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Invasion note

Human-mediated escalation of a formerly eradicable problem: the invasion of Caribbean frogs in the Hawaiian Islands

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Abstract

Two species of neotropical frog, *Eleutherodactylus coqui* and *E. planirostris*, have been introduced into the State of Hawaii via the horticulture trade. *E. coqui* was introduced prior to 1988 and *E. planirostris* was first reported in 1994. Since these dates frog colonies have rapidly spread accidentally and intentionally and frog abundance within colonies has grown rapidly. Although these frogs were originally restricted to horticulture sites, they are now found in residential areas, resorts and hotels, and public lands. Due to the high potential biomass of introduced frogs there are realistic anthropogenic and ecological concerns associated with the spread of these frogs. Though there currently is a tool that can be used for localized control of frogs in limited circumstances, overall efforts by Federal, State, and County agencies to control the frog in Hawaii have been hampered by limited authorities and funds, disbelief in the threat, and the reluctance to act.

With a few notable exceptions (e.g. the brown treesnake [*Boiga irregularis*] and cane toad [*Bufo marinus*]), the dynamics of invasions among reptiles and amphibians have been poorly studied. This presumably is because most of these species are not perceived to pose the severe ecological threats that the more numerous and obvious invasions of alien mammals and plants do. Unfortunately, this perception is not necessarily correct because alien reptiles and amphibians may degrade invaded ecosystems via subtle alterations of trophic dynamics that are difficult to discern (e.g. Fritts and Rodda 1998), an unsurprising result given the high numbers or standing biomass that many such populations may attain (Burton and Likens 1975a, b; Stewart and Pough 1983; Pechman et al. 1989; Campbell 1996; Rodda et al. 2001). We think it likely that the difficulty of observing and measuring trophic disruptions has served to dampen attention to the dynamics of reptile and amphibian invasions.

In explaining invasion dynamics, it is increasingly clear that useful information is not restricted to biological parameters. To the contrary, as is recognized in epidemiological studies (Wobeser 1994), biotic, social, and environmental factors interact to determine the eventual outcome of alien species introductions. This is clear in the case of recent invasions of *Eleutherodactylus* frogs in Hawaii, for which we reported the introduction and spread of three species within the state primarily via the nursery industry (Kraus et al. 1999). These frogs are native to various islands of the Caribbean, directly develop into small frogs from eggs laid in moist leaf litter or leaf

axils, and attain a maximum size of approximately 4–5 cm. We predicted several negative ecological and social consequences would likely result should the frogs become widely established in Hawaii. Since that time (early 1998, Kraus et al. 1999), *Eleutherodactylus* populations have exploded in Hawaii, and it appears that this invasion was detected sufficiently early that it offers an opportunity to identify some of the early dynamics of a rapid successful invasion and how that invasion has been facilitated by cultural practices and societal constraints. The present clarification of causative societal dynamics facilitating this invasion may assist in preventing the spread of newly introduced alien amphibians elsewhere, such as in the Galapagos Islands (Snell and Rea 1999) and New Zealand (Low 1999).

It was reported by Kraus et al. (1999) that three species of *Eleutherodactylus* were introduced into Hawaii: *E. coqui*, *E. martinicensis*, and *E. planirostris*. This report was based on identifications provided by experts having long experience with this difficult and speciose (>600 species) genus. The identification of *E. martinicensis*, however, turns out to have been incorrect; all specimens identified as that species are in fact *E. coqui*. This has been verified in two ways. First, subsequent to our report, we obtained from R. Crombie a taped call of *E. martinicensis* recorded in Guadeloupe. That call is easily distinguished from the call of *E. coqui*, and it has never been heard by us in hundreds of hours of night-time collecting activity at dozens of *Eleutherodactylus* sites in Hawaii, including the two sites originally reported to contain *E. martinicensis*. Second, we have borrowed well-preserved samples of both *E. martinicensis* (USNM 283058-78) and *E. coqui* (USNM 221040-62) to identify morphological differences that might serve to distinguish them (a comparison apparently not made by earlier researchers). Two external characters serve to readily differentiate the two: (1) *E. martinicensis* has digital discs with a smoothly rounded anterior margin, while *E. coqui* has digital discs with a straight anterior margin; and (2) *E. martinicensis* has a distinct white chevron above the anus, which *E. coqui* lacks. For both of these characters, all preserved Hawaiian frogs in the collections of the Bishop Museum, including those earlier reported as *E. martinicensis*, match *E. coqui*. Hence, there is no evidence that *E. martinicensis* has been introduced to Hawaii; earlier identifications to that effect were based on sub-optimally preserved material and are incorrect. The previously published identifications of *E. coqui* and *planirostris* in Hawaii remain correct (Kraus et al. 1999).

The ecological range of *E. coqui* in Hawaii continues to expand. In our previous report, we had evidence of frogs only from relatively low elevations (0–670 m), but speculated that they would pose ecological problems if allowed to invade mid-elevation native forests (900–2000 m). We now can verify the ability of *E. coqui* to thrive and successfully overwinter at higher elevations in Hawaii. A large population at 920 m elevation has survived and expanded since 1997. In addition, a set of four populations at 1170 m elevation first appeared in 1999 and successfully survived the winters of 1999–2000 and 2000–2001. The latter locality is at the upper elevation (1200 m) that the species occurs in its native Puerto Rico (Schwartz and Henderson 1991), and it remains to be seen whether the species can expand to higher altitudes in Hawaii (forest extends to >2000 m in Hawaii).

Population expansion has been dramatic. At the time of our original report (early 1998), we knew of eight sites having *Eleutherodactylus* on Hawaii Island, 12 on Maui, and one on Oahu. As of 30 August 2001, we have seen specimens from 101 sites on Hawaii Island (and have documented 124 other credible populations based on descriptions of frogs or calls), 36 on Maui, 14 on Oahu, and two on Kauai. Some of this increase surely represents sites in existence at the time of our earlier report but unknown to us. However, the number of such sites is certainly small, and most sites clearly have become established since 1998. We are led to this conclusion for three reasons. First, a cumulative plot of reports received by us shows an exponential increase since 1998 (Figure 1); second, most new populations were quite small when first reported, indicating their recent establishment; third, in numerous instances, we have been able to trace through conversations with affected landowners the time at which newly reported populations were first established. This is feasible because of the conspicuous nature of the frogs' calls (Kraus et al. 1999). In all such cases, frogs were reported to us very soon after they were first noticed (within six months, and often within days, of first detection). It appears that we happened upon this invasion (in early 1997) just as it began its logarithmic phase of expansion (Figure 1). Since our earlier report of *Eleutherodactylus* introductions to Hawaii, the rate of *Eleutherodactylus* population expansion has exceeded our original predictions. In several instances we have investigated, populations rapidly expanded to dozens

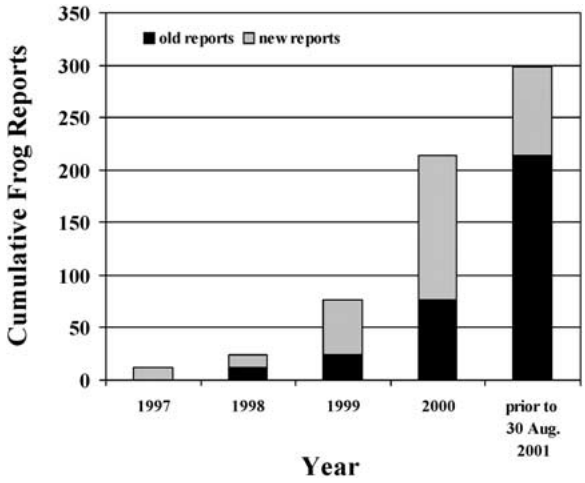

Figure 1. Cumulative growth in number of frog populations on the islands of Hawaii, Maui, Oahu, and Kauai in the State of Hawaii, USA, between 1997 and 30 August 2001. Multiple reports of frog sightings at the same locality are only counted once. Only credible reports are included, by which we mean localities for which we have directly observed specimens or for which the report is accompanied by an accurate description of the frog or call.

of calling individuals within approximately six months of the first few frogs being noticed.

This raises the question of how long it took these species to enter logarithmic growth from the time of their first arrival. We previously reported the earliest known instance of *E. coqui* in Hawaii as 1992, based on the recollection of the landowner on Hawaii Island having the largest known infestation (which we presumed to be the earliest). Subsequently, we have been told by the owner of the largest infestation on Maui that frogs were noticed on his property around 1988. Allowing for the fallibility of memory, these dates may be used to bracket an estimate that *E. coqui* was present in Hawaii from five to 10 years before population densities led to sufficiently common dispersal from infected nurseries to result in an explosion of new populations.

The relatively quiet call of *E. planirostris* makes that species less conspicuous, and it is, correspondingly, more difficult to reliably estimate its time of arrival in Hawaii. Typically, the species seems to be overlooked until such time as it develops large populations, making frogs more likely to be flushed from daytime retreats during nursery operations or gardening activities. Judging from its apparently more restricted range in Hawaii, it seems likely that it has been present in the state for less time and represents a separate invasion from that of *E. coqui*. The earliest report we have for *E. planirostris* is approximately 1994, although this should be interpreted as an estimate of latest possible date of introduction, and it is likely the frog was present earlier but overlooked. Given its limited range on Hawaii Island and recent introduction to Oahu, Kauai, and Maui, it seems likely that *E. planirostris* arrived in Hawaii sometime in the early 1990s. If so, it may be that it has yet to undergo its most explosive phase of population growth. More likely, it is more widespread than we realize, but under-reported because it is inconspicuous.

We earlier presented evidence that *Eleutherodactylus* has spread in Hawaii largely via the nursery trade and we remarked on one reported, though unverified, instance of intentional spread on Hawaii Island. We now have additional evidence confirming these two means of spread, although the former is clearly more important.

First, we now have many additional records of nurseries, residences, and resorts becoming infested with frogs via receipt of plant materials from infected nurseries. Furthermore, at least five department stores that have nursery sections (two on Oahu, one on Maui, and two on Hawaii Island) have received and sold infected plants over the past three years (e.g. Edwards 2001). In these cases, because of the high turnover of retailed plant materials, re-infection of store stocks with frogs from source nurseries has been an ongoing problem. Several residential sites have unambiguously become infected from these retail sources. In these cases, property owners reported that frogs were first detected on their property on the night of plant acquisition. These detections include observation of frogs in, or exiting from, recently purchased plants.

We can now verify that the one reported instance of intentional establishment of *E. coqui* in a previously uninfected part of Hawaii Island (Kraus et al. 1999) has been hugely successful. A large population now infests several acres at the site of intentional release and is clearly expanding its range into adjacent rainforest. Furthermore, since our original report, we have discovered that at least two gardening societies on Hawaii Island have had members actively transporting *E. coqui* around the island with the intent of establishing populations in members' gardens. One of these involved members of a water-garden club who erroneously thought these strictly terrestrial frogs would enhance their ponds. Other instances of illegal intentional establishment of *E. coqui* in natural areas on Hawaii Island are suspected for three reasons: (1) absence of a nearby

nexus with the landscaping/nursery trade, which serves as the usual mode of inoculating new populations; (2) establishment at deliberately conspicuous sites in natural areas (such as at the entrance sign to Hawaii Volcanoes National Park), and (3) the presence of a small cadre of individuals on Hawaii Island, including, but not restricted to, the garden club members noted above, who advocated the spread and/or protection of the frogs (Singer 2001).

Advocacy of *E. coqui* spread has been either for perceived amenity reasons or for the alleged biocontrol of insect pests (Greenwell 2001), with mosquitoes and tropical nut borers (*Hypothenemus obscurus*) most frequently cited (e.g. Fullington 1999; Singer 2001). The former argument reflects the opinion of some individuals who think the frogs sound pleasant (e.g. Fullington 1999), although this decision is typically rendered only upon hearing small choruses. The biocontrol argument is false: within its native range, *E. coqui* rarely feed on dipterans, including mosquitoes (Stewart and Woolbright 1996). We have similar results for populations in Hawaii (Campbell et al., unpublished data). In the case of the nut borer, the cryptic life history of that beetle never brings it into contact with the frogs, making biocontrol unlikely if not impossible. Yet such evidence and logical argument make little headway with local advocates for *E. coqui*, and the emotional pitch of some members of the latter group has led to claims equating invasive-species control with racism (cited in Hurley 2001) and attempts to redefine the frogs as 'Hawaiian' by fiat (Singer 2001).

In our earlier report, we predicted a series of negative ecological and societal consequences to result if *E. coqui* were allowed to become widely established. But our judgment was too conservative, overlooking additional concerns brought to our attention by affected citizens: (1) the potential effect on Hawaii's export nursery industry should shipments be rejected or destroyed for harboring frogs, and (2) infestation of private land leading to weaker property values or preventing sale of infested properties (Allison 2001; Fujimori 2001; Steinberg 2001). Frustration with *E. coqui* has led several landowners to attempt to rid themselves of the problem using a variety of novel, and dangerous, chemical means (each directly reported to us by those using the chemicals). One landowner heavily doused the inside of his house with a variety of insecticides in the mistaken belief the frogs resided therein; another sprayed her mango tree with household insecticides not approved for use on foods or crops; another sprayed kerosene on a tree in which frogs were calling and lit it in an unsuccessful attempt to remove the problem.

Until recently, the only legal method for frog control in Hawaii was hand-capture, which may be a successful technique if populations are sufficiently small (<10–20). One individual adopting this approach met with considerable success by using a tape loop of an *E. coqui* call to stimulate males to repeatedly call until captured by hand (a method we too have successfully used). In general, the rapid spread of *E. coqui* (and associated noise disturbance) has led many citizens to express to us their considerable willingness to eradicate their infestations, if a reliable means of control were available. The US Environmental Protection Agency (US EPA) recently granted an emergency registration (Section 18) to hand-spray caffeine for *Eleutherodactylus* control in limited situations by certified pest-control operators within the state in response to an application prepared and submitted by the Hawaii Department of Agriculture; however, additional restrictions imposed on that registration by the latter agency are so onerous as to make label compliance extremely expensive.

It is well known that invasion via multiple loci is the most effective means of establishing alien species in new environments (Mack 1985; Moody and Mack 1988; Mack and Moody 1992), and the unregulated establishment of multiple infestations via the nursery trade is a key factor in the success of *Eleutherodactylus* species in Hawaii. Hence, the question logically arises as to why the intra- and inter-island spread of the frogs through nursery material has not been regulated, even though recognized for years as the major pathway of dispersal (Kraus et al. 1998, 1999). The supplemental means of spread, intentional transport by *Homo sapiens*, has been illegal since May of 1998. Why has criminalization of this activity proven ineffective in closing that pathway?

First, it should be noted that responsibility for action rests solely with State government because the intrastate nature of spread precludes a nexus for Federal jurisdiction. The nursery pathway has not been effectively reduced or controlled because State government currently has limited authority to effectively address invasives spread through that pathway and lacks sufficient staff to address the numerous incipient invasions already ongoing. Further limitations have been the failure of certain staff of the responsible State agencies to take the threat posed by frogs seriously and a reluctance to use available legal authority. This probably resulted for two inter-related reasons: failure to

believe that a little frog could possibly constitute a real problem, and an already full schedule of control operations against other, clearly threatening, alien pests. It is clear that all factors (limited authorities and funds, disbelief in the threat, and reluctance to act) combined to delay government response to these frog invasions for several years. These same limitations are likely to be even more severe for other reptile and amphibian invasions in the many governmental jurisdictions that lack Hawaii's general sensitivity to the threats posed by invasive species.

One action State government has taken is public education and outreach on the problem since 1998. Additionally, the State has helped to fund the series of laboratory and field studies assessing techniques for *Eleutherodactylus* control. Screening of a wide variety of surfactants, registered insecticides, pharmaceutical products, and food additives identified caffeine as a potential toxicant that could be used to control frogs (Campbell et al., unpublished data) and these data were used to support the US EPA registration noted above. The caffeine registration has probably arrived too late to halt the *Eleutherodactylus* invasion of Hawaii Island because populations now number in the hundreds and frogs in the tens or hundreds of thousands, making it difficult to impose a kill rate that exceeds the recruitment rate. However, judicious application of caffeine could serve to protect other islands in the chain if utilized quickly and competently. The growing concern among many nursery owners to avoid infection, given the fear that infested exports could be destroyed or returned for harboring frogs, may also serve to generate greater interest in stemming the spread of frogs via the nursery pathway, whether by government or by private action, but this remains to be seen. Lastly, of course, the frog-control techniques developed in Hawaii may prove useful for treating similar invasions that have recently begun in the Galapagos and New Zealand (Low 1999; Snell and Rea 1999), or prove effective for eradicating future incipient invasions of alien frogs in Hawaii or elsewhere.

In the case of intentional transport of frogs, State government has taken the initiative to make such actions illegal, but such rules are inherently difficult to enforce, requiring the unlikely circumstance that a perpetrator be caught *in flagrante delicto*. This is a difficult standard to meet; hence, the law has largely served an educational role in emphasizing to the public the serious nature of this invasion, a role assisted by many printed and televised news reports since late 1998. Thus, for both means of spread, effective government action to contain frog invasions, though widely expected from the public, did not materialize in a timely fashion.

At the time of writing our original report, we stated 'most, and possibly all, populations of *E. coqui* and *E. martinicensis* (sic) are susceptible to eradication because numbers are still low at most sites and because males can readily be targeted for removal ...' This statement, though made only four years ago, is clearly untrue today, primarily because of societal failure to rectify the problem through recognized government channels. In this context, *Eleutherodactylus* invasions in Hawaii provide a broader cautionary lesson: preventing ecological degradation by alien species will not result simply from increased understanding of the ecological dynamics of invasions but must include understanding and altering the cultural dynamics that breed and exacerbate such problems.

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