman and Tattersall, 1981). Endemic West Indian animals, such as the agouti and feral pig, were carried by aboriginal peoples from South America to the islands of the Caribbean (Olson, 1982; Steadman et al., 1984). On many islands iguana (*Iguana iguana*) (Grant, 1937) and red-footed tortoise (*Geochelone carbonaria*) (MacLean, 1982) are considered as viable food sources and were likely transported to the Caribbean by the Amerindians.

Consequently, and as others have suggested (Barbour, 1912; Barrau, 1978; Kaiser and Henderson, 1994), it is highly feasible that the Amerindians introduced *L. fallax*'s ancestor as a food supply to various islands in the Caribbean.

Barbour (1912), believing *L. pentadactylus* and *L. fallax* to be the same species (*L. fallax* was not classified as a separate species until 1923) wrote, "This species, with an enormous distribution over the South American mainland, has been recorded from but three West Indian islands, - Dominica, St. Kitts and St. Lucia. This distribution strongly suggests an artificial introduction as an article of food. It may, however, have been extirpated upon other islands where it once occurred for this very reason". It is then confusing why Barbour in the same text would write, "An argument against their artificial introduction, we may cite Father Labat, who, in his accurate and engrossing narrative entitle 'Nouveau voyage aux iles d'Amerique,' [in French] informs us that, 'In Martinique and on a few other islands one finds the most beautiful frogs in the world, they are called toads because their appearance resembles those found in Europe, that is their skin is grey with yellow and black spots or stripes; they don't stay in water, but in the woods where they crow very loud, especially at night. Their flesh is white, tender and delicate. Only the head is discarded.'" This description does accurately describe *L. fallax*, and there does not appear to be any portion of Father Labat's statement that would argue against introduction.

Kaiser and Henderson (1994) 'speculate' that Amerindian settlers introduced this frog and support their speculation by citing Barrau (1978). In this original French text, Barrau describes a situation of over-hunting and the effects of the introduction of domesticated animals (pets, pigs, bovines) to Martinique, "The following species became extinct or endangered: agouti *Daysprocta*, the giant frog *Leptodactylus*, the iguane *Iguana* - (which was so popular that the island was named after it "Luanacaera") le lamantin *Trichechus* which was found along the coasts, the large "pilor" rat". There is no other mention of frogs or Amerindians. It is possible that this and other mistranslations of original text have led to confusion regarding the location of particular species on

various islands.

DISCUSSION

Reconstructing the historical geographic distribution of *L. fallax* is problematic. In some cases, earlier conclusions have been based on inaccurate translations. In others, speculations were made without substantive evidence. However, historical accounts and museum collections support the reconstruction of the historical distribution of *L. fallax* to include the Commonwealth of Dominica, Montserrat, St. Kitts, Martinique, and possibly St. Lucia, Antigua, Guadeloupe and Nevis. Due to recent attempts to introduce the species, it may have briefly occurred on Puerto Rico. It is unlikely that it ever occurred on the Dominican Republic, Jamaica, or Trinidad. Vicariance as a mode of introduction for any Lesser Antillean species is not supported by paleogeographic data. Dispersal via rafting is supported for some species, but it is highly unlikely in the case of *L. fallax* for several reasons. First, King et al. (2005) showed through antimicrobial peptides that *L. fallax* and *L. pentadactylus* share a common ancestor. Because of the range of *L. pentadactylus*, and theoretically that of the ancestor, rafts would have had to originate from northern or north-eastern South America to reach the Caribbean. By observing the combined movements of southern and northern equatorial currents, trade winds and buoy trajectories (Molinari et al., 1981), it is noted that the ocean currents in this region move in a north-westerly direction. Rafts originating from South America, under normal weather conditions, would not reach the Lesser Antilles.

Second, it is possible that non-normal weather conditions (hurricanes) could carry a raft to the Lesser Antilles. But the current distribution of *L. fallax* is on the west coast and central portions of Montserrat and the Commonwealth of Dominica. Hurricanes would deliver rafts to the east coast.

Third, successful rafting would necessitate an ocean voyage of hundreds of miles and a time frame of between two and four weeks (Censky, 1998). Due to the permeability of amphibian skin, it is not probable that a frog could withstand such a trip.

And lastly, although some historical references attest to the possibility of "flying" as a dispersal mechanism of frogs, the probability of such a natural phenomenon makes this an unlikely scenario.

Introduction of the ancestor of *L. fallax* by Pre-Columbian Amerindians as they colonized these islands appear to be the most likely mechanism. Frogs were considered a food staple and this type of strategy has been employed by these and other peoples during island colonizing events. As reported in Barbour, 1912, Father Labat said, "Their flesh is white, tender and delicate". Recent discussions have occurred on whether or not *L. fallax* should be reintroduced to islands on which it may

have previously been found. Two terms need to be appropriately defined: introduction and naturalization. Introduction is “the deliberate or accidental release of a species into a country in which it is not known to have occurred within historic times (Lever 2003)”. Naturalization is, “the establishment in the wild of self-maintaining and self-perpetuating populations of an introduced exotic species unsupported by, and independent of humans (Lever 2003)”. The ancestor of *L. fallax* can clearly be classified as an “introduced exotic” but at some point, once it became established, it would have become a “naturalized” species.

It must be remembered that ecosystems are not static and change with time. As biologists and conservationists, we must decide at what point in time we desire to preserve a biotic community. For example, suppose a prairie had been a forest before bison migrated and destroyed the trees. Do we maintain the land as a prairie or do we try to return it to the previous state of a forest? The same can be asked about the islands of the Lesser Antilles: Do we return the islands to a state before *L. fallax* was introduced or after introduction but before local extinction?

A real world situation occurred on the Hawaiian island of Nihoa (Lockwood and Latchinsky, 2008). In this case, the government hired pest managers to eliminate the gray bird grasshopper (*Schistocerca nitens*) from the island. The insect was first observed in 1977. But how did it arrive on Nihoa? Did it “stowaway” on some type of vessel or was it carried by wind from another location? Accidentally introduced by humans or a natural occurring pioneer event? Should this make a difference? And why was this species being considered for eradication? Why not other exotic species? Yes, it was destroying local vegetation, but the endangered Nihoa miller bird (*Acrocephalus familiaris*) was recovering due to the grasshopper as a food source. Are the plant species more “valuable” than the miller bird or the grasshopper? So why choose a time frame in the history of Nihoa before the arrival of the grasshopper? These are all questions that must be answered. In the end, no action was taken- not because a decision was made to save the grasshopper, but because no method of extermination could be found that would not harm other species.

Based on historical biogeography, the ancestor of *L. fallax* should be considered an introduced, exotic species on each of the islands on which it is and was found. Since it is not an endemic species, a strict point of view would dictate that it should not be reintroduced to any of the islands. But the islands of the Lesser Antilles are volcanic in origin and, therefore, no species is native. Such islands are colonized by immigrating pioneering species whether naturally dispersed or, as in this case, artificially introduced. If this line of reasoning is followed, then can any species, in an island ecosystem, ever be considered a native?

More importantly, is the present frog the same as the ancestral frog? *L. fallax* currently is not found on any mainland masses. Therefore, it has either become extinct

from the mainland or it may represent a speciation event that occurred after the original frogs were transported to the islands. Easteal (1981) concluded, “The colonization of a new area by a species may be a major event in the evolution of that species and can result in the formation of a new species. This can occur if the colonizing event itself causes isolation between different populations, which then diverge genetically as the result of micro-evolutionary processes or if the colonizing event itself, in cases where it involves few individuals, brings about a radical genetic change in the founding population”.

Regardless, whether it is an ancestral or new species, this frog is found nowhere else in the world except on these few islands and, therefore, should be considered a recent endemic to the Lesser Antilles. Its survival may be dependent on its reintroduction to the islands of St. Kitts/Nevis, Antigua, Guadeloupe, Martinique, St. Lucia and the careful management of the frogs on all the islands. All attempts should be made to establish it to its historical home range.

This research demonstrates that without a thorough review of historical documents and museum collections, the historical distribution of a species may be impossible to ascertain. Consideration of the present and past geographical distribution of a species, the means by which a species first occurred, and current threats to its continued existence must all be assessed in order to delineate appropriate and viable conservation strategies.

Conflict of interests

The authors have not declared any conflict of interests.

ACKNOWLEDGEMENTS

We would like to acknowledge the following people for their help and support. Anne-Sophie Blank of the Department of Anthropology and Languages at the University of Missouri – St. Louis for her translation of the original French documents. John Simmons of the University of Kansas – Lawrence for allowing frog specimens to be examined at the Natural History Museum. Patricia Neitfeld of the National Museum of the American Indian for permitting the examination of Amerindian artifacts. Lennox Honeychurch, historian of the Commonwealth of Dominica, for information regarding Amerindian tribes. The Forestry Department of the Commonwealth of Dominica for information regarding the status and natural history of the mountain chicken frog.

REFERENCES

- Barbour T (1912). A contribution to the zoogeography of the East Indian Islands. Mem. Mus. Comp. Zool. Harvard College 44(1):251.
- Barbour T (1937). Third list of Antillean reptiles and amphibians. Bull. Mus. Comp. Zool. Harvard College 82(2):79-107.

- Barrau J (1978). Biogeographie ou ethno-biogeographie? Une reflexion a propos de La Martinique, et plus generelement des Petites Antilles. *Compt'e rendu des s'eances de la Soci'et'e de biog'eographie* 7: 83-96.
- California Academy of Sciences (2014). <http://research.calacademy.org/>.
- Censky EJ (1998). Over-water dispersal of lizards due to hurricanes. *Nature* 395:556.
- Coe D (1994). *America's First Cuisines*. University of Texas Press, Austin. pp 156-157.
- Crisci JV, Katinas L, Posadas P (2003). *Historical Biogeography: An Introduction*. Harvard University Press, Cambridge.
- Duellman WE (1999). The West Indies and Middle America: Contrasting Origins and Diversity. In: Crother B, editor. *Caribbean Amphibians and Reptiles*. Academic Press, San Diego, pp 359-363.
- Easteal S (1981). The history of introductions of *Bufo marinus* (Amphibia: Anura): A natural experiment in evolution. *Biol. J. Linn. Soc.* 16:93-113.
- Fielden HW (1889). Notes on the reptiles of Barbados. *Zoologist*, ser.3, 13:295-298.
- Gibson RC, Buley KR (2004). Maternal care and obligatory oophagy in *Leptodactylus fallax*: A new reproductive mode in frogs. *Copeia* 1:128-135.
- Grant C (1937). Herpetological notes with new species from the American and British Virgin Islands. *J. Agric. Univ. P. R.* 21:503-522.
- Groome JR (1970). *A Natural History of the Island of Grenada, West Indies*. Caribbean Printers Limited, p. 32.
- Guilding L (1828). Observations on the Zoology of the Caribbean Islands. *Zool. J.* 3:403-408.
- Harvard University Museum of Comparative Zoology. 2008. www.collections.mcz.harvard.edu/Herp/AmphDetail.cfm.
- Henderson RW, Powell R. (1999). West Indian Herpetoecology. In: Crother B, editor. *Caribbean Amphibians and Reptiles*. San Diego: Academic Press, San Diego, pp. 263-264.
- Hetwolfe H, Levins R (1972). Biogeography of the Puerto Rican Bank: Flotsam transport of terrestrial animals. *Ecology* 53(1):112-117.
- Heyer WR (1979). Systematics of the *Leptodactylus pentadactylus* species group of the frog genus *Leptodactylus* (Amphibia: Leptodactylidae). *Smithson. Contrib. Zool.* 0(301):1-41.
- Honeychurch L. 2002. The leap at Sauteurs: The lost cosmology of indigenous Grenada. www.cavehill.uwi.edu/bnccde/grenada/conferences/papers/LH.
- Kaiser H (1994). *Leptodactylus fallax* Mueller Mountain Chicken, Crapaud. *Catalogue of American Amphibians and Reptiles* 0(583):1-3.
- Kaiser H, Henderson RW (1994). The conservation status of Lesser Antillean frogs. *Herp. Nat. Hist.* 2(2):41-56.
- King JD, Al-Ghaferi N, Abraham B, Sonnevend A, LePrince J, Nielsen PF, Conlon JM (2005). Pentadactylin: An antimicrobial peptide from the skin secretions of the South American bullfrog *Leptodactylus pentadactylus*. *Comp. Biochem. Physiol., Part C: Toxicol. Pharmacol.* 141:393-397.
- King W (1962). The occurrence of rafts for dispersal of land animals into the West Indies. *Q. J. Fla. Acad. Sci.* 25:45-52.
- Lescure J (1979). Etude taxinomique et eco-ethologique d'un amphibien des petites Antilles. *Bulletin du Musaeum national d'histoire naturelle, Section A, zoologie, biologie et aecologie animals* 1(4):757-774.
- Lescure J (1983). Introductions passives et actives de reptiles et d'amphibiens dans Les Antilles et Les Guyanes. *Compt'e rendu des s'eances de la Soci'et'e de biog'eographie* 59:59-70.
- Lesure RG (2000). Animal imagery, cultural unities, and ideologies of inequality in early formative Mesoamerica. In: Clark JE, Pye ME, editors. *Olmec Art and Archaeology in Meso America*. Yale University Press, New Haven and London, pp. 193-215.
- Lever C (2003). Preface. In: *Naturalized reptiles and amphibians of the world*. Oxford University Press, Oxford, p. vi.
- Lockwood JA, Latchinsky (2008). Confessions of an entomological hit man. *Conservation* 9(3):14-19.
- MacLean WP (1982). *Reptiles and Amphibians of the Virgin Islands*. Macmillian Caribbean, London, pp. 21-22.
- Malhotra A, Thorpe RS (1999). *Reptiles and Amphibians of the Eastern Caribbean*. MacMillian Education Ltd. London.
- McAfee L (1917). Showers of organic matter. *Mon. Weather Rev.* 45:217-224.
- Molinari RL, Spillane M., Brooks I, Atwood D, Duckett C (1981). Surface Currents in the Caribbean Sea as Deduced from Lagrangian Observations. *J. Geophys. Res.* 86(C7): 6537-6542.
- Myers GS (1953). Ability of amphibians to cross sea barriers with especial reference to Pacific zoogeography. *Proc. Seventh Pac. Sci. Congr.* 4:19-26.
- Olson SL (1982). Biological Archeology in the West Indies. *Fla. Anthropologist* 35(4):162-168.
- Proctor GR (1973). A saga of frogs. *Jamaica J.* 7(4):29-31.
- Rouse I (1992). *The Tainos: Rise and Decline of the People Who Greeted Columbus*. Yale University Press, New Haven and London, pp. 8-32.
- Schoener A, Schoener TW (1983). On the voluntary departure of lizards from very small islands. In: Rhodin AGH, Miyata K, editors. *Advances in Herpetology and Evolutionary Biology*. Cambridge: Harvard Press pp. 491-498.
- Schoener A, Schoener TW (1984). Experiments on dispersal: Short-term floatation of insular anoles with a review of similar abilities in other terrestrial animals. *Oecologia* 63:289-294.
- Steadman DW, Pregill GK, Olson SL (1984). Fossil vertebrates from Antigua, Lesser Antilles: Evidence for late Holocene human-caused extinctions in the West Indies. *Proc. Natl. Acad. Sci. U. S. A.* 81:4448-4451.
- Sussman RW, Tattersall I (1981). Behavior and Ecology of *Macaca fascicularis* in Mauritius: A preliminary study. *Primates* 22:192-205.