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Research Article

Case study of a Rapid Response Removal Campaign for the invasive alien green iguana, *Iguana iguana*

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Abstract

The Invasive Alien Green Iguana (IAGI), Iguana iguana, has spread worldwide via the pet trade, as stowaways and via other means and has become a pest species of global concern. It also represents a major threat to the endemic Lesser Antillean Iguana, Iguana delicatissima, on St. Eustatius. Following the capture of an adult female IAGI on St. Eustatius in early 2016, we conducted a Rapid Response Removal Campaign (RC) from April 2016 to January 2017. Three sets of directed visual surveys totaling 409.5 observer hours and covering a combined trajectory of 114.2 km realized only a single detection of a hybrid that was later removed. During the remainder of the campaign period, an additional four IAGI hybrids were opportunistically detected and removed thanks to park staff or community involvement. Since the end of the campaign, eight additional detections and removals have been realized, three of which were IAGIs caught while offloading freight in the harbour and five of which were hybrids caught in surrounding suburban areas. We suggest that at least four distinct IAGI introductions to St. Eustatius occurred between 2013 and 2020. Our results show the value of motivating and mobilizing stakeholders and the public at an early stage of an invasion. Since the program's initiation, eight of the 13 iguanas detected for culling were thanks to public and key stakeholder support and involvement. Four years after our campaign, the number of IAGIs and their hybrids still appear to be limited and concentrated in and around inhabited areas. Additional removal campaigns should be initiated as soon as possible, firmly based in public outreach, motivation and engagement. New legislation is needed to prohibit the importation, possession and harbouring of IAGIs or hybrids and to provide a framework for long-term structural funding required for effective control and removal. Routine fumigation and rigorous inspection of arriving cargo to eliminate the risk of stowaway IAGIs are also recommended. Culling of IAGIs is recommended for the port of St. Maarten, which serves as a major point of dispersal of IAGIs to St. Eustatius and likely also other islands in the region.

Key words: community engagement, invasive species, invasive reptile, hybridization, island

Introduction

Biological invasions are a major global concern and have significant consequences for biodiversity, the environment, agriculture, livelihoods, health and culture in affected regions (Pyšek et al. 2020). These effects tend



to be much stronger on islands than on continents (Russell et al. 2017). Worldwide, the most impactful invasive animals are generally mammals such as feral livestock, cats and rats for which many eradications have been undertaken (e.g. Campbell and Donlan 2005; Howald et al. 2007; Campbell et al. 2011). In recent years, however, the Invasive Alien Green Iguana (IAGI) has become a species of high worldwide concern as an invasive species. From its origins in South America, it has spread extensively throughout the Caribbean (Falcón et al. 2012) and is now rapidly spreading elsewhere throughout tropical and subtropical regions of the world, including Asia (Falcón et al. 2013, Van den Burg et al. 2020).

The Lesser Antillean Iguana, *Iguana delicatissima*, is a highly endangered Lesser Antillean endemic species (Van den Burg et al. 2018a) native to the Dutch Caribbean island of St. Eustatius. The species is classified as Critically Endangered on the IUCN Red List and has already been lost from most Caribbean islands on which it naturally occurred (Van den Burg et al. 2018a). Today, the IAGI is a recognized principal cause for its endangerment throughout its remaining range due to displacement by and hybridization with the IAGI (Knapp et al. 2014). Since the extinction of the endemic rice rat, *Pennatomys nivalis*, during the European colonial era, either due to introduction of invasive rodents/mammals or habitat destruction (Brace et al. 2015), *I. delicatissima* has been and still is the largest surviving endemic land vertebrate of St. Eustatius.

Awareness that the IAGI is a serious threat to *I. delicatissima* developed only gradually. For decades the IAGI was regarded as a merely compatible coexisting species. For instance, Wijffels (1976) opined that *I. delicatissima* was "absolutely not being supplaced by the IAGI advancing from South America as has been assumed for many decades". Three decades later, in their review on the conservation state of reptiles of the Lesser Antilles, Powell and Henderson (2005) only indicated the possibility of hybridization as among the many threats to the species but gave it no further priority or urgency. In the *Lesser Antillean Iguana Species Profile* by Pasachnik et al. (2006) hybridization was mentioned, however, only in passing and was not highlighted as a principal threat. Likewise, in his review paper on the ecology and conservation of the Lesser Antillean Iguana, Knapp (2007) highlighted the threat of hybridization with the IAGI to the genetic integrity of the species, but offered little to prioritize it as a principal conservation concern.

By the early 2010s, expert opinions shifted, as they began to view the IAGI as a threat to the conservation of *I. delicatissima*. For instance, in 2012, the IAGI was described as a "potentially disastrous" future threat to the Lesser Antillean Iguana on St. Eustatius by Van Buurt and Debrot (2012) and later by Vuillaume et al. (2015). In 2013, Debrot and Boman (2013) and Debrot et al. (2013) listed the introduction of the IAGI as one



of the top four threats to the native iguana population on St. Eustatius. Finally, today, the most recent Species Action Plan for *I. delicatissima* recognizes "displacement through competition and hybridization with *I. iguana*" as a key factor in the loss of the Lesser Antillean Iguana from many islands (Knapp et al. 2014).

In 1992, the *I. delicatissima* population on St. Eustatius was estimated at approximately 300 animals, in 1998 at less than 300 animals, and in 2004 at about 425 (275-650) individuals (Reichling 1999; Fogarty et al. 2004). The most recent population survey concluded that, notwithstanding protective measures, the status of the native iguana had not improved significantly in the eight years since the 2004 assessment (Debrot and Boman 2013). The long-term prospects for the species worsened dramatically when, on 22nd February 2016, St. Eustatius National Parks (STENAPA) reported the capture of a gravid adult female IAGI. Recognizing the magnitude of this threat to the native I. delicatissima population, we swiftly initiated a rapid response removal campaign (RC) in an attempt to rid the island of this emergent threat and by April 2016 we had initiated the first of three directed removal surveys. Here we report on the results of our RC, the objectives of which were to: a) provide an initial assessment of the state of the IAGI invasion; b) engage community support in addressing this threat; c) evaluate the effectiveness of directed removal surveys and; d) recommend further actions required to deal with this most vital risk to the critically endangered *I. delicatissima* population.

Materials and methods

The IAGI can be readily distinguished from *I. delicatissima* based on several morphological characteristics such as the presence of a large subtympanic scale, nasal horns, large nuchal tubercles, a flat instead of bumpy top of the head, the presence of black rings around the tail and the absence of the thick sub-labial scales that typify *I. delicatissima* (Breuil 2013). F1 hybrids of the two species have a mix of these characteristics and are distinguished by a much smaller size and more forward placement of the subtympanic scale and dull-black rings around the tail (Figure 1). The most important signs for field detection of IAGIs and their hybrids at a distance are the black rings around the tail, a spiky dorsal crest and the presence of a large to very large subtympanic scale, most prominent on adult males.

Green iguanas are generally shy and successfully use camouflage to avoid detection. Therefore, due to this low detection probability, two well-experienced, iguana spotters (H. Madden and T. van Wagensveld) were assigned to conduct three sets of directed visual surveys spread out over the course of a year. The three sets of surveys were conducted in April 2016, August–September 2016 and January 2017, respectively. Our campaign period



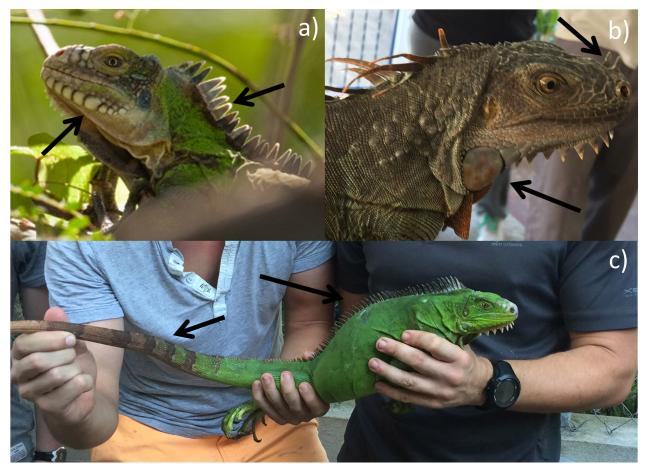


Figure 1. Key distinguishing phenotypic characteristics of a) *I. delicatissima* with arrows pointing to thick sub-labial scales and stout triangular dorsal spines, b) a specimen of Invasive Alien Green Iguana (specimen 2) caught prior to our Rapid Response Removal Campaign with arrows pointing at the large subtympanic scale and nasal spikes and c) a presumed F1 hybrid (specimen 7) with arrows pointing at the tempered-black tail rings and the spiky dorsal crest (all photos: STENAPA).

is defined as the whole period from April 2016 to January 2017. Opportunistic removals, however, continued after the campaign ended thanks to the continuing public awareness effort and broad community support. In this assessment we include information on IAGIs seen and culled both before and subsequent to our campaign, up through December 2020.

Extensive genetic sampling in 2015 showed that, until that time, there was no evidence of hybridization of IAGI into the *I. delicatissima* population (Van den Burg et al. 2018b). Making use of the most up-to-date leads, all directed search effort using line transects was concentrated in an area of up to about 200 m around locations at which IAGIs had been caught, or suspected IAGIs or hybrids had been reported. This was done to maximize actual chances of detection and was based on the presumed early stage of the IAGI invasion in 2016, during which animals should not have yet spread extensively. Searches included the harbour area as a main suspected point of entry to the island for all three sets of directed surveys. This also meant that the exact search areas covered greatly overlapped but were adjusted each time depending on the most recent actual or likely sightings of IAGIs or their hybrids (Figure 2). The distances covered during these line transect surveys were recorded and mapped, as was the time and number



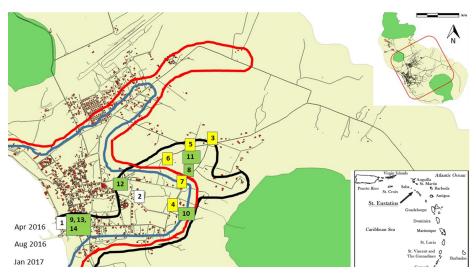


Figure 2. Map outlining the outer borders of the area envelope in which three sets of Rapid Response directed removal surveys (colored lines) were conducted; April 2016, August 2016 and January 2017. The known locations of Invasive Alien Green Iguanas and hybrids captured and culled, shown as white rectangles (before April 2016), yellow rectangles (April 2016 to January 2017) and green rectangles (January 2017 to December 2020), where numbers shown correspond to the specimen numbers in Table 2. Location of capture of specimen 15 is unknown and therefore not included on the map.

Table 1. Effort and results of the three directed surveys executed during 2016 and 2017 in an effort to find, capture and cull Invasive Alien Green Iguanas (IAGI) and hybrids on St. Eustatius.

Survey#	Time period	Days with search	Average search	Person-hours Distance		Surface	IAGI or hybrids
		activity (n)	team group size (n)	spent (hr)	covered (km)	surveyed (ha)	detected (n)
1	Apr 2016	7	2.2	72.0	23.8	47.6	0
2	Aug-Sept 2016	21	2.4	154.5	40.0	80.0	0
3	Jan 2017	12	4.3	183.0	50.4	100.8	1
	Totals:	40	3.2	409.5	114.2	228.4	1

of persons searching. The effective total visual widths of the transects varied greatly depending on vegetation density or visual obstruction by buildings and differed from roughly 10 to 50 m. With more intensive searching than applied by us in earlier work (Debrot et al. 2013) and with the generally more open suburban terrain and greater range of sight, this time our searches averaged about 10 m in width to either side of the line transects. Transect surveys were (practically) always performed by two experienced iguana spotters walking side by side, each focusing on a separate side of the transect. The only exception was for eight search hours (out of the total of 154.5 August 2016 search hours) that involved an expert observer working alone. The core group of two expert spotters was often accompanied by additional volunteers (once as many as nine) of mixed experience, tagging along to learn, help detect and help catch. Table 1 shows that the average search team size for the two first directed survey periods was only slightly above the core team size of two but that during the third period on average two or more volunteers additionally joined in the search. In total, 409.5 observer hours were spent during the three sets of directed surveys in and around areas where IAGIs or hybrids had been captured, seen or reported by the public. Searches were spread out over a



total of 40 days and covered a total trajectory of 114.2 km and an (overlapping) searched surface area of 228.4 ha (Table 1).

Iguana activity differs during the course of the day. Individuals seek out customary vantage points for basking as early as a half hour after sunrise (Van Marken Lichtenbelt et al. 1993). After initial basking they disperse more widely during mid to late-morning feeding and then generally retreat to shade during the midday heat. Line transect surveys were conducted from 7:30 am to 1:00 pm and our search strategy was adjusted according to iguana activity. Table 1 provides information on the total time spent, the distance and surface areas covered, as well as the average number of participants during each of the three directed transect surveys. Total transect distances covered differed per day, varying between two and 3.4 km for a mean length of 2.6 km per survey day. Vegetation height was highly variable in the largely suburban habitat surveyed. The vegetation was maximally 8-10 m high and generally consisted of a mix of grassy fields, scattered bushes, fruit trees or fence-line trees. Iguanas were often detected in the first half of the morning basking in the sun on rooftops, wall tops, or the top branches of higher trees. During the periods between which the three sets of directed surveys were held, as well as in the four years since, all additional IAGI captures were based on opportunistic detections from park staff and personnel and from the public and stakeholders.

The total number of inhabitants on St. Eustatius is less than 3,500, mainly concentrated in the capital Oranjestad. Public support for the RC was deemed essential (Vane and Runhaar 2016). In this small, tight-knit community, the nature conservation and agricultural sectors carry a high public profile and visibility, and thanks to extensive close personal contacts, the locals leading our effort were well-known. Also, all agencies involved in the nature and agriculture sectors are strongly embedded in the island community. Focused involvement of key institutional and community leading figures (who were well-connected, willing to communicate and whom the public respect and are willing to cooperate with) greatly facilitated broad support for the initiative. Hence, prior to starting the campaign, the agricultural, veterinary, customs services and general public were informed of the need for the RC. This was done using a combination of folders distributed to home-owners and the general public, a broadcasted radio interview, newspaper articles and social media presenting explanatory images for distinction of the two species and their hybrids, as well as a bumper sticker initiative (Figure 3). Bumper stickers and 'how to spot the IAGI/hybrid Iguana' handbooks were distributed to community members of all ages. Many vehicles sported the bumper sticker. The handbook (Powers 2016) and folders contained illustrations of both the native I. delicatissima and the IAGI, illustrating the key diagnostic phenotypic characteristics of the species. Numerous local radio shows, social media articles and in-school lessons were produced by STENAPA during the campaign





Figure 3. Selection of media headlines forming part of the campaign to engage the St. Eustatius public in the IAGI and hybrid removal campaign: A) The Daily Herald (TDH), September 23, 2016; B) TDH April 6, 2017; C) TDH, August 6, 2016; D) Bionews #12, 2018; E) TDH September 15, 2016; F) TDH, February 18, 2016; G) STENAPA Facebook post, May 6, 2020; H) TDH, April 19, 2016; I) Bes Reporter, February 2, 2017.

period. The regional newspaper *The Daily Herald* (distributed throughout St. Maarten/St. Martin, Saba, St. Eustatius and Anguilla) published five articles on the removal effort in 2016: February 18, April 23, March 8, May 8,



August 6 and September 15. Because the problem with IAGIs and hybrids had clearly not been eliminated after the campaign ended in January 2017, STENAPA continued providing attention to the issue and additional newspaper articles appeared on March 27 and May 2, 2018 and December 21, 2020. Other media attention for the IAGI removal campaign was given on March 23, 2016 (BioNews Newletter 23), October 17, 2016 (radio), February 2, 2017 (BES Reporter), April 17, 2017 (CaribischNetwerk), May 2018 (BioNews 13), and October 11, 2018 (Twitter). A local "iguana hotline" and website link were established and publicized through STENAPA's social media accounts to alert STENAPA to suspicious sightings and even encourage volunteers for "iguana patrols" (outreach@statiapark.org). Via these channels, the public was urged to help by calling the park and/or the coordinating staff member on her mobile phone to report any likely sightings of IAGIs. An invasive species workshop was hosted by the local Caribbean Netherlands Science Institute in November 2017. One of the goals of the workshop, attended by representatives of STENAPA, Public Health, the St. Eustatius Agriculture, Livestock and Fisheries Service (LVV) and the port authorities, was to educate associated border staff how to recognize the IAGI and hybrids.

All leads obtained for possible IAGIs, were followed up with a visit to each indicated location to conduct a search, generally within a day of the suspected sighting or more quickly if the animal happened to be in sight at the moment the lead came in. When an invasive iguana was not found, the site was revisited in the days thereafter to determine whether any IAGI or hybrids could be detected. All animals that could be captured by hand were humanely euthanized by the local vet; those that were out of reach were shot with an air rifle by a staff member of LVV. The specimens culled were stored in a freezer for further study. All subsequent directed surveys included these areas, as well as additional areas when new suspected sightings were reported by the public or actual captures were made. In general, the search areas were clustered around the inhabited portion of the island, starting from the harbour of Oranjestad, the suspected main point of entry of the IAGIs. Several locally-active, affiliated organizations (STENAPA, Wageningen University and Research, Caribbean Netherlands Science Institute and LVV) extensively conduct research and nature and livestock management activities in remote areas of the island and never noted anything to suggest IAGIs or their hybrids have (even up to our date of manuscript submission) spread outside Oranjestad or its immediate surroundings. Therefore, all RC directed survey effort was focused in areas most likely assumed to harbour the IAGA or its hybrids.

Results

At the start of our campaign, R. Hensen, former head of LVV, provided us photographs and information on a juvenile IAGI he had caught and euthanized



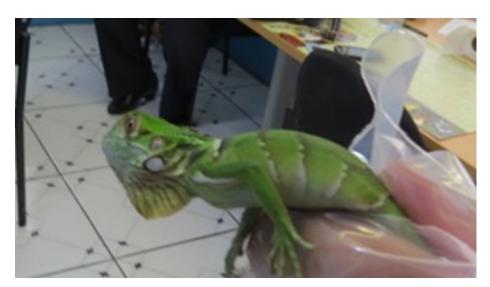


Figure 4. Juvenile Invasive Alien Green Iguana caught at the St. Eustatius harbour and euthanized by R. Hensen in 2013, exact date unknown. Photo taken at the office of the St. Eustatius Agriculture, Livestock and Fisheries Service by R. Hensen.

from the harbour area in 2013, thus documenting the first known introduction event (Figure 4). This specimen was not a direct result of our campaign but is still important to report as it provides a considerably earlier date for a first documentation of the IAGI on the island. Based on inquiries prior to our campaign, local accounts indicated that the IAGI we caught in 2016 (specimen 2) and based on which our campaign was coordinated, had been introduced as a pet but later escaped (Jesse et al. 2016). However, curiously, the specimen showed no common external signs of damage due to captivity (e.g., deformed snout and/or broken toes or nails).

During the campaign period, five hybrid iguanas were caught and culled. However, our three directed surveys yielded only a single detection of a hybrid (Table 1). The animal could initially not be retrieved despite several attempts to resight it. Nevertheless, it is believed to correspond to hybrid specimen 7 (Table 2) because of its similar size and identical capture location three months later, as based on a follow-up tip by the resident home owner. In contrast to the directed surveys, incidental detections by the public and park management staff and personnel, yielded four captures during the campaign. After the campaign ended and directed surveys were discontinued, eight more iguanas were opportunistically caught and culled, three of which were juvenile to young adult IAGIs intercepted in the harbour and five of which were hybrids caught in and around Oranjestad. Of these, six had been detected by the public and stakeholders while two had been detected by park staff and personnel. With two of the specimens documented in this study culled before our campaign, we here report on a total of 15 culled iguanas (Table 2). Most of these were young-adult hybrids, two of which were found gravid with eggs upon capture. During the whole study period, no IAGIs or hybrids were detected or reported from outside



Table 2. Overview of culled Invasive Alien Green Iguanas (IAGI) and hybrid iguanas in St. Eustatius. NA: not available; SVL: snout to vent length; VT: length of vent to tail-tip; TL: total length; U: unintentional; I: intentional; IS: incidental detection by park personnel or staff; IP: incidental detection by stakeholder or public.

Specimen number	Specimen type and order of capture	Date of capture	Year of likely separate introduction events	Period in relation to removal campaign	Type of detection	Maturity stage/sex	SVL (cm)	VT (cm)	Weight (kg)
1	IAGI 1	?/?/2013	2013 (U)	before	IP	Juvenile/NA	NA	NA	NA
2	IAGI 2	2/17/2016	2016 (I)	before	IP	Gravid/female	40.7	79.9	2.18
3	Hybrid 1	7/27/2016		during	IP	Subadult/male	19.3	15.6*	0.33
4	Hybrid 2	8/30/2016		during	IS	Adult/female	26.5	63.7	0.63
5	Hybrid 3	10/10/2016		during	IS	Adult/female	NA	NA	NA
6	Hybrid 4	10/19/2016		during	IP	Adult/male	26.9	67.0	1.40
7	Hybrid 5	1/24/2017		during	DS	Adult/female	32.5	79.6**	1.89
8	Hybrid 6	3/23/2017		after	IP	Adult/male	33.1	68.8**	2.30
9	IAGI 3	3/30/2017	2017 (U)	after	IP	Juvenile/NA	NA	NA	NA
10	Hybrid 7	4/21/2017		after	IP	Adult/female	27.3	62.2	2.30
11	Hybrid 8	4/18/2018		after	IP	Gravid/female	33.0	99.1	1.92
12	Hybrid 9	3/31/2020		after	IS	Gravid/female	26.0	29.9*	NA
13	IAGI 4	10/28/2020	2020 (U)	after	IP	Juvenile/male	17.0	40.5	NA
14	IAGI 5	12/12/2020		after	IP	Adult/female	31.0	49.0	NA
15	Hybrid 10***	NA		after	IS	Subadult/NA	24.4	33.7	NA

^{*} half of tail missing

Oranjestad or its immediate surroundings, despite our intensive field research activities in those areas.

After our initial capture of an adult IAGI in 2016, all other incidents involving non-hybrid IAGIs concerned juveniles or young adults intercepted in the St. Eustatius harbour. In March 2017, one subadult IAGI was caught while attempting to escape from cargo being unpacked in the harbour. In October 2020, a juvenile IAGI jumped onto a forklift during the unloading of cargo and was caught. Another young adult IAGI was caught in the harbour area in December 2020 and, based on similarity in size and proximity in time of detection, is believed most likely to be associated with the October 2020 specimen (Table 2). In summary, our results indicate a total of one likely intentional and three almost certainly unintentional introductions spanning the eight-year period 2013-2020. Neither the local 'iguana hotline' nor the website link for reporting suspected iguanas yielded any positive identifications of IAGIs. Most local residents and stakeholders contacted STENAPA rangers directly when they saw a potentially invasive iguana. Despite a disappointing attendance of customs officials to the invasive alien species workshop, some harbour staff were able to recognize IAGI and through this three (specimens 9, 13 and 14) were captured shortly after their presumed arrival in St. Eustatius. Since campaign initiation and up to the present, eight of the 13 iguanas detected for culling can be primarily ascribed to public and key stakeholder support and involvement. The fact that most IAGIs and hybrids were reported to STENAPA by the public and stakeholders and caught long after completion of the RC attests to the achievement of lasting community support.

^{**} tip of tail missing



Discussion and conclusions

Rapid response campaigns can greatly lower the cost of invasive species removal (Alvarez and Solís 2018), and not surprisingly there is much recent literature available on decision models and governance frameworks for implementing such systems for early detection and rapid response (e.g. Kraus and Duffy 2010; Martinez et al. 2018; Burgos-Rodríguez and Burgiel 2020; Reaser et al. 2020). Even so, while often called for (e.g. Rocha et al. 2020), actual case studies of implemented RCs with which to inform future campaigns are relatively few (e.g. Genovesi 2005; Hodgkins et al. 2012; Caffrey et al. 2018). According to Genovesi (2005) and Caffrey et al. (2018), this is most likely because of the often limited ability to detect early invasions and rapidly react due to inadequate legal frameworks and scarcity of resources. Also for the IAGI, Knapp et al. (2020) recently emphasized the need for action, but pointed out that this has typically come very late, in which case all that remains feasible is culling and control. Examples of very late action include the case of Florida, where the IAGI was introduced around 1966 but the first legal measures were only (unsuccessfully) attempted in 2020 (Knapp et al. 2020) and Puerto Rico, where the species was introduced in the 1970s, but a management plan was only recommended in 2012 (Lopez-Torres et al. 2012). In the Dominican Republic, where the species was likely introduced in the early 1990s importation was only prohibited 20 years later, after the species had already invaded the whole island (Pasachnik et al. 2012). Finally, in the Cayman Islands where the species was likely introduced in the 1990s, the first island-wide culling only took place in 2018 (Rivera-Milán and Haakonsson 2020). In the case of the IAGI on St. Eustatius, a fortuitous early detection presented us with a unique opportunity for a potentially successful eradication/containment campaign.

Based on our findings, and contrary to several recent reports and publications (Van Wagensveld and Van den Burg 2018; Van den Burg et al. 2018b), the first documented record of the IAGI on St. Eustatius dates from 2013, not 2016. The animal caught in the harbour and euthanized in 2013 was evidently a juvenile. At the time of its capture, LVV was of the opinion that it was an isolated introduction event and that euthanizing it would eliminate the threat of invasion. Therefore, aside from a brief search in the harbour area, no further attention was given to the incident. The first IAGI caught in 2016, and around which our response was coordinated, was a large, gravid adult female IAGI with 29 eggs, caught approximately one km from the harbour on the outskirts of Oranjestad. Based on local inquiries, it was determined that the animal in question had likely been introduced as a pet (Jesse et al. 2016). According to Van den Burg et al. (2018a), the 2017 introduction event involved four IAGI, of which three managed to escape. Based on what is known about growth and maturation



in the IAGI (e.g., Van Marken Lichtenbelt and Albers 1993), none of our detections or removals could reasonably correspond to any of these escaped animals and their actual fate remains unknown. Three lines of evidence suggest that the IAGI invasion in St. Eustatius is still at a relatively early stage. Firstly, only a single adult IAGI (that had been purposefully introduced as a pet) has so far been found on the island (located close to its point of escape), secondly, all juvenile IAGIs have been recorded at their point of entry in the Oranjestad harbour and thirdly, a 2015 genetic assessment found no indication of hybridization in 289 I. delicatissima blood samples collected from the wild (Van den Burg et al. 2018b). This means that containment and/or eradication of the IAGI and hybrid iguanas on St. Eustatius should still be feasible. A factor likely to help limit the spread of IAGI out of Oranjestad towards the north is the grassy to barren central section of the island with largely unsuitable habitat (Debrot et al. 2013) and the airport runway which practically cuts the island into two isolated halves.

Pluess et al. (2012a, b) examined the effect of various factors typically considered critical to eradication success in 136 eradication campaigns and 75 species. They found that factors such as reaction time, the level of knowledge and insularity were all unrelated to eradication success. Only the spatial extent of the infestation was significantly related to the eradication outcome (Pluess et al. 2012a, b). In the case of the St. Eustatius IAGI, our work suggests that the spatial extent of IAGI and hybrids distribution (if still present) is still quite limited. Even four years after the campaign, numbers of the IAGI and its hybrids were all found in and around inhabited areas, and their likely main point of entry is the island's harbour. Therefore, we conclude that it may not be too late to fully quell the invasion. Preferably, additional RCs should be initiated as soon as possible as the F1 hybrids are fertile and can reproduce (e.g. Breuil 2013). When egg-laying is successful, F2 hybrids should also soon appear. This is a tremendous challenge to eradication, as F2 hybrids resulting from backcrossing with I. delicatissima show a much wider range of intermediate and often less-pronounced distinguishing characteristics, making them much harder to distinguish from pure I. delicatissima (Breuil 2013). Once hybridization progresses beyond the F1 level, much more laborious and costly genetic testing of individual animals is required to reliably distinguish hybridized animals for culling. Therefore, immediate action must be taken to prevent any surviving F1 hybrids from successfully reproducing.

IAGI encounter rates during our directed surveys were clearly extremely low, even though we carefully targeted these surveys to those areas of highest likelihood of detection. On the contrary, most detections were incidental and primarily based on tips received from the public and other community stakeholders. In addition, more animals were actually culled after than during the campaign period. Thus, a key message from our



assessment is that for species with low detection probability, a longer, broad-based community effort might be more (cost) effective than shorter intensive survey efforts. In their draft Joint Invasive Alien Species Strategy, Smith et al. (2014) stress the need to involve the public in Invasive Alien Species (IAS) campaigns at an early stage. As also discussed by Vane and Runhaar (2016), lack of support for IAS removal and eradication is typically the principal obstacle to success. Our RC, which was extensively publicized in various ways and through a variety of media, was successful in achieving broad and lasting community support and engagement. Our results further corroborate that motivating and mobilizing community support and engagement can clearly make a critical contribution towards a RC. This may especially be the case for species with low detection probability combined with low densities, which make directed surveys relatively costly and ineffective. We suggest that under such situations it may be wise not to spend limited resources on extensive surveying but instead on intensive public outreach and education campaigns. The small island setting, close-knit community, high public profile and leading-figure roles of the local campaign initiators also likely played an important role in achieving such broad community support and stakeholder engagement.

IAGIs caught escaping from cargo or from the cargo platform in the harbour are assumed to have been accidental introductions and indicative of an introduction event taking place. Therefore, from 2013 to 2020, we believe to have documented four separate IAGI introduction events, three of which were accidental and due to stowaway animals in cargo arriving in port (2013, 2017, 2020) and one of which was likely intentional (2016). In order to safeguard the existence of I. delicatissima on St. Eustatius for posterity under such high and continuing threat levels, additional preventative and control measures will be required. Of utmost priority will be to implement (and enforce) local legislation, combined with training of border officials to prevent repeated entry of the IAGI from neighboring islands (Debrot and Boman 2013; Debrot et al. 2013; Debrot et al. 2018). However, institutions on St. Eustatius have been found to be grossly in need of additional financing, staffing and general capacity in order to be able to effectively address not only nature management in general (Van Beek et al. 2015) but also the IAS issue (Smith et al. 2014). Only a combination of legally mandated measures, structural funding and effective implementation can ultimately help keep St. Eustatius free of the IAGI.

Unfortunately, according to the most recent national review of progress made towards biodiversity conservation goals, the authors concluded that since the Dutch Caribbean IAS action plan was drafted, "no action has been taken on any of the islands" (Sanders et al. 2019). Establishing a legal framework to prevent introduction and make it illegal to possess live IAGI or its hybrids is an urgent policy priority. Only then is a legal foundation for structural funding and intervention provided. The current draft St. Eustatius



Nature Ordinance being considered for ratification states (in Art. 1.9) that it should be "prohibited to release and/or import specimens of non-indigenous or genetically modified species of flora and fauna into the wild." However, as the IAGI is notoriously prone to escape, difficult to retrieve, highly fecund and will readily hybridize with the native *I. delicatissima*, possession of live IAGI (including eggs), even in captivity, should also be fully prohibited. Supplementary ordinances will, therefore, clearly be needed.

As soon as possible, follow-up RCs should be conducted to reengage local nature, agricultural and border agencies and the public by means of personal contacts, involvement of community leading figures and public outreach in this small island community. A key practical recommendation is to implement decontamination treatment of shipments using biocide applications (Wittenberg and Cock 2005) and provide periodic inspection training to border staff, especially since officials rotate between the different Caribbean Netherlands islands on a regular basis. The border staff need to be able to recognize the IAGI and its hybrids (as well as other invasive alien species as listed by Smith et al. 2014) followed by immediately reporting of sightings to STENAPA, and preferably euthanizing animals themselves to exclude any chances of later escape. All cases of escape prior to euthanization should be reported immediately STENAPA to allow prompt follow-up action and all euthanized iguanas should be provided to STENAPA for documentation and specimen-storage purposes.

Not only do IAGI introductions pose a major danger to *I. delicatissima* on St. Eustatius and other islands of the Lesser Antilles, but also to other regional endemic iguana species and/or subspecies, three of which have only recently been described, namely Iguana melanoderma, from the nearby Caribbean Netherlands island of Saba, I. i. sanctaluciae from St. Lucia and I. i. insularis from St. Vincent and Grenada (Breuil et al. 2019, 2020). In order to give these last few large endemic island vertebrates a chance of survival, it will be essential to keep their island refuges free of the IAGI. The largest and most persistent source of IAGI in the Lesser Antilles is likely to be the port of St. Maarten that, for decades has been the largest Lesser-Antillean tourism and container shipping hub (Kester 2002; Pérez-Salas 2012; Ito et al. 2020). To reduce the threat of accidental stowaway or hitchhiking iguanas from the shipping hub of St. Maarten to nearby Anguilla and St. Barthèlemy where I. delicatissima have small populations surviving on the IAGI-free satellite islands of, respectively, Prickly Pear East and Île Fourchue (Van der Burg et al. 2018a), we recommend the port of St. Maarten carry out regular iguana culling within their grounds in order to reduce the risk of further spreading IAGI to the surrounding islands. IAGIs are being successfully culled on Grand Cayman island by the Cayman Islands Department of the Environment using a bounty system as incentive to hunters (Rivera-Milán and Haakonsson 2020 and J.F. Burton pers communication). As the iguana is an appreciated culinary delicacy



throughout the Caribbean, allowing harvest for consumption purposes, as is also being promoted regionwide in the case of the invasive Lionfish, *Pterois volitans* (e.g. Chapman et al. 2016; Blakeway et al. 2019), might also be a more sustainable incentive for the culling of this invasive species on St. Maarten.

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Authors' contribution

Debrot: funding acquisition, study design, coordination and writing, selection of journal and potential reviewers; Boman: data collection and review; Madden: design, field data collection, writing and review.

Ethics and permits

All work was carried out in accordance with St. Eustatius rules and regulations and took place under auspices of the local park management authority, STENAPA.

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