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The history of introductions of *Bufo marinus* (Amphibia : Anura); a natural experiment in evolution

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The Central American toad, *Bufo marinus*, has been extensively introduced throughout the Caribbean and Pacific regions and is now one of the most widespread of terrestrial vertebrates. Details, such as the sources and dates of introductions, the number of individuals introduced and the fates of the introduced populations have been documented and are described. The availability of this historical information makes the introductions of great potential value as a series of evolutionary experiments. They can be used to study the way in which allopatric populations diverge genetically and the effects of population bottlenecks of known size on the genetic characteristics of populations, and to examine theories of rapid speciation caused by genetic revolutions associated with founder events.

KEY WORDS:—Biogeography – biological control agent – *Bufo marinus* – colonizing species – evolution – experiment – history – introduced species – speciation – toad.

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DEDICATION

The potential significance of the history of introductions of *Bufo marinus* was first perceived, in a general sense, by the late Michael Sabath. This paper is dedicated to his memory.

INTRODUCTION

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 new species. This can occur if the colonizing event causes isolation between different populations, which then diverge genetically as the result of micro-evolutionary processes (Mayr, 1963), or if the colonizing event itself, in cases where it involves very few individuals, brings about a radical genetic change in the founding population (Mayr, 1954; Carson, 1968, 1975, 1978; Templeton, 1980).

Colonization can result from natural events or from the deliberate or accidental introduction of a species by humans. Species introductions resulting from human intervention have occurred frequently during the past few thousand years, and have caused significant alterations to the distribution of the earth's biota (Elton, 1958). These transplantations of species are of great interest. They are, in effect, field experiments in evolution and as Waddington (1965) points out are "potentially much more informative than most laboratory experimental work, since they have faced the introduced species, not with some simple defined change in selection conditions, but with a whole new ecological system in which the species has to find a place for itself".

Unfortunately, in most cases the important details of the introductions have not been documented—the experiments have proceeded unobserved. There are some notable exceptions. One of the most extensive, and probably the best documented history of, introductions of any species is that of the marine toad, *Bufo marinus* (L.). *Bufo marinus* occurs naturally in Mexico, Central and tropical South America, and on the island of Trinidad. Its natural range is shown in Fig. 1. It extends from approximately 27°N latitude in northwestern Mexico to approximately 10°S latitude in central Brazil (Zug & Zug, 1979). During the past 200 years, the species has been deliberately introduced to many places in the Caribbean and Pacific regions, mainly as a biological control agent and mainly by the sugar cane industry.

Because of their deliberate nature, many of the introductions are individually well documented. There is, however, no comprehensive account of their entire history. Three accounts do exist (Oliver, 1949; Honnegger, 1970; Tyler, 1975); all are very incomplete and contain little detailed information. The purpose of the present paper is to provide a detailed description of the history of introductions of *B. marinus,* particularly of those aspects which may have been important in the evolution of the species. These include the sources and dates of the introductions, the numbers of individuals introduced, the ways in which the parent populations were sampled and the fates of the introduced populations. The fact that details of this kind are documented for the history of introductions of *B. marinus* makes it of great potential significance as an evolutionary experiment and this potential will be discussed.

Figure 1. Natural distribution of *B. marinus*, from Zug & Zug (1979).

METHODS AND SOURCES

The information contained in this paper is derived from published literature, unpublished documents and museum records. If museum records exist from places other than on continental America and the immediately adjacent islands (e.g. Trinidad), it is assumed that the species was introduced to those places, even if there is no actual record of an introduction. Every museum in Europe, North America, South America, Asia and Australia with herpetological collections (based on the listing in *Herpetological Review,* 1978) was requested to provide records of their collections of *B. marinus*. All museums responded, and most provided information, although one major museum, the Field Museum of Natural History, Chicago, did not provide copies of its holdings. The identification of specimens in museum collections has not been verified. I have depended on the curatorial staff of the museums for identification.

Where conflicting reports about the details of introductions exist, these are discussed. In general, the earliest report is taken as the most accurate one, official records of introductions are taken to be more precise than published accounts, and reports made by the people who were directly involved in making the introductions are preferred over other reports.

THE HISTORY OF INTRODUCTIONS

Figures 2, 3 & 4 summarize the major events described in detail in this section. Appendix 1 is a list of all places to which *B. marinus* is known to have been introduced. Not all the records of the species from these places are included in the Appendix. In most cases, the records or reports providing the most information about the introductions of the species are listed with, in some cases, one or more additional corroborative sources. Complete listings of records of *B. marinus* in Australia, the Pacific and the Caribbean are contained in Boughton & Sabath (1980) and Easteal *et al.* (1981, a, b).

Martinique, Barbados and Jamaica

The first two reported introductions of *B. marinus* were from Cayenne, in French Guiana, to Martinique and from Martinique to Barbados. All that is known about these introductions is that they occurred before 1844 (Waite, 1901). Schomburg (1971) reports that the species was also introduced to Barbados from Guyana in approximately 1833; and Mungomery (1935a) states that "from French Guiana it [*B. marinus*] was introduced to Barbados prior to 1850...". Mungomery's comment occurs in a very cursory summation of the history of introductions and probably refers to introduction that occurred via Martinique. There were thus two separate introductions to Barbados, one from Guyana and the other from French Guiana via Martinique, however, neither the exact dates nor the numbers of individuals involved in either introduction is known.

The toads survived in Barbados and in 1848 were present in large numbers all over the island (Schomburg, 1971). By 1916, they had become less numerous (Clark, 1916); and by 1933 their numbers had declined dramatically (Hawaiian Sugar Planter's Association [HSPA], unpubl. documents), due to the drying up or oiling over of breeding ponds induced as part of an anti-malarial programme on the island (HSPA unpubl. documents; Anonymous, 1936; Tucker, 1940). Grant (1959) reported that the species was "of such spotty occurrence as to appear scarce in comparison to its number on other West Indian islands".

In 1844, an introduction was made to Jamaica from Barbados (Waite, 1901); it is not known how many individuals were introduced. Honnegger (1970) cites Waite (1901) as stating that an introduction was made to Jamaica in 1844 from Guyana. Waite, however, stated that the introduction was from Barbados and not from Guyana as Honnegger suggests.

Puerto Rico

The species was introduced to Puerto Rico from Barbados and Jamaica. The first introduction was made in 1920 from Barbados (Wolcott, 1934; Danforth, 1925; May, 1926; Dexter, 1932; Tucker & Wolcott, 1935). Tucker & Wolcott (1935) state that the number introduced was less than two dozen and both Danforth (1925) and Wolcott (1950) put it at 12. Wolcott (1934) reports that all the introduced toads were collected from the same locality (feeding under a beehive). The shipment was released at the Puerto Rican Agricultural Experiment Station at Mayaguez (May, 1926). A second introduction of 40 individuals was made to Puerto Rico from Jamaica in 1928–24 (Dexter, 1932; Volkenberg, 1935; Wolcott, 1935). They were released at Rio Piedras near San Juan (Wolcott, 1950).

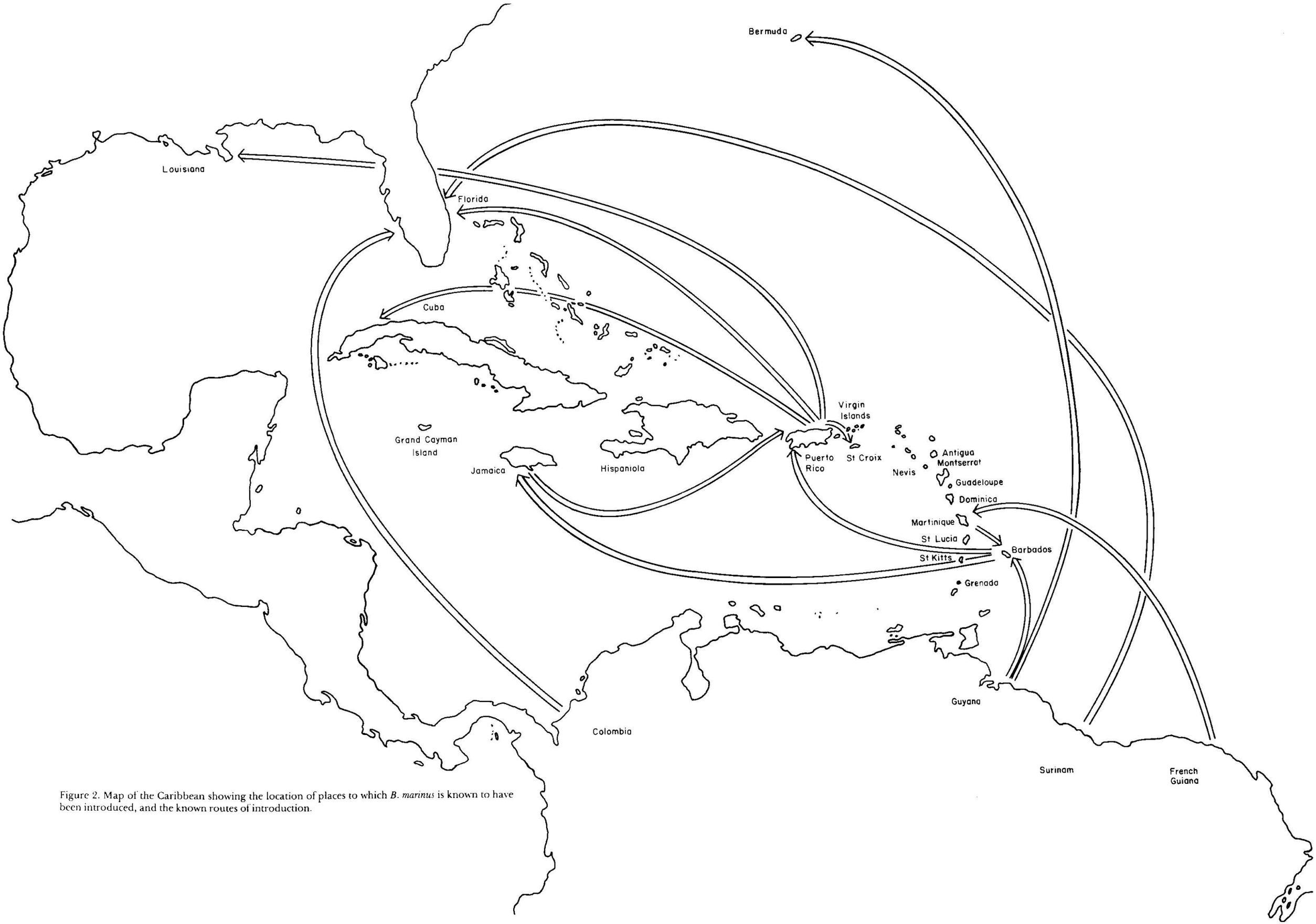

Figure 2. Map of the Caribbean showing the location of places to which *B. marinus* is known to have been introduced, and the known routes of introduction.

Danforth (1925) reports that D. W. May imported toads to Puerto Rico from Trinidad in 1920 and released them at the Experimental Station at Mayaguez. May (1926) does not mention that he made such an introduction and since the date and site of release of this reported introduction are the same as May's introduction from Barbados, it seems likely that Danforth is in fact referring to the Barbados introduction, and that toads were not imported to Puerto Rico from Trinidad. Tyler (1975), in his summary of the history of introductions, lists an introduction to Puerto Rico from Trinidad in 1920. He apparently refers to Danforth's report which I presume to be mistaken.

Both releases in Puerto Rico were successful. Wolcott (1935) reports that in less than a year toads were numerous about the points of release, and Tucker & Wolcott (1935) report that the toads were able to "reproduce to an enormous extent". Within ten years of the original introduction, toads had spread throughout the coastal regions of the island, and were also found infrequently in

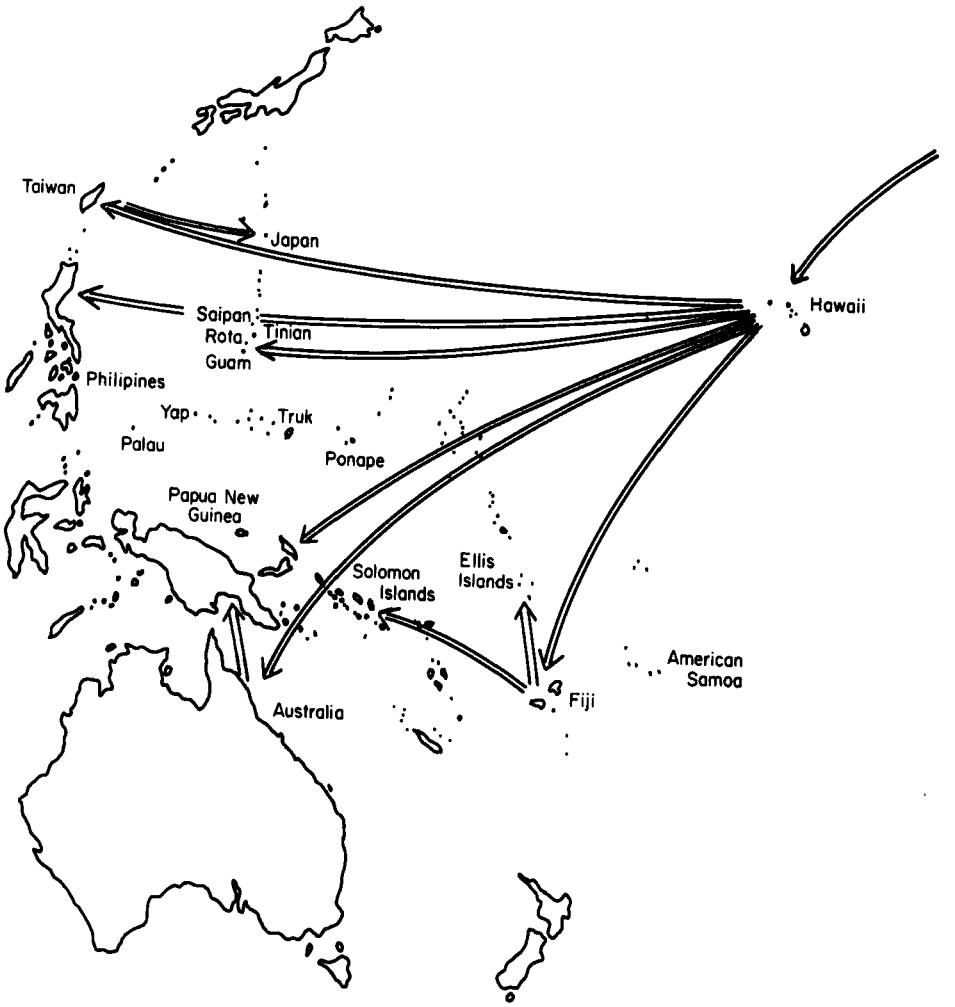

Figure 3. Map of the West Pacific showing the location of places to which *B. marinus* is known to have been introduced, and the known routes of introduction.

the interior (Wolcott, 1935). Much of this rapid spread was due to man, although few records were made of deliberate transfers (Wolcott, 1935). Several hundreds were taken from Cartegena lagoon near Lajas and released at Isabela (Wolcott, 1935). Shipments of 2–2000 were made from the Mayaguez release to various parts of the island, including a single shipment to Aguirre Sugar Company consisting of 1114 individuals (Leonard, 1933). Wolcott (1950) proposed that the descendents of the Jamaican introduction populated the eastern and northern coastal areas of the island, and that the progeny of those from Barbados occupied the western and southern sections. This proposal is consistent with the geographical positions of the initial release sites. In 1933, the species had become numerous throughout its distribution, but by 1935 its abundance had declined (Wolcott, 1935) and, subsequently, the population numbers apparently remained at a relatively low level (Wolcott, 1937, 1950).

Other Caribbean islands

There are several other islands in the Caribbean to which *B. marinus* has been introduced, although little is known about most of these introductions.

Buide (1967) reports that the species was introduced to Cuba from Puerto Rico in 1946, and that it has since become extinct there.

The species was introduced to Antigua, and Lynn (1957) suggests that the introduction occurred after 1934, as Dunn (1934) specifically remarked on its absence from the island. This seems unlikely, since Clark (1916) reported its presence there and stated that by 1916 it had become less numerous than it had once been on the island. It is possible that the population derived from the earlier introduction had become extinct by 1934 and that another introduction was made after that date.

An introduction was made to St Croix from Puerto Rico in October 1934, and released at the Agricultural Experiment Station (Grant, 1936). Within two years of its introduction there it had spread 1½ miles east and 6 miles west (Grant, 1936).

The species has also been introduced to Grenada (Barbour, 1914), St Lucia, St Kitts, Nevis, Montserrat (Barbour, 1914, 1937), St Thomas, Guadeloupe, Hispaniola (both in Haiti (Williams, Shreve & Humphrey, 1963) and the Dominican Republic (Cochran, 1941)), St Vincent, St Christopher (Schwartz & Thomas, 1975) and Vieques (Heatwole, Sade & Hildreth, 1963), and there are museum specimens of the species collected from Dominica, but almost no information is available about any of these introductions. Clark (1916) reported that the species had become extinct on St Vincent. Philibosian & Yutema (1976) suggest that the introduction to St Thomas was made either from Puerto Rico or St Croix in the early 1940's.

Bermuda

Around 1855 the species was introduced to Bermuda from Demarara in Guyana (Waite, 1901). Waite (1901) reports that Captain Vesey, who instigated the introduction, released "about two dozen" individuals in his garden. Before he was able to do this, however, some of the shipment was "purloined . . . by a native" on its way from Hamilton, its port of arrival, to Captain Vasey's residence in

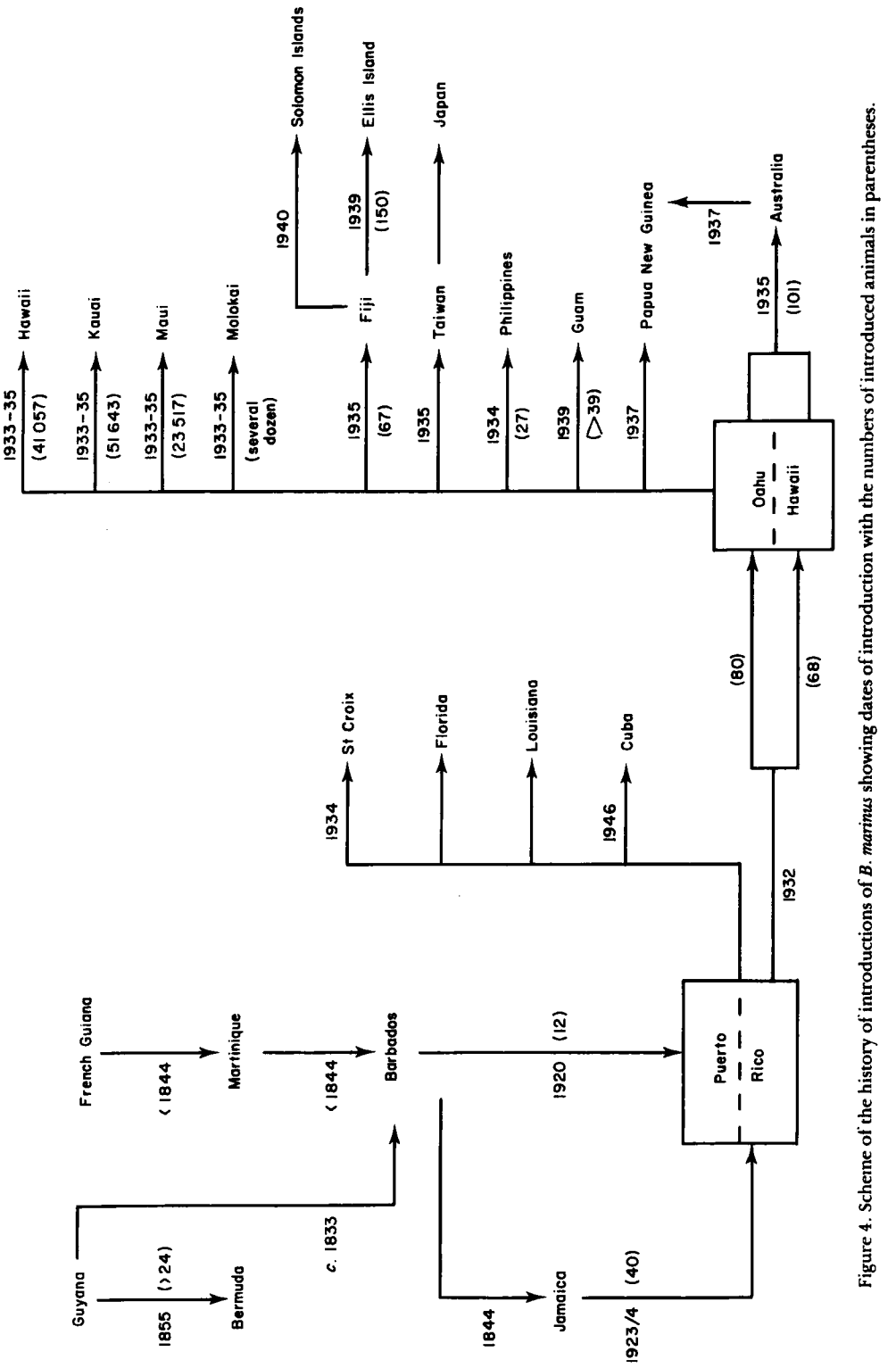

Figure 4. Scheme of the history of introductions of *B. marinus* showing dates of introduction with the numbers of introduced animals in parentheses.

Devonshire. There is no way of determining the extent of the theft and therefore no way of knowing how many individuals were introduced. The species has survived in Bermuda and is now found on all the larger islands and some of the smaller ones, although it is absent on Ireland Island (Wingate, 1965).

Following introduction to Bermuda, the species underwent an initial population explosion followed by a decline (Wingate, 1965). Pope (1917) reported that several years after their first appearance, the toads had so greatly increased in number that "in the spring the roads near their spawning places were not infrequently made black by hordes of the animals", but that their numbers greatly decreased subsequently.

United States mainland

On the US mainland the species occurs naturally only in southern Texas (Taylor & Wright, 1932; Zug & Zug, 1979) but has been introduced to Louisiana and Florida.

There were several introductions made to Louisiana, at least one of which was from Puerto Rico (HSPA unpubl. documents). These documents state that these introductions were unsuccessful, although MacLean, Kellner & Dennis (1977) report the species as present in Grande Terre.

The first introduction to Florida was from Puerto Rico at some time before 1936. Two hundred individuals were introduced and released at Canal Point and Belle Glade, on the shores of Lake Okeechokee in the southern part of the state (Riemer, 1959). The second purposeful introduction was made, again from Puerto Rico, at some time before 1944, the release being made at Clewiston, also on the shore of Lake Okeechokee (Riemer, 1959). Additional introductions are alleged to have been made at Pensuco, 10 miles north west of Miami (Duellman & Schwartz, 1958), and on the west coast at the Bass Biological Laboratory at Englewood (Riemer, 1959). All these introductions are generally considered to have been unsuccessful (Riemer, 1959; Duellman & Schwartz, 1958; Krakauer, 1968, 1970).

By 1957, a population was established in the Miami area (Duellman & Schwartz, 1958, Riemer, 1959). This population was probably derived from approximately 100 individuals accidentally released before May 1955 at the Miami International Airport by an animal importer (King & Krakauer, 1966; Krakauer, 1968). The population remained for several years in the western part of Miami, close to the airport, but in 1958 started to appear in other areas (Krakauer, 1968). In 1963 and 1964 toads were deliberately released at Pembroke Park, Broward County, and at Kendall, Dade County, respectively (King & Krakauer, 1966). The individuals released at Kendall came from Surinam, all the other releases were of individuals from Colombia.

Following introduction and successful establishment, the toads became very abundant. Krakauer (1968) reports that the population increased to the extent that it became a public nuisance. In 1966, the distribution of the species extended from Homestead in southern Dade County, north to Pembroke Park and Hollywood in Broward County, and from the Intracoastal Waterway west to the Everglades (King & Krakauer, 1966).

Hawaii

An introduction of 149 individuals of the species was made to the Hawaiian island of Oahu from Puerto Rico in April 1932 (Pemberton, 1934); 68 were released in the Manoa Arboretum at the upper end of Manoa Valley and 80 were released in a taro patch adjoining the HSPA Waipio substation (Anonymous, 1932; Pemberton, 1933). The remaining one individual is unaccounted for. The toads were collected by C. E. Pemberton while he was attending the International Congress of Sugar Cane Technologists in San Juan. It is likely that he collected the toads in San Juan and that they were the progeny of the specimens introduced from Jamaica, since San Juan is in the north west of Puerto Rico, very close to Rio Piedras, where the Jamaican introduction was released.

If the toads introduced from Barbados were to have been included in the shipment made to Hawaii, the Barbados derived population would have had to have spread 175 km around the coast from Mayaguez, where it originated, to San Juan in the 12 years between its introduction in 1920 and the time of the shipment to Hawaii in 1932. Sabath (pers. comm.) estimated that the average linear rate of spread of *B. marinus* since its introduction to Queensland, Australia has been 9.3 km per annum. At this rate, it would have taken the toads 19 years to have spread to San Juan from Mayaguez, and they could therefore not have done so by 1932. It is possible that toads were accidentally taken from Mayaguez to the San Juan district, but unlikely that they were deliberately transported, since there were already toads present in the San Juan area. It is most probable that the 148 individuals taken to Hawaii were all descended from the 40 introduced to Puerto Rico from Jamaica in 1924.

Following introduction, both the Waipio and the Manoa populations flourished, and in August 1933 the HSPA started to spread the toads throughout the major Hawaiian islands. During the first year of the spread, almost all the toads came from the Waipio population (Pemberton, 1934; F. A. Bianchi, pers. comm.), and the location of this population makes it likely that it was the source of almost all the subsequent distributions (F. A. Bianchi, pers. comm.). Between August 1933 and July 1935, more than half a million toads were spread throughout the islands of Hawaii, Kauai, Maui, Molokai and Oahu (HSPA, unpubl. documents). Following introduction, the toads became very abundant (Pemberton, 1934; Mungomery, 1935a; Oliver & Shaw, 1953), but Oahu residents now report that they are less numerous than they once were.

Table 1 summarizes the details of the spread of *B. marinus* through the Hawaiian islands. A total of at least 633 872 were transported. The records are incomplete and do not include the destinations of many of the shipments. More than half are unaccounted for in this way. Of the 307 934 that are accounted for, by far the largest portion (191 717) were spread within Oahu; 41 057 were taken to Hawaii, 51 643 to Kauai, and 23 517 to Maui. Although there is no official record of introductions to Molokai, at least two shipments were sent there, each consisting of several dozen juvenile toads, during the time when shipments were being sent to the other major Hawaiian islands (F. A. Bianchi, pers. comm.).

In addition to providing the source for the spread of toads to the other Hawaiian islands, the Oahu population was the source of introductions to several other places in the Pacific region.

Table 1. Numbers of toads known to have been introduced to the major Hawaiian islands for every six month interval between August 1933 and July 1935. There are no records of toads distributed before or after these dates. The destinies of more than half (325 938) of the 633 872 toads distributed are not known. (Source: HSPA, unpubl. documents)

Island	Aug–Dec 1933	Jan–June 1934	July–Dec 1934	Jan–June 1935	Total
Hawaii	12	185	6000	34 860	41 057
Kauai	52	111	4000	47 480	51 643
Maui	67	0	7000	16 450	23 517
Molokai	0	0	0	0	Several dozen
Oahu	758	65 504	125 460	0	191 717
					307 934
Total	947	68 667	253 157	199 201	633 872
			Total unaccounted for		325 938

Micronesia, Taiwan and Japan

There were two separate introductions to Guam from Hawaii (HSPA, unpubl. documents). Thirty-nine individuals were imported in May 1937, and an unknown number was imported on 25 September of the same year. The introductions were successful and by 1939 the toads had been deliberately spread throughout the island and had become common in the lowland areas (HSPA, unpubl. documents).

Toads were also introduced to several other Micronesian islands. Stohler & Cooling (1945) and Downes (1948) report their presence on Tinian, Gressitt (1954) records them from Ponape, and Savage (1960) records them on the Palau islands. There are museum records from the Palau islands of Arakabesan, Kayangel and Koror, and from Yap and Saipan. There is no information about any of these introductions. Honneger (1970) cites Downes (1948) as stating that the introduction to Tinian was made from Hawaii at some time before 1945. However, Downes made no mention of when or from where the species was introduced to Tinian, but states that "the immediate source of the introduced stock is unknown to me". Honnegger (1970) also cites Savage (1960) as stating that the introduction to Palau was made from western Mexico, although Savage makes no such claim.

In 1935, an unknown number of toads was taken from Oahu, Hawaii to Taiwan (Lever, 1938), resulting in the successful establishment of the species there (Kaburaki, 1939). Toads are now also found on the island of Minami-Daitojima in the Ryuku Archipelago, Japan, and were possibly introduced there from Taiwan (Matsui, 1975).

Fiji, Ellis Islands, Solomon Islands and Samoa

Sixty-seven half grown and adult toads were introduced from Oahu, Hawaii, to the Fijian island of Vitu Levu in February 1936 (Jack, 1936; HSPA, unpubl. documents). They were maintained at Lautoka and allowed to breed. Breeding

commenced immediately and colonies (consisting, presumably, of tadpoles and/or juveniles) were released in May and June of that year in Suva, Nasium and Navuso, Viti Levu (Jack, 1936). Lever (1937) reports that a colony of tadpoles was released at Navua in September 1937, and that tadpoles and adults were sent from Viti Levu to Tavenui Island in May and September 1937, respectively. He also reports (Department of Agriculture, Fiji, unpubl. documents) that they were introduced to Rambi Island. By 1938 they had been spread throughout the main island of Vitu Levu, and to the islands of Vanua Levu, Tavenui, Rambi, Kadavu (Lever, 1938) and are now also found on Ovalau (J. C. Pernetta, pers. comm.).

In November 1939, 150 adult toads were sent from Suva, Fiji, to the Funafuti Atoll in the Ellis Islands, and from there they were taken to Vaitupu Atoll (Lever, 1942). It is not known if these introductions were successful. In February 1940, toads were sent from Fiji (presumably Viti Levu) to the Solomon Islands, where they were released on several islands including Guadelcanal (Lever, 1942). They are now present on at least six of the Solomon islands (see Appendix 1). Honnegger (1970) cites Brown (1952) as stating that an introduction was made to the Solomons from Hawaii in 1940, but Brown in fact made no such statement.

The species was also introduced to American Samoa (Simmonds, 1957; HSPA, unpubl. documents) but no information about the introduction is recorded.

Philippines

Bufo marinus was introduced to the Philippines from Oahu, Hawaii, in 1934 (Lever, 1938; Rabor, 1952; HSPA, unpubl. documents). The HSPA records of the shipment state that 27 half grown and adult toads, collected at Waipio, were introduced. Rabor (1952), however, reports that about 50 were introduced. His estimate, made 24 years after the event, is based on the recollections of the man responsible for making the introduction, Dr Merio, and not on official records. I take the HSPA record as the accurate estimate of the numbers introduced.

The toads were first released in Manila, and later deliberately spread throughout the island of Luzon. In 1935 or 1936 they were taken to Negros Island, and between 1936 and 1939 to Guimaras and Panay Islands. In 1949 and subsequently, they were taken from Negros to Mindanao Island (Rabor, 1952). The species apparently experienced a population explosion in many areas following introduction (Rabor, 1952; Alcala, 1957), but by 1957 on Negros Island, at least, the population had declined (Alcala, 1957).

Papua New Guinea

Bufo marinus was first introduced to Papua New Guinea from Hawaii in 1937 (Lever, 1942; Zug, Lindgren & Pippet, 1975; HSPA, unpubl. documents). The release was made at Karavat, New Britain and involved a large number of individuals (Commonwealth of Australia, 1938). There is also a record of an introduction to Papua New Guinea from Australia in 1937 (Commonwealth of Australia, 1940), and there is hearsay evidence that in 1938 the Department of Public Health brought the toads to Port Moresby for use in human pregnancy tests, and that these toads were either released or escaped (Pippet, 1975; Zug *et al.*, 1975). Following introduction, the toads were distributed throughout the

territory (Commonwealth of Australia, 1940). There are no records of where the releases were made. Zug *et al.* (1975) have summarized the distribution of the species in Papua New Guinea in 1972.

Australia

The events surrounding and following the introduction of *B. marinus* from Oahu, Hawaii to Australia are well documented. On 1 June 1935, 102 individuals (51 females and 51 males) were collected from both the western suburbs of Honolulu and the HSPA Waipio Substation (Mungomery, 1935b, 1936). The collections included both fully and half grown individuals (Mungomery, 1935b); at least 50 of the larger individuals were collected from Honolulu (Mungomery, 1936). The proximity of the western suburbs to Manoa Valley makes it very likely that the toads caught there were derived from the original release at the Manoa Arboretum, and thus the shipment to Australia was derived from both the initial releases of toads in Oahu, at Waipio and Manoa. The toads arrived at Gordonvale, North Queensland on 22 June 1935, one half-grown male having died *en route* (Mungomery, 1935b).

The toads were maintained at the Meringa Sugar Experimental Station, and allowed to breed in captivity (Mungomery, 1936). Breeding started in July 1935 and the population rapidly increased and was widely distributed throughout the cane growing areas of Queensland. By January 1936, at least 12 females had laid eggs (Mungomery, 1936). Kinghorn (1938) reported 52 records of egg masses in the Maringa district by 1938. Between August 1935 and 1 April 1936, 41 800 young toads were distributed in the Cairns, Gordonvale, Innisfail and Tully districts, in addition to which several thousand more escaped naturally from the lagoons in which they had bred (Mungomery, 1936). Distribution to these areas had been discontinued by July 1937 (Mungomery, 1937). At some time before April 1936, the Australian Federal Government placed a ban on the further spread of toads (Bell, 1936a); this ban was removed in September of the same year (Bell, 1936b). Between then and July 1937, toads were liberated in the Mossman, Babinda, Ingham, Bambaroo, Giru, Ayr, Mackay, Bundaberg and Isis districts (Mungomery, 1937). By March 1937, more than 1 560 000 eggs had been laid and approximately 62 000 toadlets had been caught and distributed (Kinghorn, 1938).

From these initial points of liberation, the area occupied by the species has increased exponentially at a rate of approximately 8.1% per annum (Sabath, Boughton & Easteal, 1981). Covacevich & Archer (1975) and Sabath *et al.* (1981) have described the distribution of the species in 1974. It extended from the Archer River on Cape York Peninsula to the Tweed River on the Queensland-New South Wales border. An isolated population also exists in northern New South Wales (Van Beurden & Grigg, 1980). The species has not reached the limit to its expansion in Australia; the results of a recent survey (1979) showed that its range had increased between 1974 and 1979.

Miscellaneous

Bufo marinus was introduced to Egypt in 1937, probably from Hawaii, but was unable to breed there and did not survive (HSPA, unpubl. documents).

A shipment of 150 toads was taken from Puerto Rico to Mauritius but the toads were not allowed to be landed when they arrived (HSPA, unpubl. documents).

Tyler (1975) reports that in February 1975 an Australian Broadcasting Commission newscast mentioned that some 'giant Cane Toads' imported from Australia to a private zoo in Bangkok, Thailand, had escaped. It is not known if *B. marinus* has become established on continental Asia as a result of this introduction.

DISCUSSION

When a population is isolated from the main body of a species either by the colonization of a new area or by the intervention of an extrinsic barrier to migration, it will, if it remains isolated, diverge genetically from the parent population as a result of microevolutionary changes and may eventually become sufficiently distinct to form a separate species.

If the isolated population is formed from only a few individuals, the isolating or founder event itself may directly affect the genetic characteristics of the founding population. It can do this in two ways. Firstly, as a result of sampling error it may cause the amount of genetic variability to be reduced and the genetic distance between the ancestral and founder populations to be increased. Secondly, in some circumstances, as demonstrated by Templeton (1979), it may bring about a genetic revolution of sufficient magnitude to cause the formation of a new species.

This history of introductions of *B. marinus* provides opportunities to study each of these effects.

Gradual allopatric divergence

To study the way in which originally identical or very similar populations undergo divergence following isolation, it is necessary to observe a situation in which it is known that the isolation involved a large number of individuals and that there is therefore no possibility of the isolating event itself having an effect on the rate or mode of divergence as a result of sampling error.

The spread of *B. marinus* to the Hawaiian islands is just such a situation. The populations on Kauai, Hawaii, Maui and Molokai were started, between 1933 and 1935, from many thousands of the progeny of the 148 individuals introduced to Oahu from Puerto Rico in 1932 (see Table 1). It is unlikely that there has been any significant migration of toads between the islands since 1935, and the populations are therefore effectively isolated from each other. The way in which they diverge genetically can now be monitored. They have already undergone considerable divergence in less than 50 generations (Easteal & Sabath, unpubl. data).

Population bottleneck effects

A founder event involving a sudden reduction in population size, or a population bottleneck, may affect at least three evolutionarily significant genetic characteristics of the founding population. It may decrease the average

heterozygosity of individuals and the number of alleles per polymorphic locus, and it may increase the initial genetic distance between the founding and the ancestral populations.

Nei, Maruyama & Chakraborty (1975) and Chakroborty & Nei (1977) have described the theoretical effects of population bottlenecks on these three parameters. Their models make precise predictions, and since the exact numbers of individuals involved in many of the introductions of *B. marinus* are known (see Fig. 3), the effects of these introductions can be directly compared with the predictions of the population bottleneck models.

The history of introductions of *B. marinus* thus provides a good opportunity to test these models.

Speciation via genetic transilience

Templeton (1980) introduced the phrase 'genetic transilience' to describe "a rapid shift in a multi-locus complex influencing fitness in response to a sudden perturbation in genetic environment". He demonstrated experimentally that a genetic transilience could occur in response to a simulated founder event, and that it could give rise to a new species (Templeton, 1979). He stressed that such events were very unlikely and probably rarely occur since they require a set of stringent conditions. In addition to the existence of an epistatic, multi-locus complex, they require a situation in which a founder event produces a large change in the inbreeding effective population size and thus creates an intensive selective bottleneck (Templeton, Carson & Sing, 1976). The variance effective size of the ancestral population, the sample size of the founders and the variance effective size of the founder population must also be as large as possible, subject to the constraint that the change in the inbreeding effective size be large, so that the founders may have sufficient genetic variability to respond to the selective bottleneck (Templeton, 1980). The conditions that are likely to give rise to such a situation, and hence to a genetic transilience, are listed in Table 2. Since many of these conditions are relative and have not been quantified, a discussion of the degree of correspondence to them by any particular species must be vague. Templeton (1979), however, was able to effect a genetic transilience with *Drosophila mercatorum,* and therefore this species and his experimental procedures can be assumed to provide at least the minimum necessary conditions for the occurrence of a genetic transilience.

The circumstances of the history of introductions of *B. marinus* together with certain aspects of its biology correspond very well with Templeton's conditions (see Table 2).

Bufo marinus has a haploid number of 11 chromosomes (Beckert & Doyle, 1969; Cole, Lowe & Wright, 1968; Volpe & Gebhardt, 1968; Griffin, Scott & Papworth, 1970; and Brum-Zorrilla & Saez, 1973) which is similar to the number in other amphibian species (Becak *et al.,* 1970, 1971) but greater than the number of five for *Drosophila mercatorum* (Templeton, Sing & Brokaw, 1976). The number is therefore at least large enough to permit a transilience.

The total genomic map length of *B. marinus* is not known but the absolute quantity of DNA per cell is 8.7 pg (Griffin *et al.,* 1970), which is towards the lower end of the range of values for amphibians but above the range for mammals, birds and reptiles (Goin, Goin & Bachmann, 1968) and most invertebrates (White, 1977). It is not known how many crossover suppressors exist in the

Table 2. Optimal organismic characteristics and founder event conditions for the occurrence of a genetic transilience (after Templeton, 1980), and correspondence to these by *B. marinus*

	Bufo marinus
Genome	
Chromosome number large	$n=11$
Total genomic map, length large	unknown
Crossover suppressors few and easily lost	unknown
A system of epistatic polygenes with several major genes	unknown
Population general	
Average number of offspring large	yes
Overlapping generations	yes
High level of genetic variability	yes
Ancestral population	
Large and panmictic	yes
Sample of ancestral population (for large panmictic ancestral population)	
Random sample either over entire range or from local deme, or:	
Correlated sample from local deme	yes
Founder population	
Open niche allowing population flush	yes
Initial density low	no
Initial subdivided population structure	in some instances
Reproductive value of founders high	yes
Mating system	
Assortative	unknown
Sexual selection of mate recognition system	unknown
Imprinting, partially learned sexual behaviour	unknown

genome of *B. marinus,* or if it contains systems of epistatic polygenes containing several major genes.

The average number of offspring of *B. marinus* is large; females lay between 10 000 and 20 000 eggs at one time (Pemberton, 1934; Kinghorn, 1938; Tyler, 1976; pers. obs.) and can lay more than once a year (Kinghorn, 1938). Breeding is opportunistic and in many areas occurs during wet weather at any time of the year (Leonard, 1933; Pemberton, 1934; Zug *et al.,* 1975; pers. obs.). Adults can survive for 15 years in captivity (Pemberton, 1949) and probably often survive several breeding seasons in the wild. *Bufo marinus* populations therefore have overlapping generations.

Australian and Hawaiian populations have been shown to have exceptionally high levels of electrophoretically detectable genetic variable (Easteal & Sabath, unpubl. data), and it is likely that the parent South American populations also have high levels of genetic variability.

Very little is known of the structure of *B. marinus* populations, but the species is known to be locally very abundant, for example, in Papua New Guinea it occurs in densities of up to 300 individuals ha^{-1} in semi-urban areas (Zug *et al.,* 1975).

This, together with the fact that populations have expanded very quickly to occupy new areas, demonstrating that individuals are capable of rapid long distant movement, suggests that populations consist of large panmictic units.

The samples taken in making the introductions were probably almost all from single locations and may have been random or correlated.

The fact that the species has expanded at such a great rate and been so successful in almost all the places to which it has been introduced, is evidence of the existence of open niches in those places which the species has been able to exploit, and population flushes are known to have occurred after many introductions.

The initial density of introduced populations has not been low, but in some cases, where deliberate local distribution of the toad has occurred following introduction, there has initially been an artificially created subdivided population structure. The reproductive value of the founders has been high and they have, in most cases, reproduced very successfully.

Unfortunately, nothing is known of the mating behaviour of *B. marinus,* and therefore it is not known if the species corresponds to Templeton's conditions in this respect.

Bufo marinus has been introduced to at least 90 distinct places. Although some of the introductions, such as those to the Hawaiian islands, have involved large numbers of individuals, many and probably most have involved very few. Assuming the existence of an appropriate multi-locus complex, it is probable as a prediction of Templeton's theory, that at least one of these introductions has given rise to a genetic transilience leading to the formation of a new species.

The history of introductions of *B. marinus* is thus, in effect, an experiment designed to test Templeton's theory of speciation via genetic transilience.

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APPENDIX

List of countries (and islands) to which *B. marinus* is known to have been introduced with details, where available, of the sources of introductions, dates of introductions and numbers of individuals introduced, and including the sources of information.

Country	Source of introduction	Date of introduction	Numbers introduced	Source
American Samoa		before 1957		Simmonds, 1957
Tutuila Island				USNM (1976)
Antigua		before 1916		Clark, 1916
				MCZ (1960)
Australia	Oahu, Hawaii	1935	101	Mongumery, 1935a
Dunk Island				Boughton & Sabath, 1980
Fantome Island		1957		Floyd *et al.*, 1981
Frazer Island				Boughton & Sabath, 1980
North Stradbroke Island				Boughton & Sabath, 1980
Orpheus Island				Boughton & Sabath, 1980
Palm Island		1964		Floyd *et al.*, 1981
Barbados	Martinique	before 1844		Waite, 1901
	Guyana	*c.* 1888		Schomburg, 1971
				MCZ (1879)
Bermuda	Guyana	1855	>24	Waite, 1901
				MCZ (1906)
Cuba*	Puerto Rico	1946		Buide, 1967
Dominica				Gressitt, 1954
Dominican Republic		before 1941		Cochran, 1941

Egypt*		1937		HSPA (unpubl. document)
Ellis Islands				
Funafuti Atoll	Viti Levu,	1939	150	Lever, 1942
Vaitupu Atoll	Funafuti Atoll			Lever, 1942
Fiji	Oahu, Hawaii	1935	67	Jack, 1936
Kandavu		before 1938		Lever, 1938
Rambi		1937		Lever (unpubl.)
Tavenui	Viti Levu	1937		Lever, 1937
				CMNH
Ovalau				Pernetta (pers. comm.)
Vanua Levu		before 1938		Lever, 1938
Viti Levu	Oahu, Hawaii	1935	67	Jack, 1936
Grand Cayman Island		before 1887		MCZ (1887)
Grenada		1870's		MCZ (1870's)
				Barbour, 1914
				MCZ (1966)
Guadeloupe				MCZ (1962)
				Schwartz & Thomas, 1975
Guam	Oahu, Hawaii	1937	>39	HSPA (unpubl. document)
				USNM (1945)
Haiti		1932		Williams *et al.*, 1963
				UZM (1935)
Ile de la Gonave				YPM
Jamaica	Barbados	1844		Waite, 1901
				MCZ (1865)
Japan				
Minami-Daitujima	Taiwan			Matsui, 1975
Martinique	French Guiana	before 1844		Waite, 1901
				MCZ (1879)
Montserrat		before 1879		MCZ (1879)
				Barbour, 1914
Nevis		before 1914		Barbour, 1914
				MCZ (1922)
Palau				Savage, 1960
Arakabesan Island		before 1955		CAS (1955)
Kayangel Island		before 1955		CAS (1955)
Kerrar Island		before 1954		CAS (1954)
Papua New Guinea	Hawaii	1937		Comm. Aust., 1938
	Australia	1937		Comm. Aust., 1940
Bali Witu Island		1970		Zug *et al.*, 1975
Baluan Island				Zug *et al.*, 1975
Bangatang Island				Zug *et al.*, 1975
Buka Island		1938		Zug *et al.*, 1975
Bougainville		1940		Zug *et al.*, 1975
Emira Island		before 1944		MVZ (1944)
				Zug *et al.*, 1975
Garua Island				Zug *et al.*, 1975
Karkar Island		1958		Zug *et al.*, 1975
Lambon				Zug *et al.*, 1975
Los Negros		before 1952		Brown, 1952
Manus Island		1942–45		Zug *et al.*, 1975
				Brown, 1952
Mortlock Island				Zug *et al.*, 1975
New Britain	Oahu, Hawaii	1937	many	Comm. Aust., 1938
				Zug *et al.*, 1975
New Ireland	New Britain			Tyler, 1975
		1942–45		Zug *et al.*, 1975
Normanby Island		1945		Zug *et al.*, 1975
Rogeia Island		1942–45		Zug *et al.*, 1975

Rooke Island				Zug *et al.*, 1975
Wito Island				Zug *et al.*, 1975
Philippines	Oahu, Hawaii	1934	27	HSPA (unpubl. document)
				Rabor, 1952
Guimaras Island		1936–39		Rabor, 1952
Luzon Island	Oahu, Hawaii	1934	27	HSPA (Unpubl. document)
				Rabor, 1952
Marinoluque Island				CM
Mindanao Island	Negros Island	1949 & subsequently	30	Rabor, 1952 USNM (1979)
Mindoro Island				CAS
Negros Island	Luzon Island	1935–36		Rabor, 1952
Panay Island		1936–39		Rabor, 1952
Ponape				USNM (1930)
Puerto Rico	Barbados	1920	12	Wolcott, 1934
				May, 1926
	Jamaica	1923–24	40	Dexter, 1932
Cayo Santiago		before 1968		Heatwole *et al.*, 1968
Mona Island				MPM
Vieques		before 1936		UMMZ (1936)
Rota Island		before 1945		Heatwole *et al.*, 1968 USNM (1945)
St Christopher		before 1904		BMNH (1904)
St Croix		before 1935		UZM (1935)
St Kitts		before 1914		Barbour, 1914
St Lucia		before 1879		MCZ (1879) Barbour, 1914
St Thomas		before 1888		UZM (1888) Schwartz & Thomas, 1975
St Vincent*		before 1916		Clarke, 1916
Saipan		before 1961		USNM (1961)
Solomon Islands	Fiji	1940		Lever, 1945
Baniki Island		before 1945		Lever, 1945
Buka Island		before 1968		MCZ (1968)
Guadelcanal	Fiji	1940		Lever, 1945
Gavutu Island		before 1944		UMMZ (1944)
Malaita Island		before 1952		Brown, 1952
Vanikora Island		before 1956		BMNH (1956)
Taiwan	Hawaii	1935		Lever, 1938
Tinian		before 1945		Stohler & Cooling, 1945
USA				
Florida		before 1955		King & Krakauer, 1966
				Krakauer, 1968
Hawaii	Puerto Rico	1932	148	Pemberton, 1934
Kauai	Oahu	1933–35	51 643	HSPA (unpubl. document)
Hawaii	Oahu	1933–35	41 057	HSPA (unpubl. document)
Maui	Oahu	1933–35	23 517	HSPA (unpubl. document)
Molokai	Oahu	1933–35		HSPA (unpubl. document)
Oahu	Puerto Rico	1932	148	Pemberton, 1934
Louisiana				
Grande Terre				Maclean *et al.*, 1977
Yap		before 1946		UIMNH (1946)

*Become extinct since introduction.

Abbreviations: BMNH, British Museum (Natural History); CAS, California Academy of Sciences; CM, Carnegie Museum; CMNH, Cincinnati Museum of Natural History; MCZ, Harvard University, Museum of Comparative Zoology; MPM, Milwakee Public Museum; MVZ, University of California, Museum of Vertebrate Zoology; UIMNH, University of Illinois, Museum of Natural History; UMMZ, University of Michigan, Museum of Zoology; USNM, United States National Museum; UZM, Universitetes Zoologiske Museum; YPM, Yale University, Peabody Museum.