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Predation of Jamaican rock iguana (*Cyclura collei*) nests by the invasive small Asian mongoose (*Herpestes auropunctatus*) and the conservation value of predator control

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The introduced small Asian mongoose (*Herpestes auropunctatus*) has been widely implicated in extirpations and extinctions of island taxa. Recent studies and anecdotal observations suggest that the nests of terrestrial island species are particularly vulnerable to mongoose predation, yet quantitative data have remained scarce, even for species long assumed to be at risk from the mongoose. We monitored nests of the Critically Endangered Jamaican Rock Iguana (*Cyclura collei*) to determine nest fate, and augmented these observations with motion-activated camera trap images to document the predatory behaviour of the mongoose. Our data provide direct, quantitative evidence of high nest predation pressure attributable to the mongoose, and together with reported high rates of predation on hatchling and juvenile iguanas (also by the mongoose), support the original conclusion that the mongoose was responsible for the apparent lack of recruitment and the aging structure of the small population that was 're-discovered' in 1990. Encouragingly however, our data also demonstrate a significant reduction in nest predation pressure within an experimental mongoose-removal area. Thus, our results indicate that otherwise catastrophic levels of nest loss (at or near 100%) can be ameliorated or even eliminated by removal trapping of the mongoose. We suggest that such targeted control efforts could also prove useful in safeguarding other threatened insular species with reproductive strategies that are notably vulnerable to mongoose predation (e.g., the incubation of eggs on or underground).

Key words: Cyclura collei, Jamaican Iguana, *Herpestes auropunctatus*, mongoose, IAS trapping, nest predation, reptile conservation

INTRODUCTION

Among the world's 100 worst invasive species, the small Asian mongoose (*Herpestes auropunctatus,* Patou et al., 2009) has been implicated in extirpations and extinctions across its introduced range (Lever, 1994; Lowe et al., 2000; Barun et al., 2011). Insular faunas and especially terrestrial reptiles and ground nesting birds, have proven highly vulnerable to predation by the mongoose (Case & Bolger 1991; Hays & Conant 2007; Lewis et al., 2011; Barun et al., 2011). Few question that the introduced mongoose negatively impacts native island species, particularly vertebrates, and a compelling body of inferential evidence supports this conclusion (Gorman, 1975; Case & Bolger, 1991; Yamada & Sugimara, 2004; Hays & Conant, 2007; Watari et al., 2008). Direct evidence, however, remains scarce (Henderson 1992; Lever, 1994; Borroto-Páez & Woods, 2012). Indeed, some have questioned the reputation of the small Asian mongoose as a "driver" of island extinctions, and have argued that the evidence of alleged impacts remains inconclusive (Baldwin, et al.,1952; Corke, 1992; Hays & Conant, 2007).

In the Caribbean, an important biodiversity hotspot, the mongoose is widespread, occupying at least 33 islands, including all of the Greater Antilles (Myers et al., 2000; Barun et al. 2011). The mongoose was introduced in the late 1800's (Espeut 1882) to control agricultural pests, primarily introduced rats (e.g., *Rattus rattus, R. norvegicus*), but the results of this bio-control effort remain ambiguous (Baldwin et al., 1952; Seaman, 1952; Seaman & Randall, 1962; Hinton & Dunn, 1967; Nellis & Everard, 1983; Hoagland et al., 1989). Mongooses are known predators of introduced rat species; however, they are opportunistic omnivores that are largely terrestrial and diurnal in behaviour (Kavanau, 1975; Nellis & Everard, 1983; Simberloff et al., 2000; Barun et al., 2011). In contrast, the rat species they were introduced to target are both nocturnal and one, *R. rattus,* is predominately arboreal (Nellis & Everard, 1983). Because of differences in activity patterns, microhabitat use, and the availability of alternative diurnal terrestrial prey, mongooses were a poor choice for their intended purpose.

Since their introduction to the Caribbean, significant losses of the region's biodiversity have been attributed to predation by the mongoose. For example, Hedges & Conn (2012) suggest that 14 of 39 recently described

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Caribbean skinks may already be extinct, and attribute their loss to predation by the mongoose. Diurnal terrestrial snakes (e.g., *Alsophis* spp, *Liophis* spp, *Clelia* spp) and lizards (e.g., *Cyclura* spp, *Ameiva* spp, *Celestus* spp) (Henderson, 1992; Powell & Henderson, 2005; Powell & Inchaustegui, 2009), ground and low nesting birds (Wetmore, 1927; Raffaele et al., 1998), and terrestrial mammals (Woods & Ottenwalder, 1992; Borroto-Páez & Woods, 2012) across the Caribbean have suffered species extinctions, extirpation of populations, or have decreased in abundance. Depredation of sea turtle nests by mongooses is also widely reported (Seaman & Randell, 1962; Hays & Conant, 2007), and more recently Leighton et al. (2009) concluded that the mongoose was the primary source of sea turtle nest mortality in Barbados. In Jamaica a similar trend among Hawksbill turtle (*Eretmochelys imbricata*) nests is likely (Pers. Obs.).

In Jamaica, the mongoose has been implicated in the loss of at least six endemic species, including a mammal (Jamaican Rice Rat, *Oryzomys antillarum*), several birds (Uniform Crake, *Amaurolimnas concolor concolor*; Jamaican Pauraque, *Siphonorhis americana*; Jamaican Petrel, *Pterodroma caribbaea*), and two reptiles (Jamaican Giant Galliwasp, *Celestus occiduus*; Jamaican Black Racer, *Hypsirhynchus ater*) (see Lewis et al., 2011). Other endemic Jamaican species that were once common are now scarce, and the mongoose is considered the primary cause of their decline (Henderson, 1992; Vogel et al., 1996). However, quantitative data confirming the impacts of mongoose predation on threatened Jamaican fauna have been few, and conclusions regarding the mongoose have been based largely on anecdotal accounts (Vogel et al., 1996; but see Lewis et al., 2011).
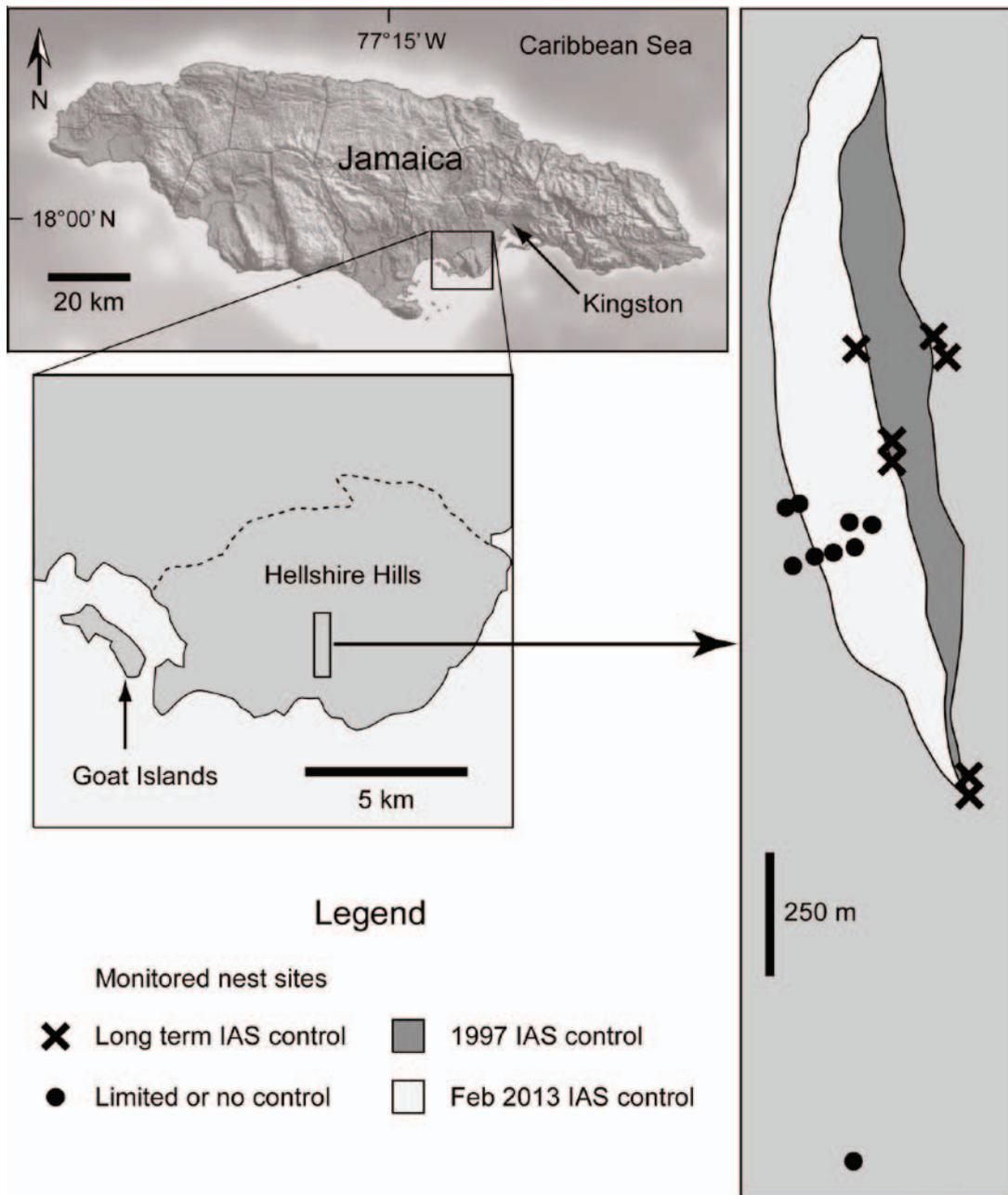
Fig. 1. Map of Jamaica with inset showing Hellshire Hills (Study area) and the Goat Islands

Fig. 2. Three types of iguana nest sites: A) Communal soil nest - showing two recently arrived gravid females, two post-partum females defending their nests and one female that emerged from laying her eggs, B) Rock-Hole nest - a female iguana has just laid her eggs at this site and is peering into her nest, C) Artificial or Man-made nest site–with a post-partum female and a gravid female fighting over nest space

On the Jamaican mainland, the endemic iguana (*C. collei*) was thought to have been extirpated within a few decades following the introduction of the mongoose, and by the early 1900's the species was known only from the mongoose-free Goat Islands (Barbour, 1910). However, by 1925 mongooses were also introduced to the Goat Islands and by 1930 iguanas were considered scarce; then, during a six-month period in 1944, surveys by the Institute of Jamaica suggested that at most a few dozen aged adults were all that remained. Most of these were moved into captivity to make way for a World War II, U.S. military base, and when the aging captives eventually

died out the Jamaica iguana was considered extinct (Lewis, 1944). Although other factors such as habitat destruction, hunting by people for food, and predation by domestic cats, dogs, and feral pigs likely played a significant role in decimating iguana populations, the mongoose is said to "have preyed upon the eggs and the young lizards with amazing thoroughness" (Lewis, 1944).

Several species (e.g., Antiguan Racer, *Alsophis antiguae*, Bridled Quail Dove *Geotrygon mystacea*, Cuban Solenodon, *Solenodon cubanus*) that the mongoose is thought to have eliminated have since been rediscovered, albeit most of those species remain close to extinction (Parker, 1936; Westermann, 1953; Nellis & Everard, 1983; Nowak, 1991; Sajdak & Henderson, 1991). Similarly, in 1990 the Jamaican iguana was rediscovered, and in 1993 a Population and Habitat Viability Analysis (PHVA) concluded that fewer than 100 aging adults remained, juvenile recruitment was negligible, and the mongoose was the primary threat to the iguanas' persistence in otherwise suitable habitat (Captive Breeding Specialist Group, 1993). In an effort to prevent their impending extinction several emergency conservation measures were implemented:

(1) From 1991 until the present (2016), two small communal nest sites have been monitored (visually and more recently with camera traps) and protected (live traps and fenced barriers) against Invasive Alien Species (IAS), during both nesting and hatching seasons. A portion of hatchlings are collected and enter a captive headstart program, in which they are raised to a size considered secure from most introduced predators before being released back into the wild, and

(2) in 1997 an IAS control program was initiated in the 'core' iguana area (~2 km^2 limestone depression, containing the only known iguana nesting sites) using live trapping that primarily targets the mongoose (Wilson et al., 2004).

Since 2004, other nesting areas outside of the 1997 IAS control area have been identified. In an effort to improve and monitor the efficacy of overall conservation measures, and specifically to investigate the use and success of other iguana nesting sites outside of the IAS control area, we incorporated the deployment of camera traps into our monitoring program.

The objectives of this study were to quantify the impact of mongoose predation on iguana nests, and to assess the utility of a trap-removal program designed to mitigate mongoose impacts. Using a combination of direct observations and camera traps we monitored a range of known and suspected iguana nest sites in areas with and without IAS control and recorded iguana and mongoose activity at these sites.

Field-Site Description: The Hellshire Hills
Located in the Portland Bight Protected Area (Espeut, 1999) on Jamaica's central southeast coast, the Hellshire Hills (17⁰54' N, 77⁰58' W) comprise a 110 km^2 area of dry tropical forest over a raised white limestone peninsula,

Table 1. Summary of camera trap survey showing number of Trap Nights (TN), photo-capture data, and % of target species recorded for 16 nesting areas during three Jamaican iguana nesting seasons. X=camera not set, nest not used, camera failure. Nest sites 1-7, were in areas of long-term IAS control and nest sites 8-16 in areas with No IAS control or limited (recent) control.

Treatment	Nest Site	Number of Trap Nights (TN)				Number of photos				Photo % of target species		
		2010	2012	2013	Total	2010	2012	2013	Total	% Iguanas	% Mongooses	% Other spp.
LONG-TERM IAS CONTROL	1	6	X	X	6	397	X	X	397	98.2	0	1.8
	2	4	46	54	108	496	1022	1586	3104	95.1	<0.7	4.2
	3	20	20	27	67	2434	15285	13566	31285	94.5	0	5.5
	4	16	13	24	53	3612	7533	3740	14883	94.1	0	5.9
	5	X	18	X	18	X	501	X	501	51.2	0	48.8
	6	X	26	17	43	X	1510	96	1606	97	0	3
	7	15	X	X	15	19	X	X	19	100	0	0
								Totals	51795	90	0	10
LIMITED OR NO IAS CONTROL	8	7	7	38	52	57	1783	515	2355	88.4	7	4.6
	9	X	26	35	61	X	82	212	294	14	<0.5	85.5
	10	16	29	39	84	62	780	441	1306	61.2	30	8.8
	11	X	22	36	58	X	326	121	441	48	42.9	9.1
	12	X	22	42	64	X	124	797	914	42	29.4	28.6
	13	X	32	X	32	X	2046	X	2046	85.4	7.5	7.1
	14	11	26	28	65	158	1001	419	1578	62	9.6	28.4
	15	X	21	24	45	X	367	615	982	85.2	2.7	12.1
	16	X	4	23	27	X	23	69	92	65.2	19.6	15.2
								Totals	9988	61.3	16.6	22.1
				Total TN's=798			Total # of photos=61783					

bordered by a rugged coastline to the south and west; Jamaica's second largest city—Spanish Town— lies to the north and the urban centers of Portmore and Hellshire Beach to the east (Fig. 1). As the 'crown jewel' of Jamaica's largest protected area, the Hellshire Hills contain the largest tract of intact dry tropical forest in Central America and the West Indies (McLaren et al., 2011; Neill, 2013), and is regarded as a biodiversity 'hotspot within a hotspot' (Lewis et al., 2011). The area is also considered of global importance as a Key Biodiversity Area (KBA) designated by the Critical Ecosystems Partnership Fund (CEPF), and is recognised by the Alliance for Zero Extinction as a site facing an 'imminent extinction' (Ricketts et al., 2005).

Our study was conducted in the least disturbed interior of the Hellshire Hills (Fig.1). This area is bisected along a collapsed north-south geological fault that forms a series of large, steep sided depressions that represent the most prominent features in the Hellshire Hills landscape. These rugged karst limestone depressions now support all that remains of the remnant Jamaican iguana population.

Nest types and sites
Soil deposits are scarce throughout the Hellshire Hills and accumulated deposits in exposed sites are important iguana nesting resources. Several of these soil deposits within the largest depression are known to harbor communal iguana nesting sites (Fig. 2A). In addition, the western slope of the main depression contains several areas of open karst pavement that support a number of smaller, more dispersed nesting sites, including a small red soil nesting site and a series of rock-hole nest sites (Fig. 2B). Several head-started iguanas established a similar set of rock-hole nests in 2007, south of the main depression nesting areas, on westerly slopes of karstified rock pavement at the edge of a smaller depression.

Two communal nest sites within the large depression were identified in 1990-91; additional nest sites were located during the period 2004-2008, and two artificial nest sites (one in 2004, the other in 2012) were constructed within the IAS control area and have proven successful (Fig. 2C). In total, we have identified five soil-nesting sites (including the two artificial nests sites) and four rock-hole nesting sites within the 1997 IAS control area. Before 2013, one soil nest site (up to three nests) and 17 rock-hole nests were known outside of the 1997 IAS control area. However, several of those nests were used only periodically, with weather conditions and predator disturbance thought to be factors in the use or abandonment of some nests.

Although nest type (i.e., soil vs. rock hole) varied between the areas under investigation (IAS control: 5 soil nest sites, 4 rock-hole nest sites; No IAS control: 1

Table 2. Number of camera trap photos of species photographed at 16 active Jamaican iguana nesting areas during three nesting seasons (2010, 2012, 2013); nest sites 1-7, were in areas of long-term IAS control and nest sites 8-16 in areas with No IAS control or limited (recent) control. X=camera not set, nest not used, camera failure.

Nest Site #	Iguana 2010	Iguana 2012	Iguana 2013	Mongoose 2010	Mongoose 2012	Mongoose 2013	Pig 2010	Pig 2012	Pig 2013	Cat 2010	Cat 2012	Cat 2013	Dog 2010	Dog 2012	Dog 2013	Birds 2010	Birds 2012	Birds 2013	Hutia 2010	Hutia 2012	Hutia 2013	Other non-natives 2010	Other non-natives 2012	Other non-natives 2013
1	390	X	X	0	X	X	0	X	X	0	X	X	0	X	X	6	X	X	0	X	X	1	X	X
2	495	927	1529	0	0	0	0	0	0	0	0	0	0	0	0	1	68	23	0	27	22	0	0	12
3	2382	15214	13400	0	0	0	24	1	24	0	38	3	0	0	0	24	31	139	0	0	0	0	1	0
4	3604	6788	3610	0	6	0	0	0	0	0	5	3	0	0	0	6	734	125	0	0	0	0	0	0
5	X	258	X	X	0	X	X	0	X	X	12	X	X	0	X	X	231	X	X	0	X	X	0	X
6	X	1485	73	X	0	0	X	0	0	X	17	0	X	0	0	X	8	23	X	0	0	X	0	0
7	19	X	X	0	X	X	0	X	X	0	X	X	0	X	X	0	X	X	0	X	X	0	X	X
8	55	1599	428	2	151	19	0	0	0	0	0	6	0	0	0	0	30	44	0	0	0	0	3	18
9	X	35	6	X	3	3	X	2	3	X	0	72	X	0	0	X	42	90	X	0	15	X	0	23
10	47	572	172	5	140	241	3	9	0	0	8	6	0	0	0	7	48	0	0	3	0	0	0	18
11	X	121	94	X	183	9	X	0	3	X	16	0	X	0	0	X	0	6	X	0	3	X	6	6
12	X	34	353	X	26	245	X	0	0	X	48	0	X	0	0	X	16	192	X	0	0	X	0	0
13	X	1748	X	X	155	X	X	0	X	X	0	X	X	0	X	X	143	X	X	0	X	X	0	X
14	141	458	380	4	148	1	2	0	0	0	11	0	0	0	0	12	384	38	0	0	0	0	0	0
15	X	243	594	X	12	15	X	7	0	X	19	3	X	0	0	X	70	0	X	0	0	X	16	3
16	X	16	44	X	7	11	X	0	0	X	0	2	X	0	0	X	0	9	X	0	0	X	0	3

soil nest site and 17 rock-hole nest sites), we believe all iguana nests, regardless of type (soil, rock-hole and artificially constructed nests), are equally attractive to the mongoose. Before the establishment of IAS control in 1997, observations of mongooses investigating communal nesting sites were not uncommon (Vogel & Kerr, 1992; E. Duffus pers. comm.), and following initiation of IAS control small seasonal increases in mongoose capture rates have been noted in the vicinity of iguana nest sites during nesting and hatching periods (unpublished data). Furthermore, observations of mongoose visitation at iguana nests (e.g., fresh mongoose tracks or scats at nest entrances) in non-IAS controlled areas are noted with regularity.

METHODS

Invasive Alien Species (IAS) control

In 1997 a trap loop (ca. 0.5 km^2) of ~20 live box traps was established within two large depressions that contained the majority of the remaining iguana population; that part-time effort was expanded in mid 1999 when 55 live box traps were opened 365 d/yr. By 2004 the trap loop contained ~75 live box traps, comprising mostly cat (66cm L x 22cm W x 22cm H) and mongoose (50cm L x 18cm W x 18cm H) sized traps. Mongooses are relatively easy to trap (Coblentz & Coblentz, 1985; Roy et al., 2002; Yamada & Sugimara, 2004), and both trap sizes proved effective for mongoose captures. The larger cat-sized live box traps are however, better suited to capturing larger iguanas (for population monitoring) and perhaps increase rates of feral cat capture (another target of the trapping program).

Four months prior to the 2013 nesting season a new trap line with an additional 105 cat-sized live box traps was added along the outer western slopes of the two large central depressions, connecting with the initial 1997 trap loop. This effort doubled the size of the IAS control area; included three more recently (2006, 2007, 2008) identified nesting areas (approx. 25% of all known iguana nests), and increased the number of traps deployed to approx. 190.

Camera trap surveys

Camera trapping surveys were conducted during the 2010, 2012 and 2013 nesting seasons from the third week of May (when oviposition generally begins) through early July. In 2010 we deployed eight digital Bushnell Trophy Cam units (Bushnell Outdoor Products Inc., 9200 Cody Overland Park, KS 66214-1734, USA) at eight nest site locations, five inside the long-term 1997 IAS control area and three outside of this mongoose-removal area. In 2012, twelve Reconyx PC800 Hyperfire Professional

semi-covert IR units (Reconyx, Inc., 3828 Creekside lane, Suite 2 Holmen, WI 54636, US) were deployed at 14 nesting site locations, five inside the long-term 1997 IAS control and nine outside of the IAS control area. In 2013 twelve Reconyx PC800 Hyperfire Professional semi-covert IR units were deployed at 14 nesting site locations, all of which were within the expanded IAS control area. In both 2012 and 2013, cameras from two early season nests were later moved to monitor two late season nests (i.e., 12 cameras were used to monitor 14 nests sites).

In most cases camera units were secured to trees with elastic straps. In locations where a suitable tree was unavailable, tri-pods constructed from dead wood strapped together with zip-loc cable ties were used to position cameras. Depending on the field of view required, cameras were set between 0.5 — 1.5 m in height and directed down towards the target area. Each unit was fitted with two silica gel desiccant pellets, a Sandisk 4 GB memory chip and powered by 8 (Bushnell) or 12 (Reconyx) eneloop AA rechargeable batteries. We used normal trigger settings (three pictures per trigger, one-second interval between pictures, and 0 seconds between successive triggers) together with the nighttime picture illuminator option. Date and time were imprinted on each photograph taken with the Bushnell cameras and, date, time, and temperature readings were recorded on the Reconyx models.

We monitored all nest sites using a single camera at each site, with the exception of the Upper Communal Nest Site (inside the 1997 IAS control area) — this larger site required two cameras to ensure adequate coverage; we therefore considered these two cameras to constitute a single unit (i.e., coverage of a single nesting area). In all other cases a single camera provided adequate coverage, because surveys were focused on the presence and activities of iguanas and mongooses in small areas of interest (nest entrances). Camera traps were erected and activated at known and suspected nest sites and remained active through the iguana-nesting season (mid-May–early July).

When possible, camera traps were deployed prior to nest initiation based on data from previous nesting seasons. Cameras were also deployed when nesting activity (i.e., test digs, soil spray or fresh scratches at rock hole nest entrances) was detected at other sites during regular nesting season surveys within the core iguana area.

Data analysis

During three iguana nesting seasons (May–July 2010, 2012, 2013) camera traps were used to monitor 16 different nest site areas (~ 160 individual nests) for 798

Table 3. Proportion (%) of iguana and mongoose photos by year (2010, 2012, 2013) and area (with and without IAS control).

	2010	2012	2013	IAS control	No control
Mongoose	0.15	2.6	2.45	0.01	13.8
Iguana	98.6	91	93.26	96.86	74.41

Trap Days (TD) with one TD=24 hours, see Table 1. We report the number of images of each species or species group (i.e., birds) per site and year (Table 2).

Relative Abundance Indices (RAI's) representing nest predation intensity were generated from photographic rates recorded at iguana nest sites with and without IAS control; this allowed us to examine the temporal pattern of mongoose nest predation, and to assess the effectiveness of the mongoose control program. All photo encounters (regardless of independence) of mongoose at the 16 monitored nest sites, were summed for three nesting seasons and then divided by the number of TD's at each site and multiplied by 100 (# of photos/TD's X 100=RAI) then the RAI's of the two groups (IAS control VS No control) were compared using a Generalised Linear Mixed Model (GLMM implemented using the GLMER function, LME 4 package, Bates et al. 2015) with time as a random effect, to examine for differences in mongoose visitation (Predation intensity). Although the GLMM data were not strictly independent, the result was supported by additional independent t-tests that compared camera traps that recorded mongooses with those that did not; we also calculated the number of individual (i.e., identified as unique) mongooses at sites with IAS control and without.

To document the details of mongoose predatory behaviour at iguana nest sites we divided images into five categories: (1) Mongoose present at nest sites, (2) Mongoose entering or exiting iguana nest (3) Mongoose with iguana egg in mouth, (4) Mongoose scent marking objects (e.g., shrubs, rock features) near the entrances of iguana nests, and (5) Negative interactions between mongoose and nest guarding female iguana; image data are considered for each nest site and by area (i.e., IAS control/no control) and year (3 nesting seasons).

To record the relationship between time of iguana oviposition and mongoose visitation patterns we identified the oviposition dates of as many gravid female iguanas as possible from camera trap images. The occurrence and dates of mongoose visits were then tallied for the week preceding and the three weeks subsequent to oviposition. We also measured diel
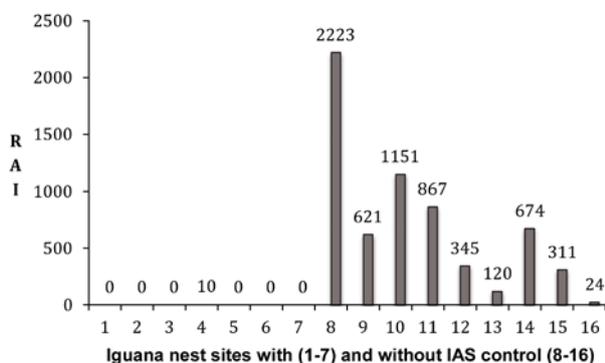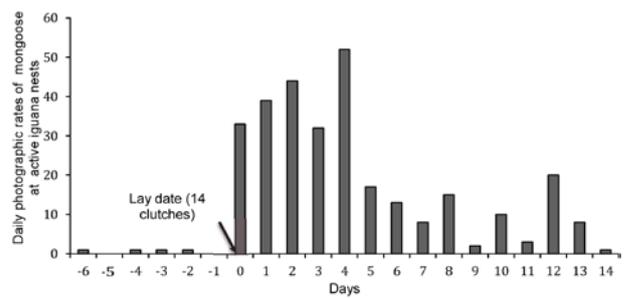
Fig. 4. Daily photo capture rates of mongooses at recently deposited iguana nests (n=14), beginning one week prior to oviposition through two weeks post-oviposition.

patterns of behavioural activity (mongoose and iguana) in the vicinity of iguana nests. Image capture times of each species were grouped into one-hour intervals to produce a nest visitation plot.

We determined nest predation during regular visual nest surveys that were augmented with information from photographic data. To compare the loss of iguana nests at nesting areas with and without IAS control we analyzed annual nest data with 2 X 2 contingency tables using Barnard's exact tests (Calhoun 2013; R Core team 2014). Nest predation was either documented directly (e.g., evidence of egg shells or photographic images of egg removal by mongoose) or inferred from repeated evidence of visitation by mongoose (e.g., mongoose scats, tracks, or images of mongoose entering or exiting active iguana nests) and subsequent abandonment of the nesting attempt by the iguana. Thus, we categorised nests as either being depredated by the mongoose or not; we could not determine whether all non-depredated nests were ultimately successful (i.e., produced hatchlings). Female iguanas show strong nest site fidelity, often using the same nest site repeatedly for many years. Therefore, to ensure data independence (i.e., the potential for repeated measurements/nesting observations of the same individuals during multiple years), we analyzed iguana nest data for each of the three nesting seasons separately.

RESULTS

Camera trap sampling effort and species recorded
The camera trap nest site surveys resulted in a total of 61798 images from 16 Jamaican iguana-nesting sites (~160 individual nests) over the 2010, 2012 and 2013 nesting seasons (Table 1). Iguanas, specifically nesting female iguanas, were responsible for 92.7 % (57314 images) of all photos recorded. Birds, mostly Turkey vultures (*Cathartes aura*), Ground Doves (*Leptotila j. jamaicensis*), Caribbean Doves (*Zenaida aurita zenaida*) and Stolid Flycatchers (*Myiarchus s. stolidus*) were the next highest group represented. However, if only IAS are considered, then the mongoose accounted for 1386 images (or 74 %) of the photo visits recorded at iguana nest sites (Table 3), feral cats (*Felis catus*) 298 images (16 %), feral pigs (*Sus scrofa*)55 images (~ 4%), marine toads (*Rhinella marina*) 65 images (4 %), and rats (*Rattus rattus*) 45 images (~ 3 %).

Fig. 3. Relative Abundance Indices (RAI) derived from camera trapping data, of mongoose at Jamaican Iguana nest sites with and without IAS control for the 3 nesting seasons by site. Iguana nest sites 1–7 have long-term IAS control, whereas iguana nest sites 8–16 are outside of this area afforded IAS trapping protection
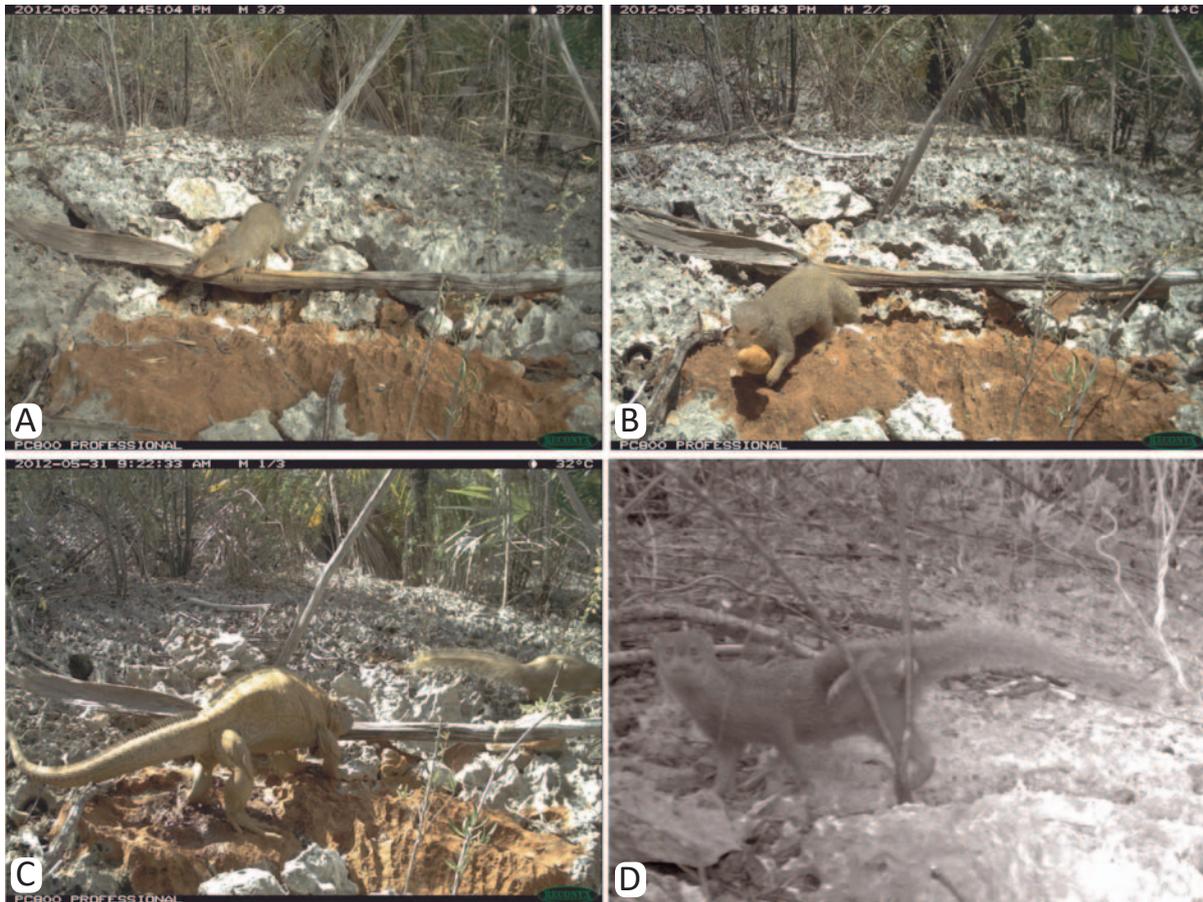
Fig. 5. A) Mongoose present at the entrance to an active iguana rock-hole nest. B) A mongoose exits an iguana rock-hole nest with an iguana egg in its mouth. C) Iguana and mongoose interaction - a female iguana chases a mongoose from her rock-hole nest site. A wet patch beneath the female iguana can be seen where the mongoose had punctured a stolen egg and some of the contents had drained onto the ground. D) A mongoose scent marks the entrance to an active iguana rock-hole nest, mongoose were observed entering this nest > 40 times in the following 6 days.

The majority (~84 % or 51795 images) of the total photo set was recorded from nest sites inside the long-term (1997-present) IAS control zone; this excludes nest sites with limited IAS control in 2013 (see below). Within the long-term 1997 IAS control zone, camera traps at the two communal soil nest sites recorded 75 % (46170 images) of the total photo set. These two communal nesting sites contain the largest proportion of nests laid by reproductive females in the remaining Jamaican iguana population. Approximately 122 nests were deposited at these nest sites (2010–28 nests, 2012–40 nests, and 2013–54 nests) — 74 % of the total nests monitored (n=167). The remaining 5630 images from the five other nest sites within the 1997 IAS control zone represented an additional 16 nests. Therefore, within the 1997 IAS control zone, 44 % of the monitored iguana nesting sites contained 84 % (138) of the nests recorded during the three nesting periods.

Outside of the zone with long-term IAS control, camera traps recorded 9998 images from nine nesting sites with 26 (16%) nests monitored over the three nesting seasons. Data from camera traps are available for 23 nests; one camera failed to produce suitable images due to shadows and wind-blown vegetation, and two rock-hole nest sites were abandoned soon after gravid female iguanas were recorded. Visual observations of mongoose activity (i.e., fresh mongoose tracks entering a rock-hole nest in 2010 and 2013, several fresh mongoose scats at the entrance to another rock-hole nest, and a mongoose fighting with two iguanas underground and between two nests, also in 2013) were also recorded at three nests that were all outside of the IAS control area.

IAS control

In 1997 we documented an initial mongoose capture rate of 7 mongooses/100 TN's, which was reduced by over an order of magnitude by early 1998 (down to 0.25 mongooses/100 TN's) (Lewis et al. 2011). For the period under investigation here, we estimate the 2010 and 2012 mongoose capture rate at ~ 0.16/100 TN's based on ~1 mongoose per week, using ~75 - 80 live box traps. As part of a planned IAS control zone expansion, together with a higher density of traps, mongoose capture rates (per TN) were further reduced in 2013.

Individual recognition and abundance of the mongoose

We estimated the number of individual mongooses in each season from camera trap images that captured either multiple individual mongooses in the same image, or single individuals that could be distinguished by size or sex. Within the IAS control zone a single
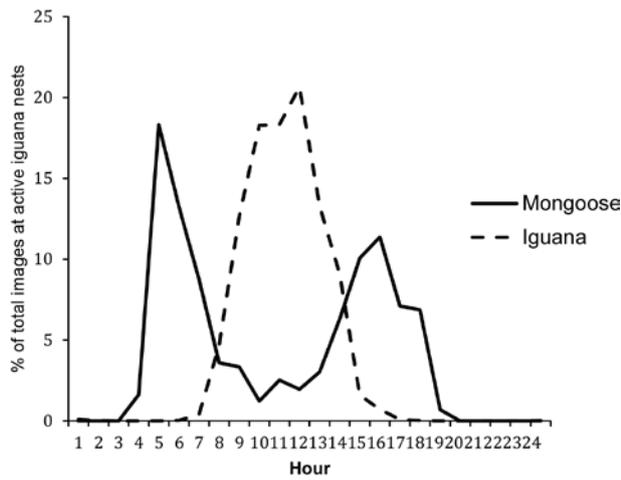
Fig. 6. Diel activity patterns of mongooses and female iguanas at active iguana nests derived from camera trap images.

juvenile mongoose was documented at a nesting site during the 2012 nesting season. Outside of the IAS control zone during the 2010-nesting period all monitored nests (N=4) received mongoose visitation with four individuals identified (adult male, small male, adult female, a juvenile). In 2012 mongooses visited all 10 monitored nests, and at least five individuals were identified (large adult male, two small males, adult female, and a juvenile), and again in 2013 mongooses visited all 12 monitored nests with 8 individuals identified (adult male, two small males, adult female, small female, three juveniles).

Mongoose visitation at Jamaican Iguana nests
In areas without IAS control, mongoose visitation at active Jamaican Iguana nests has been observed with regularity (Vogel 1994, Pers. Obs. 2004 to 2010, 2012, 2013). Results of visual surveys augmented with camera trapping data in the 2010, 2012, and 2013 nesting seasons showed high rates of nest visitation by the mongoose. Nest visitation rates (by mongooses) expressed as RAI's (#images/TN *100) serve as our proxy for predation intensity (Fig. 3). Nest sites inside of the IAS control zone had significantly (GLMM, t=2.31, P=0.02) lower rates of mongoose visitation. Outside of the IAS control zone, evidence of mongoose visitation was recorded at all monitored nests (n= 29) during the three nesting seasons. The difference between mongoose presence (recorded by camera traps) at monitored nest sites inside and outside of the IAS control area was also significantly different (Inside IAS=1 of 15 camera traps recorded a mongoose; Outside IAS=All 20 camera traps recorded mongooses, Independent t-test, t4=3.36, P=0.02), as were comparisons between the number of identified individual mongooses between IAS control (one juvenile individual) and no IAS control sites (17 individuals, Independent t-test, t4=4.3, P=0.01).

Mongoose activity at monitored nest sites
Inside the IAS control zone camera traps recorded the presence of a mongoose at one monitored nest site during the three nesting seasons (Fig. 3). This record

comprised a sequence of 6 images (2 image capture events) of a single juvenile mongoose that passed through during a 1-hour period on a single day; that individual was trapped and removed the following day. Inside the IAS control zone there were no images or other evidence of mongooses entering, exiting or otherwise disturbing active iguana nests (n=138).

Outside of the IAS control zone, however, camera traps captured 1223 images of mongoose activity (456 separate image capture events: one image capture event=a sequence of three images bracketed by one second intervals) from all monitored nest sites during all three nesting seasons (n=29). Mongooses were recorded entering, exiting and or removing eggs from 24 nests, a further two nests were abandoned by female iguanas following repeated scent marking by mongooses. Three other nests (two monitored visually and one at which the camera trap had malfunctioned) that had been used in previous years showed no evidence of use by iguanas during the period under investigation; however, evidence of mongooses and other IAS were recorded from these sites.

We also determined oviposition dates of 14 iguana nests outside of the IAS control area that received mongoose visitation. We recorded 331 images at these nests during a three-week period (beginning one week prior to oviposition). The frequency of mongoose visitation increased dramatically following oviposition; 10 % of all mongoose visits to active iguana nests were recorded the day of oviposition, and 70% of mongoose visits occurred within the first week following oviposition (Fig. 4). Images recorded at three sites showed female iguanas defending their nests against the mongoose (Fig. 5C), and daily activity patterns by the mongoose indicate avoidance of nest-guarding iguanas by focusing their nest assaults around times when the female iguanas are least active (Fig. 6).

Nest mortality inside and outside of the IAS control area
We used a combination of camera trap images and direct observations of mongoose activity to classify nests as
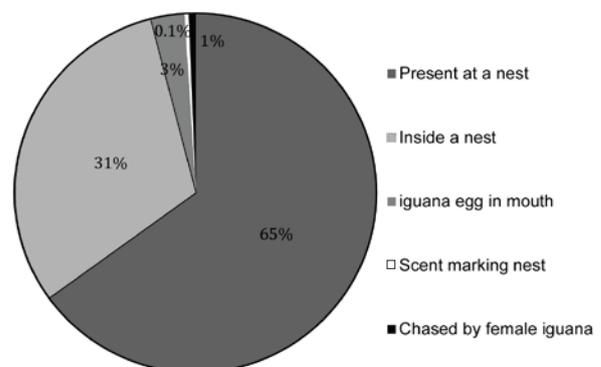
Fig. 7. Mongoose activity at active iguana nests during three iguana-nesting seasons based on camera trap images (n=1223) of mongooses recorded, 1. Present at a nest, 2. Entering or exiting an iguana nest, 3.Stealing iguana eggs, 4. Scent marking iguana nests and 5. Negative interactions with female iguanas.
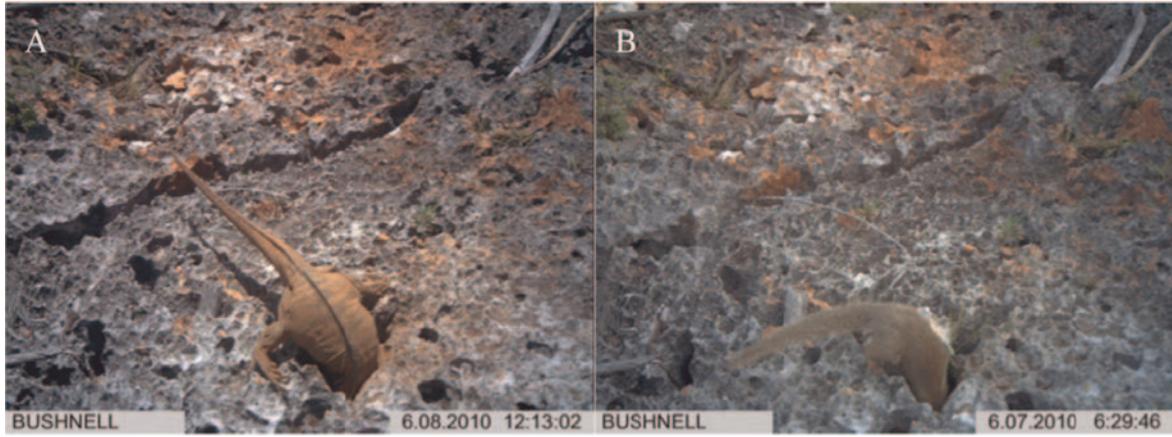
Fig. 8. A) Camera trap photo of gravid iguana entering a rock hole nest site. B) A mongoose intrusion into the same iguana rock-hole nest.

either 'depredated or likely depredated'. Among the nests assigned as 'depredated by the mongoose' we included the two nests initiated by females that were later abandoned. These nests suffered depredation by mongooses in other years (i.e., mongoose tracks in nests and discarded egg shells nearby), and both sites were visited immediately after female iguanas initiated nest excavation. In addition, several mongooses scent marked (i.e., chest and anal rubbing against rocks/shrubs at nest entrances) and/or urinated at these sites prior to abandonment by the female iguana; it is unknown whether these gravid iguanas found alternative locations for egg laying. The activities of mongooses at active iguana nests are summarised in Fig. 7, with examples of these activities in Fig. 5A-D, and Fig. 8A-B.

Predation of iguana nests by the mongoose was significantly different between areas with and without IAS control in all three nesting seasons (Barnard's exact tests, 2010, Wald T=5.66, p<0.0001; 2012, Wald T=7.21, p<0.0001; 2013, Wald T=8.12, p<0.0001). As such, we classified 100% of monitored iguana nests outside of the IAS control zone as depredated by the mongoose. Inside of the 1997 IAS control zone there were no records of mongoose entering or exiting active iguana nests, or any other evidence of nest loss due to the mongoose (Fig. 9.). Aside from female iguanas, the mongoose was the only species recorded entering or exiting active iguana nests.

Fig. 9. Mongoose depredation of active iguana nests (n=150), in areas with and without IAS control, during three nesting seasons was highly statistically different based on Barnard's exact tests (2010, Wald T=5.66, p<0.0001; 2012, Wald T=7.21, p<0.0001; 2013, Wald T=8.12 , p<0.0001).

Fig. 10. A mongoose steals a Jamaican iguana egg from a nest before the guarding female iguana is active.
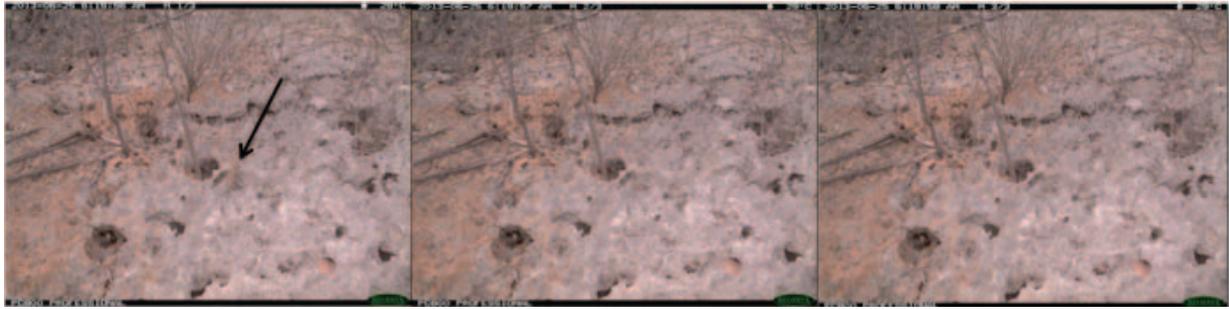
Fig. 11. An arrow points to a mongoose tail tip, barely visible in a single image from three frames.

DISCUSSION

Although evidence suggesting that the mongoose has been a major driver of extirpations and extinctions in the West Indies and elsewhere is abundant (Nellis, 1979; Case & Bolger, 1991; Hays & Conant, 2007; Barun et al., 2011; and references therein), this notorious IAS has had its defenders, and quantitative data on affected species have been rare, with sea turtles being a notable exception (Seaman & Randell, 1962; Nellis & Small, 1983; Leighton et al., 2008; Leighton et al., 2009). This study provides incontrovertible evidence of negative impacts of the small Indian mongoose on nesting attempts by the Critically Endangered Jamaican Iguana. We also document details of mongoose predatory behaviour that are consistent with the high rates of nest loss documented in areas not benefitting from mongoose removal efforts. Importantly, our results indicate that focused removal trapping in iguana nesting areas can significantly reduce iguana egg losses attributable to the mongoose.

An accomplished egg predator
The mongoose is a notorious egg predator (Lariviere, 2015). For example, in Hawaii alone the eggs of eight federally listed endangered or threatened birds are known prey of the mongoose (Stone et al. 1994). This mongoose trait was recognised soon after their widespread introduction to Pacific and Caribbean sugar cane growing regions in the 1880's. Reported declines in rodent populations precipitated the rapid spread of the mongoose to other islands and archipelagos (Nellis & Everard, 1983). Within 10 years mongooses had impacted the poultry industry and were implicated in the loss of 'important' ground nesting game birds and lizards in Hawaii (Evening Bulletin, 1895; The Honolulu Republican, 1900; The Hawaiian Gazette, 1904; The Hawaiian Star, 1904; The Hawaiian Star 1911) and the Caribbean (Espeut, 1882; Hill, 1897; Palmer, 1899). The decline, extirpation and extinction of ground nesting birds and other terrestrial fauna in the decades following the mongoose's introduction provide strong circumstantial evidence of its culpability (Urich, 1931; Baldwin et al. 1952; Seaman, 1952; Pimentel, 1955; Nellis & Small, 1983; Coblentz & Coblentz 1985; Case & Bolger, 1991; Hay & Conant 2007; Lewis et al. 2011). Numerous anecdotal accounts add further support that the mongoose is a destructive nest predator (Baldwin et al., 1952; Seaman & Randell, 1962; Baker & Russell, 1979; Nellis & Everard, 1983; Townsend, 2006, Lewis et al., 2011); however, quantitative data are limited.

Banko (1992) reported that approximately 62% of 39 Hawaiian 'Nene' goose (*Branta sandvicensis*) nest failures between 1978–1981 were due to mongoose predation, and of 485 chicken eggs placed in 'Nene' nesting habitat, 97% were taken by mongooses (Banko 1988). In Puerto Rico's Luquillo experimental forest, Kepler (1977) determined that nest losses of the endemic burrow nesting Puerto Rican tody (*Todus mexicanus*) were greater than 80%; although not quantified, the nest burrows of Jamaican todies (*Todus todus*) are also regularly excavated by mongooses (Pers. Obs.) Mongooses are also major predators of sea turtle nests with nest losses of 100% at some beaches in the Eastern Caribbean (Nellis & Small 1983), although a broad range of variables including predator experience, predator-prey densities, habitat heterogeneity, prevailing weather, and trapping can affect predation intensity (Small, 1982; Leighton et al. 2008; 2009; 2011).

Patterns of mongoose visitation at iguana nest sites
The timing of mongoose visits to iguana nests indicates that nest detection occurs rapidly. Only a few mongoose visits were recorded in the week prior to oviposition of iguana nests, following oviposition, however, mongoose visitation commenced immediately and intensified during the first week (Fig. 4). Leighton et al., (2009) identified the mongoose as the primary nest predator of Hawksbill turtles in Barbados and reported that the median time to detection of nests was two days. Data from experimental (artificial) nests suggested that olfactory surface cues (soil disturbance and residues from laid clutches and female turtles) were particularly important in attracting mongooses to those sites (Leighton et al., 2009).

Like sea turtles, the preferred nesting habitat of iguanas is specific and limited, often resulting in concentrations of nests in particular areas. Mongooses are highly food conscious and behaviourally adaptable animals (Nellis, 1989). Relative to similar sized terrestrial carnivores (mean home range 11–20 hectares, Linstedt, et al. 1986), mongooses have small home ranges (~ 2-5 hectares–Nellis, 1989) that often overlap widely both among and between sexes; accordingly, densities may vary significantly. In the Caribbean mongoose densities may vary from 0–14+/hectare (Nellis & Everard, 1983;

Hoagland et al. 1989), and are influenced by the abundance of resources (Quinn & Whisson, 2005). A response in mongooses known as 'food envy' (Ewer, 1963) may result in high densities around particular resources. Nellis & Everard (1983) reported 27 mongooses trapped around a rubbish site in Grenada, and in St Croix 37 individuals were trapped in 5 days at a small poultry farm.

Because of their uniform pelage mongooses are difficult to visually discern as individuals, particularly those of the same sex, or age, or across long periods of time (nesting seasons). During the three nesting seasons we identified at least 4 individuals in 2010, 5 individuals in 2012 and 8 individual mongooses in 2013, all at nest sites without IAS control. Although, highly conservative, our estimate suggests a minimum mongoose density of 2.8 mongooses per hectare; while density is an important factor it is their persistent and accomplished foraging behaviour that render the mongoose such a destructive IAS.

We found that mongooses focused most of their activity at nests when iguanas were least active, with pulses of visitation recorded in the early morning (Fig. 10) and late afternoon. However, mongoose raids continued opportunistically throughout the day, particularly at times when female iguanas retreated from nesting sites to seek shade (Fig. 6). Of 26 nests that camera traps recorded mongoose visitation (i.e., nest sites outside of the IAS control zone), only one nest was recorded with fewer than 10 camera trap images of mongoose. The majority of camera traps recorded many images of mongooses, particularly in the week post-oviposition, (e.g., > 40 images of mongoose visitation per nest). These data are actually conservative, because different cameras (i.e., 2010 Bushnell, 2011 vs. 2012 Reconyx), and the height, angle and distance of camera from nest entrances varied between nests and years -- factors that may effect the efficiency of camera trap performance (Kelly & Holub, 2008; Rowcliffe, et al. 2011; Ancrenaz, et al. 2012) and small carnivores are likely under-reported by camera traps (Pirie, et al. 2016). For example, Fig. 11 shows an image sequence that recorded just the tip of a mongooses tail entering an iguana nest in a single image, suggesting other visits may have been missed completely.

The convergence of predators on iguana nest sites has been noted for a range of species (Rand & Robinson, 1969; Christian & Tracey, 1981; Dugan et al., 1981; Werner, 1983; Rivas et al., 1998), although most reference predators preying on hatchlings. In the dry forests of the Greater Antilles iguanas are often the largest remaining native vertebrates and at nesting times when iguanas are concentrated at nesting sites, represent a considerable resource to IAS predators. The reproductive season for many dry forest species (both native and introduced) coincides with the first (May-June) of two annual periods of peak precipitation, with the aftereffect of higher overall predator densities during the iguana-nesting period.

Due to the size and shape of the mongoose all iguana nests are potentially accessible. Their aggressive and persistent attacks on nests, sometimes in small groups (Nellis & Small 1983; Banko, 1988), and the potential for such resources to attract a high density of mongooses (Leighton, et al. 2008) for weeks or months, make mongooses the primary direct threat to the remnant Jamaican iguana population. Indirectly, the sociality and activities of mongooses also increase the olfactory signal of iguana nesting areas (e.g., urine, chest and anal scent markings, depredated iguana eggs on the surface), potentially attracting higher densities of other IAS (e.g., cats, pigs, and dogs), and thereby increasing the predation risk of both nests and adult iguanas.

Live trapping of mongoose: a successful conservation strategy

Most of the communal nest sites used by Jamaican Iguanas are subjected to continuous IAS control and are therefore exposed to very low mongoose visitation rates (Fig. 3). Nevertheless, our IAS trapping data suggest that mongooses do converge on these sites annually, during both nesting and hatching seasons, as evidenced by a small increase in the numbers of mongoose trapped near these sites (unpublished data). The communal nest sites used by Jamaican Iguanas appear very similar to those described by Rand & Dugan (1983) for Green Iguanas (*Iguana iguana*) nesting in Panama. The network of tunnels contain egg chambers dug into the harder soil along the sides of tunnels, soil is packed around the egg masses, and tunnel entrances are plugged with packed soil. If a mongoose breaches a tunnel entrance a large number of eggs are easily accessible with minimal effort. Given that the two primary communal nest sites that were monitored over the 3 nesting seasons comprised 74 % of the nests (n=122) and yielded >750 hatchlings (>98% of all known hatchling iguanas), mongoose trapping appears to have been very successful at eliminating mongoose predation of iguana nests within this protected site. Indeed, trap removal of the mongoose may be all that stands in the way of near or complete nesting failure for the imperiled iguana.

Vulnerable nesting strategies

Physically comparable to other known nest predators (i.e., weasels, ferrets and stoats) (Mcdonald & Murphy, 2000; Dowding & Murphy, 2001), the mongoose has long been regarded as a virulent nest predator (Stone et al., 1994), although direct evidence has remained rare (Hays & Conant, 2007). Our results demonstrate that the mongoose is capable of quickly locating active iguana nests (Fig. 4); once located they apparently make repeated raids until all eggs are taken. Mongooses were also documented scent marking (Fig. 5C) vegetation at the entrances of three iguana nests, suggesting territorial competition for these valuable seasonal resources (Gosling & Roberts, 2001). These results provide direct evidence that iguana nests are highly vulnerable to mongoose predation; and because mongoose's are also effective predators of hatchling iguanas (Ottenwalder, 2000 a, b; Lewis, 1944), we argue that mongoose predation of early life stages is,

at present, the primary threat to the persistence of the species in otherwise intact habitat.

Our results provide support for earlier conclusions about the loss of Jamaican Iguana nests due to mongoose predation (Vogel et al., 1996). Moreover, together with behavioural data provided by camera trap images, this study provides a graphic account of a species under imminent threat from an IAS predator. Other factors undoubtedly contributed to the extirpation of the iguana from most of its historical range, and additional factors represent threats where the species persists (e.g., illegal tree cutting for charcoal production). However, nest loss (this study) and high rates of predation on hatchling and juvenile iguanas by the mongoose (pers. obs.; also see Lewis et al., 2011) appear to represent an overwhelming threat to the species. At present the remnant population is being augmented annually through the release of captive-reared 'headstarters', and is also provided with a significant degree of protection from IAS impacts through the implementation of a continuous trap-removal program focused on the mongoose. As a result, *C. collei* is regarded as 'conservation dependent', because cessation of those activities would likely precipitate a population crash (see Turtle Conservation Fund, 2002; Wilson, 2011; Wilson et al., 2016).

Consequently, we echo the suggestion of Lewis et al., (2011), that removal-trapping programs may be crucially important in averting future extinctions, and that such control programs should be encouraged — and funded. Improved IAS control and eradication protocols and advances in available technology may someday obviate the need for 'control' trapping; but at present it appears to be essential if the extinction of the Jamaican Iguana in the wild is to be averted.

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