MOVEMENTS AND NESTING OF THE LESSER ANTILLEAN IGUANA (*IGUANA DELICATISSIMA*) FROM DOMINICA, WEST INDIES: IMPLICATIONS FOR CONSERVATION

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Abstract.—The Lesser Antillean Iguana (*Iguana delicatissima*) is endemic to the Lesser Antilles and listed as Endangered according to the IUCN Red List of Threatened Species. Dominica supports the largest population of *I. delicatissima* because of its relatively undisturbed coastal habitat. Though habitats on Dominica are relatively intact, the species is impacted by non-native species, escalating habitat loss and degradation, hunting pressure, and road mortality. To inform and expand management options on the island, we investigated nesting and hatchling-emergence activity at coastal nest sites, post-nesting migrations of females, and the impacts of roads on iguana movements. We also tested the efficacy of a mitigation strategy aimed at reducing road mortality. The nesting season on Dominica is from February to September, though peak activity occurs from April to June. We documented a skewed female sex ratio at coastal sites, along with increases in daily capture rates, during the nesting season. Females make round-trip movements (up to 4,070 m) from inland areas to coastal slopes and are thus vulnerable to vehicular collision. Over 216 days from 2007–2010, we documented 102 iguanas struck by vehicles along the Caribbean coastal road. Most mortalities were females (83%) followed by males (14%) and hatchlings (3%). Mortality rates per day after an awareness campaign and after signs were erected were reduced by almost half. We discuss the utility of using communal nest sites as indicators to assess both the number of breeding females and, indirectly, the potential for hatchling recruitment into the population.

Abstract.—De Antillen Leguaan (*Iguana delicatissima*) is een endemische soort van de Kleine Antillen en staat op de IUCN Rode Lijst als bedreigd geclassificeerd. Dominica herbergt de grootste *Iguana delicatissima* populatie vanwege de relatief onverstoorde kusthabitat. Hoewel het leefgebied op Dominica betrekkelijk intact is gebleven, staat de soort onder druk door invasieve diersoorten, toenemende verarming en afkalving van habitat, jachtdruk, en sterfte door het verkeer. Om de situatie in kaart te brengen, en de beheersmogelijkheden op het eiland te vergroten, onderzochten we de nestactiviteit en de bewegingen na het uitkomen van de eieren op de aan de kust gelegen nestgebieden, het migratiegedrag van wijfjes na het nestelen, en de impact van verkeerswegen op leguanenverplaatsingen. We hebben ook de doeltreffendheid getest van een mitigatiestrategie gericht op reducering van verkeerssterfte. Op Dominica wordt genesteld van Februari tot en met September. De meeste activiteit vindt plaats van April tot en met Juni. Gedurende het nestseizoen op de aan de kust gelegen studielocaties registreerden we een sex ratio van meer wijfjes dan mannen, tezamen met een toename in de dagelijkse aantallen wijfjes welke werden afgevangen. Wijfjes maken rondtrekkende bewegingen (tot 4,070 m) van landinwaarts gelegen gebieden naar de hellingen aan de kust en lopen daarmee het gevaar om aangereden te worden. Over een periode van 216 dagen tussen 2007–2010, registreerden wij 102 aangereden leguanen langs de Caribische kustweg. De meeste sterfgevallen waren wijfjes (83%) gevolgd door mannetjes (14%) en pas uitgekomen jongen (3%). Het sterftecijfer werd na een bewustmakingscampagne en het plaatsen van waarschuwingsborden met bijna de helft gereduceerd. We bepraken het nut van het gebruik van nestplaatsen als indicatoren om de aantallen nestelende wijfjes te bepalen, en indirect, het potentieel aan pasgeborenen ter versterking van de populatie.

Abstract.—L'Iguane des Petites Antilles (*Iguana delicatissima*) est endémique des Petites Antilles et est classé dans la catégorie En danger par La Liste rouge des espèces menacées de l'UICN. La Dominique abrite la plus importante population de *I. delicatissima* du fait de son habitat côtier relativement indemne de dérangements. Bien que les habitats de la Dominique soient relativement préservés, l'espèce est impactée par des espèces non indigènes, qui augmentent la perte et la dégradation des habitats, ainsi que par la pression de chasse, et la mortalité sur les routes. Afin de recueillir des informations et d'étendre les possibilités de gestion sur l'île, nous avons étudié l'activité de ponte et d'émergence des nouveau-nés sur des sites de ponte côtiers, les migrations des femelles après la nidification, et les impacts des routes sur les déplacements d'iguanes. En Dominique, la ponte se déroule entre février et septembre, bien que le pic d'activité se situe entre avril et juin. Nous avons relevé un sex ratio biaisé envers les femelles sur les sites côtiers, ainsi qu'une augmentation des taux de captures journaliers, pendant la saison de ponte. Les femelles réalisent

des migrations aller-retours (jusqu'à 4,070m) depuis les zones intérieures jusqu'aux pentes côtières et sont donc vulnérables face aux collisions routières. Sur 216 jours entre 2007 et 2010, nous avons relevé 102 iguanes victimes de collisions le long de la route côtière caribbéenne. La majorité des mortalités concernaient les femelles (83%), suivies par les mâles (14%) et les nouveau-nés (3%). Les taux journaliers de mortalité par collision avec des véhicules ont été presque réduits de moitié après une campagne de sensibilisation et la pose de panneaux. Nous discutons de l'utilité de se servir des sites de ponte collectifs comme indicateurs pour estimer le nombre de femelles gestantes et, indirectement, le potentiel de recrutement des nouveau-nés dans la population.

Key Words.—communal nesting; migration; morphology; road mortality; telemetry

INTRODUCTION

The Lesser Antillean Iguana (*Iguana delicatissima*; Fig. 1) is a large species living up to 25 years with a maximum recorded snout-vent length (SVL) of 43.4 cm (Breuil et al. 2010). The iguana once occupied most islands from Anguilla to Martinique in the West Indies. However, based on historical range data, the total population of *I. delicatissima* has most likely declined ≥ 70% since European contact, and the existing population is fragmented (Breuil et al. 2010). Moreover, only three island populations (Îles de Petite Terre, La Désirade, Dominica) are considered relatively stable, while others have been extirpated within the last decade. The proximate drivers for these contemporary extirpations are habitat destruction, hunting, introduction of exotic predators and competitors, and hybridization with Green Iguanas (*I. iguana*). Consequently, the Lesser Antillean Iguana is listed as Endangered according to International Union for Conservation of Nature Red List of Threatened Species criteria (Breuil et al. 2010) and can now be found only on the islands of Anguilla, St. Barthélemy (including the islands of Île Fourchue), St. Eustatius, Guadeloupe (including only the islands of Basse-Terre, Îles de Petite Terre, La Désirade), Dominica, and Martinique (including Îlet Chancel and Ramier; Knapp et al. 2014). Dominica is believed to support the largest single population of *I. delicatissima* due to the extent of available coastal habitat, whereas Les Îles de la Petite Terre supports the highest population density.

The Lesser Antillean Iguana occupies a diverse suite of habitats across its range, including xeric scrub, dry scrub woodland, littoral woodland, mangrove, as well as lower and mid-altitude portions of transitional rainforest. The diversity and condition of these habitats varies by island and iguanas demonstrate unique natural history attributes relative to their environment (see Henderson and Powell 2009 for detailed synopsis of natural history). Therefore, any management program for the Lesser Antillean Iguana must include specific ecological data relative to habitat features. For example, some female *I. delicatissima* inhabiting larger volcanic islands migrate annually from island interiors to nest communally along coastal slopes (Knapp et al. 2014).

During these migrations, gravid females are highly vulnerable to vehicular collisions along coastal roads. However, the extent of mortality and its demographic effects are unknown for any population in the Lesser Antilles. Therefore, investigations are crucial to determine the timing and migration routes of nesting females, rates of road mortality, and road attributes that increase the susceptibility to vehicular collision.

The congregation of migrating females at coastal nesting sites provides a cost effective and efficient opportunity to quantify female populations over time. The relationship, however, between non-nesting to nesting populations in an area must be understood for accurate island-wide extrapolations, and to assess the health of coastal habitats. The relative contribution of specific nesting sites to the overall island population is also critical for prioritizing protection for highly influential nesting areas. Furthermore, understanding specific threats while females are at nest sites would refine mitigation strategies.

In an effort to inform conservation management for *I. delicatissima,* we investigated individual morphometrics and sex ratios within and outside the nesting season, post-nesting migrations of females, and the impacts of coastal roads on iguana movements. We also studied nesting ecology and hatchling emergence from the most important nest site identified in the study. Finally, we tested the acute efficacy of a mitigation strategy aimed at

FIGURE 1. The Lesser Antillean Iguana (*Iguana delicatissima*), Dominica. (Photographed by Charles R. Knapp).
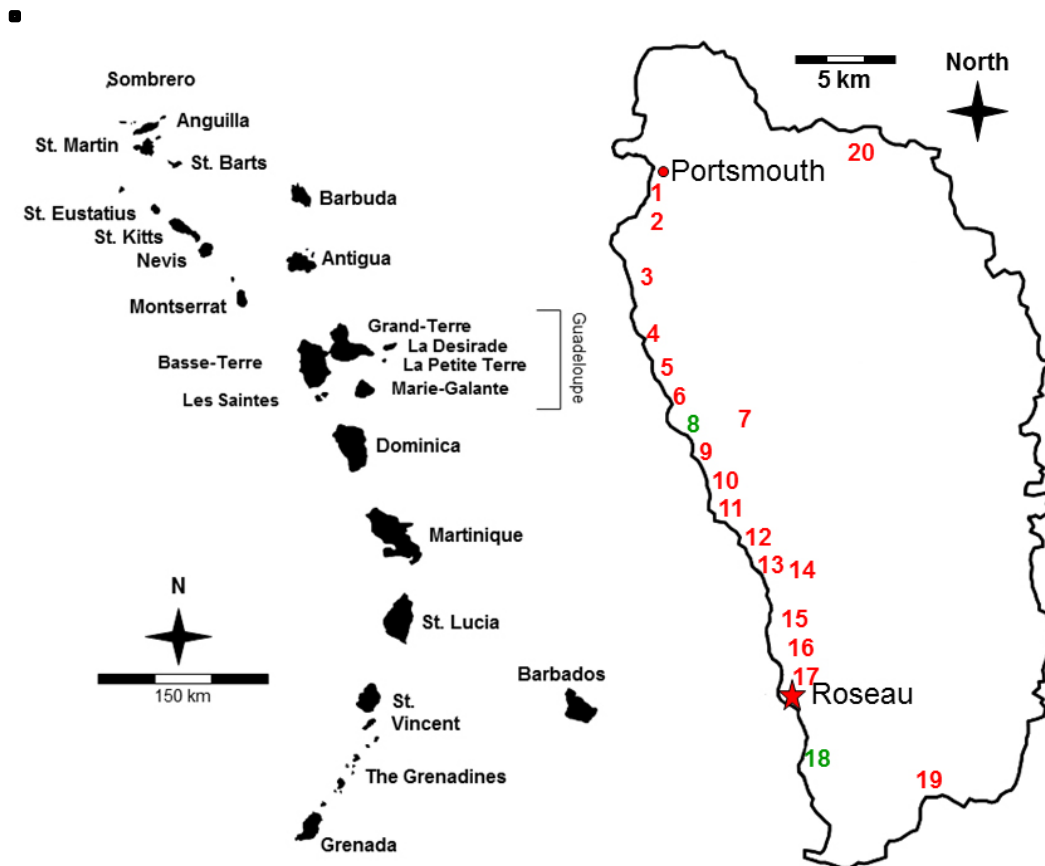
FIGURE 2. Map of Lesser Antilles, West Indies (left) along with capture locations for *Iguana delicatissima* on Dominica (right). Numbers indicate capture locations: (1) Ross University Campus; (2) Picard; (3) South Bioche slope; (4) Colihaut; (5) Coulibistrie Quarry; (6) Coulibistrie; (7) Roche d'Or Estate; (8) Batali Beach; (9) Salisbury; (10) Salisbury/Macoucheri slope; (11) Mero; (12) St. Joseph; (13) Layou; (14) Layou Valley; (15) Hummingbird Inn; (16) Goodwill; (17) Roseau; (18) Champagne Bay; (19) Grand Bay; and (20) Woodford Hill. Green numbers (8 and 18) represent the communal nest sites in this study.

reducing road mortality. Results from this study are not only applicable to I. delicatissima from Dominica but aspects can be applied to conspecific and congeneric populations across the Lesser Antilles.

MATERIALS AND METHODS

Study area and field seasons*.*—Dominica is one of the largest of the eastern Caribbean islands (48 km long and 24 km wide) with a maximum altitude of 1,447 m. This study was conducted on the Caribbean (leeward) coast, which is characterized primarily by xeric woodland and relatively low rainfall (< 2,000 mm) with a pronounced dry season from February to May. The vegetation is primarily deciduous with leaves falling during the dry season (Malhotra et al. 2007).

We conducted research during two continuous field seasons (April through June; August through September) each year from 2007 to 2009, and from April through June 2010. Our April through June field seasons coincided with female migrations to nest sites and nesting activity while the August through September field seasons

coincided primarily with hatchling emergence. We searched for iguanas across the island but the majority of effort, and most captures (18 of 20 sites; Fig. 2), occurred in villages and natural areas on the Caribbean side of the island (see Knapp and Perez-Heydrich 2012). Captures (71%) were concentrated on the coastal slopes of the two recorded communal nest sites at Batali Beach (15°27′01.15″N; 61°26′49.92″W) and Champagne Bay (15°14′48.20″N, 61°22′22.09″W). The Batali Beach site is a Caribbean coastal slope 350 m in length located south of the Batali River. Female iguanas converge on the slope during the nesting season but concentrate most of their nesting in one communal area. The Champagne Bay nesting site is a Caribbean coastal slope 350 m in length located adjacent to the Soufriere-Scott's Head Marine Reserve. Iguanas can be found nesting along the entire slope and not necessarily concentrated at one communal site.

Morphometrics, tail breaks, and capture history*.*— We captured free-ranging iguanas by noose to record morphometrics including snout-vent length (SVL), tail

length (TL) from unbroken tails, body mass (BM), head width (HW), and maximum dorsal spine length. We noted tail breaks and determined sex by cloacal probing for hemipenes. For long-term identification of individual iguanas, we affixed a unique combination of 4-mm colored glass beads through their dorsal crest (Rodda et al. 1988), and injected PIT tags beneath the epidermis on the right dorsolateral side directly anterior to the pelvis. We log-transformed all morphologic variables and compared SVL between sexes using t-tests. We used ANCOVA with SVL as a covariate to assess differences between sexes in TL, BM, HW, and maximum dorsal spine length. In analyses where the slopes were not significantly different ($P > 0.05$), interaction terms were deleted and the analyses recalculated to investigate possible differences in intercepts (Sokal and Rohlf 1995). We analyzed data only from iguanas considered adults ($\geq$ 25.0 cm SVL) based on the smallest female confirmed gravid during the study. We used BM data only from females captured during the non-nesting season because most females in the nesting season were captured either gravid, or after having recently oviposited. We compared tail break frequencies by sex, as well as sex ratios of all captures during nesting and non-nesting field seasons using chi-square tests. Daily capture rates were compared between seasons using a t-test. Results are reported with ± 1 SD and significance level set at α = 0.05 throughout the paper.

Telemetry.—We affixed radio transmitters (Holohil Systems, Inc., Carp, Ontario, Canada; model RI-2C, 11.3 g) using a suture technique (described in Goodman et al. 2009) to the anterior dorsal crest of 9 and 21 female iguanas in 2008 and 2009, respectively. Females were captured after ovipositing at the Batali communal nest site. Transmitter-to-BM ratios ranged from 0.7–1.3%, below the recommended threshold of 7.5% for arboreal lizards (Knapp and Abarca 2009). We tracked females from April to June, and August each year using a hand-held 3-element Yagi directional antenna and a TRX-48S receiver (Wildlife Materials, Inc., Carbondale, Illinois, USA). Only one location per tracking day was recorded for each relocated iguana.

Nesting ecology and hatchlings.—To document nesting activities, we erected an observation blind overlooking the communal nest site at Batali Beach and observed iguana activity for a minimum of one hour every other day from April to June, 2008 and 2009. The communal nesting area is located 20 m from the Caribbean Sea in an exposed portion of the west coastal slope (~ 45°). The slope remains exposed and nearly vegetation-free because of continuous digging by females during the nesting season (Fig. 3). We also observed and documented nesting females opportunistically at the Champagne Bay nesting site over the course of the study.

In order to record patterns and numbers of emerging hatchlings, we constructed a 98 m² enclosure of construction plastic surrounding approximately 50% of the main communal nesting area at Batali communal nest site (Fig. 3). The enclosure was erected from August to September in 2008 and 2009. We monitored the enclosure a minimum of six times per day from 0630 to 1830. Hatchlings were either captured by hand or removed from buckets that were sunk along the fence at the bottom of the enclosure. We also monitored the enclosure using camera traps and time-lapse video. Iguanas collected at the enclosure were weighed, measured, marked numerically with white correction fluid, and released outside the enclosure. In order to speed processing time and eliminate possible complications detecting hemipenes, we did not determine sex via probing or permanently mark hatchling iguanas from the enclosure.

Road mortality.—Each field season from April 2008 to June 2010, we drove one of two coastal road segments (north and south) every other day to record locations of road mortalities. The Caribbean coastal road is narrow (~ 4.5 m wide), curves extensively, veers inland for bridge crossings when rivers meet the sea, and passes through natural areas, plantations, smaller villages, and the capital. Land to the east of the road can vary from cliffs to flat topography, while the west side is edged typically by coastal slope or beach. The north segment ranged from the Batali River to Dublanc (11 km). The south segment ranged from the Batali River to Champagne Bay (29 km). Mortalities were also recorded opportunistically when a deceased iguana was spotted while driving regardless of reason. We augmented our records through confirmed reports from the Dominica Forestry, Wildlife and Parks Division. When permissible according to the condition of carcasses, we performed necropsies and recorded sex and SVL for all iguanas, and clutch size, egg length, egg width, and egg mass for

FIGURE 3. Batali communal nest site used by *Iguana delicatissima* on Dominica. The site is enclosed by a drift fence measuring approximately 14 m x 7 m. (Photographed by Charles R. Knapp).

FIGURE 4. Bumper sticker to protect *Iguana delicatissima* distributed on Dominica. The same iguana character was used in the road signs. (Artwork and design by Joel Friesch and John Binns).

gravid females. We analyzed the relationship between SVL and clutch size using least squares regression.

In May 2008, we initiated an awareness campaign focusing on the need to protect iguanas. Until the end of the study, we lectured at schools, presented to the Dominica Forestry, Wildlife and Parks Division officers and at the University of the West Indies Dominica campus, conducted radio and television interviews, and distributed bumper stickers across the island asking people to slow for iguanas (Fig. 4). Preliminary mortality results suggested that the highest concentration of vehicular collisions occurred in the 870 m stretch of road above the communal nest site at Batali Beach. Therefore, on 1 July 2009, road signs asking people to slow for iguanas were erected on the north and south ends of this road segment above the Batali communal nest site. All recorded collisions in this study occurred during the nest migration period (April to July) each year. To control for differences in survey duration from April to July before and after signs were erected, we calculated mortality rates per day before (122 survey days) and after (94 survey days) erecting signs. Rates of collisions pre- and post-signing were evaluated using chi-square tests.

RESULTS

Morphometrics, tail breaks, and capture history.— We captured 1,410 free-ranging iguanas (excluding hatchlings from the enclosure) representing 1,127 individuals. Snout-vent length ($t = 1.073$, df $= 866$, $P = 0.284$) and BM (ANCOVA: $F_{1,213} = 3.601$, $P = 0.059$) for adult iguanas in our study did not differ statistically between males and females (Table 1). However, TL (ANCOVA: $F_{1,752} = 60.426$, $P < 0.001$) and maximum dorsal spine length (ANCOVA: $F_{1,863} = 388.147$, $P < 0.001$) did differ statistically by sex (Table 1). Slopes for head width were heterogeneous between sexes (ANCOVA: $F_{1,561} = 18.032$, $P < 0.001$) suggesting that as males grow, HW increases at a higher rate proportionally (Fig. 5). Tail break frequencies between all males (6.0%; 18 of 302 males) and females (4.5%; 37 of 825 females) in the study did not differ statistically ($\chi^2 = 1.037$, df $= 1$, $P = 0.309$). Tail break frequencies also did not differ ($\chi^2 = 2.293$, df $= 1$, $P = 0.130$) between males (7.3%; 14 of 191 males) and females (4.6%; 31 of 677 females) classified as adults in our study (> 25.0 cm SVL).

Despite accounts of iguanas inhabiting the east (Atlantic) side of Dominica, we only captured two iguanas on the northeast side (Woodford Hill) and one iguana on the southeast side (Grand Bay) despite 176 person hours of searching. Iguanas are less dense on the east side of Dominica and the tall trees make capture difficult. Instead, iguanas were captured at 18 locations on the Caribbean slope at elevations up to 315 m above msl. We did, however, observe a pair of iguanas regularly in the trees of the Picard Gorge (550 m above msl) opposite the parrot viewing overlook on the Syndicate Nature Trail in the Morne Diablotin National Park (reported initially in Malhorta et al. 2007). Sex ratios of captured iguanas differed significantly by season ($\chi^2 = 28.744$, df $= 1$, $P < 0.001$) with relatively more females (72%, 894 females from 1,246 total captures) being captured in the nesting versus the non-nesting season (51%, 84 females from 164 total captures). Indeed, 63.4% of all 1,410 captures in the study were females from our field seasons that corresponded with nesting (April to June). Captures per day were significantly greater ($t = 4.998$, df $= 157$, $P < 0.001$) during the nesting (mean daily captures $= 9.6 \pm$ (SD) 3.9 (range, 3–23 daily captures) versus non-nesting (mean daily captures $= 5.7 \pm$ (SD) 3.3 (range, 1–12 daily captures) seasons.

Telemetry.—Telemetered female iguanas ranged in SVL from 29.5 to 35.9 cm (mean $= 32.7$ cm) and in BM from 900 to 1,620 g (mean $= 1,174$ g), and were tracked from 3 to 119 days post-oviposition (mean $= 40$ days) in the Batali River Valley. Because of challenges associated with radio-tracking in a narrow valley with steep slopes (e.g., rebounding transmitter signal,

inaccessible slopes), only 18 of 30 females were relocated a mean of 11.1 ± 4.3 times (range, 2–17 relocations). Mean distance of last relocation was 1,248 ± 1,077 m (range, 45–4,070 m) from the communal nest site. Mean elevation recorded at last relocation was 87 ± 83 m (range, 12–315 m). Though some females lingered at the communal nest site prior to moving inland, we recorded females returning up the valley at daily rates up to 467 m (1,403 m total distance for the individual tracked over three days). The only female telemetered in both tracking seasons was last relocated within 300 m of the previous year (3,100 m from nest site).

Nesting ecology and hatchlings.—The description of nesting female activity is based on composite observations of more than 50 females, primarily at the

TABLE 1. Means and standard deviations of un-transformed body-size values for *Iguana delicatissima* on Dominica. Ranges are in parentheses and sample sizes in brackets.

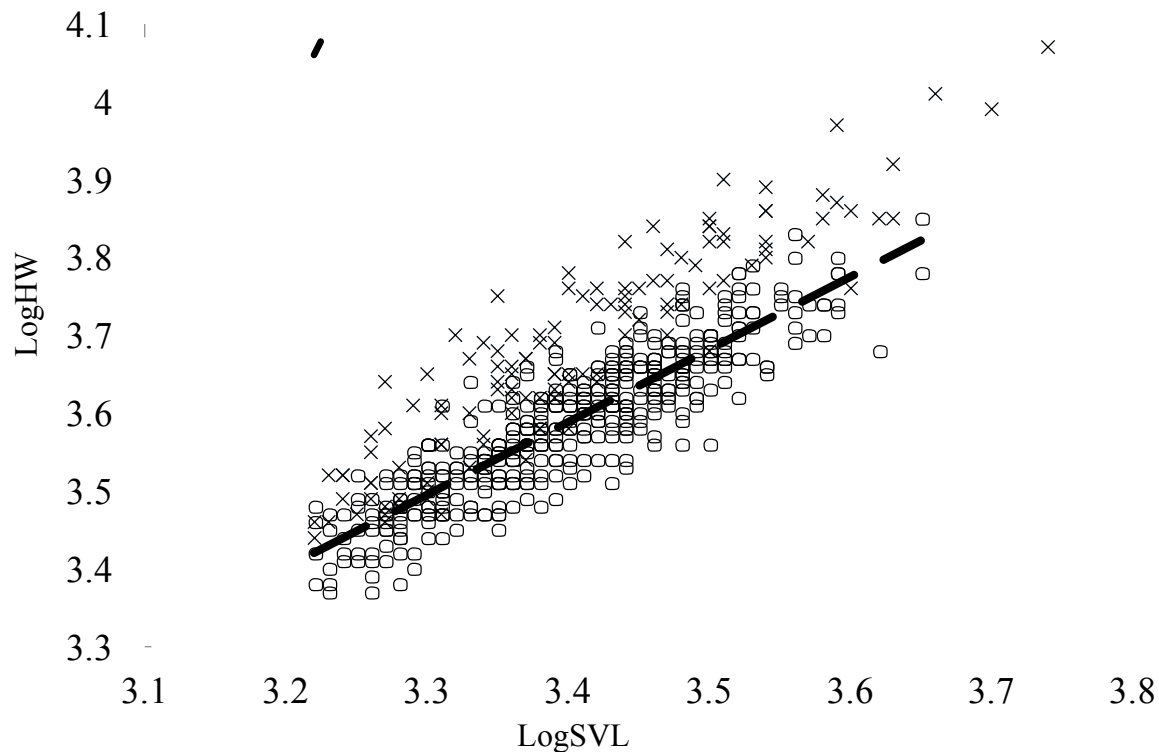|	Body mass (g)	SVL (cm)	TL (cm)	HW (mm)	Max. dorsal spine (mm)
Males	1,304.5 ± 523.2 (610–3,690) [191]	30.3 ± 3.6 (25.0–42.8) [191]	77.3 ± 6.3 (66.6–97.9) [172]	40.2 ± 5.6 (31.1–58.4) [125]	20.1 ± 3.9 (12.4–28.8) [191]
Females	1,130.8 ± 223.8 (790–1,560) [26]	30.0 ± 2.7 (24.0–38.6) [677]	75.0 ± 4.9 (64.6–90.3) [617]	36.3 ± 3.4 (29.1–47.2) [440]	15.9 ± 2.5 (7.8–27.7) [675]
Hatchlings	15.7 ± 2.1 (8.8–21.8) [1,117]	7.8 ± 0.3 (6.2–8.8) [1,117]	21.3 ± 1.28 (15.0–23.8) [1,117]	—	—

FIGURE 5. Relationship between log-transformed snout-vent length and head width for adult *Iguana delicatissima* from Dominica. Open circles and the dashed trend line represent females. Crosses and the solid trend line represent males.

Batali nest site, over three nesting seasons (2008–2010). Copulation events were observed opportunistically at Batali on 24 April and 5 May 2007, 16 and 25 April 2008, 25 April 2009, and 17 and 20 April 2010. At the Batali communal nest site, nesting activity begins in earnest at the start of April and peaks in mid-May. Although infrequent, recently emerged hatchlings were captured on 3 May and 15 June 2008 at Champagne Bay and Batali Beach, respectively. Additionally, recently emerged hatchlings have been reported in December (Arlington James, pers. obs.). Assuming a three-month incubation period (Breuil et al. 2010), these records suggest that nesting season on Dominica is from February to September.

Hundreds of females converge on communal nest sites from April to June and congregate in trees that retain their foliage (e.g., *Capparis* spp.) during the dry season. As many as 15 female iguanas, with one male, were observed within a 5 m tree-crown diameter at the Batali communal site. At the Batali nest site we captured 76, 102, and 227 females during the 2008, 2009, and 2010 nesting seasons, respectively. Of the 405 adult female iguanas captured during the 2008–2010 nesting seasons, 9.4% ($n = 34$) were recaptures from the previous season, though camera traps confirmed additional marked, uncaptured females in the area. Over the same three-year nesting period, we captured 56, 41, and 69 female iguanas at the Champagne Bay nest site, of which 4.2% ($n = 7$ recaptures of 166 adult females) were recaptures from the previous nesting season.

Female iguanas excavate burrows primarily in the morning and late afternoon, but we have confirmed via camera traps that females can also dig midday. As many as eight iguanas were observed digging at one time. Females are extremely wary while on nesting slopes and flee when minimally disturbed (e.g., view of human observer at distances > 30 m). Exploratory activity and excavation are similar to those described in aggregating Green Iguanas in Panamá (Rand 1968). The soil at the Batali nest site is fine and prone to erosion and collapse so we did not excavate burrows in order to preserve the integrity of the nesting slope. However, we did probe more than 15 burrows and they were all more than 1 m long. Females also nest along beaches and we observed iguana nest excavations resulting in sea turtle eggs being ejected from nests.

Similarly to gravid Green Iguanas that excavate at communal nest sites (Rand 1968), gravid *I. delicatissima* will defend their burrow while in progress, but the aggression fades once spent females exit burrows and finish covering the entrance. Indeed, we did not observe females actively guarding nests from the surface. Spent females left immediately after nest closure and retreated to surrounding trees before migrating back to their activity centers. As with Green Iguanas at the same communal nest site in Panamá (Rand 1968), eggs from previous nesting females are often ejected when late-arriving females excavate new nests. On 31 occasions from 27 April to 30 June 2008, we recorded a total of 160 eggs (range, 0–22 eggs per day) ejected from the site. This total is considered a minimum as ejected eggs were assuredly missed during the season. The constant digging by females and the fragile structure of the slopes can result in rock slides. We recorded two deaths ostensibly as a result of iguanas being hit by falling rocks. We also recorded an iguana trapped by dirt and rocks anterior to its hind legs as it was emerging from its nest burrow. Another iguana was buried headfirst in a burrow with only her tail exposed above the surface. Based on necropsy data from 34 road-killed females, mean clutch size was 12.5 ± 5.2 eggs (range, 4–26 eggs). There was a significant positive relationship between SVL and clutch size ($F_{1,14} = 6.152$, $P = 0.026$; Fig. 6). Mean recorded egg mass was 19.6 ± 2.8 g (range, 10.0–23.7 g), mean egg length was 45.3 ± 3.1 mm (range, 31.3–51.8 mm), and mean egg width was 29.5 ± 2.4 mm (range, 24.0–34.5 mm).

At the Batali nest site enclosure, we collected 713 and 548 hatchlings from 17 August to 17 September 2008 and 16 August to 14 September 2009, respectively (Table 1). It is likely that hatchlings escaped, however, as heavy rain events caused breaches in the fence on two occasions each year. Hatchlings typically emerged from the ground between the hours of 0630 and 1000, or between 1300 and 1600. Mean daily emergence rates from the enclosed nest area in 2008 and 2009 were 22.3 ± 15.7 hatchlings (range, 0–58 hatchlings) and 17.8 ± 15.8 hatchlings (range, 1–61 hatchlings), respectively (Fig. 7). The most significant predator of iguana hatchlings is the Dominican Ground Lizard (*Ameiva fuscata*). In the 2008 nesting season, we recorded a minimum of eight predation events involving *A. fuscata* as these lizards patrolled the communal nesting area and entered emergence holes. During the 2008 nesting season, we also observed four snakes (*Alsophis sibonius*), a marine crab (*Grapsus grapsus*), and an American Kestrel (*Falco sparverius*) preying on iguana hatchlings.

Road mortality.—A total of 102 iguanas was recorded killed on roads from 2007 to 2010. Of the 72 iguanas that could be sexed reliably, 83% ($n = 60$) were females, 14% ($n = 10$) males, and 3% ($n = 2$) hatchlings. Most iguanas (57%, $n = 58$) were struck and killed on the 870 m segment of road above the Batali Beach communal nest site. At least 34 (57%) of the 60 females were gravid and migrating to the nest site. The remaining 29 females were assumed to be returning inland after recent coastal nesting activity. This assumption is supported by a marked, non-resident female that was killed eight days after oviposition, the absence of eggs in other females, and the lack of documented road kills outside the nesting season. Mortality rates per day from vehicle collisions
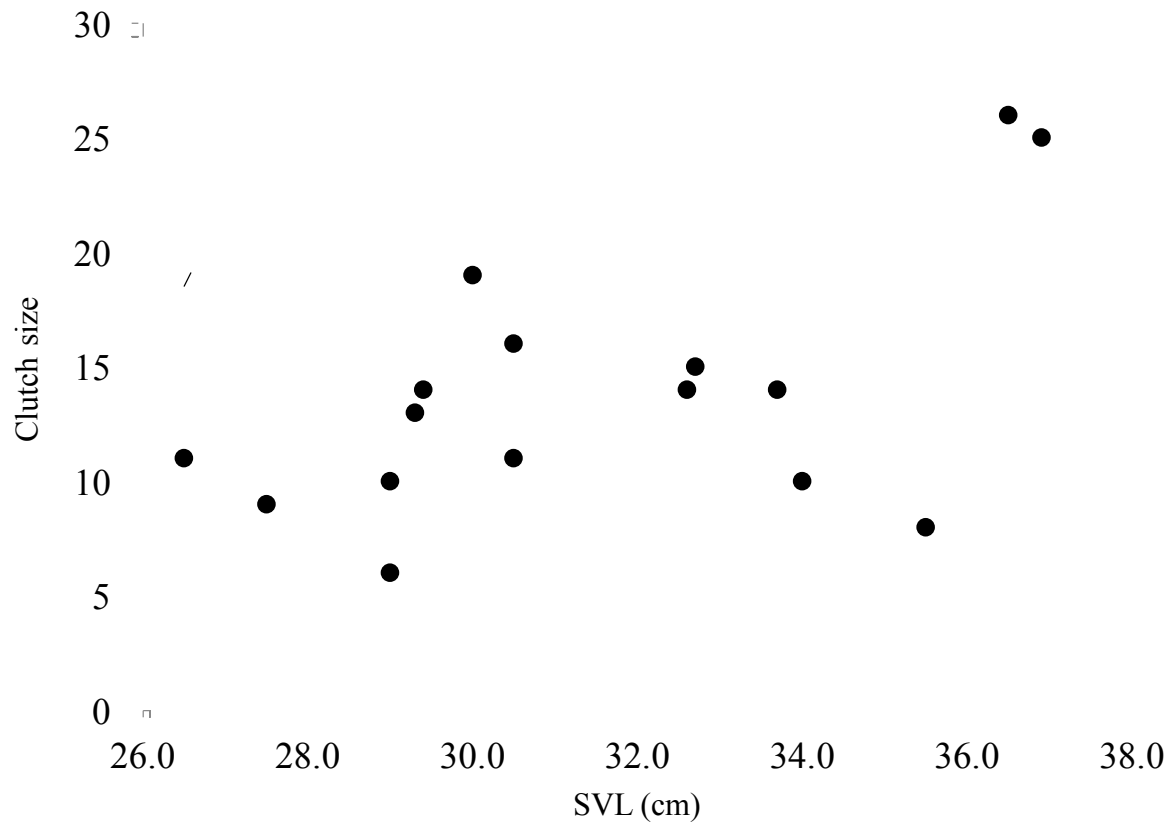
FIGURE 6. Relationship between snout-vent length and clutch size for adult *Iguana delicatissima* from Dominica.
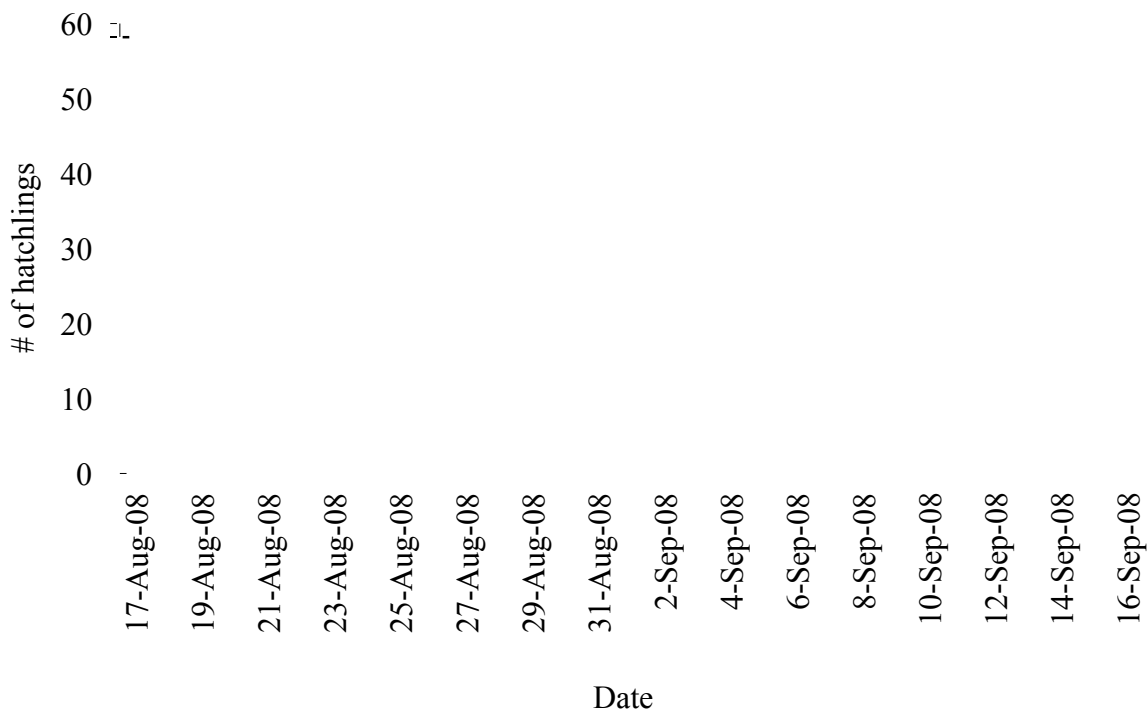

FIGURE 7. Daily emergence of *Iguana delicatissima* hatchlings from 17 August to 17 September 2008 at the Batali communal nest site, Dominica.

after the awareness campaign and signposting were reduced significantly across the island (0.6 versus 0.32 collisions per day; χ^2 = 24.863, df = 1, P < 0.001), above the Batali communal nest site (0.35 versus 0.18 collisions per day; χ^2 = 12.356, df = 1, P < 0.001), and over the remaining coastal road (0.25 versus 0.14 collisions per day; χ^2 = 6.721, df = 1, P = 0.009; Fig. 8).

DISCUSSION

Adult male and female Lesser Antillean Iguanas on Dominica do not differ statistically in SVL or BM, which is unusual (e.g., Wikelski and Trillmich 1997; Beovides-Casas and Mancina 2006; Pasachnik et al. 2012) within the Iguaninae (*sensu* Iguana Taxonomy Working Group of the IUCN SSC Iguana Specialist Group (ITWG) this volume) but may be attributed to an abundance of females in our sample. Male *I. delicatissima* do, however, attain larger maximum body sizes (Table 1). Controlling for SVL, males have longer tails and dorsal spines than females, which is consistent with sexual dimorphism in the congener *I. iguana* (Fitch and Henderson 1977). Longer TL in male iguanas may be influenced by sexual selection. Huyghe et al. (2013) reported that male Common Lizards (*Zootoca vivipara*) with longer tails had a higher probability of mating with females. The difference in tail length of adults could also be attributed

to the arboreal ecology of the species. Arboreal lizards tend to have relatively long tails used for balance (Ji et al. 2002). For example, TL represents 75% of total adult body length in the arboreal Oriental Garden Lizard (*Calotes versicolor*) (Ji et al. 2002), while TL represents 72% of total adult length in *I. delicatissma* from Dominica. In contrast, TL represents a smaller percentage of total adult length in ground-dwelling lizards such as the Gila Monster (*Heloderma suspectum*) and Beaded Lizard (*Heloderma horridum*) (32% and 44%, respectively; Gienger and Beck 2007), *Cyclura rileyi nuchalis* (60%; Iverson et al. this volume), and *Liolaemus aparicioi* (66%; Ocampo et al. 2012). The balance benefits of longer tails in large arboreal male *I. delicatissima* may confer advantages in territorial disputes among branches; however, further research is needed to elucidate any sex-specific advantages of greater lengths.

The divergence of HW as adults grow is expected because many male reptiles that exhibit male-male combat demonstrate larger head sizes than females (Alberts et al. 2002; Gienger and Beck 2007). Tail break frequencies for this arboreal species (up to 7.3%) were lower than reported for terrestrial iguana species from other genera such as *Cyclura* (up to 64.5%; reviewed in Hayes et al. 2012) and *Ctenosaura* (up to 51.9%; Pasachnik et al. 2012; Pasachnik 2013) and similar statistically between sexes in this study. The lower break
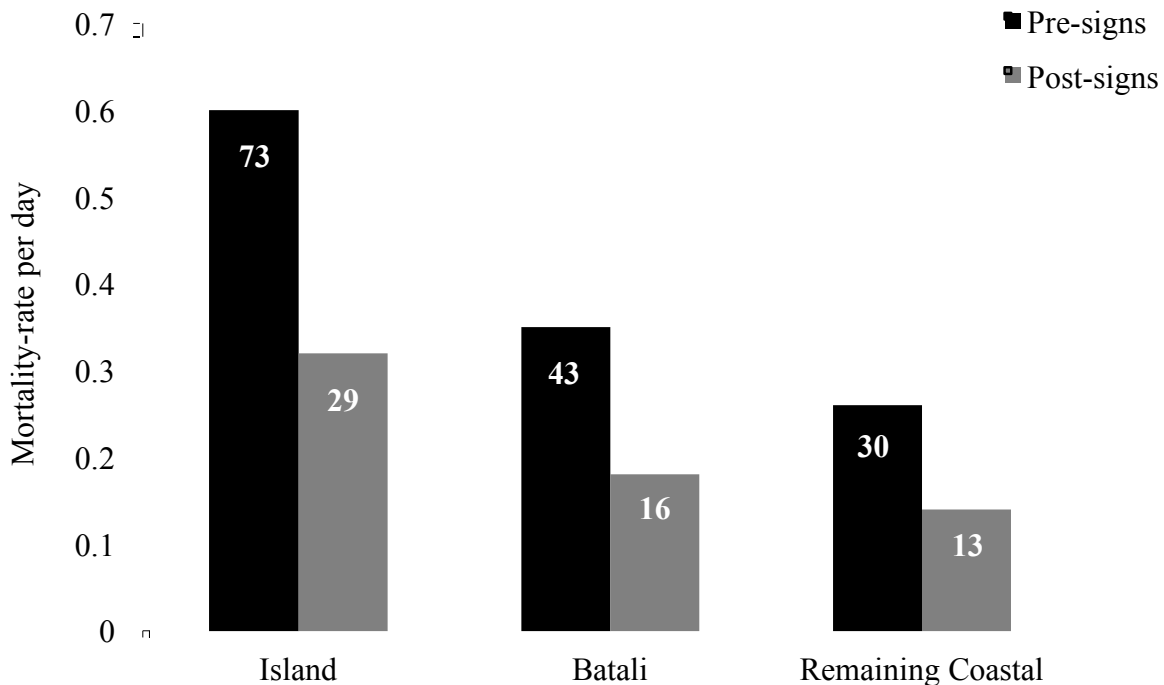

FIGURE 8. Raw mortality rates per day of *Iguana delicatissima* from vehicle collisions before and after the start of an awareness campaign and sign postings above the Batali communal nest site on Dominica. Graph represents data from the entire island, only the 870 m stretch of road above the Batali nest site, and the remaining coastal road. Sample sizes are embedded within the bars.

frequencies may be associated with reduced predation pressure on an arboreal insular iguana species or more resource allocation on the island (Iverson et al. 2004). The lower break frequencies in females may also potentially be attributed to a lack of nest defense in *I. delicatissima* on Dominica. Nest defense in spent females occurs in many other iguana species including *Amblyrhynchus cristatus*, *Brachylophus* spp., *Conolophus pallidus*, *Cyclura* spp., and *I. iguana* (reviewed in Wiewandt 1982; Iverson et al. 2004), and is suspected to elevate tail break frequencies in females (Knapp 2000). Arboreal lizards that experience tail loss may be impacted more significantly because of impaired locomotor abilities such as speed, endurance, momentum, and balance (reviewed in Clause and Capaldi 2006; Maginnis 2006; Bateman and Fleming 2009). Hence, selection may favor a reduction in tail autotomy in arboreal species.

Sex ratios of captured iguanas were skewed significantly toward females in the nesting season. The skewed sex ratio along with increases in daily capture rates during the nesting season were the result of females that migrated from inland areas to coastal sites. With this species, the skewed sex ratios and inflated population numbers during the nesting season, regardless of island, must be considered when analyzing longitudinal population trends (e.g., Lorvelec et al. 2011) as estimates will vary widely depending on the time of year and intra-island location of surveys. Considering these factors, annual female nesting effort at communal sites could be a useful indicator to assess both the number of breeding females and, indirectly, the potential for hatchling recruitment into the population. Moreover, in the absence of labor-intensive monitoring programs, the capacity to assess annual activity and variation in nesting coastal populations provides managers with a simple strategy for assessing trends in Lesser Antillean Iguana populations, assuming that nesting areas can be located and annual survey efforts remain constant.

The potential utility of assessing population trends via communal nesting sites underscores their sensitivity to perturbations. Tourists and livestock can trample communal sites and destroy nest chambers (Breuil 2009). The concentration of nesting females at communal sites also increases their susceptibility to poaching. We observed an excavating female, that was close to the coastal road above the Batali site, taken by a person who only had to step out of his car. At times, coastal slopes on Dominica are used to dump trash and large items such as appliances. The Batali communal nest site was compromised during the 2009 nesting season when items including appliances and tires were discarded down the slope directly above the nest site. Signs were posted at the incipient dumpsite but the activity continued.

Coastal slopes in the Caribbean are also sensitive to extreme weather events such as hurricanes, which undermine their integrity, trigger landslides, or cause severe erosional furrows (Walker et al. 1991). In August 2007, Hurricane Dean struck Dominica causing part of the slope above the Batali communal nesting site to fail, resulting in the loss of hatchlings and nests (Knapp and Valeri 2008). Therefore, preserving the integrity of coastal slopes by enforcing a no dumping policy and constructing coastal roads away from nesting slopes to reduce the potential for landslides must be made a priority for any serious effort at protecting nesting populations of *I. delicatissima*.

Admittedly, redirecting roads may pose a challenge because in tropical island systems such as the Caribbean, road construction and development occurs primarily along coastal areas. Furthermore, construction practices in these systems rarely consider the impacts of development on terrestrial wildlife (Myers et al. 2000; Knapp 2004). Indeed, reptiles are particularly susceptible to the effects of roads, which are unequivocally a major source of mortality for many species and likely pose risks to population viability (Andrews et al. 2008). For example, hundreds of Green Iguanas (*I. iguana*) from Isla de Salamanca in Columbia have been reported killed by vehicles during the breeding season (Harris 1982). On Salamanca, both male and female Green Iguanas were reported on the road, whereas with *I. delicatissima* on Dominica, vehicles kill females disproportionately. This disparity is the result of female migrations to and from nest sites and could prove particularly harmful, especially since disproportionate deaths have the potential to perturb sex ratios, resulting in demographic side effects that destabilize the population (Marchand and Litvaitis 2004).

We identified a < 1 km stretch of road above the Batali nesting site that is responsible for the majority of iguanas (57%) killed by collisions with vehicles. Our ability to identify a relatively short stretch of roadway that is disproportionately responsible for iguana deaths is important and serves as a conservation opportunity. The high costs of physical structures such as overpasses, limits their installations to a few sites and are most likely not realistic for island nations. Other less costly measures (e.g., signposting as in this study) are not effective if installed over long stretches of roads (Malo et al. 2004), therefore our targeted approach using signposting along a < 1 km stretch of road in association with outreach campaigns offers a reasonable chance for success.

Fortunately, the results from our outreach campaign and signposting suggest that these initiatives can play a role in reducing collision mortality. Continuous outreach messaging can be a challenge for some island nations and thus more work is needed to determine the sustained efficacy of a combined campaign of messaging and signs, or signs only. We suspect, however, that without consistent messaging leading up to the nesting season, people will revert back to unsafe and fast driving because female movements are seasonal and easily forgotten. Another mitigation option is the installation of rumble strips on the

pavement to remind drivers to reduce speed through sensitive areas.

Based on our extensive search of coastal slopes on the Caribbean side of Dominica, in addition to interviewing people along the coast, the communal nest site at Batali appears to be the most important remaining nesting area on the island. We recorded 713 and 548 hatchlings in 2008 and 2009, respectively, with an additional 160 eggs ejected from nests in 2008. Based on the mean clutch size in this study (12.5 eggs) and estimated eggs ejected ($n = 160$), at least 70 and 57 female iguanas used the area that was enclosed in 2008 and 2009, respectively. However, our enclosures around the nest site included only an estimated 50% of the main site, and 30% of the available nesting area on the entire slope. Factoring the area of the entire slope, and mortality due to vehicle collisions prior to reaching the nest site, we estimate conservatively that 260 female iguanas use, or attempt to use, the Batali nesting slope each year.

The nesting site at Champagne Bay is also important but less concentrated, as females nest intermittently along the 350 m slope. The Champagne Bay nest site is adjacent to a marine protected area, which offers some protection for nesting females. However, the site is a tourist attraction and visitors often walk down the boardwalk and along the slope, thus disrupting nesting activity. Spotting scopes, interpretive graphics, visual barriers, and discussions with guides would enhance the tourist experience during the nesting season and offer further incentive to protect the area.

Telemetry data suggest that female iguanas can make long-distance migrations (recorded up to 4,070 m) from inland areas to coastal nesting sites. Migration of females from normal activity centers to distant nesting sites is typical of iguanids (Wiewandt 1982; reviewed in Iverson et al. 2004). Green Iguanas have been observed migrating up to 3 km to a communal nest site in Panamá (Montgomery et al. 1973; Bock et al. 1989). The most extreme example of female migration (exceeding 10 km to a 1,500 m maximum altitude) includes Galápagos Land Iguanas (*Conolophus subcristatus*) from Fernandina Island in the Galápagos. The costs associated with this long-distance migration are high and estimated to constitute half of the reproductive effort (Werner 1983). The energetic costs associated with nesting migrations on Dominica may influence the frequency of nesting and is worth further scrutiny (see below).

The use of telemetry in this study greatly extended the maximum range of movement recorded previously for *I. delicatissima* (1,800 m; Breuil 2000). All but three of the 18 females from the Batali communal nest site returned and remained within the Batali River Valley. Indeed, the one female tracked in both years made the equivalent round-trip migration and was relocated in the same area as the previous year, suggesting that the valley and coastal slopes are intricately connected. Our relocations underscore the importance of preserving intact migration corridors for females. The three females that exited the Batali River Valley returned to the Coulibistri River Valley immediately north of Batali. Future research will focus on the genetic representation of females at the Batali communal nest site to better understand its relative importance along the Caribbean coast of Dominica.

It is assumed that *I. delicatissima* nests once per season and some have suggested twice per season (Day et al. 2000). We therefore expected more recaptures at the nesting sites of females that nested the previous year. Our low recapture rates of previous nesters (9.4% at Batali and 4.2% at Champagne Bay), and the seemingly lack of alternative nesting areas for females to use, suggest that perhaps reproduction is arrested in some years. Others have reported less-than-annual reproduction in iguanids. Abts (1987) recorded an annual frequency of reproduction in female Common Chuckwallas (*Sauromalus obesus*) to be from 0% to 95% (mean = 52%) while Laurie (1990) reported an annual nesting frequency from 1.0 to 87.9% (mean = 51%) for female Marine Iguanas (*Amblyrhynchus cristatus*). More recently, Iverson et al. (2004) recorded on average only one in three female Allen Cays Rock Iguanas (*Cyclura cychlura inornata*) nest each year. Green Iguanas are considered to nest annually (Bock et al. 1985), or biannually in populations near the equator (Rand and Green 1982). However, Bock et al. (1985) recorded annual return rates to a communal nest site to be only 30–45%. These data combined suggest that less than annual reproduction may be a common life history characteristic in iguanas (Iverson et al. 2004) and warrants additional research.

The Lesser Antillean Iguana faces manifold threats throughout its range and Dominica is one of the last strong-holds for the species. The island of Dominica represents a significant opportunity to conserve *I. delicatissima*, specifically because of the relatively expansive and undisturbed coastline, low human population density, and relatively low development pressure. Currently, Dominica is home to the largest population of *I. delicatissima* (Knapp et al. 2014) and protecting the species there provides a means to connect different landscapes using charismatic species as conservation flagships. Currently on Dominica, parrots are considered a flagship for inland mesic forests, while sea turtles represent beach habitat. The coastal scrub areas, however, lack such a focal species and *I. delicatissima* has charisma and conservation appeal. By being large, conspicuous, and exhibiting interesting behavior, the species has the potential to serve as a flagship (Caro and O'Doherty 1999). Elsewhere, such as in The Bahamas and Galápagos, iguanas are used with variable success to serve as flagship species and support ecotourism (Knapp 2004, 2007). We suspect, based on our experience on Dominica, that the iguana can serve the same purpose if a concentrated effort is made to promote

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