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First record on fecundity of an *Iguana* hybrid and its implications for conservation: evidence for genetic swamping of *Iguana delicatissima* populations by non-native iguanas

Timothy P. van Wagensveld[1,#,*] and Matthijs P. van den Burg[2,#]

The Lesser Antillean iguana, *Iguana delicatissima* Laurenti, 1768, is a large herbivorous iguana historically ranging from Anguilla to Martinique (Knapp et al., 2014). Following the International Union for Conservation of Nature (IUCN) Red List of Threatened Species™ criteria, the conservation status of this species was recently changed from Endangered to Critically Endangered due to the severity of threats throughout its native range (van den Burg et al., 2018a). The main threat that *I. delicatissima* faces, besides those of anthropogenic origin and invasive predators, is widespread occurrence and hybridisation with the invasive and non-native Green iguana, *Iguana iguana* Linnaeus, 1758 (Knapp et al., 2014; Vuillaume et al., 2015; van den Burg et al., 2018a,b). Green iguanas have become widespread throughout the Caribbean and in the Pacific region (Falcón et al., 2012, 2013), and are known to introduce and transfer pet-trade skin infections to native reptile species (Hellebuyck et al., 2017). Identification between both parental species and hybrids is possible through either morphological characteristics (Breuil, 2013), or molecular data (Malone et al., 2000, 2017; Stephen et al., 2013; Vuillaume et al., 2015; van den Burg et al., 2018c). Both *I. iguana*, and *Iguana* hybrids have caused severe genetic pollution of *I. delicatissima* populations in areas where they have managed to establish, as is the case on several islands in the Guadeloupe archipelago (Vuillaume et al., 2015), ultimately leading to the loss of genetically pure populations of *I. delicatissima*. This process, caused by hybridisation and introgression, is defined as genetic swamping (Rhymer and Simberloff, 1996; Todesco et al., 2016). To date, no *I. iguana* invasion has been mitigated and several island populations no longer have genetically pure *I. delicatissima* individuals (Knapp et al., 2014; van den Burg et al., 2018a). Most of these invasive iguana populations are already well established and widespread throughout *I. delicatissima* populations, which makes their removal difficult or even impossible, due to both financial and practical reasons, a common occurrence in invasion biology (Simberloff et al., 2013). Given its continued decline, major research is focused towards *I. delicatissima* conservation and research (e.g. natural history) of genetically pure populations (Knapp and Perez-Heydrich, 2012; Debrot et al., 2013; Knapp et al., 2016; Judson et al., 2018; van den Burg et al., 2018c), though we propose that understanding the natural history of both hybrid individuals and populations is also important for science and conservation. Firstly, such data will provide an understanding of, the thus far unstudied, establishment and invasion dynamics of *I. iguana* and their hybrids. Secondly, even though pure *I. delicatissima* individuals are no longer present on several islands, we lack an understanding of the ecological impacts of these substitute hybrids. So far, to our knowledge no study has addressed natural history characteristics of *I. delicatissima* x *I. iguana* hybrids, though Bochaton et al. (2016) made comments on osteological features. Here, we describe the first record on *I. delicatissima* x *I. iguana* hybrid fecundity based on a single individual caught on St. Eustatius, in the Dutch Caribbean.

On St. Eustatius, it is suspected that the arrival of likely one single adult female *Iguana iguana* in 2016 (Jesse et

[1] Reptile, Amphibian & Fish Conservation the Netherlands, P.O. Box 1413, 6501 BK Nijmegen, The Netherlands.
[2] Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, P.O. Box 94248, 1090 GE Amsterdam, The Netherlands.
[#] Both authors contributed equally to this manuscript.
[*] Corresponding author. E-mail: t.vanwagensveld@ravon.nl

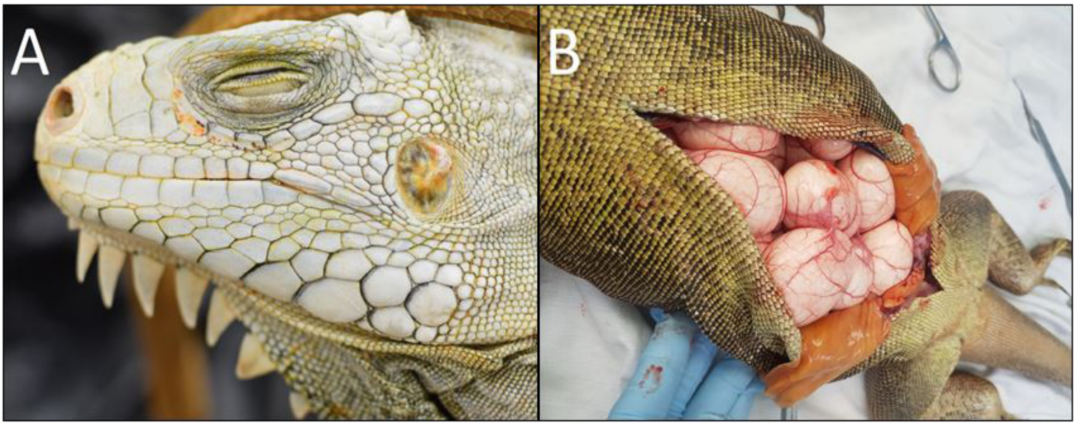

Figure 1. The here reported hybrid female iguana (*Iguana delicatissima* x *Iguana iguana*), captured on St. Eustatius (A). The hybrid abdomen opened up, revealing the egg mass (35 in total) (B). Photos by Tim van Wagensveld (A), and Danielle van Dommele (B).

al., 2016) led to at least two hybridisation events with genetically pure *I. delicatissima* (van den Burg et al., 2018b). Since 2016, ten presumably F1 hybrids from two reproduction events have been discovered (van den Burg et al., 2018b; unpublished data, RAVON). On the 18 April 2018, at 11:06 h, an adult hybrid female was captured (17.48473°N, -62.97614°W, WGS 84), subsequently euthanised, and stored at the Caribbean Netherlands Science Institute (CNSI) (voucher number: Hybrid-10), St. Eustatius, Caribbean Netherlands. Briefly, the absence of a large subtympanic plate, 8 gular spines, shape of the gular spines, presence of nuchal tubercles, and presence of black strips on the tail, pointed towards an F1 hybrid (Breuil, 2013; Fig. 1A). The hybrid measurements were; (snout-vent length, SVL) = 36.5 cm; tail length = 87.5 cm; mass (including eggs) = 1.92 kg (Fig. 1B). After examination, this female appeared gravid, carrying 35 eggs of which 25 were fertilized based on the presence of blood vessels. The hybrid iguana was caught approximately two weeks prior to the expected clutch laying date (Sharon Veira, pers. comm.). A genetic sample of the gravid female was collected and all eggs were preserved at CNSI for future study. Given no additional data from the eggs were collected before preserving them in alcohol we refrained from measuring weight and length dimensions given the potential for bias. Although little information on reproduction is known from the St. Eustatius population, the timing of this capture appears to coincide with the local nesting season of *I. delicatissima* (unpublished data, RAVON), as we observed four gravid *I. delicatissima* females *in-situ* during fieldwork between 10–15 March 2018. The large size and location of this hybrid female suggests that it belonged to one of the same clutches that showed genetic signatures of F1 hybrids (van den Burg et al., 2018b). The F1 hybrid assignment of this individual is further supported by data on growth rate (Wikelski and Romero, 2003) and age at first reproduction (Zug and Rand, 1987), which do not support the presence of a gravid >F1 iguana. Hence, the short period of documented hybridisation events on St. Eustatius, makes it extremely unlikely that >F1 hybrids of such size already could occur within the population.

Clutch size within the *Iguana* genus varies greatly, with clutch sizes ranging between 4–30 eggs for *I. delicatissima* (Knapp et al., 2014) and between 9–71 eggs for *I. iguana* (Rand, 1984; Alvarado et al., 1995; Bock, 2014). Although mean *I. iguana* clutch size is ~35 (Bock et al., 2018 and references therein), for *I. delicatissima* these data are limited, but mean clutch size was 12.5 on Dominica (Knapp et al., 2016). Interestingly, no study has yet assessed whether reproduction output differs among genetic clades within *I. iguana* (Stephen et al., 2013). However, previous studies found reproductive output to be smaller in *I. iguana* populations that inhabit dry habitat compared to wet-habitat occurring populations (van Marken Lichtenbelt and Albers, 1993). Clutch size is positively correlated with SVL in these and other species of Iguaninae (Rand, 1984; van

Marken Lichtenbelt and Albers, 1993; Alvarado et al., 1995; Iverson et al., 2004; Gutsche, 2005; Knapp et al., 2006; Aguirre-Hlidalgo, 2006; Knapp et al., 2016), and both female *I. delicatissima* and *I. iguana* can grow larger than the female hybrid which measured 36.5 cm SVL (Alvarado et al., 1995; Knapp et al., 2016; van den Burg et al., 2018a; Bock et al., 2018). Therefore we believe that the maximum clutch size for the captured female hybrid could exceed 35 eggs. In fact, the largest female hybrid on Grande-Terre measured 42 cm SVL (unpublished data, Association Le GAIAC), illustrating the potential size that female hybrids can reach. Thus, given the aforementioned positive correlation between clutch size and SVL, and that female hybrids can attain a larger SVL, a larger maximum clutch size for *Iguana* hybrids is very plausible. Further collection of fecundity data of F1 and >F1 hybrids would provide more insight in the variation and maximum clutch size of *Iguana* hybrids.

Although based on a single observation, we have shown that *Iguana delicatissima* x *Iguana iguana* hybrids are likely to attain larger clutch sizes compared to *I. delicatissima*. This increased recruitment rate indicates the necessity for rapid removal after the first signs of an *Iguana delicatissima* x *Iguana iguana* hybrid invasion to prevent any genetic pollution. In general, detection of early invasions allows for more efficient invasive species management, and comes with less mitigation costs (Simberloff et al., 2013). Interestingly, an explosive increase in population size, as found for invasive *Iguana iguana*, has so far not been observed for invasive *Iguana delicatissima* x *Iguana iguana* hybrid populations. For example, invasive *I. iguana* on Grand Cayman experienced an increase from a few individuals to hundreds of thousands within two decades (Haakonsson, 2016). These high densities of invasive iguanas can only be controlled, and complete removal is deemed as impossible. Therefore, efforts directed at removing invasive iguanas on a continuous basis, particularly during early invasive stages, are highly recommended. This should however, be coupled with increased biosecurity measures to prevent further invasive species introductions.

Concluding, we provide first data on reproductive output of an *Iguana delicatissima* x *Iguana iguana* F1 hybrid, which was larger than the maximum reproductive output recorded for *I. delicatissima*. In addition to the larger body size and aggressive nature of *I. iguana*, our data highlights another factor that contributes to the range-wide disappearance of the native and Critically Endangered *Iguana delicatissima* throughout the Lesser Antilles as proposed by van den Burg et al. (2018b), these data imply that genetic swamping, due to higher hybrid recruitment rates, contributes to the decline of *Iguana delicatissima* populations where hybridisation is ongoing.

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