use of the genus *Bufo*; more recent taxonomic treatments have suggested the use of *Chaunus* (Frost et al. 2006) and *Rhinella* (Chaparro et al. 2007). Beginning in the early-to-mid 1800's the species was intentionally introduced to islands in the Caribbean, including to Jamaica in 1844, and subsequently throughout the southern Pacific in the early 1900's, as a biological control agent to combat rats and invertebrate pests of sugar cane (Lever 2001; Lewis 1949). Like all members of the genus, *B. marinus* secretes a powerful bufogenin toxin, which is often fatal if ingested by naïve species that have not co-evolved with *Bufo* species. When introduced outside of its normal range and in the absence of its own controlling predators, *B. marinus* can establish itself quickly and reach phenomenal densities (up to 2138 individuals/ha: Freeland 1986; Lever 2001). Listed as one of the world's 100 worst invasive species by the IUCN, *B. marinus* is now a ubiquitous component of many tropical islands, including all major sugar cane producing islands in the West Indies.

Commonly, the deleterious impacts of invasive alien species (IAS) are manifested in competition with or predation on native species (e.g., Boland 2004; Fritts and Rodda 1998). In the case of the cane toad however, negative impacts may be most consequential at another trophic link: frog-eating predators dying as a result of ingesting (or attempting to ingest) this highly toxic species. For example, *B. marinus* has been implicated in population crashes and localized extirpations among diverse taxa, including dasyurid marsupials, reptiles, and at least one ground-nesting bird in Australia–a continent that possesses a largely non-toxic native anuran fauna, and, not surprisingly, a variety of frog-eating mammals, reptiles, and birds (e.g., Boland 2004; Phillips et al. 2003; Rayward 1974; Taylor and Edwards 2005). As a consequence, and in contrast to the usual roles of invasives as competitors, pathogens, or predators, the primary issue in Australia is the danger to native wildlife posed by the presence of an inappropriate and toxic prey species (Crossland 1998; Phillips et al. 2003).

Although cane toads have existed on Jamaica for more than 160 years and are found in nearly all terrestrial habitats, published literature regarding their relationships with native species is restricted to anecdotal reports of foraging observations and inspection of toad stomach contents (Lewis 1949). To our knowledge, there are no reports suggesting that *B. marinus* may represent a threat to native predators on Jamaica or, indeed, anywhere in the West Indies where it has been introduced. Here we report definitive evidence that such a potential exists. Specifically, we present data indicating that the cane toad is preyed on by the endemic Jamaican boa (*Epicrates subflavus*; Boidae; IUCN RedList Vulnerable), and that such events can lead to the death of the snake.

Study areas and methods

In the course of field work and year-round residence in the Hellshire Hills and Cockpit Country we have now observed at least two instances of *E. subflavus* succumbing to toxic assault resulting from *B. marinus* ingestion. Additional *E. subflavus* carcasses have been encountered in both locations, and the circumstances surrounding those discoveries suggest that the deaths may also have been attributable to *B. marinus*.

Hellshire Hills

The Hellshire Hills form a limestone peninsula roughly 114 km^2 along the southern coast of Jamaica. The area supports the only remaining population of the critically endangered Jamaican iguana (*Cyclura collei*), among other threatened endemic wildlife species (Wilson and Vogel 2000). Cane toads are relatively common in the Hellshire Hills, despite the probable absence of any suitable breeding sites (i.e., standing water). However, the northern edge of the peninsula has been used extensively for aquaculture (primarily tilapia *Oreochromis* spp), and the presence of numerous artificial ponds and associated flooded pools have generated ample breeding habitat for *B. marinus*. Thus, although the toads do not appear to breed in the Hellshire Hills, they are nevertheless present throughout the peninsula. That the Hellshire Hills are the driest portion of the island (averaging fewer than 100 cm of rainfall annually) and consist of rugged limestone outcrops and open canopy dry forest, attests to the tenacity of *B. marinus*.

Cockpit Country

The region known as Cockpit Country, located in northwestern Jamaica, is a distinct portion of an elevated limestone plateau that forms the central spine of the island. The plateau has eroded over millennia by rainfall and underground drainage to form an area of conical hills, separated by depressions ('cockpits') and small valleys. This important forested area encompasses the largest blocks of contiguous moist and wet limestone evergreen forest on Jamaica, including the 22,327 ha Cockpit Country Forest Reserve. The area is recognized for its high levels of site-endemic biodiversity and also as a stronghold for many island-endemic species, including *E. subflavus* (Oliver 1982). *B. marinus* is extremely common in peripheral, edge habitat of agriculture and rural communities, where the toads breed in man-made ponds and roadside puddles. While toad densities are considerably lower in the core, interior forest, we have observed large (SVL ~ 15 cm) individuals in the center of the Cockpit Country Forest Reserve (Koenig, unpubl. data).

Results

Hellshire Hills

On 4 July 2005 we found a freshly dead *E. subflavus* (SVL ~ 120 cm) in a small (0.5 m × 0.5 m) limestone depression that was partially filled with water from recent rains (17.86635N, 76.96493 W). In this same temporary pool was a similarly freshly dead *B. marinus* (approximate SVL = 100 mm). Although interactions between the boa and the toad were not observed, their position in the same small pool, and their similar, freshly dead status, strongly suggest that both animals died as a result of a predator–prey interaction. Whether the boa actually ingested (and subsequently ejected) the *B. marinus*, or whether the toad was simply "mouthed" could not be determined, but we surmise that the toad was at least in the snake's mouth long enough to deliver a fatal dose of toxin; the toad probably succumbed to suffocation due to either ingestion or constriction.

On 18 March 2005 we observed a second, freshly dead *E. subflavus*. This specimen was also found after a period of significant precipitation–the conditions during which *B. marinus* are especially active, and therefore most likely to be encountered by boas. In addition to these two fresh specimens, we have also observed older carcasses or skeletal remains on three other occasions over the past 12 years. In all cases the relatively intact remains suggested that the snakes were not predation victims, and were not even severely scavenged after death–consistent with mortality due to lethal ingestion.

Cockpit Country

On 5 March 2007 we observed definitive evidence of *E. subflavus* being fatally poisoned by *B. marinus* in Windsor, Trelawny (18.35556N; 77.64694W). At approximately 1300 h we found a medium-sized female boa (SVL = 157 cm; mass = 2040 g, post-mortem [see below]) stretched out on a pile of old bricks, in a habitat consisting of an abandoned coffee farm with a regenerating edge forest. Despite the boa's size, she gave very little muscular resistance when hand-captured. As we proceeded to process her (e.g., confirmation of a PIT-tag originally inserted on 3 July 2006), she began displaying unusual neurologic symptoms: notably a wide gaping of her mouth followed by a cocking of her head that gave an appearance of the upper cervical vertebrae and associated muscles being locked and paralyzed. We placed her in a large terrarium for observation. Her initial movements can only be described as an extremely inebriated bar patron, crawling home after last-call. Respiration was deep and rapid (e.g. 10 inhalations per minute). After several minutes her respiration became shallow and slowed to two inhalations per minute. Within 2 h the boa died. Post-mortem, we surgically extracted a large cane toad (SVL = 110 mm, mass = 92 g), which had been ingested head-first and was lodged in the esophagus.

We have also encountered three slightly decomposed carcasses and one skeleton for which the causes of death were unknown. None appeared to have been severed by a machete–a common cause of mortality of boas on the edge of Cockpit Country. In the case of the skeleton and one of the carcasses, we found the remains on the private property of Windsor Research Centre, which has had a successful community awareness program about boas for over 10 years; it is therefore highly unlikely that anyone visiting the property killed either of these two boas.

The other two carcasses were encountered during an on-going radio-telemetry study of the home ranges and habitat preferences of *E. subflavus* in Windsor. On 29 June 2009, we recovered one medium-sized (SVL ~120 cm) carcass, approximately 60% decomposed, within the home range of a radio-tagged female boa (18.35789N; 77.64964W). Then, on 27 August 2009, we recovered the carcass of the aforementioned radio-tagged female (18.35838N; 77.65017W), whose movements we had been monitoring since 19 January 2009. At capture (21 December 2008), her snout-vent length measured 178 cm and her weight was 2500 g. On her final pre-mortality location fix, 24 August 2009, she was observed to be alive, coiled in the branches of a tree. We note that post-mortem, her transmitter was scavenged and moved approximately one meter from her slightly coiled body. The small pockets of soil amidst the limestone talus surrounding both the transmitter and the carcass showed evidence of either rat (*Rattus* sp.) or mongoose (*Herpestes javanicus*) scratchings. However, and as with the first carcass found near this site, her carcass (~50% decomposed) showed no further signs of having been scavenged directly. Dorsal skin remained intact from snout to the tip of her tail. We also note that in none of these carcasses did we find direct evidence of ingested cane toads: there were no bones or other biological material of cane toads mixed with the boa remains.

Discussion

We have presented definitive evidence that cane toads are consumed by adult Jamaican boas, and that the resulting toxic assault can result in the death of the snake. To the best of our knowledge, this is the first report of a West Indian species succumbing to the toxic effects of *B. marinus* ingestion in the wild. We are aware of only one other observation of toxicity, where a captive Hispaniolan Boa (*E. striatus*) died after swallowing a cane toad (J.M. Wunderle, Jr., pers. comm.). The key conservation question which must now be raised from our multiple anecdotal observations is whether lethal poisoning is a significant threat to the persistence of Jamaica's endemic and vulnerable boa, which is also the island's top native terrestrial predator. Unfortunately, an accurate assessment of the boa population is not available for any area of the island, nor are historical densities known. The species appears to be widespread and in some areas not uncommon, albeit difficult to detect. Moreover, it would be impossible to attribute possible population reductions to the influence of the toad, given the other known sources of boa mortality and population limitation (e.g., persecution, habitat loss). Nevertheless, our observations suggest that toad-induced mortality could be an under-appreciated and significant source of mortality for adult boas.

The Jamaican boa evolved in a relatively benign oceanic island ecosystem. Unlike the neighboring islands of Cuba, Hispaniola, and Puerto Rico, where their respective endemic *Epicrates* evolved with species of native *Bufo* (formerly *Peltophryne*), the introduction of *B. marinus* presented a novel toxin to Jamaican wildlife. Thus, even though the colonizing ancestor of the Jamaican boa from Central America likely had some level of tolerance to bufogenins because of its co-evolution with mainland *Bufo* species, the absence of highly toxic anuran prey on Jamaica eliminated selective pressures for maintaining resistance. Indeed, we speculate that the Jamaican boa is likely the most sensitive of all the endemic Greater Antillean *Epicrates*, as noted by the absence of reports from the wild on mortality-following-ingestion of cane toads on the other large islands. However, as noted by Wunderle (pers. comm.), *E. striatus* also appears to be sensitive to *B. marinus* toxins; although sensitive, because it co-evolved with native *Bufo* on Hispaniola, *E. striatus* may avoid all species of *Bufo*. In Puerto Rico, juvenile *E. inornatus* feed on *Eleutherodactylus* spp., but there are no reports of this boa feeding on native *Bufo* or on *B. marinus* (A. Puente-Rolón, pers. comm.). The Puerto Rican boa may also have evolved to avoid *Bufo* spp. Alternatively, as on Jamaica, detecting cane toad poisoning may be extremely difficult because of the naturally cryptic behavior of *Epicrates* and the rapid rate of decomposition in the tropics following death. Other West Indian boas may be dying in the wild after ingesting *B. marinus*, but the impact has not been documented due to difficulties associated with detection. Overall, it is notable that reports of snakes consuming *Bufo* species in the West Indies, and *B. marinus* in particular, are effectively non-existent (see Henderson and Powell 2009; Schwartz and Henderson 1991).

To assess the magnitude of the threat that cane toads present to Jamaican boas, controlled experiments are needed to determine boa sensitivity to variable concentrations of toad toxins (see Phillips et al. 2003). Although cane toads have been present on Jamaica for more than 160 years, it is clear from our observations that Jamaican boas have not yet learned to avoid this toxic prey species. If only large size-classes of boas (e.g. mature individuals that have already begun breeding) are vulnerable, perhaps because they have a relatively large gape to ingest a large volume of cane toad toxins relative to the boas' body mass (Phillips et al. 2003), or ingest multiple toads (Kidera and Ota 2008), then selective pressures to avoid cane toads may be weaker than if immature boas were to experience high rates of mortality following ingestion. Alternatively, smaller boas may spend more time foraging arboreally, whereas larger boas may be more terrestrial and, consequently, have higher encounter frequencies with cane toads (see Wunderle et al. 2004). Finally, if indeed larger boas are more vulnerable to toad toxins, the Jamaican boa might be experiencing sex-biased mortality against females, which tend to attain larger sizes than males (unpubl. data). Any speculation at this time, however, is premature: our observations of relatively large carcasses may simply be a re ection that small boas decompose extremely quickly and we have as yet been unsuccessful in detecting these events.

In addition to endorsing toxicity studies, we highlight concerns for the management of boa habitat across Jamaica. Because cane toads occur in virtually all terrestrial habitats on the island, they represent a threat throughout the boa's full ecological range. Of special concern is the extent to which new roads and development fragment remnant patches of large forested areas. As noted by Brown et al. (2006), roads facilitate dispersal of toads by providing a corridor for easy movement; in addition, the potholes that form in un-maintained tarmac or dirt roads provide semi-permanent breeding ponds–a reservoir which is normally a limiting factor in a karst limestone landscape. Indeed, our study underscores the imperative that large tracts of forest must be protected from disturbance in order to reduce contact between harmful invasive species (which ourish in human-modi ed environments) and Jamaica's native and endemic wildlife.

Of course, all phases of the cane toad's life history are toxic, so it is not just adult cane toads that pose a threat to native wildlife species. A variety of other species probably prey on cane toads of various sizes, so it is likely that a host of other species may be suffering from this toxic invasive. Some, such as Turkey Vultures (*Cathartes aura*), appear to have learned to feed safely on roadkill cane toads by pulling away the soft belly skin and consuming the internal organs, leaving the skin and avoiding the paratoid glands (Koenig, pers. obs.; see also, Taylor and Edwards 2005). Other Jamaican species probably attempt to consume various life stages of the cane toad, but evidence of impacts and tolerance to toxins have not been reported or investigated. In addition to other Jamaican species, predators on other islands in the Caribbean are also doubtless at risk of bufotoxin poisoning. Unfortunately, there are currently no methods for effectively controlling or eradicating cane toads. At best then, efforts can be made to reduce the potential for cane toads spreading from source populations into sensitive wildlife areas; of course, this potential certainly adds impetus to any efforts to control or eradicate *B. marinus* as a conservation activity. At a minimum, Jamaica's natural resource managers and veterinary division should use our observations to ensure that no additional species with known toxic properties are imported to Jamaica.

Acknowledgments SEK would like to thank Michel Milinkovitch for donating passive implantable transponders (PIT-tags) to enable identi cation of individual Jamaican boas in Windsor. Radio-tracking of boas is made possible through the support of Craig Rudolph and the US Forest Service, US Peace Corps, and Windsor Research Centre. BSW would like to thank the International Iguana Foundation, the Disney Worldwide Conservation Fund, the Fort Worth Zoo, and an anonymous donor for much appreciated support of the Jamaican Iguana Recovery Group.

References

Boland CRJ (2004) Introduced cane toads *Bufo marinus* are active nest predators and competitors of rainbow bee-eaters *Merops ornatus*: observational and experimental evidence. Biol Cons 120:53–62

Brown BL, Phillips BL, Webb JK, Shine R (2006) Toad on the road: use of roads as dispersal corridors by cane toads (*Bufo marinus*) at an invasion front in tropical Australia. Biol Cons 133:88–94

Chaparro JC, Pramuk JB, Gluesenkamp AG (2007) A new species of arboreal *Rhinella* (Anura: Bufonidae) from cloud forest of southeastern Peru. Herpetologica 63: 203–212

Crossland MR (1998) Ontongenetic variation in toxicity of tadpoles of the introduced *Bufo marinus* to native

Australian aquatic invertebrate predators. Herpetologia 54:364–369

Dixon JR (2000) Amphibians and reptiles of Texas. Texas A&M University Press, College Station TX. 421 pp

Freeland WJ (1986) Populations of cane toad *Bufo marinus* in relation to time since colonization. Aust Wildl Res 13:321–330

Fritts TH, Rodda GH (1998) The role of introduced species in the degradation of island ecosystems: a case history of Guam. Annu Rev Ecol Syst 29:113–140

Frost DR, Grant T, Faivovich J, Bain RH, Haas A, Haddad CF, de Sa RO, Channing A, Wilkinson M, Donnellan SC, Raxworthy CJ, Campbell JA, Blotto BL, Moler P, Drewes RC, Nussbaum RA, Lynch JD, Green DM, Wheeler WC (2006) The amphibian tree of life. Bull Am Mus Nat Hist 297:1–370

Henderson RW, Powell R (2009) Natural history of West Indian reptiles and amphibians. University Press of Florida, Gainesville

Kidera N, Ota H (2008) Can exotic toad toxins kill native Ryukyu snakes? Experimental and field observations on the effects of *Bufo marinus* toxins on *Dinodon rufozonatum walli*. Curr Herpetol 27:23–27

Lever C (2001) The cane toad: the history and ecology of a successful colonist. Westbury Publishing, West Yorkshire

Lewis CB (1949) Toads and frogs. In: Lewis CB (ed) Glimpses of Jamaican Natural History, Vol. 1. The Institute of Jamaica, Kingston, pp 24–26

Oliver WLR (1982) The coney and the yellow snake: the distribution and status of the Jamaican Hutia *Geocapromys brownii* and the Jamaica Boa *Epicrates subflavus*. Dodo 19:6–33

Phillips BL, Brown GP, Shine R (2003) Assessing the potential impact of cane toads on Australian snakes. Conserv Biol 17:1738–1747

Rayward A (1974) Giant toads–a threat to Australian wildlife. Wildlife 17:506–507

Schwartz A, Henderson RW (1991) Amphibians and Reptiles of the West Indies: descriptions, distributions, and natural history. University of Florida Press, Gainesville Florida, 720 p

Taylor R, Edwards G (eds) (2005) A review of the impact and control of cane toads in Australia with recommendations for future research and management approaches: a report to the vertebrate pests committee from the national cane toad taskforce. Submitted to the Northern Territory Minister for the Environment and to the Natural Resource Management Ministerial Council, Australia, http://www.feral.org.au/ref_docs_images/CaneToadReport2.pdf

Wunderle JM, Mercado JE, Parresol B, Terranova E (2004) Spatial ecology of Puerto Rican boas (*Epicrates inornatus*) in a hurricane impacted forest. Biotropica 36:555–571

Zug GR, Zug PA (1979) The marine toad, *Bufo marinus* a natural history resume of native populations. Simthsonian Contributions to Zoology, No. 284. Smithsonian Institution Press, Washington, DC