

1 **Find me if you can: Pre- and Post-hurricane Densities of the Red-bellied Racer (*Alsophis***  
2 ***rufiventris*) on St. Eustatius, and a review of the genus in the Caribbean**

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17

18 **ABSTRACT.**--- We estimated population densities of the red-bellied racer (*Alsophis*  
19 *rufiventris*) on the Caribbean island of St. Eustatius in 2011, 2018 and 2019 to determine the  
20 likely influence of hurricanes Irma and Maria (September 2017), in addition to evaluating abiotic  
21 parameters which may be correlated with its presence. Surveys were conducted at seven sites in  
22 2011 prior to the hurricanes, and at 81 and 108 sites in 2018 and 2019 respectively posterior to  
23 the hurricanes. A total of 8.2 ha was surveyed in 2011, and 11.42 ha in 2018/2019. The pre-  
24 hurricane (2011) racer density estimate was 9.2/ha (min 7.3 - max 11.6); post-hurricane estimates  
25 were 4.6/ha (min 3.4 - max 6.0) in 2018 and 5.0/ha (min 3.8 - max 6.5) in 2019. The pre-  
26 hurricane encounter rate of individual racers was 16.0 snakes/hour compared to 0.34 snakes/hour  
27 in 2018 and 0.41 snakes/hour in 2019 (post-hurricane). The decrease in encounter rates between  
28 2011 and 2019 implies a negative impact of the hurricanes on racer abundance. Based on  
29 calculations of detection probability (0.02 in 2018 and 0.03 in 2019), post-hurricane lambda

30 estimates were 1.82 (95% CI 0.66 - 5.01) in 2018 and 1.60 (95% CI 0.39 - 6.65) snakes/ha in  
31 2019. Given the current small size of the remaining population and the presence of invasive  
32 species across the snake's range, this species could be at risk of local extirpation. We suggest  
33 conservation actions such as invasive species management and habitat restoration to enable  
34 further recovery.

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36 Key words: Caribbean; Dry forest; Island; N-mixture model; Snake; Transect; Unmarked; Wqid.

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## INTRODUCTION

42

43 The frequency of hurricanes in some tropical areas can be a strong determinant of the  
44 structure and composition of biotic communities (Odum, 1970; Walker et al., 1991; Wunderle et  
45 al., 2004). Although structural vegetation damage is a primary direct effect of severe hurricanes  
46 to mature forests (Boose et al., 2004; Eppinga and Pucko, 2018), food limitation is a significant  
47 indirect effect (Cely, 1991). Animals may respond to these indirect effects by altering their diet  
48 or relocating to less affected areas or habitats (Wundele et al., 2004). The Lesser Antilles is a  
49 group of islands in the Caribbean archipelago, an area characterized by frequent hurricanes, with  
50 multiple or major hurricanes striking every eight to nine years (Elsner et al., 1999; Tartaglione et  
51 al., 2003). In Puerto Rico, Hurricanes Hugo (1989) and Georges (1998) brought storm force  
52 winds that defoliated trees, resulting in reduced cover for the Puerto Rican boa (*Epicrates*  
53 *inornatus* Reinhardt, 1843) and limited access to arboreal sites (Wunderle et al., 2004). As a  
54 result, boas were more visible in the post-hurricane ( $0.20\% \pm SE 0.03$ ) compared with the pre-

55 hurricane ( $0.11\% \pm 0.02$ ) period, suggesting that the species was more abundant than previously  
56 thought (Wunderle et al., 2004). Nevertheless, the forest systems of these islands have adapted to  
57 withstand frequent storms (Odum, 1970; Doyle, 1981), and species occurring within these  
58 systems may have broad habitat breadths (Waide and Reagan, 1996), including snakes in the  
59 genus *Alsophis*.

60  
61       Habitat selection is a fundamental determinant of animal distribution and densities.  
62 Reptiles and amphibians often tend to have their distribution restricted by environmental  
63 variables. Example of this are well known, and variation in environmental variables that  
64 influences reptiles' distribution include canopy cover (Wunderle et al., 2004; Schlaepfer and  
65 Gavin, 2001), substrate (Wunderle et al., 2004), humidity (Brown and Shine, 2002), temperature  
66 (Brown and Shine, 2002), vegetation type (Stumpel, 2004), time of day (Stumpel, 2004), as well  
67 as hurricane impacted sites (Wunderle et al., 2004). An example of environmental variation  
68 influencing snake behavior includes forest cover; this was observed in the black rat snake  
69 (*Pantherophis obsoletus* Say, 1823) which thermoregulates at forest edges (Blouin-Demers and  
70 Weatherhead, 2001), while the Santa Catalina rattlesnake (*Crotalus catalinensis* Linnaeus, 1758)  
71 in the Gulf of California avoids high soil temperatures in specific periods of the year (Martins et  
72 al., 2008). Preferred structured canopy and microclimatic variations influence habitat selection in  
73 the broad-headed snake (*Hoplocephalus bungaroides* Schlegel, 1837) in Australia (Pringle et al.,  
74 2003), while Malayan pit vipers' (*Calloselasma rhodostoma* Kuhl, 1824) movements were  
75 positively correlated with relative humidity (Daltry et al., 1998). In small Colubrids, preferred  
76 locations have been shown to be influenced by soil moisture conditions. (Elick et al., 1972).

77

78           The Caribbean is classified as a biodiversity hotspot due to its high levels of species  
79   endemism (Mittermeier et al., 2004). Unfortunately, the restricted geographic ranges of endemic  
80   species puts them at greater risk of extinction from local impacts (e.g., habitat loss, invasive  
81   species; Catford et al., 2012), especially specialist species with limited dispersal abilities,  
82   restricted population sizes and reduced adaptive capacity (Chichorro et al., 2019; Staude et al.,  
83   2020). Snakes in the genus *Alsophis* once occupied over 100 islands, from the Bahamas to  
84   Dominica in the Lesser Antilles (Henderson and Sajdak, 1996). However, habitat degradation,  
85   human persecution, and the introduction of the Indian mongoose (*Herpestes javanicus* Geoffroy  
86   Saint-Hilaire, 1818) and black rat (*Rattus rattus* Linnaeus, 1758) have resulted in more  
87   extirpations and extinctions than any other reptilian or amphibian genus in the region (Henderson  
88   and Tolson, 2006). Today, several Lesser Antillean species, including *Alsophis antiguae* (Parker,  
89   1933), *Alsophis rijgersmaei* (Cope, 1869), and *Alsophis rufiventris* (Duméril, Bibron and  
90   Duméril, 1854), are considered threatened or endangered (Daltry et al., 2001; Henderson and  
91   Powell, 2009). Five species of *Alsophis* exist in the Lesser Antilles, each occurring on a single or  
92   small number of islands. *Alsophis antillensis* (Schlegel, 1837) has the largest range, occurring on  
93   the Monserrat, Guadeloupe, and Dominica island banks. *Alsophis rijgersmaei* occurs only on the  
94   main islands of the Anguilla Bank, *A. antiguae* on the Antigua Bank, *A. sanctonum* (Barbour,  
95   1915) on the Isles des Saintes Bank near Guadeloupe, and *A. rufiventris* on the Saba and St.  
96   Christopher Bank (Maley, 2004). We have been unsuccessful at locating information on  
97   population size estimates or densities for these species, except for general comments highlighted  
98   below:

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100

### **Historical and Present Knowledge of *Alsophis* Species**

101           The Antiguan racer (*Alsophis antiguae*) has not been collected in at least 80 years and is  
102 likely extinct due to mongoose predation (Sajdak and Henderson, 1991). However, Great Bird  
103 Island off the Antiguan coast supports a population of *A. antiguae sajdaki* (Henderson, 1990),  
104 which in 2001 was thought to total approximately 80 individuals (Daltry et al., 2001). It is  
105 unlikely that Great Bird Island (0.083 km<sup>2</sup>) can support more than approximately 100 individuals  
106 because of resource limitations (Daltry et al., 2001). Following translocations from Great Bird  
107 Island to Rabbi Island, Green Island (2002) and York Island (2008), the total area of occupancy  
108 for *A. antiguae sajdaki* increased to 63 ha. Since translocation, the species appeared to thrive in  
109 its new habitats where it immediately began reproducing. Since then, the Antiguan snake  
110 metapopulation is estimated to have increased to > 1,100 individuals (Daltry et al., 2017).  
111 Nevertheless, these racers and their habitats remain potentially vulnerable to invasive mammals  
112 such as rats (*Rattus* spp.), cats (*Felis catus* Linnaeus, 1758), dogs (*Canis lupus* Linnaeus, 1758)  
113 and mongooses, in addition to harmful developments, and hurricanes (Daltry et al., 2001; 2017).

114  
115           *Alsophis antillensis antillensis* was thought to be extinct from Guadeloupe, where both  
116 Basse-Terre and Grande-Terre have mongoose populations. In 1990, Sadjak and Henderson  
117 (1991) visited Terre-de-Haut and detected eight racers in three days. They also visited Terre-de-  
118 Bas, where they detected six *A. a danforthi* in three days. More recently, Breuil (2009) reported  
119 sightings from a survey in 2003 of *Alsophis antillensis* in Basse-Terre and Grande-Terre and on  
120 Ilet à Cabrit (new locality for Les Saintes as *Alsophis sanctonum sanctonum*) despite the  
121 presence of cats, mongooses, rats, and humans.

122

123           *Alsophis rijgersmai* occurs on Anguilla and St. Barthelemy, where Sadjak and Herderson  
124 (1990) conducted two surveys of six and three days and observed three and five snakes  
125 respectively. The species is also presumed to occur on Scrub Island off the eastern coast of  
126 Anguilla. St. Martin/St. Maarten has a dense mongoose population and racers are thought to have  
127 been extirpated; the most recent report of *A. rijgersmai* on this island is from 1951 (Brongersma,  
128 1959).

129  
130           Daltry *et al.* (1997) reported ‘high densities’ of *A. rufiventris* on Saba and St. Eustatius,  
131 especially in upland areas, but warned of the risk of complacency due to the islands’ small sizes  
132 and fragile ecosystems. During field research on St. Eustatius in March 1997, Daltry *et al.*  
133 captured and measured 40 (35 male; five female) live racers. Based on interactions with local  
134 residents, the authors suggested that the species was already declining on St. Eustatius as a result  
135 of habitat loss, human persecution, and predation by black rats and domestic cats. The racer’s  
136 population density was not estimated for either island, but was said to be ‘very abundant’ within  
137 its current distribution range, with robust populations on both islands. The species appeared to be  
138 more abundant on Saba than St. Eustatius (e.g., one racer was detected every thirty minutes in  
139 the Saban rainforest, whereas sightings on St. Eustatius occurred ‘much less frequently’; Daltry  
140 *et al.*, 1997). On St. Eustatius, racers appeared to be most abundant in the Quill National Park  
141 (Daltry *et al.*, 1997). From 3 - 23 June 2004, Savit *et al.* (2005) encountered 182 racers along a  
142 single hiking trail on the western slope of the Quill. The authors determined that the highest racer  
143 encounter rates were along sections of the trail that contained the most rocks. Rocks may be  
144 attractive to snakes due to the availability of refuges or because prey species may refuge in  
145 cavities surrounding rocks, *A. schwartzi* (Lazell, 1972), was closely associated with rocks in the

146 Quill. From September to December 2016, Zobel (2016) surveyed three hiking trails in the Quill  
147 where she captured, recaptured and PIT-tagged 68 racers (36 male; 32 female).

148

149 *Alsophis sibonius* (Cope, 1879), formerly considered a subspecies of *Alsophis antillensis*,  
150 is endemic to Dominica. During a seven-day survey of the island, Sadjak and Henderson (1991)  
151 found nine racers in Cabrits peninsula. In 2008, White *et al.* (2008) encountered 19 snakes based  
152 on 267 min of focal animal observations in a survey of snake activity and habitat associations.  
153 Sadjak and Henderson (1991) observed two *A. a. manselli* racers in a four-day survey on  
154 Montserrat in 1987. Local residents were said to be familiar with the snake, and mongooses were  
155 not observed or reported.

156

157 *Borikenophis* (formerly *Alsophis*) *portoricensis* (Reinhardt and Lütken, 1862) inhabits the  
158 Puerto Rican Bank, including Puerto Rico mainland and the Virgin Islands. MacLean (1982)  
159 reported the species to be rare or extirpated on the larger Virgin Islands but still moderately  
160 common in Puerto Rico and many smaller islands (Barun *et al.*, 2007). Total snake encounters  
161 over a five-year study period (2001-2005) numbered 205, however population abundance or  
162 density was not estimated (Barun *et al.*, 2007).

163

164 Introduced and invasive mammalian predators such as rats, cats, dogs and mongooses  
165 pose a threat to most species of racers (Seaman and Randall, 1962; Henderson, 1992). This is the  
166 case for *A. rufiventris* on St. Kitts and Nevis, which is thought to have been extirpated by the  
167 mongoose following its introduction circa the early 1900s (Sadjak and Henderson, 1991;  
168 Borroto-Páez and Woods, 2012). Consequently, the current range of *A. rufiventris* in the Lesser

169 Antilles is now limited to the two smallest islands of the Caribbean Netherlands: Saba and St.  
170 Eustatius. These last remaining habitats represent just 10.9% of the racer's original range of 302  
171 km<sup>2</sup> (Fig. 1; Sajdak and Henderson, 1991). Besides invasive species, other external factors that  
172 contribute to population declines include volcanic activity (Young and Ogradowczyk, 2008),  
173 hurricanes (Daltry, 1991; 2006; Zobel et al., 2018), development (Daltry et al., 2017), road kills  
174 by traffic (Hypolite et al., 2007), and habitat loss and alteration (Henderson and Tolson, 2006).

175

176 ***Hurricane impacts.*** Rising sea surface temperatures are predicted to cause more frequent  
177 and intense hurricanes in the Caribbean (Webster et al., 2005; Biasutti et al., 2012). The 2017  
178 Atlantic hurricane season recorded six major hurricanes, including hurricanes Irma (cat. 5,  
179 maximum wind speed 285 km h<sup>-1</sup>) and Maria (cat. 5, max. wind speed 280 km h<sup>-1</sup>;  
180 [www.nhc.noaa.gov/](http://www.nhc.noaa.gov/)). In addition to the natural and anthropogenic disturbances mentioned  
181 above, major hurricanes can increase the risk of extinction of Caribbean reptile species -  
182 especially those with restricted distributions and small, closed populations (Powell and  
183 Henderson, 2005). Our research was conducted prior to and following two major hurricanes  
184 which impacted St. Eustatius in 2017, causing extensive damage to forest vegetation (Eppinga  
185 and Pucko, 2018). Insular populations that have evolved in the absence of mainland predators  
186 and competitors are considered especially vulnerable (Powell, 2006). Whereas the critically  
187 endangered Lesser Antillean iguana (*Iguana delicatissima* Laurenti, 1768) has been the focus of  
188 extensive conservation efforts on St. Eustatius over the past few years (Debrot et al., 2013; van  
189 den Burg et al., 2018; van Wagensveld and van den Burg, 2018), the red-bellied racer has  
190 received less attention (Powell, 2006). This was in part due to the belief that the species was  
191 thriving, especially in the Quill (HM, pers. obs.). On a hike to the crater rim (~400 a.s.l), casual



192 hikers would regularly encounter snakes and the population was thought to be stable. However,  
193 many island species are in various stages of decline, and less enigmatic reptile species have been  
194 ignored by even professional conservation biologists (Powell, 2006). Despite its current  
195 classification under IUCN criteria as Vulnerable (Daltry and Powell, 2016), (in 1996 it was  
196 classified as Endangered; Daltry et al., 1997), the population was potentially impacted following  
197 two major hurricanes in September 2017. In many cases, as evidenced earlier in this paper,  
198 baseline data are lacking. Whilst some preliminary studies have been conducted on *A. rufiventris*  
199 on St. Eustatius (e.g., Daltry et al., 1997; Savit et al., 2005; Zobel et al., 2018), we present the  
200 first quantitative assessment of the population. The results of this study can be used as a baseline  
201 to monitor long-term population trends and survival of the racer in the context of environmental  
202 and ecological changes.

203

204       Occupancy is defined as the probability of a site being occupied by a species (MacKenzie  
205 et al., 2002); fluctuations in occupancy estimates provide a robust proxy for population stability.  
206 Such estimates are particularly useful for sparsely populated or cryptic species that are difficult  
207 to detect (Beaudrot et al., 2016). The goal of our study was to estimate abundance, detection  
208 probability and site occupancy of the red-bellied racer at three different time periods. We  
209 hypothesized that if the racer's population size was stable based on surveys conducted prior to  
210 and post hurricanes, this would suggest that snakes are resilient to changes. If the racer's  
211 abundance estimates varied, however, this would suggest that external factors (direct and  
212 indirect) are impacting life history characteristics and vulnerability of the species. An additional  
213 goal of our study was to determine the influence of specific geographic and ecological covariates

214 on site occupancy, abundance and detection probability and abiotic/biotic variables which may  
215 be correlated with the presence of the racer.

216

## 217 **METHODS**

### 218 **Study Area**

219 Our study took place on St. Eustatius (17°28'N, 62°57' W), a small (21 km<sup>2</sup>) island with  
220 a human population of approximately 3,900 (Statistics Netherlands, 2018) located approximately  
221 12.5 km north-west of St. Kitts (Fig. 1). Temperature typically ranges from 25 to 33°C. Average  
222 annual rainfall is 986 mm, with upper elevations of the Quill receiving 1,500 – 2,000 mm per  
223 year (Rojer, 1997; van Anandel et al., 2016). Our study took place within and outside the  
224 boundaries of the Quill (~220 ha) and Boven National Parks (~320 ha). Vegetation in the Quill  
225 ranges from evergreen seasonal secondary forest inside the crater and higher slopes to thorny  
226 woodland below 250 meters (Stoffers, 1956). Vegetation in Boven comprises dry forest  
227 fragments with areas of open, grassy shrubland (van Anandel et al., 2016).

228

### 229 **Species Description and Behavior**

230 The red-bellied racer (hereafter 'racer') is a moderately sized (max total length: male =  
231 1179mm; female = 976 mm (Daltry et al., 1997); male = 1046 mm; female = 1070 mm (this  
232 study)), sexually dimorphic colubrid (Maley et al., 2006). Racers are variable in color and  
233 pattern, and members of the same species may vary morphologically on different islands. A  
234 diurnal species, the racer forages through leaf litter in search of lizards (*Anolis* spp. Daudin,  
235 1802), frogs (*Eleutherodactylus johnstonei* Barbour, 1914), iguana (*Iguana delicatissima*  
236 Laurenti, 1768) hatchlings and the occasional egg (Powell et al., 2005). Despite growing to a

237 length of approximately one meter, it is considered a small snake that is harmless to humans. If  
238 captured, however, it will release an unpleasant-smelling cloacal secretion (Malhotra and  
239 Thorpe, 1999). Nevertheless, the racer is often persecuted by people who fear them (Powell,  
240 2006) and encounters with humans can result in the demise of the snake. While the racer's  
241 venom is capable of subduing its prey, its small size and rear-facing fangs prevent it from  
242 attacking larger victims. Little is known about *Alsophis'* breeding habits, however a captive  
243 breeding program at Jersey Zoo resulted in *Alsophis antiquae* producing 11 eggs, of which five  
244 hatched (Daltry et al., 2001).

245  
246 The racer shows remarkable sexual dimorphism, whereby males and females can be reliably  
247 distinguished (Daltry et al., 1997). Males are predominantly chocolate brown to black on the  
248 dorsum with conspicuous paler brown/yellow blotches; females are predominantly grey to  
249 medium brown dorsally with darker streaks (Daltry et al., 1997). Additionally, female racers  
250 typically have longer and broader heads than males. Male racers can also be distinguished by the  
251 higher number of pairs of subcaudal scales. The tails of adult males are also noticeably thickened  
252 at the base and relatively long, accounting for 26.4–30.9 % of the snake's total body length  
253 (Daltry et al., 1997).

254  
255 Racers are found in a variety of natural and altered habitats, ranging from thorny  
256 woodland to moderately mesic hillsides. The species was previously described as 'thriving' by  
257 Maley et al. (2006), being common even in close proximity to human activity and habitation.  
258 The Quill and Boven National Parks are considered important habitats for the racer (Daltry et al.,  
259 1997). Besides the introduced brahminy blind snake (*Indotyphlops braminus* Daudin, 1803;

260 Snyder et al. 2019), the only other native snake species that occurs on St. Eustatius is the  
261 Leeward Blindsnake (*Antillotyphlops geotomus* Thomas, 1966; van Wagensveld et al. 2020). *A.*  
262 *rufiventris* has few natural predators but has been observed being consumed by American Kestrel  
263 (*Falco sparverius* Linnaeus, 1758; HM pers. obs.). However, the species is threatened by non-  
264 native species such as free-roaming cats, dogs, chickens (*Gallus gallus domesticus* Linnaeus,  
265 1758), and black rats (Henderson, 1992). Black rats are thought to attack racers, especially when  
266 rats are hungry or defending young (Daltry et al., 1997). The racer is too small to be able to  
267 consume adult rats (Daltry et al., 1997). Attacks on the snake, on the other hand, may have  
268 implications for the reproductive success of racers, which can lose portions of their tail (where  
269 the hemipenis and retractor muscles are located; Daltry, 2006). Daltry et al. (1997) reported 55%  
270 of captured snakes with incomplete tails, indicative of likely heavy predation pressure on St.  
271 Eustatius and Saba. House mice (*Mus musculus* Linnaeus, 1758), while present on St. Eustatius  
272 (Madden et al., 2019), are not thought to constitute a threat to the snake. The presence of free-  
273 roaming herbivores in the Quill and Boven (Madden, 2020) could indirectly impact racers  
274 through trampling or loss of vegetation through grazing (McCauley et al., 2006), however this  
275 has not been studied. Fortunately the island is currently not occupied by the mongoose, whose  
276 introduction to other Caribbean islands is thought to be responsible for numerous reptile  
277 extirpations (Table 1; Henderson, 1992; Powell and Henderson, 2005; Powell et al., 2005).

278 **Table 1.** Overview of all islands in the Lesser Antilles where *Alsophis* sp. is known to have been  
279 present, or is currently present, and the presence or absence of mongoose. On at least five islands  
280 *Alsophis* has been extirpated and in all cases the presence of mongoose is known (Powell and  
281 Henderson, 2005). Adapted from Powell and Henderson (2005).  
282

<b>Island</b>	<b>Mongoose</b>	<b><i>Alsophis</i></b>
Anguilla	No	Yes
Antigua	Yes	No

Dominica	No	Yes
Great Bird	No	Yes
Guadeloupe	Yes	No
Marie-Galante	Yes	No
Montserrat	No	Yes
Saba	No	Yes
Scrub	No	Yes
St. Barthelemy	No	Yes
St. Christopher & Nevis	Yes	No
St. Eustatius	No	Yes
St. Martin/St. Maarten	Yes	No
Terre-de-Bas	No	Yes
Terre-de-Haut	No	Yes

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283

284

285 **Surveys: *Pre-hurricane Surveys*.** Specific survey locations on the Quill include four areas:  
286 NW facing slope (range 238-350 m.a.s.l.), SW facing slope (range 220-400 m.a.s.l.), and East  
287 facing slope/Botanical Garden (range 106-220 m.a.s.l.) and inside the crater (range 300-351  
288 m.a.s.l.). Location of each area surveyed is indicated in Figure 2. At each site, snakes were  
289 located using transects along the trail (10 m wide on each side) and/or perpendicular to the trail  
290 in the NW and SW areas and inside the crater; for these three locations, eight people survey in  
291 parallel transects, at 6 m apart (50 m wide total) and 350 long, covering an area of 1.7 ha each  
292 (see Online Supporting Information Table S1 for specific areas). Surveys commenced after 9:00  
293 h and finished around 14:00 h, between 21st January 2011 and 24th January 2011. When a snake  
294 was detected, a parallel point was selected at an equivalent position from the center of the

295 transect, these are called null points thereafter. At each point (snake and null), all measurements  
296 described below were conducted. We calculated snake density by dividing the number of  
297 individuals detected by the calculated area of each transect.

298

299 ***Environmental Measurements (Pre-hurricane).*** On each point where a snake was detected  
300 or the null point, we conducted the following measurements: air temperature and relative  
301 humidity with a hand-held meter; hemispherical photography pointing above the place, with a  
302 digital camera with a fish-eye lens, to use it to calculate leaf area index and canopy cover  
303 (HemiView 2.1 software, Delta-T/Dynamax); photography of the area enclosed in a 1m<sup>2</sup> frame  
304 placed on the forest floor, to use it to measure the fractions of bare soil, green vegetation,  
305 leaf litter, rocks and wood; depth of the litterfall using a ruler and measuring five points inside the  
306 frame; location and elevation with a GPS receiver.

307

308 ***Post-hurricane Surveys.*** In 2018 and 2019 we surveyed racers in the Quill and Boven  
309 National Parks (total survey area 11.42 ha). Surveys were conducted from December 2017 to  
310 May 2018, and from March to June 2019. To maximize detection and minimize disturbance, all  
311 surveys were conducted along existing hiking trails. Using the existing network of trails allowed  
312 us to survey snakes in an otherwise steep topographical environment with, at times, rocks or  
313 dense vegetation. We conducted surveys along a 100-meter line transect by looking and listening  
314 for *A. rufiventris* while walking at a very slow pace. All surveys were conducted between 0700  
315 and 1900 hrs. Once detected, the perpendicular distance of the snake from the center of the  
316 transect was measured with a tape measure.

317

318 ***Morphological Measurements and PIT-tagging of Snakes.*** We measured morphological  
319 characteristics of 60 racers (20 in 2018 and 40 in 2019; snout – vent; vent – tail; total length, cm)  
320 and weighed individuals using a pesola scale (g). We scanned all captured racers for a PIT tag  
321 during surveys in 2018 and 2019. In 2019, if no PIT tag was detected in the captured snake we  
322 inserted one (10.9 x 1.6 mm) using a 2mm sterile needle (Online Supporting Information Table  
323 S2). After sterilizing the skin, the PIT tag was placed subcutaneously in the mid-body region on  
324 the mediolateral side. Markings on the body and other morphological differences described  
325 earlier enabled us to confidently determine the sex of captured individuals.

326

327 ***Ecological and Geographic Covariates.*** The following covariate data were collected:  
328 elevation (m): measured with a handheld GPS; temperature (°C): measured with a temperature  
329 gauge; cloud cover: estimated by eye, categorical (0–4; 0= no cloud, 4 = full cloud); habitat: 6  
330 habitats were selected based on vegetation descriptions by de Freitas et al., (2014; Fig. 1);  
331 rainfall: total monthly rainfall from the previous month was included in the dataset following the  
332 completion of surveys (data downloaded from <http://www.seawf.com/rainhist2.php>).

333

334 ***Habitat descriptions.*** We split our survey areas into six habitat types based on vegetation  
335 descriptions by de Freitas et al. (2014; Fig. 2): 1. *Pisonia-Justicia* and *Pisonia-Bothriochloa* hills  
336 (H1, H2). Elevation: 13 - 177m; 2. *Pisonia-Eugenia* mountains (M5). Elevation: 155-354 m; 3.  
337 *Pisonia-Eugenia*, *Chionanthus-Nectandra* and *Capparis-Antirhea* mountains (M5, M3b, M6).  
338 Elevation: 275-354 m; 4. *Myrcia-Quararibea* (M1). Elevation: 296-400 m; 5. *Coccoloba-*  
339 *Chionanthus* and *Chionanthus-Nectandra* mountains (M2, M3a). Elevation: 393-534 m; 6.  
340 *Capparis-Pisonia* mountains (M4). Elevation: 80-275 m.

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## STATISTICAL ANALYSES

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### Pre-hurricane Methods

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*Abiotic and Biotic Variables Influencing Detection.* To assess potential relationships between the presence and absence of *Alsophis* (where a snake was located or not) correlated with biotic and abiotic variables we used a model selection approach with a generalized linear model (GLM). Variables evaluated included leaf litter depth, percentage of bare soil, percentage of litter, percentage of green vegetation, percentage of wood, soil temperature, above-ground air temperature (30 cm), and leaf area index above the site where the snake or control site was located. Data for the control site (null point) were collected at a position in the other half of the transect equivalent to the one where the snake was found. These data were only collected for 2011 surveys. The biotic and abiotic data for 71 sites where snakes were located and 75 control sites were collected.

354

We tested for collinearity using kendall's correlation analysis. We performed pairwise correlations, whereby all correlations were below  $\pm 0.39$  except air and soil temperature (cor = 0.49), thus we eliminated air temperature from further analysis. We performed a GLM analysis with a binomial link (snake presence or absence; Crawley, 2007; Weigelt & Kreft, 2013). Models were ranked according to the corrected Akaike's Information Criterion (AICc) and the model with the lowest AICc is considered the best-fit model (Akaike, 1974; Sugiura, 1978). Those models with AICc differences  $<2$  relative to the best-fit model were also considered as plausible (Arnold, 2010). The 95% normal confidence intervals of the coefficients are calculated from the most parsimonious models. All GLM analyses were performed in *R* (R Development



364 Core Team, 2013) using the *MASS* package (Venables & Ripley, 2002) and the *dredge* function  
365 in the *MuMIn* package (Barton, 2019) for comparing all models.

366

367 ***Post-hurricane Methods.*** Density estimation: We used the Schnabel index to estimate  
368 population size based on marked and recaptured snakes in 2019, and compared this with  
369 marked/recaptured snakes from 2016 (Zobel, 2016). We used a likelihood-based, single-season  
370 occupancy model (MacKenzie et al., 2017) in the package ‘wqid’ (Meredith, 2020) to estimate  
371 site occupancy ( $\psi$ ) in relation to habitat and elevation, while accounting for detectability ( $p$ ).  
372 During wildlife surveys, individuals can go undetected, either because they are truly absent at the  
373 sampling site, or because they are present, but were not observed. Visiting each sampling site on  
374 multiple occasions enables the estimation of detection probability, which can be incorporated  
375 into occupancy modeling to correct for imperfect detection (MacKenzie et al., 2002). Occupancy  
376 models link a state model determining occupancy at each site with an observation model for  
377 detection, which is conditional on occupancy. Occupancy models were based on three  
378 assumptions: (i) the racer population in each site was closed to birth, death, immigration, and  
379 emigration during the sampling period; (ii) counts at each site were independent; and (iii)  
380 individuals were not double counted within a single sampling occasion (Murray and Sandercock,  
381 2020). We first modeled detection probability and then occupancy probability. We subsequently  
382 used a built-in covariate function which estimated detection in relation to whether the species  
383 had previously been detected or not. The function ‘occSStime’ allowed us to include a time trend  
384 in our analysis based on survey effort. The function ‘occSSrn’ (Royle and Nichols, 2003)  
385 provided an estimation of site occupancy ( $\psi$ ), average number of individuals per sample, lambda  
386 ( $\lambda$ ) and sampling detection probability ( $p$ ). Finally, we repeated some of the analyses with the

387 package ‘unmarked’ (Fiske and Chandler, 2011) using a basic N-mixture model to estimate racer  
388 abundance ( $\lambda$ ) and detectability ( $p$ ). This allowed us to test the influence of covariates such as  
389 rainfall, temperature, week of the year on abundance estimates. Quadratic terms for all variables  
390 were also included to account for the possibility of non-linear responses. We ranked the resulting  
391 models using Akaike’s Information Criterion, corrected for small sample size (AICc; Burnham  
392 and Anderson, 2002) in the package ‘MuMIn’ (Barton, 2020) where the detection model with the  
393 lowest AICc is best-fitting. All analyses were performed in the R environment version 4.0.3.

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## RESULTS

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### Presence of *Alsophis* with Biotic and Abiotic Variables

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A total of 128 different models were evaluated and eight models had  $\Delta\text{AICc} \leq 2$  with a total weight of 0.398 (Table 2). The only variables that were consistent among all eight models was litter depth and fraction of bare soil, which were negatively correlated with the presence of snakes. Leaf Area Index (LAI) and the soil temperature were both positively correlated with the presence of snakes. All seven variables were included in at least one of the models. The average coefficients of the best models resulted in wide confidence intervals in four of the seven variables which were included in the models. Evaluating the confidence intervals as estimated from the multiple models only two variables were consistent in that they excluded zero (the null model), fraction of bare soil and litter depth, both of which had a negative effect on snake occurrence (Fig. 3).

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**Table 2.** Top models for the presence of snakes, AICc, corrected Akaike Information Criterion, delta = change in AICc as compared to the best model, weight = the weight of the model as compared to all other models in the analysis. The last line in italics represents the worst model.

<b>% bare soil</b>	<b>% green vegetat ion</b>	<b>% litter</b>	<b>% wood</b>	<b>Leaf Area Index</b>	<b>Litter depth</b>	<b>Soil temp</b>	<b>df</b>	<b>logLik</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>weight</b>
-3.933	NA	NA	NA	NA	-0.022	0.057	3	-90.75	187.69	0	0.07
-3.343	NA	NA	NA	0.238	-0.017	NA	3	-90.8	187.77	0.083	0.067
-3.957	NA	NA	NA	0.143	-0.024	0.035	4	-89.95	188.21	0.516	0.054
-3.188	NA	NA	1.269	0.206	-0.017	NA	4	-90.09	188.49	0.796	0.047
-4.442	NA	-1.06	NA	NA	-0.02	0.086	4	-90.25	188.80	1.108	0.04
-4.541	NA	-1.23	NA	0.159	-0.021	0.066	5	-89.28	189.02	1.33	0.036
-3.273	1.223	NA	NA	0.229	-0.018	NA	4	-90.57	189.45	1.756	0.029
-3.711	NA	NA	0.679	NA	-0.021	0.05	4	-90.60	189.51	1.817	0.028
-3.846	0.854	NA	NA	NA	-0.023	0.054	4	-90.65	189.60	1.908	0.027
<i>NA</i>	<i>0.657</i>	<i>-0.6</i>	<i>NA</i>	<i>0.12</i>	<i>NA</i>	<i>-0.004</i>	<i>4</i>	<i>-95.39</i>	<i>199.08</i>	<i>11.39</i>	<i>0</i>

411

412           ***Pre- and post-hurricane Survey Densities and Encounter Rates.*** Pre-hurricane snake  
413 densities/ha were higher than post-hurricane densities across all comparable habitats. For  
414 example, in the Quill crater, pre-hurricane densities varied between 11.9 (min 7.5 - max 18.7)  
415 and 22.4 (min 9.1 - max 51.3) snakes/ha, whereas post-hurricane densities varied between 0 (min  
416 0 - max 4.9) and 2.1 (min 0.4 - max 8.4) snakes/ha (Fig. 4). Similarly, in the Botanical  
417 Garden/Around the Mountain S, densities decreased from 13.2 (min 7.3 - max 23.1) snakes/ha in  
418 2011, to 3.3 (min 1.1 - max 9.2) snakes/ha in 2018 and 0 (min 0 - max 3.9) snakes/ha in 2019  
419 (Fig. 4). We excluded the northern hills, where we only found one snake, and the Quill rim,  
420 which we did not survey in 2011 (Figure 3). In 2011 (pre-hurricane), based on 146 transect  
421 surveys (21-24 January), we encountered 64 racers. Post-hurricane, we detected 54 individuals in  
422 2018 (based on 1,468 transects) and 60 in 2019 (based on 1,084 transects). This translates to a  
423 raw encounter rate across all habitats surveyed of 16.0 snakes/hour in 2011, 0.34 snakes/hour in  
424 2018 and 0.41 snakes/hour in 2019.

425  
426           ***Post- hurricane Survey Population Size.*** We conducted surveys in 2018, following  
427 Hurricanes Irma and Maria, and in 2019, surveying an area of 6.6 ha in the Quill National Park  
428 and 4.8 ha in Boven National Park. Average transect length was  $100.73 \pm 0.35$  m. Line transects  
429 were repeated a minimum of two and a maximum of 24 times at different sites. Average transect  
430 time was  $7.08 \pm 0.11$  minutes. Estimates of population size varied among sites surveyed. Using  
431 data from PIT-tagged snakes and based on the Schnabel index estimate of marked and recaptured  
432 snakes, we calculated a population size of 44.39 ( $\pm 0.46$ ) in 2016 based on a survey area of 3.5  
433 ha in the Quill. For 2019 we calculated a population size of 310.5 ( $\pm 0.16$ ) based on a survey area  
434 of 6.6 ha in the Quill, and 249 ( $\pm 0.18$ ) based on a survey area of 4.8 ha in Boven (Table 3).

435 **Table 3.** Overview of 2018 and 2019 site occupancy ( $\psi$ ; the probability of a site to be occupied)  
 436 and mean abundance ( $\lambda$ ; average individuals per sample) estimates per habitat (with upper and  
 437 lower confidence intervals and SD) of *Alsophis rufiventris* on St. Eustatius. 1 = Northern hills; 2  
 438 = Quill main trail; 3 = Quill Around the Mountain S (upper); 4 = Quill crater; 5 = Quill rim; 6 =  
 439 Botanical Garden/Around the Mountain S (lower). Black text = wiqid; red text = unmarked.

Year	Habitat	$\psi$	low CI	upp CI	$\lambda$	SD
2018	1	0.488 0.806	0.224 0.374	0.759 0.997	0.264	0.168
2018	2	0.774 0.966	0.355 0.568	0.955 1.000	1.785	0.288
2018	3	0.925 0.850	0.289 0.422	0.997 0.999	2.001	0.189
2018	4	0.978 0.888	0.208 0.467	1.000 1.000	2.011	0.102
2018	5	0.994 0.920	0.141 0.507	1.000 1.000	2.865	0.355
2018	6	0.998 0.946	0.092 0.540	1.000 1.000	1.544	0.227
2019	1	0.883 0.973	0.229 0.237	0.995 1.000	1.631	0.515
2019	2	0.798 0.655	0.237 0.074	0.981 1.000	5.062	1.920
2019	3	0.675 0.941	0.235 0.195	0.933 1.000	6.548	0.922
2019	4	0.521 0.743	0.211 0.097	0.816 1.000	6.181	0.876
2019	5	0.364 0.891	0.145 0.158	0.659 1.000	14.045	5.403
2019	6	0.231 0.824	0.065 0.125	0.565 1.000	3.246	1.114

440

441

442 **Abundance estimates.** Estimated racer densities per hectare in 2011, 2018 and 2019

443 mainly varied in their differences among habitat types but also varied greatly in the dispersion of

444 the estimates among years (Fig. 4). The naïve occupancy (i.e., proportion of sites the species was  
445 detected;  $\psi$ ) of racers was 84% (48% - 99% CI) in 2018, and 80% (32% - 99% CI) in 2019.  
446 Racer occupancy increased with increasing elevation in 2018, but decreased with increasing  
447 elevation in 2019. Occupancy varied across the six habitats sampled, but exhibited similar  
448 patterns in 2018 and 2019 (Figs. 5a and 5b). Site occupancy and mean abundance estimates per  
449 habitat for 2018 and 2019 are provided in Table 5. Mean detection probability ( $p$ ) per transect  
450 was 0.05 (0.03 - 0.07 CI) in 2018, and 0.07 (0.05 - 0.11 CI) in 2019 (package: 'wqid'). In 2018,  
451  $p$  was 0.02 (0.01 - 0.06 CI), and 0.03 (0.01 - 0.12 CI) in 2019 (package: 'unmarked'). During  
452 2018 surveys,  $p$  increased from 0.05 (0.03 - 0.07 CI) to 0.09 (0.03 - 0.21 CI) with a previous  
453 racer detection. During 2019 surveys,  $p$  did not increase with a previous detection. The number  
454 of surveys was not an important predictor of  $p$  in 2018, however  $p$  increased significantly in  
455 2019 with more (15 - 20) visits (Fig. 6). Estimated mean abundance ( $\lambda$ ) per transect was 1.82  
456 (0.66 - 5.01 CI) in 2018, and 1.60 (0.39 - 6.65 CI) in 2019 (package: 'wqid'). Estimated  $\lambda$  was  
457 1.90 in 2018 and 4.50 in 2019 (package: 'unmarked'). When habitat and elevation were included  
458 as fixed effects, mean  $\lambda$  was 1.72 (SD  $\pm$  0.52) in 2018 and 4.69 (SD  $\pm$  4.16) in 2019. This  
459 translates to a population estimate across the entire study area (11.42 ha) of 139.40 in 2018 and  
460 506.16 in 2019. Snake abundance increased with elevation, however the observed rate of  
461 increase among years was different, showing a drastic increase in 2019, while the rate of increase  
462 in 2018 was small (Fig. 7). Occupancy rates varied dramatically between the two years, showing  
463 an occupancy rate of 80% or more at elevations of 150m in 2018, while the occupancy rate at all  
464 elevations was more or less equal at all elevations ( $\pm$ 65%; Fig. 8). Site occupancy in 2018 ranged  
465 from 0.49 (0.22 - 0.76 CI) in the northern hills to 0.99 (0.14 - 1.00 CI) along the crater rim of the  
466 Quill, though we note the very large confidence intervals. Conversely, occupancy in 2019 ranged

467 from 0.23 (0.07 - 0.57 CI) in the botanical garden/lower Quill slopes to 0.88 (0.23 - 1.00 CI) in  
468 the northern hills.

469

470 Habitat type did not appear to influence abundance ( $\lambda$ ) and site occupancy ( $\psi$ ) estimates  
471 in 2018 and 2019; note that the 95% confidence intervals for each habitat type are very wide and  
472 encompass each other. This was independent if the analysis was performed with 'wqid' (Fig. 9a)  
473 or 'unmarked' software (Fig. 9b). Inside the crater,  $\psi$  estimates decreased from 0.98 (0.21 - 1.00  
474 CI) in 2018 to 0.52 (0.21 - 0.82 CI) in 2019.  $\lambda$  estimates (average number of individuals per  
475 transect) were lowest in the northern hills ( $0.26 \pm \text{SD } 0.17$ ) and highest along the crater rim ( $2.87$   
476  $\pm 0.36$ ) in 2018.  $\lambda$  estimates were lowest in the botanical garden/lower Quill slopes ( $3.25 \pm \text{SD}$   
477  $1.14$ ) and highest along the main Quill trail ( $14.05 \pm 5.40$ ) in 2019. Occupancy rates differed  
478 among years, and the effects of covariates on detection estimates were only significant in 2018:  
479 survey time positively influenced detection probability ( $1.90 \pm 0.26$ ), whereas the effects of week  
480 of the survey ( $-0.20 \pm 0.14$ ), rain ( $-0.18 \pm 0.18$ ) and temperature ( $-0.08 \pm 0.15$ ) were negative.  
481 The effects of covariates on detection and occupancy estimates in 2019 were negligible ( $\Delta\text{AICc}$   
482  $< 2$ ). Covariate models only shared survey time, week of survey and rainfall, the other variables  
483 only showed up in one of the models.

484

## 485 DISCUSSION

486

487 Quantitative estimates of abundance are essential for the recognition, management, and  
488 recovery of vulnerable, threatened, and endangered populations and species. Unfortunately,  
489 obtaining such estimates is often difficult, especially for rare organisms (Conroy et al., 2008).  
490 Worldwide, >82% of snake species have not been evaluated by the International Union for

491 Conservation of Nature (IUCN) or are classified as data deficient (IUCN, 2020). Snakes are  
492 generally secretive animals with low abundances, leading to difficulty in detection and the  
493 perception that many species are impossible to monitor (Urbina-Cardona, 2008; Luja et al., 2008,  
494 Durso et al., 2011). Unfortunately, this has led to a lack of information about the status of most  
495 snake populations (Durso et al., 2011). We aimed to address this by producing the first  
496 quantitative assessment of hurricane impacts on an endangered snake species with an extremely  
497 restricted range.

498  
499 Hurricanes can significantly alter the structure of biotic assemblages within hours of  
500 impact (Wiley and Wunderle, 1993; Widmer et al., 2004; Vilella and Fogarty, 2005; Schriever et  
501 al., 2009; Nicoletto 2013), and could cause local extirpation of some species (Schoener et al.,  
502 2017). The intensity and frequency of hurricanes has increased over recent decades (Emanuel,  
503 2013, Trenberth 2005, Webster et al. 2005), and assessing their influence on biodiversity,  
504 although challenging, is of increasing importance. There is a general dearth of information on the  
505 effects of hurricanes on snake species, although Marroquín-Páramo et al. (2021) recorded a  
506 significant decrease in snake abundance and species richness in the disturbed tropical dry forest  
507 of Jalisco, Mexico, following hurricanes Jova (2011) and Patricia (2015). A decrease in  
508 predatory reptile species such as *A. rufiventris* could affect the local food web (Spiller and  
509 Schoener, 1998; Schoener et al., 2001).

510  
511 Various studies have revealed differing responses of herpetofauna following hurricanes,  
512 with some species or assemblages increasing or decreasing their abundance, richness and  
513 diversity, while others remain unchanged (Reagan, 1991; Woolbright, 1991; Schoener et al.,



514 2001; Gunzburger et al., 2010; Nicoletto 2013; Suazo-Ortuño et al. 2018b). The cumulative  
515 effects of two or more hurricanes usually result in a significant abundance decrease for specialist  
516 species, but an increase for generalist species (McCoid, 1996; Schriever et al., 2009; Selman,  
517 2015). For example, in Louisiana following hurricanes Ivan (2004), Katrina and Rita (2005),  
518 *Thamnophis proximus* (Say in James, 1823) and *Agkistrodon piscivorus* (Lacépède, 1789) were  
519 observed to increase in abundance in levee and marsh habitats (Schriever et al., 2009). The  
520 structural effects of major hurricanes on forest ecosystems include tree damage/mortality  
521 (Eppinga and Pucko 2018) and an increase in leaf litter, which might affect the heterogeneity of  
522 the forest floor (Bellingham et al., 1996) and alter the structure and composition of herpetofauna  
523 assemblages, although this may be less pertinent on St. Eustatius given its small size and limited  
524 reptile diversity (Powell et al. 2005). Nevertheless, such changes may cause snakes to decline in  
525 abundance or disappear from some sites (Suazo-Ortuño et al., 2018a); indeed, our results show  
526 that post-hurricane racer density decreased dramatically inside the Quill crater compared to  
527 before the hurricanes. The racer population likely declined substantially within the first year  
528 post-hurricane, but exhibited signs of recovery after two years. This implies that the species may  
529 be resilient to hurricanes and could recover to pre-hurricane densities within approximately five  
530 years, provided no additional hurricanes make landfall on St. Eustatius during that time. Pre-  
531 hurricane data revealed that racers preferred sites without bare soil and with shallow litterfall  
532 depth. There was a small positive relationship between racer occurrence and soil temperature and  
533 fraction of green vegetation and wood litter on the ground, in addition to higher leaf area index.  
534 The higher leaf area index may suggest that racers are less likely to be observed in direct sunlight  
535 and prefer some amount of shade, however evaluating this variable independently showed no  
536 such pattern (GLM, binomial response,  $p > 0.05$ ).

537

538           Mean racer abundance increased across all habitats between 2018 and 2019, exhibiting  
539 similar patterns per habitat in both years. Specifically, abundance was highest in upper elevations  
540 of the Quill, especially along the crater rim, compared to Boven and the Botanical Garden/lower  
541 Quill slopes. This may be linked to greater quantities of prey such as *Anolis* lizards at higher  
542 elevations (Diaz et al., 2005). Alternatively, racers may prefer moist, unfragmented habitats at  
543 higher elevations with fewer shrubs and taller trees (Savit et al., 2005). Abundance estimates  
544 increased in line with increasing elevation in both years. We posit that the Quill's higher  
545 elevational habitats (<600 m) are preferred by racers compared to the northern hills (296 m;  
546 DCNA 2014). This is also consistent with Daltry et al. (1997) who observed more racers in the  
547 Quill than the drier northern hills, and with other researchers who have selected the Quill to  
548 research racers (e.g., Savit et al., 2005; Zobel, 2016). Generally, however, racers are habitat  
549 generalists and have been observed across the entire island (pers. obs. HM). Our results also  
550 suggest that racers are more likely to be detected on cooler days, supporting our suggestion that  
551 the higher elevations of the Quill offer preferential habitat for the species. The effects of  
552 temperature on snake populations have been studied in temperate (Weatherhead et al., 2002) and  
553 Mediterranean climates (Zamora-Camacho et al., 2010), but we were unable to find relevant  
554 comparative studies of diurnal terrestrial snake species from the tropics. Moreover, it is possible  
555 that racer abundance and occupancy is influenced by other factors that were not accounted for  
556 during data collection (i.e., canopy cover, rock cover, leaf litter cover, prey abundance).

557

558           The Quill and Boven are separated by an airport and areas of agriculture and human  
559 habitation. Given that the parks likely support small, fragmented racer populations, if local

560 extinction occurs in one area, natural recolonization may be inhibited by barriers of unsuitable  
561 habitat (Sewell et al., 2012). Additionally, we were unable to quantify the effects of invasive  
562 species which may impact *Alsophis* populations, however we note that free-roaming goats are  
563 present in both survey areas, with higher densities in the northern hills than the Quill (Madden,  
564 2020). McCauley et al. (2006) suggest that snakes could be affected by free-roaming herbivores  
565 through trampling or loss of vegetation through grazing; the latter is certainly evident on the  
566 outer slopes of the Quill and the remaining forest fragments of Boven. A roaming animal control  
567 project is currently being initiated by the government of St. Eustatius (BES Reporter, 2020), part  
568 of which involves the installation of a fence across the southern boundary of Boven National  
569 Park followed by the removal of non-native herbivores. This should result in the recovery of  
570 vegetation and reduce the risk of disturbance/trampling of racers by roaming goats. Black rats  
571 are also present in various densities across all vegetation types on St. Eustatius, but are more  
572 prevalent in forested areas (Madden et al., 2020). Thus the Quill is an ideal habitat for black rats  
573 as well as racers, and the coexistence of both species could have negative impacts on the racer  
574 population, as suggested by Daltry et al. (1997). Currently there are no plans to control or  
575 eradicate rats or free-roaming livestock from the Quill, which would be effective short-term  
576 conservation measures for the persistence of the racer population. Herpetofauna perform various  
577 regulating ecological functions in forest ecosystems (Cortés-Gomez et al., 2015) and can modify  
578 forest processes such as regeneration and nutrient cycling (Felix et al., 2004). Secondary dry  
579 tropical forest ecosystems play a buffering role that promote herpetofauna resilience, thus their  
580 importance for racer persistence cannot be underestimated, especially in line with increasing  
581 hurricane frequency and intensity (Marroquín-Páramo et al. 2021). Long-term monitoring to  
582 assess hurricane impacts, as well as changes in abundance and occupancy, will play an important

583 role in the conservation of racers within St. Eustatius' forest ecosystems, especially under the  
584 predicted future scenarios of anthropogenic climate change.

585

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599

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985

## FIGURES

986 **Figure 1.** Distribution of *Alsophis rufiventris* on the St. Christopher and Saba banks. Dots  
987 indicate locality records, X's mark extirpated populations on St. Kitts and Nevis, and red stars  
988 mark fossil localities (adapted from Maley et al., 2006).

989

990 **Figure 2.** Map of St. Eustatius showing 2011 survey areas (yellow stars), 2018 and 2019  
991 transects (red lines), 20m contours (black lines) and vegetation types. Adapted from de Freitas et  
992 al. (2014).

993

994 **Figure 3.** Mean coefficients of the selected models and their 95% confidence intervals.  
995 Confidence intervals are estimated from variation of the coefficient among the eight most  
996 parsimonious models (selected models). Vertical line represents a coefficient of zero.

997

998 **Figure 4.** Estimated density ( $\pm$  SE) per hectare of *Alsophis rufiventris* on St. Eustatius based on  
999 surveys conducted in 2011 (left), 2018 (middle) and 2019 (right). Note that in 2011 the Northern  
1000 Hills (H1-H2) and Quill rim (M5) were not surveyed.

1001

1002 **Figure 5a.** Mean abundance ( $\pm$  SE) per transect per habitat of *Alsophis rufiventris* on St.  
1003 Eustatius based on surveys conducted in 2018 and 2019. 1 = Northern hills; 2 = Quill main trail;  
1004 3 = Quill Around the Mountain S (upper); 4 = Quill crater; 5 = Quill rim; 6 = Botanical  
1005 Garden/Around the Mountain S (lower). Package: wqid.

1006

1007

1008 **Figure 5b.** Mean abundance ( $\pm$  SE) per transect per habitat of *Alsophis rufiventris* on St.  
1009 Eustatius based on surveys conducted in 2018 and 2019. 1 = Northern hills; 2 = Quill main trail;  
1010 3 = Quill Around the Mountain S (upper); 4 = Quill crater; 5 = Quill rim; 6 = Botanical  
1011 Garden/Around the Mountain S (lower). Package: unmarked.

1012

1013 **Figure 6.** Detection probability (%) of *Alsophis rufiventris* in relation to sampling effort (number  
1014 of surveys) on St. Eustatius based on transect surveys conducted in 2018 and 2019.

1015

1016 **Figure 7.** The effect of elevation on abundance ( $\lambda$ ) estimates of *Alsophis rufiventris* on St.  
1017 Eustatius based on transect surveys conducted in 2018 and 2019.

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1019 **Figure 8.** The effect of elevation on site occupancy estimates ( $\psi$ ) of *Alsophis rufiventris* on St.  
1020 Eustatius based on transect surveys conducted in 2018 (blue line) and 2019 (red line). Package:  
1021 wqid.

1022

1023 **Figure 9a.** Site occupancy estimates per habitat of *Alsophis rufiventris* on St. Eustatius based on  
1024 surveys conducted in 2018 and 2019. 1 = Northern hills; 2 = Quill main trail; 3 = Quill Around  
1025 the Mountain S (upper); 4 = Quill crater; 5 = Quill rim; 6 = Botanical Garden/Around the  
1026 Mountain S (lower). Package: wqid.

1027

1028 **Figure 9b.** Site occupancy estimates per habitat of *Alsophis rufiventris* on St. Eustatius based on  
1029 surveys conducted in 2018 and 2019. 1 = Northern hills; 2 = Quill main trail; 3 = Quill Around  
1030 the Mountain S (upper); 4 = Quill crater; 5 = Quill rim; 6 = Botanical Garden/Around the  
1031 Mountain S (lower). Package: unmarked.

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