

Expansion of *Eleutherodactylus johnstonei* in Northern South America: Rapid Dispersal Through Human Interactions

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Among amphibians, *Eleutherodactylus johnstonei* (Fig. 1) is rivaled in its propensity for range expansion only by the toad *Bufo marinus* (Kaiser 1997). However, whereas *B. marinus* made its biggest expansion jump, from South America to Australia, through purposeful human intervention and for a presumed agricultural benefit, *E. johnstonei* seems to move from one urban center to another continuously, at irregular intervals, both with and without the deliberate help of *Homo sapiens*: A compelling reason for carefully documenting the expansion of *E. johnstonei* is that it has been shown (Ovaska 1991; Pough et al. 1977; Stewart and Martin 1980) that its behavioral ecology and physiology allow it to colonize successfully where few other anurans can live, and that it may itself be a catalyst for the disappearance of other species (Hardy and Harris 1979). As a species with direct development, *E. johnstonei* does not require standing water for reproduction and

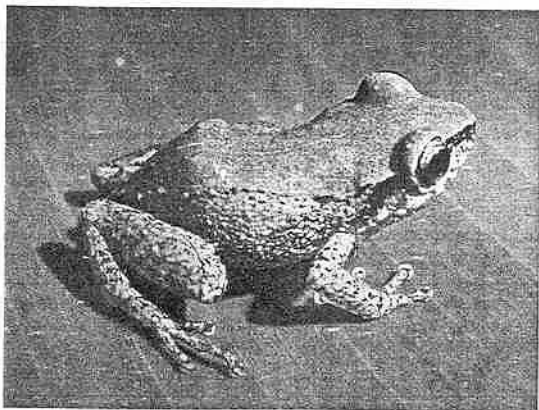


FIG. 1. *Eleutherodactylus johnstonei* from an empty lot in Irapa, Estado Sucre, Venezuela. This specimen is voucher LSUPC F-1388, a male of 27 mm snout-vent length that was photographed on 4 September 2001.

is therefore all the more capable of settling into novel habitats. At this time, with reports of amphibian declines circling the globe, the example of this highly successful invader is instructive. We here detail the progress this species has made recently in South America, a region where dozens of native species have been impacted by human developments and the introduction of exotics, and where any additional environmental pressure on a delicately balanced frog fauna may become a tipping point (Gladwell 2000) for further declines of native frogs.

Eleutherodactylus johnstonei is a species endemic to the Lesser Antilles, though its exact island of origin has become obscured by centuries of presumably repeated human-mitigated introductions (Kaiser 1992, 1996). There have been many reports on the vectors by which these frogs move from one island to another, and conclusive evidence for both deliberate (e.g., Bequia—Lazell 1994; Bermuda—Pope 1917; Jamaica—Barbour 1910) and accidental (e.g., Dominica—Kaiser and Wagenseil 1995; Panama City—Ibáñez and Rand 1990; Trinidad—Kenny 1980) introductions is available. The first documented introduction into the South American mainland occurred prior to 1919 when a specimen was collected in Georgetown, British Guyana (Hardy and Harris 1979). This introduction was most likely accomplished by the same trade-related mechanism that carried the species throughout most of the other British dependencies in the Eastern Caribbean region (Kaiser 1992). A similar, trade-linked scenario was invoked by Lescure and Marty (1996) who encountered *E. johnstonei* in 1993 near the city center of Cayenne, the capital city of French Guiana. In surveys during the early 1970s (reported in Lescure 1981, 1983), Lescure had not heard the species in French Guiana. The most likely conduit for *E. johnstonei* into French Guiana is the trade in ornamental plants from Martinique (Lescure and Marty 1996).

An introduction of the species into Caracas, Venezuela, in the late 1950s (Juan Rivero, quoted in Hardy and Harris 1979), perhaps deliberately to introduce acoustic entertainment for a garden in the upscale suburb of Altamira, laid the foundation for its spread throughout that country and into neighboring Colombia, as detailed below. It is noteworthy that the species must have been highly restricted initially in its distribution in Caracas, as it is still absent from the thorough list published by Rivero (1961).

For verification of records, one would normally consider as confirmed only those localities for which voucher specimens or voucher photographs have been deposited in public institutions. However, in the case of “weed species,” such as *Bufo marinus* or *E. johnstonei*, we realize that sightings verifiable through more than one source should also be considered. With species such as these, their presence may be duly noted by scientists yet no material might be collected because the species is so common and encountered all the time. Thus, after a species has become established at a locality for a certain period of time and becomes an integral part of that environment, voucher specimens are unlikely to be collected unless someone were interested in specifically documenting for science what has become common knowledge locally. In Venezuela, species for which this might be the case include *B. marinus*, *E. johnstonei*, *Leptodactylus fuscus*, *Hyla crepitans*, and *H. microcephala*. Our list of localities (Table 1) therefore includes a variety of places without voucher specimens. Institutional abbreviations used are as follows: CVULA—Colección de Vertebrados, Universidad de Los Andes, Mérida, Venezuela;

EBRG—Estación Biológica de Rancho Grande, Maracay, Venezuela; EDELCA—Departamento de Ecología, Corporación Venezolana de Guayana, Electrificación del Caroni C.A., Guri, Venezuela; ICN—Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia, Bogotá, Colombia; USFJ—La Sierra University Photographic Collection, Riverside, California; MNHN—Muséum National d'Histoire Naturelle, Paris, France; RMNH—Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands; SCN—Museo de Ciencias Naturales "La Salle," Caracas, Venezuela; UIS—Universidad Industrial de Santander, Bucaramanga, Colombia; ULABG—Universidad de los Andes, Instituto de Geografía, Colección de Anfibios, Mérida, Venezuela; UVC—Universidad del Valle, Cali, Colombia; USNM—U.S. National Museum, Washington, D.C.

Explosion in Venezuela.—The Venezuelan capital of Caracas is a center for international trade and a crossroads for transportation across northern South America. Its shipping port and airport are both located along the coast just north of Caracas, in the cities of Catiá La Mar, La Guaira, and Maiquetía. Among the most significant population centers in coastal northeastern Venezuela are Barcelona, Puerto La Cruz, and Cumaná. If a species is indeed transported both deliberately and accidentally, then these traffic centers would be logical places to find that species after an initial Caracas introduction.

Specimens of *E. johnstonei* from Caracas were deliberately released in Cumaná in 1967 (Hardy and Harris 1979), preempting a likely accidental introduction. By the mid-1970s, the species had spread throughout the city and along the coast near Cumaná (Hardy and Harris 1979). Its presence at Puerto La Cruz and for the coastal cities near Caracas was reported by Kaiser and Grismer (2001), though without vouchers.

Reports from local residents indicate that *E. johnstonei* has been in residence at Simón Bolívar International Airport for over a decade. Thus, the initial spread of the species from the site of introduction in Caracas occurred by both deliberate (Cumaná) and accidental (elsewhere) means. Additional records of the species' spread in Venezuela (Table 1) were published by Gorzula (1989), Kaiser and Grismer (2001), and La Marca (1992), and a cumulative listing appeared in Barrio-Amorós (1998). Yústiz (1977) mentioned the occurrence of an exotic *Eleutherodactylus*, possibly related to *E. portoricensis*, in his list of the frogs of the city of Barquisimeto that is clearly referable to *E. johnstonei*.

A specimen of *E. johnstonei* in the collections of the EBRG in Maracay that was collected on 01 June 1998 in Naguanagua, Carabobo State, a town close to Valencia on the far side of Lago Valencia from Maracay, represents the first specimen from that state. EBRG 3681 verifies the presence of *E. johnstonei* in the city of Maracay, Aragua State. The presence of *E. johnstonei* in Miranda State, the state surrounding the Distrito Federal in which Caracas is located, is ascertained by specimen EBRG 1756. This specimen is notable because it was collected at an altitude of 1300 m which we believe to be near the limit for the species (see below).

Reports of *E. johnstonei* from Bolívar State were made by Gorzula (1989). His list included Ciudad Bolívar, Ciudad Guayana, Upata, and Campamento Guri. Whereas museum vouchers are available for Guri (SCN 10919), the records for Ciudad Bolívar and Upata were based on the observation of calling males (Gorzula, in litt.). In listing the records for Ciudad Guayana, Gorzula (1989)

used the name Ciudad Guayana as it is commonly used locally, encompassing two individual cities (Puerto Ordaz, San Félix). However, voucher specimens exist only for Puerto Ordaz town (e.g. RMNH 18488, EDELCA 5898), the western half of the Ciudad Guayana conglomerate separated from San Félix by the Caroní River.

Kaiser and Grismer (2001) reported *E. johnstonei* from Maturín and Caripe, cities in Venezuela's easternmost part. Unbeknownst to us, the species had been observed in Maturín a few years earlier and vouchered via photograph on the website of a hobby herpetologist (<http://www.meos.ch/terra-typica/amphibia/amphibia.htm>; Thomas Haag, pers. comm.). During their trip in the year 2000, Kaiser and Grismer also visited the city of Irapa, where *E. johnstonei* was not heard. During a visit in September 2001, we heard *E. johnstonei* in several localities in Irapa and conducted audio transects along all of the streets criss-crossing the downtown area (Fig. 2). It appears that the species was not present in large numbers where choruses were heard, and, at this time, its distribution throughout the city is discontinuous. Habitats for *E. johnstonei* in Irapa currently are gardens, empty lots, and construction sites, though it was still absent from the three parks in the downtown area during our survey. We also determined, through additional driving transects, that the species was not present during this period in either the downtown or surrounding areas of Güiría, the main port city on the Península de Paria, although this city is a logical next colonization locale for *E. johnstonei* after colonization of Irapa.

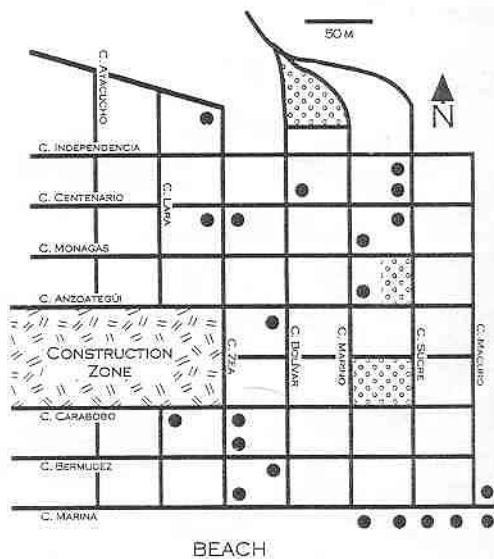


FIG. 2. Map of downtown Irapa, Estado Sucre, Venezuela. This map illustrates the distribution of *Eleutherodactylus johnstonei* in Irapa's downtown area shortly after its introduction between September 2000 and September 2001. In order to facilitate the description of localities, we considered the city's streets a grid, each of whose blocks represents four quarter squares. Filled circles indicate the quarter square in which audio transects revealed the presence of calling *E. johnstonei* males.

Expansion in Colombia.—Accounts of the invasion of *E. johnstonei* into Colombia (Table 1) have mostly been anecdotal (e.g. Kaiser 1997). Recent collecting has confirmed several localities, such as Bucaramanga (Ortega et al. 2002). Although reports supported by voucher specimens are few, the species is now also confirmed for Barranquilla and Cali (Table 1). It has apparently become established in Cartagena, but no voucher specimens are available.

The distribution of *E. johnstonei* across northern South America (Fig. 3) remains restricted to population centers. Within these locales, key habitats for *E. johnstonei* are private residences and areas where transportation of goods (such as construction materials, wood, or ornamental plants) is centered. It has been noted (Gorzula and Señaris 1998) that the occurrence of *E. johnstonei* in a residential area is generally an indicator of an elevated socioeconomic status of the residents, since the purchase of ornamental plants and the requirement of year-round watering requires considerable financial resources. This has earned the species the nickname "la rana burguesa" in some areas (Gorzula and Señaris 1998). This species has never been reported to cross from city habitats (e.g., parks, gardens, empty lots etc.), into native habitat. This is a key observation with respect to the species' competitive capacity and expansion pattern and may allay some fears about the potential impact of this species on local endemics. In Guyana, where *E. johnstonei* has existed for over 80 yrs, it has remained confined to the capital city of Georgetown, despite the proximity of agricultural land and disturbed forests; and the location of an international airport ca. 20 km to the south. Based on this pattern it is unlikely that there will be significant consequences for local endemics based on the mere presence of the species. However, if an endemic is negatively impacted by some form of human disturbance, such as short-term cutting of vegetation or residential construction in new forest tracts, *E. johnstonei* will likely move into that habitat before the native species has the opportunity to recover.

It is an interesting feature of *E. johnstonei* that its expansion

TABLE 1. Current localities for *Eleutherodactylus johnstonei* in South America. Photographic vouchers are italicized. Institutional abbreviations are listed in the text.

Locality	Voucher	Reference
Colombia		
Barranquilla	ICN	Ruiz-Carranza et al. 1996
Bucaramanga	UIS-A-0346-0350	Ortega et al. 2002
Cali	UVC 13885, <i>LSUPC F-1389</i>	F. Castro, in litt.
Cartagena	none	this paper
French Guiana		
Cayenne	MNH 1996.1003	Lescure and Marty 1996
Guyana		
Georgetown	USNM 194416-28	Hardy and Harris 1979
Venezuela		
Distrito Federal		
Caracas	USNM 194429-41	
La Guaira	none	this paper
Maiquetia	none	Kaiser and Grismer 2001
Edo. Anzoátegui		
Puerto La Cruz	none	Kaiser and Grismer 2001
Edo. Aragua		
El Castaño, Maracay	EBRG 3681	Manzanilla et al. 1995
El Limón	none	Barrio-Amorós 1998
Río Güey	none	Manzanilla et al. 1995
Edo. Bolívar		
Ciudad Bolívar	none	Gorzula 1989
Ciudad Guayana	none	Gorzula 1989
Guri	SCN 10919	Gorzula 1989
Puerto Ordaz	RMNH 18488	Barrio-Amorós 1998
Upata	none	Gorzula 1989
Edo. Carabobo		
Naguanagua, Valencia	EBRG 2090	this paper
Edo. Lara		
Barquisimeto*	none	Yústiz 1977
Edo. Mérida		
La Parroquia	CVULA 5032	Barrio Amorós 1998
Mérida	none	La Marca 1992
Edo. Miranda		
San José de los Altos	EBRG 1756	this paper
Edo. Monagas		
Caripe	<i>LSUPC F-555</i>	Kaiser and Grismer 2001
Maturín	<i>LSUPC F-556</i>	Kaiser and Grismer 2001
Edo. Sucre		
Cumaná	USNM 194442-46	Hardy and Harris 1979
Irapa	<i>LSUPC F-1388</i>	this paper
Edo. Trujillo		
Trujillo	ULABG 1158	La Marca 1992

* This population was listed as "*E. portoricensis* (= *cooki*)" by Yústiz (1977). We believe that Dr. Yústiz was trying to refer the observed individuals to a frog similar to the Puerto Rican coqui, now known as *E. coqui*. It is unlikely that he was trying to imply a synonymy of *E. portoricensis* and *E. cooki*, a distributionally highly restricted cave dweller.

seems to be limited by the availability of disturbed habitat. In collecting on all Eastern Caribbean islands with *E. johnstonei* populations, one of us (HK) found the species in seemingly undisturbed habitat in the southern Lesser Antilles only on the island of St. Lucia and in the northern part of that island chain on some of the Netherlands Antilles (Saba, St. Eustatius) and on the volcanic slopes of St. Kitts and Nevis. In all of these cases, *E. johnstonei* populations in primary habitat exist in noticeably lower densities than populations in adjacent disturbed habitats. Although this is an anecdotal observation at this time, it allows us to hypothesize



FIG. 3. Map of northern South America (Colombia, Venezuela, Guyana), indicating locations for which *Eleutherodactylus johnstonei* has been confirmed.

that the capacity of *E. johnstonei* to expand into new habitats, and to survive at great densities, is optimized by habitat disturbance. The fact that all other populations of *E. johnstonei* are apparently linked to some abiotic disturbance (e.g., volcanism, degradation of native habitat by grazing and establishment of plantations, residential construction etc.) and exist at higher densities than in the forests of the islands mentioned above validates such an hypothesis. Assuming that any abiotic disturbance reduces, or at least temporarily rearranges, the complexity of a primary habitat, this might be what allows *E. johnstonei* to quickly move into ecological niches vacated temporarily or permanently by other species.

It is apparent that *E. johnstonei* is dispersed by a variety of means. Accidental introductions occur most likely through the ornamental plant trade, as evidenced by the species' appearance in upscale residential areas. With this vector, it is impossible to differentiate whether the species arrived through plants in one residence and was subsequently distributed by the owner of that residence to friends who enjoyed the frogs's vocalizations, or whether multiple plant introductions via plants occurred. In the suburbs of Caracas, Venezuela the species is now widely spread, and its escape from gardens of select barrios in other cities (such as Bucaramanga or Cali, Colombia) is only a matter of time. Purposeful introductions in South America are unequivocally documented only for Cumaná, Venezuela, and are apparently a simple matter of releasing a few *E. johnstonei* males and females in any area with disturbed vegetation.

One of the potential barriers to the spread of *E. johnstonei* is altitude. The population of *E. johnstonei* in Mérida occurs at the highest reported altitude for the species (up to 1400 m), followed by the populations in the town of La Parroquia near Mérida (ca. 1300 m) and near Caripe (ca. 1200 m). It seems that this altitude is the maximum possible for the species in this area of the Andes. At these altitudes, the species is tightly linked to gardens in south

Mérida; no expansion from these localities has occurred at least over the last six years.

The pattern established by the spread of *E. johnstonei* in northern South America leads us to believe that the species will continue to expand its range by chance, and that there is no realistic possibility of stopping that expansion. If our current range map (Fig. 3) is considered a base map for the year 2001, predicted further points of introduction include all major cities in Colombia and Venezuela, as well as communities connected by trade and/or people movement south along the Andes into Ecuador, Peru, and Chile. It remains to be seen whether this species is capable of inhabiting higher altitude areas of the Andes (>3000 m), or disturbed sites in primary rainforests in the Orinoco and Amazon basins.

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