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Invasive rat establishment and changes in small mammal populations on Caribbean Islands following two hurricanes

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A R T I C L E I N F O

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ABSTRACT

Invasive mammals, particularly black rats (Rattus rattus), house mice (Mus musculus), and mongoose (Herpestes auropunctatus) are established on many tropical islands and threaten natural resources such as native birds, sea turtles, lizards, invertebrates, and plants. St. Croix (U.S. Virgin Islands, Caribbean) has a diversity of natural resources being protected from invasive mammals by U.S. conservation agencies. Sandy Point National Wildlife Refuge and Buck Island Reef National Monument receive among the highest density of nesting sea turtles in the region, including annual nesting populations of 50-250 leatherbacks (Dermochelys coriacea), 25-80 hawksbills (Eretmochelys imbricata), and 100-250 green turtles (Chelonia mydas). Buck Island Reef National Monument and Green Cay National Wildlife Refuge are small islands near St. Croix Island that have endangered St. Croix ground lizards (Ameiva polops) established. Rodents and mongoose threaten each of these natural resources. The goal of our study was to determine the types of small mammals (i.e., mongoose, rats, and/or house mice) that are established in each of the three hotspot locations mentioned, and to determine how two severe hurricanes (Irma and Maria) affected the small mammal populations. We used traps and tracking tunnels, which are baited ink cards placed in tunnels so that animal foot prints can be identified, to determine presence and relative abundances of small mammal species. We found that: 1) black rats invaded and established, possibly by rafting and/or swimming, Green Cay following the hurricanes, 2) house mice, rats, and mongoose were present before and after the hurricanes at Sandy Point (mice had not been documented prior to our sampling), and house mouse abundance significantly increased (>2.5 times pre-hurricane levels) 9-months after the hurricanes, and 3) the house mouse population more than doubled 15-months after the hurricanes on Buck Island. Land and resource managers benefit from knowing the composition and relative abundances of the small mammal communities, and the presence of house mice will make predator-free management efforts challenging. Surveillance using tracking tunnels enables rapid confirmation of new invasive species in isolated habitats and following large storms, as demonstrated by our finding that black rats established on Green Cay following the 2017 hurricanes.

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1. Introduction

Invasive mammals are well known to harm native species and ecosystems on islands. Invasive rodents (*Rattus* spp. and *Mus musculus* Linnaeus, 1758) have been unintentionally introduced to most continents and >80% of the major islands worldwide (Atkinson, 1985; Towns, 2009), and are among the most problematic invasive animals affecting island biodiversity (Towns et al., 2006; Angel et al., 2009; Shiels et al., 2014; Harper and Bunbury, 2015). In addition to rodents, mongoose (*Herpestes auropunctatus* Hodgson, 1836), feral dogs (*Canis lupus familiaris* Linnaeus, 1758), and feral cats (*Felis catus* Linnaeus, 1758) are prominent invasive predators that also threaten native species on islands (Seaman and Randall, 1962; Young et al., 2013, Angeli and Fitzgerald. *In Press*).

Native flora and fauna of St. Croix, in the U.S. Virgin Islands (USVI) of the Caribbean, have experienced extinctions and range reductions, possibly due to depredations by several non-native mammals, including rats, mongoose, and cats (Seaman and Randall, 1962; Morgan and Woods, 1986). For example, invasive rats consume sea turtle hatchlings on tropical islands (Gronwald et al., 2019), and in St. Croix invasive black rats (*R. rattus* Linnaeus, 1758) are known predators of both sea turtle hatchlings and the eggs and young of endangered St. Croix ground lizards (*Ameiva polops* Cope, 1863) (Witmer et al., 2007). At Sandy Point National Wildlife Refuge (hereafter Sandy Point) on St. Croix Island, >200 sea turtles (leatherbacks, *Dermochelys coriacea* Vandelli, 1761; hawksbill, *Eretmochelys imbricata* Linnaeus, 1766; and green, *Chelonia mydas* Linnaeus, 1758) nest annually, and observers found that mongoose consumed all the eggs from 25.5% of hawksbill nests (n = 35) and 35% of green turtle nests (n = 56) (C. Lombard, unpubl. data). Mongoose have also been observed digging up sea turtle nests and attempting to steal sea bird eggs, including those as large as pelicans (*Pelicanus occidentalis* Linnaeus, 1766), elsewhere in St. Croix (Seaman and Randall, 1962).

Based on these natural resource threats by invasive mammals in St. Croix, U.S. Department of Agriculture (USDA) Wildlife Services, U.S. Fish and Wildlife Service (USFWS), and the U.S. National Park Service (NPS) have been active in invasive mammal population control and eradication efforts. For example, each July from 2010 to 2013 at Sandy Point, USDA Wildlife Services removed 39–107 mongoose in traps positioned along the beach edges to protect sea turtle nest depredations by mongoose. Green Cay National Wildlife Refuge (hereafter Green Cay), which is an offshore island at the northern edge of St. Croix Island, had black rats eradicated in 2015 using diphacinone bait after several failed eradication attempts using traps (Draft Comprehensive Conservation Plan, 2009; C. Lombard, unpubl. data). Similarly, Buck Island Reef National Monument (just northeast of Green Cay) had mongoose eradicated by using traps in the 1980s (Z. Hillis-Starr, unpubl. data), and then an island-wide rat eradication was undertaken to prevent frequent black rat predation on hawksbill sea turtle eggs and hatchlings (Witmer et al., 2007), and to prepare the island for translocation of the St. Croix ground lizard in 2007. The rat eradication occurred by using diphacinone bait; however, house mice (*M. musculus*), which had gone undetected on the island until the rat eradication, quickly became prominent (Witmer et al., 2007).

When determining the best invasive predator removal strategies and management methods, it is important to identify all the mammalian predator species that are present at target sites (Courchamp et al., 2003). Rats, mongoose, cats, and dogs are known threats to sea turtles at sea turtle nesting beaches, such as at Sandy Point, yet the presence of mice and relative abundances of rats and other mammals are generally unknown. Although rats are a greater threat to sea turtles and birds than are mice, house mice are an invasive predator of interest for management because native plants and arthropods are common components of their diets (Angel et al., 2009; Shiels et al., 2013) and it is unknown if house mice are predators or competitors of St. Croix ground lizards (Witmer et al., 2007). The USFWS is considering several predator management options for Sandy Point, and one method of particular interest is a predator-proof fence installment followed by the removal of all (non-native and invasive) mammalian predators (e.g., replicating the methods of Young et al., 2013). Because rats are competitively dominant over house mice (Shiels et al., 2013), house mouse presence may be unknown in ecosystems that are commonly studied (Shiels and Ramírez de Arellano, 2018) and otherwise assumed absent until rat eradication occurs (Witmer et al., 2007). Additionally, large storms such as hurricanes can shift rodent populations, often causing large spikes in their abundances (Htwe et al., 2012), which may merit temporary or long-term adjustments in management strategies. Furthermore, given constant potential for accidental reintroduction of unwanted invasive predators through storm events and recreational access, it is essential to uphold biosecurity measures by conducting frequent small mammal surveillance in these critical island refuges. By doing this, managers can help maintain these islands predator-free and protect rare, threatened, and endangered natural resources.

The objective of this study was to determine the presence and relative abundances (via trapping or tracking tunnel activity; Shiels and Ramírez de Arellano, 2018, Madden et al., 2019) of non-native invasive mammals, with a focus on rodents (*Rattus* spp. and *M. musculus*) and mongoose, in high-interest habitats of St. Croix. Because two severe (Category 3–5) hurricanes passed St. Croix during the study period, we also compared the small mammal relative abundances just prior to and following the September 2017 hurricanes. We expected to find house mice, rats, and mongoose at Sandy Point, and mice only on Buck Island Reef National Monument and Green Cay (Draft Comprehensive Conservation Plan, 2009; Z. Hillis-Star, unpubl. data). Further, we expected that house mice would be more abundant on Buck Island Reef National Monument and Green Cay than at Sandy Point because of an absence of mongoose and other large predators and competitors on Buck Island Reef National Monument and Green Cay. Finally, we expected that the 2017 hurricanes would increase all established small mammal populations, particularly rodents.

2. Materials and methods

2.1. Study sites

Sandy Point National Wildlife Refuge (N $17^{\circ}41'$ W $64^{\circ}54'$) on St. Croix Island, USVI, was established in 1984 as the first sea turtle refuge in the USFWS refuge system. The 145 ha refuge has the longest continuous beach (4.8 km) in St. Croix (Fig. 1), where annually there are nesting population of 50–250 leatherback sea turtles, 25 to 50 hawksbill sea turtles, and 100 to 250 green sea turtles. From 2010 to 2013, the annual range of nests counted by USFWS observers was 254–1150 green turtle nests and 81–227 hawksbill nests. Black rats, mongoose, cats, and dogs are known predators at Sandy Point, and these species are often controlled using traps during the sea turtle nesting season.

Green Cay National Wildlife Refuge (N 17°46′ W 64°39′) is a 5.7 ha offshore island that is approximately 450 m from the northern shore of St. Croix Island (Fig. 1). Management efforts on Green Cay preserve habitat for the largest remaining population of the endangered St. Croix ground lizard. To help protect this lizard, repeated attempts have occurred using traps to remove invasive black rats in 2000 and 2006, but not all rats were eradicated or new ones had established by 2007 (Draft Comprehensive Conservation Plan, 2009). In 2015 black rats were confirmed as eradicated using diphacinone bait, and there have not been any invasive mammals on Green Cay since the rat eradication (C. Lombard, unpubl. data). Because of the close proximity to St. Croix Island (where black rats have long been established), Green Cay will be vulnerable to future rat re-invasions, and rat surveys have been conducted yearly using snap-traps by USFWS to ensure that the island remains rat-free. Aside from occasional visitation by land managers, humans are prohibited from visiting this island.

Buck Island Reef National Monument (N 17°47′ W 64°37′; hereafter Buck Island) is located 2.4 km off the northeast shore of St. Croix Island (Fig. 1). It is a 70 ha island that rises about 104 m a.s.l. There are no permanent water sources and it is covered by dry tropical forest vegetation. Although a few buildings and a plantation were established in 1754, the island has not been occupied by humans since the 19th century and forest cover has recovered from the past human disturbance (Witmer et al., 2007). No permanent residents are on Buck Island, but the NPS allows day-visitors to the island for purposes of hiking, picnicking, and swimming. Several species of threatened or endangered flora and fauna occur on Buck Island. Sea turtle nesting is annually quantified, and nesting populations of hawksbill sea turtles range from 50 to 80 adults and up to 250 nests (Hart et al., 2019). Black rats were eradicated (followed by a population explosion of house mice) in 2000 (Witmer et al., 2007). After island-wide rat eradication, the NPS reintroduced the endangered St. Croix ground lizard in 2007, translocating >50 individuals from Green Cay. Currently, there are no established mammals aside from house mice on Buck Island.

Two severe (Category 3–5) hurricanes (Irma and Maria) passed St. Croix in September 2017. Although Hurricanes Irma and Maria were classified as Category 5 hurricanes on the Saffir-Simpson (wind) Index during part of their passage through the region, the eye of each hurricane passed just to the north (Irma) or south (Maria) of St. Croix. Due to the distances from St. Croix to the eye of these storms, the wind speeds recorded in St. Croix were those of a Category 3 storm, and gusts reached 119 knots (93 knots sustained wind) at weather stations on Buck Island (during Irma) and Sandy Point (during Maria) (Cangialosi et al., 2018; Pasch et al., 2019). Because damage caused by each hurricane, in addition to wind speed, can also influence its category of classification, we refer to each Hurricane Irma and Maria as severe hurricanes, or Category 3–5 hurricanes, when they affected St. Croix in September 2017.

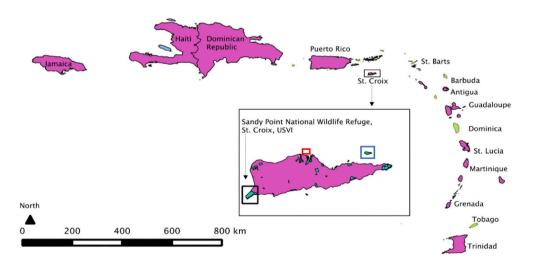


Fig. 1. Map of the Greater and Lesser Antilles, Caribbean Islands. In the magnified view of St Croix, U.S. Virgin Islands: Sandy Point National Wildlife Refuge is highlighted (black outlined box) in the southwest corner of St. Croix Island, whereas Green Cay National Wildlife Refuge (an offshore island) has a red outlined box off the north-central part of St. Croix Island, and Buck Island Reef National Monument (an offshore island) has a blue outlined box off the northeast end of St. Croix Island. The pink shade represents those islands with invasive mongoose. Most islands in the Caribbean have been colonized by one or more species of non-native rodents (i.e., *Rattus rattus, R. norvegicus*, and/or *Mus musculus*). Map provided by N.F. Angeli and modified from Ríos-López et al. (in press).

2.2. Field sampling

At Sandy Point and Green Cay, we used tracking tunnels (Shiels and Ramírez de Arellano, 2018; Madden et al., 2019) to determine the small mammals present and to monitor the changes in small mammal activity from the two severe hurricanes (Irma and Maria). Tracking tunnels consist of inked cards that are baited and placed inside a plastic tunnel. As a small mammal investigates the bait inside the tunnel, the ink is transferred onto the foot of the animal, resulting in a footprint left on the card, which can be identified to genus (Shiels and Ramírez de Arellano, 2018; Shiels et al., 2018; Madden et al., 2019). Tunnels (50 cm \times 10 cm x 10 cm; length x width x height; made of plastic) and pre-inked tracking cards (49 cm \times 9 cm; length x width; made of wax-coated paper; an 18 cm \times 9 cm [length x width] inked area occupies the center of the tracking card) were purchased from Gotcha Traps Ltd ("Black Trakka", gotchatraps.co.nz). These tracking tunnels are generally too small to survey for cats, but are ample size to detect mice, rats, and mongoose.

At Sandy Point on July 27, 2017 and June 25, 2018, we set 34 tracking tunnels. The same methodology was used in both years, which included baiting the tunnels with peanut butter and a coconut chunk, and spacing each tunnel 20–30 m apart from the east end of the refuge peninsula to the edge of the sand at the southwest end of the refuge (Fig. 2). Both peanut butter and coconut chunks are attractive baits for sampling house mice, rats, and mongoose (Pitt et al., 2015; Shiels and Ramírez de Arellano, 2018). At Green Cay, 14 tracking tunnels were established (Fig. 2) on June 26, 2018 (i.e., 9 months after the two Category 3–5 hurricanes), using the same methodology (including spacing and bait) as Sandy Point. During each survey, we recovered the tracking tunnels after 24 h of being set, and we then identified all animal tracks on tracking cards to genus. Previous studies in Puerto Rico and Hawaii revealed that house mice, rats, and mongoose visit baited tracking tunnels



Fig. 2. The three St. Croix study sites with yellow circles or lines depicting the approximate locations of the small mammal detection devices. Green Cay (upper left image) had 14 tracking tunnels for the 2018 sampling, and annual rodent snap-trapping occurs along this same transect. Sandy Point (upper right image) had 34 tracking tunnels for 2017 and 2018 sampling; red dashed lines outline the approximate eastern boundary of the refuge where human communities begin. Buck Island (lower image) had five transects where 93 snap-traps are used in annual rodent surveys. See methods for sizes of each study site. Maps modified from googlemaps.

and similar sampling devices within 24 h of placement (Pitt et al., 2015; Shiels and Ramírez de Arellano, 2018; Shiels et al., 2019).

For 2017 and 2018 evidence of small mammals at Buck Island, and 2017 evidence at Green Cay, we relied upon collaborators (i.e., C. Lombard, unpubl. data; Z. Hillis-Starr, unpubl. data) for rodent snap-trapping surveys that occurred annually or semi-annually. Both locations had Victor rat snap-traps baited with peanut butter mixed with dry oatmeal, and the traps were elevated above the ground (e.g., on tree trunks and/or branches) to limit the interference with hermit crabs. On Green Cay, 15–20 traps were used each 6 months, usually in January and July. Traps were placed along one transect that extended the length of the island (Fig. 2), and traps were clustered along the transect at several locations deemed to be favorable rat habitat. Traps were checked daily and remained set for 3–5 consecutive days. On Buck Island, there were 93 traps placed along five transects (20 traps placed on each of four transects, and 13 traps placed on one transect) along walking trails that spanned sea level to the highest point on the island (Fig. 2); sampling occurred the second week in December each year. On Buck Island, traps were set for a total of three consecutive nights, and they were checked daily in the morning. Thus, on an annual basis, the number of trap-nights (i.e., one trap set for one night is one trap-night) for Green Cay ranged from 45 to 100, whereas Buck Island always had 279 trap-nights.

2.3. Statistical analysis

We used generalized linear models with binomial errors (i.e., logistic regression) to determine if the ratios of small mammal presence (tracking) in tunnels were different between pre- vs. post-hurricane sampling (i.e., 2017 vs. 2018) at Sandy Point. Analyses were focused on house mice, rats, and mongoose; each of these species received independent testing. Statistical analyses were conducted in R version 3.4.1. We provided descriptive statistics (i.e., number of individuals per trapnight) for each sampling using snap-traps on Green Cay and Buck Island.

3. Results

House mice had not been recorded previously at Sandy Point, but they were found continuously distributed (i.e., end-toend) along the transect established at Sandy Point using tracking tunnels in both 2017 and 2018. When mouse tracking (which is indicative of mouse population abundance) was compared before (in 2017) and after (in 2018) Hurricanes Irma and Maria, there was significantly more tracking tunnels with house mouse tracks after the hurricanes (16 out of 34, or 47.1%) than just before the hurricanes (6 out of 34, or 17.6%) (z = 2.513, SE = 0.57, P = 0.0120; Fig. 3). Rat tracking at Sandy Point did not differ significantly (z = 0.983, SE = 1.18, P = 0.3260) when sampled before (3 out of 34, or 8.8%) and after the hurricanes (1 out of 34, or 2.9%). Mongoose tracking tended to be lower after the hurricane (1 out of 34, or 2.9%) relative to before the hurricane (7 out of 34, or 20.6%), but this pattern was only marginally significant (z = 1.951, SE = 1.10, P = 0.0510; Fig. 3). A feral cat and a lizard were detected in 2017, and invertebrates, particularly ants, were observed in many of the tracking tunnels in both 2017 and 2018 (Table 1).

Based on the snap-trap sampling that occurred in the few years leading up to the September 2017 hurricanes, rats (or any other mammal) had not established on Green Cay (i.e., zero individuals per trap-night; C. Lombard, unpubl. data). However, our sampling using tracking tunnels in June 2018 revealed that rats were present on Green Cay after the hurricanes, and 9 out of the 14 (i.e., 64.3%) tracking tunnels had rat tracks present after one night of sampling. The tracking tunnels with evidence of rat tracks were continuously distributed (i.e., end-to-end) across the island. There were no mouse tracks on Green Cay, and no

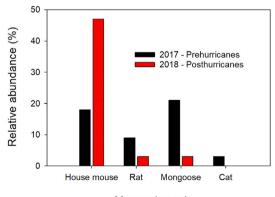




Fig. 3. Relative abundances (%) of small mammals detected in tracking tunnels prior to and following two Category 3-5 hurricanes (Irma + Maria) passing close to Sandy Point National Wildlife Refuge, St. Croix, U.S. Virgin Islands. There were 34 tracking tunnels set each year, and tunnels were checked to identify animal tracks 1 day after deployment. Note that a single tracking card can have multiple animal tracks present. Tracking, which may be used as an index of population relative abundance, of house mice increased significantly (P < 0.05) following the hurricanes.

Table 1

Results of animal visitation to tracking tunnels that were set at Sandy Point National Wildlife Refuge, St. Croix, U.S. Virgin Islands, prior to (in 2017) an after (in 2018) Hurricanes Irma + Maria. There were 34 tracking tunnels set each year, and tunnels were checked to identify animal tracks 1 day after deployment. Note that a single tracking card can have multiple animal tracks present.

Animal	2017 - Prehurricanes No. cards tracked	<u>2018 – Posthurricanes</u> No. cards tracked
Rat	3	1
Mongoose	7	1
Cat	1	0
Lizard	1	0
Ant	5	9
Total insect (including ant)	18	13

evidence of any other small mammals. Since our study, these rats on Green Cay were positively identified as the black rat (*R. rattus*).

On Buck Island, there were house mice, and not rats, in annual surveys just prior to the 2017 hurricanes, as well as in the 2017 survey (~3 months after hurricanes) and 2018 survey (~15 months after hurricanes) (Fig. 4). Although the number of mice caught were equal in the 2016 and 2017 surveys (14 individuals, or 5.0 indiv. per 100 trap-nights), the number of mice more than doubled from 2017 to 2018 (33 individuals, or 11.8 per 100 trap-nights) (Fig. 4).

4. Discussion

Surveillance using tracking tunnels enables rapid confirmation of new invasive species in areas not previously sampled, in remote locations such as islands, and following large storms (Shiels et al., 2018). At Sandy Point, we determined that house mice, rats, and mongoose were present before and after the 2017 hurricanes. Interestingly, house mice had not been documented prior to our sampling, and this was probably a result of previous small mammal surveys at the site using larger traps for larger animals (e.g., tomahawk traps with rats and mongoose targeted). By sampling the small mammal community at Sandy Point pre- and post-hurricanes, we found that house mouse abundance increased after the hurricanes, rat populations appeared unchanged, and mongoose populations tended to decrease (but only marginally significantly) after the hurricanes. Annual snap-trapping conducted by the NPS on Buck Island demonstrated that Buck Island is still rat-free, and the house mouse population that existed prior to rat eradication has continued to be successful for nearly 20 years and is still present. NPS trap data revealed that the mouse population more than doubled 15-months after the hurricanes. It has yet to be determined if, or the extent to which, the mouse population on Buck Island is affecting St. Croix ground lizards or other natural resources. By using tracking tunnels after the 2017 hurricanes at Green Cay, we determined that rats had established, probably through rafting on storm debris, swimming, a combination of rafting and swimming, or via accidental introduction by humans (e.g., a rat-infested boat landing on the island). Motivated by our sampling results on Green Cay in summer of 2018, USFWS and USDA Wildlife Services implemented a rat eradication operation on Green Cay in the summer of 2019. Land and resource managers benefit from knowing the composition of the small mammal community, and findings from our study have already influenced local natural resource management (e.g., stimulating a rat-eradication attempt of Green Cay).

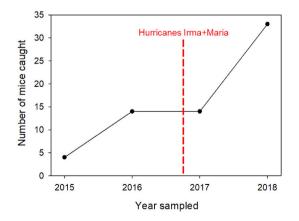


Fig. 4. Total house mice (*Mus musculus*) captured in rat traps during 279 trap-nights each year at Buck Island Reef National Monument, St. Croix, U.S. Virgin Islands. Trapping occurred for three consecutive nights, using 93 traps per night, during the second week in December each year. The two Category 3–5 hurricanes (Irma + Maria) passed close to the island in September 2017 (red dashed line). There were no rats captured during any of these periods. Data were provided by N. Hanna Holloway of the NPS.

The main island of St. Croix has well-established rat (black rats and Norway rats R. norvegicus Berkenhout, 1769), house mouse, and mongoose populations that span most of the island, and this includes both city and suburban areas. Our study has identified if these invasive mammals are present at some key natural area hot spots of St. Croix and revealed their relative abundances before and after two severe hurricanes passed by the islands. Predator control at Sandy Point mostly targets the protection of sea turtles and birds, of which rats, mongoose, cats, and dogs are the greatest threats to eggs and hatchlings. House mice have been shown to depredate seabirds on Gough Island (sub-Antarctic, where mice are three-times larger than mice in St Croix; Wanless et al., 2007) and Midway Island (north Pacific; in portions of the seabird colonies), but this behavior is extremely rare and we know of only six islands in the world where mice have been documented eating eggs, chicks, or adult seabirds (Angel et al., 2009). Instead, house mice are generally predators of insects and seeds (Angel et al., 2009; Shiels et al., 2013), and their population and ecosystem impacts are less well known than rats. Furthermore, house mice are generally seen as a lesser threat to native island species than are rats (Angel et al., 2009; Shiels et al., 2014). Nevertheless, future studies of the impacts and management of house mice are warranted, as they may be affecting plant reproduction by disrupting insect pollination and recruitment from seed (Shiels et al., 2013). At Sandy Point, house mouse eradication does not appear to require prioritization, yet if a predator-proof fence was installed to restore the native ecosystem then house mice should be a species included in the eradication plan, just like rats and mongoose (Angeli and Fitzgerald, In Press). It should be noted, however, that house mice are generally more difficult to eradicate from islands than are rats and this may be a result of the competitive dominance of rats over house mice (Angel et al., 2009; Witmer et al., 2007) and possibly lower efficacy of some of the rodenticide baits used to eradicate house mice (Witmer et al., 2007; Pitt et al., 2011).

The increase in house mice following Hurricanes Irma + Maria was a pattern observed at Sandy Point and Buck Island (St. Croix), and El Yunque National Forest (Puerto Rico). In El Yunque prior to the hurricanes, tracking tunnel evidence revealed that house mice were restricted to the roadside edges of the forest where grass cover was prominent (Shiels and Ramírez de Arellano, 2018). However, 9 months after the hurricanes house mice had spread hundreds of meters from the road into the interior forest (A. Shiels, unpubl. data), which may have been a result of their exploitation of increased grass cover and forage that occurred in the forest understory as a result of the opening of the canopy by the hurricanes. Formal vegetation surveys did not occur prior to or following the 2017 hurricanes at Sandy Point and Buck Island, yet field staff on Buck Island reported increased grass cover after the hurricanes (N. Hanna Holloway, pers. comm.), which supports the possibility that increased grass cover and food resources for mice may have helped boost mouse abundance in St. Croix. However, it is unknown if the increase in house mouse abundance at Sandy Point was fully or partially caused by the slight (but not significant) reductions in mongoose and cat (predators), or rat (competitors), presence and relative abundances (Fig. 3). Mongoose are well-known predators of house mice (Seaman and Randall, 1962), but the simultaneous changes in mongoose and house mouse tracking (and thus relative abundances) could be strictly correlative and not causal. To our knowledge, hurricane impacts to mongoose populations have not been previously documented. Both sampling at the same time of the year on Buck Island and at Sandy Point (within 1 month), and the large changes in house mouse abundance uncovered at Buck Island, Sandy Point, and El Yunque following the hurricanes, support a greater likelihood that the changes in small mammal abundances observed were likely due to the effects of the Category 3–5 hurricanes than not.

Hurricanes and other large storms may dislodge animals and animal habitat, and otherwise sweep vertebrates away from landmasses. For example, Elsey and Aldrich (2009) speculated that Hurricane Ike was responsible for moving a juvenile alligator 489 km, based on marking the alligator 6 weeks prior to finding it among mats of debris produced by the hurricane. Black rats are known to be good swimmers (Innes, 2005) and they commonly reside in a range of disturbed environments (Shiels and Ramírez de Arellano, 2019); both factors would enable them to survive rafting on debris from storms and establishing in foreign habitats. In temperate regions with rough waters, black rats have maximum swimming distances of about 300 m. However, in warmer, nearly subtropical areas (e.g., Great Barrier Island, New Zealand), some islands have been naturally colonized by black rats swimming 750 m (Innes, 2005). The most likely explanation for the arrival of black rats on Green Cay during the months following Hurricanes Irma + Maria is via dislodgement of habitat where the rat(s) were established on St. Croix Island and the ocean current swept the rat(s), and/or rats swam, the <500 m distance between the two islands. However, it is possible that humans were in part responsible for accidently transporting rats to Green Cay, and nearby boat harbors had been experiencing high rat infestations after the hurricanes (Z. Hillis-Starr, unpubl. data). It is forbidden for people to land or set foot on Green Cay; and although rare, people have been observed illegally visiting the island.

Black rats can have large home ranges and nightly movements when their densities are low (Shiels, 2010). However, it is unlikely that there was just one rat that moved along the >350 m transect and visited the 9 (of 14) tracking tunnels placed on Green Cay in a 24 h period. It is more likely that there were multiple rats when we sampled Green Cay in June 2018, even if there was one (pregnant female) that had colonized Green Cay post-hurricanes. The approximately 9 month period between Hurricane Maria (September 20, 2017) and our June 26, 2018 sampling was ample time for a significant-sized rat population to establish on the 5.7 ha island. The average litter size for black rats is 5–8, and the interval between litters averages 32 days (range 27–38) (Innes, 2005). Thus, using such estimation of litter size and rat survival, there could have been >500 individuals on Green Cay when we sampled the island 9 months after a single rat (pregnant female) would have established. Due to the many environmental and rat physiological factors that simultaneously affect rat population densities (e.g., Innes, 2005; Shiels, 2010), it is difficult to estimate population densities even when it is the objective of the study. The objective of our study was not to estimate rat population density, and tracking tunnel surveys represent an index of abundance and not a density estimate. At minimum, and based on the nightly linear distances traveled by black rats in Hawaii mesic forest (Shiels, 2010) and

the distribution of rats revealed in tracking tunnels on Green Cay, it is our estimation that there were at least a dozen black rats on Green Cay when our sampling occurred in June 2018. Due to the necessary time to build up a novel rodent population after very few individuals are introduced, and the difficulty in detecting very small populations, it was fortunate that our sampling occurred several months after the hurricanes (and likely rat establishment) on Green Cay. Similarly, Htwe et al. (2012) determined that the rodent outbreak (including black rats, house mice, and *Bandicota* spp.) in Myanmar rice fields occurred 15 months after the hurricane (Cyclone Nargis), and they surmised that the outbreak was consistent with the biological response time of rodent populations to build up from the lull produced by the major flooding event associated with the hurricane. Furthermore, the house mouse population on Buck Island did not double until the period from 3 to 15 months following the two hurricanes of 2017.

Buck Island still appears rat-free, yet reinvasion by rats to Buck Island remains a constant concern for the land and natural resource managers (primarily the NPS) because there are many visitors each day who arrive by boat and walk around on the island, often with picnics of food. Additionally, boats are allowed to park directly on the shoreline or a few meters offshore with their anchor lines connecting to the beach above the waterline. Overnight camping on boats is allowed, and even though visitors are not supposed to be onshore after sunset, it can be difficult to regulate. A greater number of traps or the use of tracking tunnels regularly distributed across the island would probably give earlier detection of a rat invasion than by using current methods; however, like Green Cay, within several months (perhaps 6–9 months) of a rat establishment event, the current rat-trapping transects would probably detect the spreading rat population that would likely occur if a rat (e.g., a pregnant female or multiple rats that successfully breed) was to establish somewhere on the island. If rats reinvaded Buck Island, and because sampling occurs just once a year (in winter), containment of the invading rats to a segment of the island would be unlikely but instead whole-island treatment probably would be needed to ensure that all rats were successfully eradicated.

House mice are less of a threat to native species conservation than are rats (Angel et al., 2009; Towns, 2009). Whereas the black rat is known to depredate many native species including vertebrates on islands where they occur (e.g., Shiels et al., 2014; Harper and Bunbury, 2015), house mice typically eat insects and plant material and not birds, lizards, or sea turtles (Angel et al., 2009; Shiels et al., 2013). Thus, there is little motivation to allocate efforts and funding into attempting to eradicate house mice that have been established for over 20 years on Buck Island. However, with the potential for future technology to lower costs to remove house mice in a safe and effective manner, and the possibility for house mice to unpredictably switch to preying on vertebrates in some years (e.g., Wanless et al., 2007), house mouse eradication from Buck Island, Sandy Point, or other areas of interest may be a more realistic consideration for the future. For any such small mammal eradications, biosecurity protocols must be in place and upheld to both prevent and rapidly address reinvasions like we documented on Green Cay following the 2017 hurricanes. Given that severe hurricanes (i.e., Category 3–5) are expected to increase in frequency in the future in the Caribbean and other regions of the world (Bender et al., 2010), land and resource managers should be prepared for the possibilities of new invasive mammals establishing and increased abundances of some already established invasive species.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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