

1 What makes *Hemidactylus* invasions successful? A case study on the island of Curaçao.

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24
25 **Abstract**

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28 *Hemidactylus* spp. (House geckos) rank among the most successful invasive reptile species worldwide.
29 *Hemidactylus mabouia* in particular has come to dominate tropical urban settings in the Western
30 Hemisphere, often rapidly displacing native species. However, the mechanisms driving displacement
31 remain unclear. Here we combine data from nitrogen and carbon stable isotopes, stomach contents, and
32 morphometric analyses of traits associated with feeding and locomotion to test alternate hypotheses of
33 displacement between *H. mabouia* and a native gecko, *Phyllodactylus martini*, on the island of Curaçao.
34 Consistent with expectations of direct food resource competition, we demonstrate substantial overlap of
35 invertebrate prey resources between the species. Additionally, we found strong evidence from both diet
36 content and stable isotope analyses that *H. mabouia* acts as an opportunistic vertebrate predator, preying
37 upon *P. martini* as well as other native and non-native reptiles. Finally, we show that *H. mabouia*
38 possesses several morphological advantages, including larger sizes in feeding-associated traits and limb
39 proportions that could offer a propulsive locomotor advantage on vertical surfaces. Together, these
40 findings suggest the establishment of *H. mabouia* likely involves a combination of both exploitative
41 interspecific competition and opportunistic predation. Given the ubiquity of *H. mabouia*, illuminating the
42 role of this species as both a competitor and a predator casts new concerns on the ecological and
43 demographic impacts of this widespread urban invader.

44 **Keywords:** invasive species, urbanization, vertebrate biodiversity loss, food web, trophic ecology, urban
45 gradient, intraguild predation

46
47 **Introduction**

48 Since the onset of the industrial revolution, the impact of invasive species on endemic fauna and
49 flora has been a central topic in the management and conservation of biodiversity worldwide (Paini et al.
50 2016; Young et al. 2017; Shechonge et al. 2019). This concern reflects dramatic losses in global
51 biodiversity and an increasing shift towards widespread homogenization of the planet's biota (McKinney
52 and Lockwood 1999; McKinney 2006; Trentanovi et al. 2013). These trends are especially acute in
53 urbanizing landscapes, which have repeatedly been shown to support higher numbers of non-native,
54 human-commensal species (Useni Sikuzani et al. 2018), such as cats (Buzan 2017; Bateman and Fleming
55 2012), rats (Bateman and Fleming 2012; Buzan 2017), and house sparrows (González-Oreja et al. 2018).
56 Following establishment, successful non-native species have been found to restructure resident
57 community assemblages by directly or indirectly altering top-down processes (e.g. predation, (Willson
58 2017; Pedersen et al. 2018)), bottom-up processes (e.g resource availability (Yam et al. 2016)), or both
59 (i.e.. "middle-out" effects, (Weber and Brown 2009)) at the expense of native taxa. In the most extreme
60 cases this can result in the extirpation or extinction of native species (Wiles et al. 2003; Toussaint et al.
61 2016; Liu et al. 2017). However, investigations into the impact and distribution of introduced species
62 have been largely restricted to species that are easily visible in the landscape (Beasley et al. 2018), are a
63 direct nuisance to humans (Bithas et al. 2018), or displace commercially important or game species
64 (Galanidi et al. 2018; Hill et al. 2004). While not misguided, this bias has left a critical gap in our
65 knowledge regarding the potential impacts of less readily observable, but equally common, non-native
66 human-commensal taxa (Morais and Reichard 2018).

67 Despite the prevalence of invasive reptiles around the world (Kraus 2015), most attention has
68 been devoted to the loss of biodiversity following the spread of a few larger bodied species such as
69 Burmese pythons (Smith et al. 2016; Willson 2017), green iguanas (Falcón et al. 2013; Burgos-Rodríguez
70 et al. 2016), and brown tree snakes (Wiles et al. 2003; Rodda and Savidge 2007; Richmond et al. 2015).
71 However, numerous smaller and more clandestine reptiles have also become globally pervasive (Kraus
72 2015; Capinha et al. 2017; Lapidra et al. 2017). These invasions, while common, often unnoticed until
73 native reptiles begin to disappear from the landscape (Kraus 2015). Such cryptic losses in biodiversity are
74 a hallmark of introduction of *Hemidactylus* spp. (House Geckos), a group commonly associated with
75 urbanized and developing areas. Over the past century, *Hemidactylus* spp. have become an established
76 feature of tropical and subtropical landscapes around the world (Carranza and Arnold 2006). Following
77 establishment, these geckos have been repeatedly linked to local extirpation and even extinction of native
78 lizards (Petren and Case 1996; Cole et al. 2005; Hoskin 2011). One species in particular, *Hemidactylus*
79 *mabouia* (Tropical House Gecko), is perhaps the most pervasive and formidable gecko to invade the
80 Western Hemisphere (Weterings and Vetter 2018).

81 Native to Africa, *Hemidactylus mabouia* is now common throughout the Americas and Caribbean
82 (Carranza and Arnold 2006). Recent studies have linked the successful establishment of this species in
83 urban and suburban environments to its ability to capitalize on the aggregation of insects around human
84 light sources (Hughes et al. 2015). Restricting the access of native geckos to these clustered food
85 resources is thought to represent a competitive advantage for *H. mabouia* that promotes high densities of
86 individuals (van Buurt 2004; Short and Petren 2011; Williams et al. 2016). As *H. mabouia* adult males
87 are noted for being particularly aggressive (Short and Petren 2011), the ability of this species to

88 aggressively restrict access to spatially clustered food resources presents a plausible hypothesis positing
89 that high densities of aggressive competitors fuel the displacement of native gecko species. However,
90 alternate hypotheses remain untested.

91 In addition to their impact as competitors, two aspects of *H. mabouia* invasions that have received
92 particularly little attention are locomotor morphology and the role of *H. mabouia* as potential predators.
93 The feeding mode of *H. mabouia* combines ambush tactics (Vitt 1983) with active pursuit of nearby prey
94 (Dornburg et al. 2016). Such a foraging mode could have selected for limb proportions that offer a
95 mechanical advantage on sheer vertical surfaces (Zaaf and Van Damme 2001). Further, it is possible that
96 the generally robust body plan of *Hemidactylus* spp. facilitates the capture of larger prey at a given body
97 size. An alternative, but not mutually exclusive, explanation for the success of *H. mabouia* comes from
98 isolated natural history reports of *H. mabouia* preying on other species of geckos (Dornburg et al. 2011,
99 2016) as well as cannibalizing conspecifics (Bonfiglio et al. 2006). These reports suggest that these
100 invaders may not only be superior competitors but may also act as predators exerting top-down control in
101 New World reptile communities. Both morphological advantages and predation have been invoked as
102 major drivers of displacement in the wake of invasions by the closely related *Hemidactylus frenatus* in the
103 Pacific (Petren and Case 1998; Petren and Case 1996; Bolger and Case 1992; Case et al. 1994; Short and
104 Petren 2012). However, both the role of morphological advantages and predation in driving the decline of
105 native gecko populations in the wake of an *H. mabouia* invasion remain unclear.

106 In this study we assess whether there is evidence for trait driven advantages or predation in the
107 invasion of *H. mabouia* in the Lesser Antillean island of Curaçao. We specifically focus on competition
108 between *H. mabouia* and the native *Phyllodactylus martini* (Dutch Leaf Tailed Gecko), as *P. martini*
109 declines have historically been linked to the invasion of *H. mabouia* (van Buurt 2004; van Buurt 2006;
110 Hughes et al. 2015; Dornburg et al. 2016). First we integrate analyses of nitrogen and carbon stable
111 isotopes with direct examination of stomach contents to test for levels of prey overlap and isotopic trophic
112 signatures consistent with hypotheses of resource competition or opportunistic predation. We additionally
113 collected morphometric measurements from traits associated with feeding and locomotion to test the
114 hypothesis that *H. mabouia* possess trait advantages over its hypothesized native competitor.

116 **Materials/Methods**

117 *Fieldwork and Data Acquisition*

118 *Hemidactylus mabouia* (n=90) and *Phyllodactylus martini* (n=71) specimens were collected at six
119 sites across Curaçao between July 2009 and September 2011: Lagun, Wespunt, CARMABI, Shete Boca,
120 Saint Anna Bay, and Willemstadt (Supplemental materials). Habitat type and species occupancy vary
121 across sampling locations. For example, both species co-occur in Lagun and Westpunt. At these sites we
122 restricted our sampling to suburban areas near natural habitats to maximize the potential of both species
123 co-occurring as *P. martini* has been found to be absent far from edge habitats in the presence of *H.*
124 *mabouia* (Hughes et al. 2015). In contrast, Shete Boca is a natural area in which *H. mabouia* are absent,
125 while Saint Anna Bay and Willemstadt are urban areas in which *P. martini* are absent. This sampling
126 design allowed us to capture a greater degree of diet breadth of each species across the island. Across
127 sites, sample locations included walls, rocks, outcrops, trees, thatch roofs, open ground, and shrubbery. At
128 no point during sampling did we document individuals of both species occupying the same structure (e.g.,
129 same wall or tree), and individuals were collected opportunistically at each site. All samples were
130 deposited in the Yale Peabody Museum of Natural History (supplemental materials). Each specimen and
131 prior to preservation, muscle biopsies were taken from each individual and dehydrated for analysis of

132 stable isotopes. Additionally, leaf samples from each locality and temporal sampling event were collected
133 and dehydrated for use as baselines in isotopic analyses. Following formalin preservation, samples were
134 transferred to 70% ethanol.

135 Specimens collected in 2011 had their stomach contents preserved in 10% formalin, and these 59
136 deposited samples were dissected, with contents identified and enumerated under a dissecting MVX10
137 microscope (Olympus Corp.; <http://www.olympus-lifescience.com/>). Prey items were identified to the
138 taxonomic groupings similar to those in other studies of Caribbean lizards (e.g., (Perry 1996)): Arachnida
139 (scorpiones), Arachnida (Araneae), Blattaria (Blattodea), Chilopoda, Coleoptera, Diptera, Ephemeroptera,
140 Hemiptera, Hymenoptera, Isopoda, Lepidoptera, Orthoptera, and “other”. Any vertebrate remains
141 encountered were additionally identified to the highest taxonomic resolution possible, and we additionally
142 identified any parasites encountered in the stomach. As formalin and alcohol preservation can have
143 heterogeneous effects on the volume of invertebrate organisms (Donald and Paterson 1977), enumeration
144 of diet contents was restricted to % frequency.

145 We further collected measurement data on 79 *Hemidactylus mabouia* for 10 morphological traits
146 associated with feeding and locomotion: snout-vent length (SVL), postorbital width, temporalis width,
147 head length, jaw length, head height, humerus length, radius length, femur length and tibia length. All
148 measurements were taken to the nearest 0.01 mm using digital calipers (Fowler Promax). Both stomach
149 content and morphological data were integrated with the dataset of Dornburg et al. (2016) who previously
150 measured *Phyllodactylus martini* specimens for the same morphological traits (n=34; Zenodo DOI:
151 10.5281/zenodo.61569) and prey items (n=69; Zenodo DOI: 10.5281/zenodo.61569).

152

153 *Stable isotopic analysis of trophic ecology*

154 Leg muscle biopsies from 21 individual *Hemidactylus mabouia* and 17 *Phyllodactylus martini*
155 legs as well as 8 plant stems and leaf baseline samples were used in nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$)
156 stable isotope analysis. Skin was removed from each muscle biopsy, and individual muscle and plant
157 baseline samples were dehydrated at 40°C degrees for 48 hours. Following dehydration, samples were
158 powderized using a bead beater (MP FastPrep24 Hyland Scientific). From each sample, 1.5 mg of powder
159 was loaded into 3x5 mm tins. Samples were analyzed at the University of California Davis Stable Isotope
160 Facility using an isotope ratio mass spectrometer. As nitrogen enrichment can vary over spatial or
161 temporal periods, quantification of trophic position for each individual was standardized using primary
162 producer baseline samples from plant leaves and stems collected at each locality (Vidal and Sabat 2010;
163 Roches et al. 2016). To account for $\delta^{15}\text{N}$ values not reflecting primary producer level values (Marshall et
164 al. 2007), baseline samples were compared across sites with aberrant samples (i.e., primary producer
165 $\delta^{15}\text{N} > \text{consumer } \delta^{15}\text{N}$) removed. Nitrogen values were standardized following Post (2002), in
166 subtracting the mean $\delta^{15}\text{N}$ of the primary producers from $\delta^{15}\text{N}$ of each individual lizard and assuming
167 fractionation of 3.4% per trophic level (Post 2002). $\delta^{15}\text{N}$ values for each species were visualized using
168 violin plots which allow for simultaneous inspection of quartiles and the underlying probability
169 distribution through integration of a rotated kernel density plot with a boxplot (Hintze and Nelson 1998).
170 We tested for differences between the mean $\delta^{15}\text{N}$ values of *H. mabouia* and *P. martini* using a Welch’s t-
171 test and additionally used Levene’s test to assess whether there was a significant difference in $\delta^{15}\text{N}$
172 variance between species. A significant positive difference in $\delta^{15}\text{N}$ between *H. mabouia* and *P. martini*
173 would be consistent with the hypothesis that individual *H. mabouia* are opportunistic vertebrate predators.
174 To test for potential differences in $\delta^{13}\text{C}$, we used the same statistical approaches as those used in the
175 analysis of $\delta^{15}\text{N}$, assuming carbon fractionation to be 0% (Post 2002). In this case, non-significant

176 differences in $\delta^{13}\text{C}$ would support the expectation that these species forage in similar habitats. All
177 analyses were conducted in R, v. 3.4.3 (R Development Core Team 2018).

178

179 *Stomach Content Analysis*

180 For each species, relative frequency of each prey item was calculated based on the total number
181 of prey items encountered across all individuals of that species. Differences in stomach contents between
182 species were visualized using a non-metric multidimensional scaling (NMDS) analysis in the vegan
183 software package (Oksanen et al. 2007; Oksanen 2011). Stress values were quantified to test if NMDS
184 ordination represents a viable indicator of species dissimilarity, with stress values less than 0.1 indicating
185 good representation of the dissimilarities (Clarke 1993). An analysis of similarity (ANOSIM; (Clarke
186 1993); (Chapman and Underwood 1999)) was used to additionally test for significant differences between
187 species, using Manhattan distances and 999 permutations in the vegan software package (Oksanen et al.
188 2007; Oksanen 2011). Differences in mean ranks were quantified using the R statistic, with values close
189 to zero indicating high similarity and values close to one indicating high dissimilarity (Chapman and
190 Underwood 1999). As *P. martini* has been found to consume different prey in rural versus suburban edge
191 habitats (Dornburg et al. 2016), NMDS and ANOSIM analyses were repeated with analyses restricted to
192 individual geckos collected in areas where both species co-occur. This allowed us to test whether pooling
193 across habitat types potentially masked differences or overlap in prey items. Additionally, differences in
194 parasite load between species were compared using a Welch's t-test.

195

196 *Comparisons of morphology*

197 We compared absolute differences in log snout-vent length (SVL) between species using an
198 ANOVA and created raincloud plots (Allen et al. 2019) visualize differences. These plots combine classic
199 boxplots with violin raw data plots to simultaneously visualize data, the difference in size quartiles, and a
200 kernel density estimate of the probability density of the SVL data. We conducted a principal components
201 analysis (PCA) to visualize the overall morphospace occupied by both species. In geckos, size has been
202 shown to covary with our target morphological measurements (Dornburg et al. 2016). As such, we first
203 regressed all the measurements per species against SVL (supplemental materials) and used the residual
204 values of individual traits regressed against SVL as data for the PCA. To assess if differences in
205 morphospace occupancy were mostly driven by uneven sample sizes, we randomly sampled equal
206 numbers of both gecko species from our data 200 times in intervals of 5 between 10 and 55. For each of
207 these 2000 datasets, we conducted a PCA and computed the mean and quantiles (25% & 75%) of the ratio
208 of *H. mabouia* to *P. martini* morphospace.

209 While morphospace visualization is advantageous for assessing the overall overlap of phenotypic
210 variation, it is possible that allometric slopes are identical between species and simply have different
211 intercepts (i.e., at a given body size a focal trait in one species is larger in one species than the other). To
212 further scrutinize our data, we used an analysis of covariance (ANCOVA) to test for differences in each
213 morphological trait between species. For each analysis, we kept log transformed SVL as the covariate and
214 treated each log transformed morphometric measurement (e.g., jaw length, limb length, etc) as the
215 response. This approach allowed us to test the potential correlation for each measured trait and SVL as
216 well as the possibility of significant differences between species that take trait covariation with SVL into
217 account. We repeated analyses with non-significant interactions removed, as inclusion or omission of
218 non-significant interactions can potentially impact ANCOVA analyses.

219 In many lizard species, including geckos, head size is a sexually dimorphic trait with males often
220 having larger heads relative to females (Kratochvíl et al. 2002; Scharf and Mieri 2013; Iturriaga and
221 Marrero 2013). As such, we used an ANCOVA assess whether morphological differences for each trait
222 were potentially masked when pooling sexes by species. For all analyses, we again kept log transformed
223 SVL as the covariate and treated each log transformed morphometric measurement as the response.
224 Finally, we assessed potential differences in total limb lengths (humerus length + radius length; femur
225 length + tibia length) between species and sexes using log transformed limb length as the response and
226 log transformed SVL as the covariate in an ANCOVA. This additional analysis facilitated additional
227 comparisons of expectations of gecko locomotion as studies often discuss differences in total limb
228 lengths.

229 Prior work has suggested large hind limbs compensate for large heads in the locomotion of
230 *Hemidactylus* spp. geckos (Cameron et al. 2013). As such, we examined scaling relationships between
231 head size and hindlimb length for both species by constructing a set of generalized linear models (GLMs).
232 We built models using sex, species, SVL, and head size as explanatory variables, with one set of models
233 using head length to quantify head size and another set using post-orbital width. All models except the
234 intercept-only null models contained an interaction term between SVL and the head size term, so that the
235 effects of head size on limb length would be controlled for overall body size. Additional candidate models
236 included (1) sex, (2) species identity, and (3) sex, species identity, and an interaction term between
237 species identity and head size. Model fit was evaluated with the Akaike information criterion with a
238 correction for small sample size (AICc). This method of model selection identifies models that predict the
239 data well while penalizing overparameterization (Burnham and Anderson 2004).

240

241 **Results**

242 *Differences in feeding ecology*

243 Analysis of $\delta^{15}\text{N}$ revealed a significant (Welch's t-test: $p < 0.00363$; $t = 3.1228$ $df = 34.272$) shift
244 towards a higher mean trophic level in *H. mabouia* versus *P. martini* (Figure 1A). In contrast, analysis of
245 $\delta^{13}\text{C}$ isotopes revealed no significant (Welch's t-test: $p < 0.4006$; $t = 0.85733$ $df = 21.812$) shift in mean
246 $\delta^{13}\text{C}$ between *H. mabouia* versus *P. martini* (Figure 1B), supporting the expectation that these two
247 species overlap in major foraging habitat type. Levene's tests did not support a significant increase in
248 $\delta^{15}\text{N}$ variance within *H. mabouia* versus *P. martini* ($F = 0.48$; $p = 0.493$), though a single *P. martini*
249 outlier point in our analysis depicted a carbon signature consistent with marine prey resource use,
250 suggesting the possibility that some individuals may opportunistically forage close to the shoreline.
251 Regardless, the difference in variance of $\delta^{13}\text{C}$ values between species was found to be non-significant
252 ($F = 0.5851$; $p = 0.4494$), even after removing this potential outlier point ($F = 7.624$; $p = 0.1546$).

253 Across 59 specimens of *H. mabouia*, we found 0 to 3 prey items per individual, which spanned a wide
254 range of invertebrates (Table 1 & Figure 2). Additionally, three individual *H. mabouia* each contained a
255 single vertebrate prey item. These prey items were identified as *Gonatodes antillensis*, *Phyllodactylus*
256 *martini*, and *Ramphotyphlops braminus*. Comparing the invertebrate prey found in *H. mabouia* to *P.*
257 *martini* revealed the two species to consume similar prey items with differences in the overall percentages
258 of prey items consumed. We find both species to generally consume the same major invertebrate prey
259 groups but at different frequencies: Arachnida (*H. mabouia* = 14%; *P. martini* = 19%); Insecta (*H.*
260 *mabouia* = 50%; *P. martini* = 58%); Isopoda (*H. mabouia* = 28%; *P. martini* = 9%). Further, the species
261 varied with regard to individual prey items and frequency within these major groupings (Figure 2 &
262 Table 1) and ANOSIM results supported significant differences between groups ($R = 0.213$, $p = 0.001$).

263 Visualizations of diet data based on NMDS analyses of invertebrate prey items for the two species
264 support a large degree of overlap in diet with *H. mabouia* utilizing the same resources as *P. martini*, but
265 with *H. mabouia* also utilizing more resources not exploited by *P. martini* (Figure 3A). Repeating
266 analyses for just individuals residing in areas of co-occurrence again supported significant differences
267 between species in an ANOSIM analysis when vertebrates were included as a prey category ($R=0.020$,
268 $p=.04$). All instances of vertebrate predation by *H. mabouia* were found in areas where the two species
269 overlap (supplemental materials). Restricting an ANOSIM analyses to just invertebrate prey items
270 supported no significant differences in diet between the two species ($R=0.018$, $p=.07$). Visualizations of
271 both the raw (supplemental materials) and NMDS analyses of the invertebrate prey item diet data for the
272 two species areas further depicted a large degree of overlap (Figure 3B). In addition to prey contents,
273 parasitism infestations by nematodes were significantly different between the two species (Welch's t-test:
274 $p < 0.0005$; $t = -3.7683$ $df = 71$), suggesting higher parasite pressure within *P. martini* (Table 1).

275

276 *Differences in morphology*

277 We found a significant overall size difference between *H. mabouia* versus *P. martini* ($F = 10.61$; p
278 $= 0.00143$), with *H. mabouia* generally being larger (Figure 4A). Three axes of a principal components
279 analysis (PCA) of morphological traits collectively capture 64.1% of the measured variation (PC1:
280 34.84%; PC2: 16.90%; PC3: 12.37%). PC1 largely captures differences in limb lengths (~39% total
281 hindlimb, 18% total front limb) and variation in the postorbital width (~24%). In contrast, PC2 mostly
282 captures variation in cranial measurements with over 70% of the loadings belonging to a combination of
283 head length (~29%), jaw length (~17%), temporalis width (~13%), and postorbital width (~13%). PC3
284 largely captured further variation in cranial morphology (Supplemental materials). Visualization of these
285 PC axes revealed a high degree of overlap between species, with *H. mabouia* occupying more
286 morphospace overall. Between PC1 and PC2 (Figure 4B) the total morphospace occupancy based on the
287 convex hull area [CHA] of *H. mabouia* was 64% larger (*H. mabouia* CHA = 18.37; *P. martini* = 11.14).
288 Similarly, between PC1 & PC3 (*H. mabouia* CHA = 22.724; *P. martini* = 5.898; Figure 4C) and PC2 &
289 PC3 (*H. mabouia* CHA = 16.532; *P. martini* = 5.474; Figure 4D) the CHAs of *H. mabouia* were larger.
290 Results of our dataset resampling analyses support that these differences were not due to sample size
291 differences alone (Supplemental materials). SVL was significantly correlated with all measured
292 morphological traits (Table 2; Supplemental materials) and ANCOVA results further support significant
293 differences between residual trait variation after accounting for SVL scaling between species for all traits
294 (Table 2; Supplemental materials). The only exception to this general trend of a significant relationship
295 between species identity and trait was head height ($F = 3.232$; $p = 0.0745$). These results were consistent
296 whether non-significant interactions were included in the analysis or not (Supplemental materials). Tests
297 for sexual dimorphism for no evidence for trait differences between male and female *P. martini*. In
298 contrast, head width was significantly different between male and female *H. mabouia*, suggesting *H.*
299 *mabouia* males have wider heads than females (Supplemental materials).

300 GLM analyses of the relationship between head size and hind limb length reveal largely
301 concordant patterns regardless of which metric (head length or post-orbital width) is used to quantify head
302 size (Table 3; supplemental materials). For both measurements, the top model (lowest AICc score) was
303 the one containing a different intercept of the relationship between head size and limb length for the two
304 species, but without a difference in slope (i.e., no interaction between species identity and the head
305 size/SVL relationship). These top models also include no effect of sex on the relationship between head

306 size and limb length, but in both cases the model that did include sex was also within or nearly within the
307 set of credible models (deltaAIC of 1.52 for head length, and deltaAIC of 2.2 for post-orbital width).

308

309 **Discussion**

310 *Hemidactylus mabouia* ranks among the most pervasive invasive lizard species in the neotropics
311 (Rödder et al. 2008; Weterings and Vetter 2018). This species has repeatedly been hypothesized to
312 represent a superior competitor that restricts access to food resources (Rocha et al. 2011; Hughes et al.
313 2015; Williams et al. 2016) and thereby promotes the extirpation of native, as well as non-native, geckos
314 (van Buurt 2004; van Buurt 2006). Our study provides support that on Curaçao, *H. mabouia* not only
315 competes with the native gecko *Phyllodactylus martini* for prey resources but can act as a predator of this
316 and other vertebrate species. Both stable isotopic and stomach contents demonstrate that *H. mabouia* will
317 readily consume vertebrate prey items that include *P. martini*, *Gonatodes antillensis* (the Venezuelan
318 Coastal Clawed Gecko), and the non-native blind snake *Ramphotyphlops braminus*. Additionally, we
319 demonstrate larger sizes in feeding associated traits and limb lengths that provide an advantage for rapid
320 forward propulsive locomotion characteristic of ambush predators for *H. mabouia* over *P. martini*. Given
321 the ubiquity of *H. mabouia* throughout the neotropics, our results provide a new perspective for
322 understanding the complexity of *Hemidactylus* spp. invasions, suggesting their potential impact to be
323 vastly underestimated.

324

325 *On the competitive advantages of Hemidactylus*

326 Prior work has suggested that *H. mabouia* directly competes with *Phyllodactylus martini* for food
327 resources (Hughes et al. 2015), suggesting resource competition is a major driver of *P. martini*'s
328 displacement. Our analyses are consistent with the expectations of a competitive exploitation hypothesis,
329 demonstrating substantial overlap of major invertebrate prey categories between *H. mabouia* and *P.*
330 *martini* when the two species co-occur (Fig. 3; Supplemental materials). These prey categories largely
331 reflect common groups of invertebrates associated with human dwellings and artificial lighting in
332 Curaçao (Dornburg et al. 2016) and are consistent with studies of the diet of *H. mabouia* in other
333 urbanizing areas (Bonfiglio et al. 2006; Iturriaga and Marrero 2013; Drüke and Rödder 2017). In addition
334 to dietary overlap, our analyses of individual stomach contents revealed *H. mabouia* to generally have
335 fewer prey items per stomach than *P. martini* (Welch's t-test: $p < 0.001$; $t = 3.31$ $df = 84.74$). A potential
336 explanation for this dissimilarity may stem from the ambush prey capture tactics of *H. mabouia*.
337 Fragments of presumably larger prey items such as roaches, beetles, and spiders were often found in the
338 stomachs of *H. mabouia* in comparison with *P. martini*. Additionally, high numbers of isopods were
339 found in some individuals. This suggests that *H. mabouia* could be opportunistically feeding on larger
340 prey as well prey encountered in daytime refugia. The latter could also explain the finding of a blind
341 snake within an individual *H. mabouia*. While partially digested fragments of invertebrate body parts
342 prohibit further testing of whether *H. mabouia* is more effectively harnessing larger prey, this hypothesis
343 raises several possibilities of how the natural history of these species influences differential patterns of
344 foraging and prey capture.

345 There are different responses to bright lighting between these species with *Hemidactylus mabouia*
346 readily foraging directly at brightly lit artificial lights (Perry and Fisher 2006; Hughes et al. 2015). This
347 strategy reduces the energetic cost of finding prey as *H. mabouia* can harness the potential of artificial
348 lights as a lure for attracting large prey resources (Gaston et al. 2013) while simultaneously gaining a
349 potential thermal advantage (Perry et al. 2008). In contrast, *P. martini* avoids direct bright lights, and is

350 often found foraging along the more dimly lit periphery of buildings (Hughes et al. 2015). As such, *P.*
351 *martini* may have an ecological disadvantage to *H. mabouia*, as the former may need to spend more time
352 locating prey. Furthermore, this small change in prey foraging may put *P. martini* in contact with
353 arthropod vectors for nematodes not encountered by *H. mabouia*, as suggested by our observation of a
354 difference in parasite infestations between species. Given that lizards are often transport hosts for
355 mammalian parasites (Incedogan et al 2014; Dornburg et al 2019), including nematodes (Goldberg and
356 Bursey 2000), further testing of differences in parasite frequencies between *Hemidactylus* and its native
357 competitors represents an exciting direction additional research of high relevance to animal health.

358 In addition to having an advantage in light tolerance, our analyses of trait morphological variation
359 suggest that *H. mabouia* has a size advantage over *P. martini*, possessing overall larger size, as well as
360 larger heads, hind limbs, and other traits (Fig. 4 & Table 2). Increases in head height and head length are
361 associated with increases in bite force and more efficient prey capture in geckos (Cameron et al. 2013;
362 Massetti et al. 2017), as well as other lizard species (Verwajen et al. 2002; Dufour et al. 2018).
363 Functionally, this advantage is thought to arise by the combination of increasing space to accommodate
364 increases in mandible adductor muscle sizes as well as changes in attachment angle that provide force
365 advantages (Herrel et al. 2001). Head sizes were larger in both male and female *H. mabouia* relative to *P.*
366 *martini*, with only head width (temporal width) significantly different between the sexes (Supplemental
367 materials). Males of the closely related *Hemidactylus turcicus* have also been found to have larger head
368 widths that are hypothesized to be the result of sexual selection (Iturriaga and Marrero 2013), and our
369 results suggest a similar pattern of dimorphism occurs in *H. mabouia*. However, larger heads also come at
370 a cost. Increased head sizes can negatively impact sprinting speed in lizards (Cameron et al. 2013), and
371 our additional finding of increased hind limb lengths in both sexes of *H. mabouia* may reflect the species
372 avoiding a fundamental locomotor trade-off (Table 3, Supplemental materials). A similar compensation
373 has been reported in *Hemidactylus frenatus* (Cameron et al. 2013) suggesting this is potentially a general
374 feature of *Hemidactylus* locomotor morphology. But, these results also raise new questions about the
375 general features and evolvability of locomotion in *H. mabouia*.

376 *Hemidactylus mabouia* has been subjected to an unintentional experiment of introduction to
377 human mediated landscapes across the new world for centuries (Goeldi 1902; Van Buurt 2004; Carranza
378 and Arnold 2006). But, whether colonization of human structures has placed this species under selection
379 for changes in locomotor morphology remains unclear. Longer hind limbs in lizards are often correlated
380 with increased sprint speeds and forward propulsion in lizards (Bonine and Garland 1999; Cameron et al.
381 2013; Winchell et al 2018), thereby providing an advantage for an ambush predator such as *H. mabouia*
382 relying on a combination of ambush and pursuit to capture prey. Additionally, recent work placing front
383 limbs into the context of gecko locomotion models (Birn-Jeffery and Higham 2016; Zhuang and Higham
384 2016) provides strong evidence that locomotor function is decoupled between fore- and hind limbs. In
385 contrast to hind limbs, which act as primary axes of propulsion, front limbs are primarily used for braking
386 and downward locomotion (Birn-Jeffery and Higham 2016). Quantifications of limb morphology across
387 major lineages of geckos suggest shorter front limbs relative to hindlimbs to be a hallmark of gecko
388 locomotor morphology, with all species having between a 10 to 35% reduction in front limb proportions
389 (Hagey et al. 2017), a finding consistent with our analysis *H. mabouia* limb proportions (Supplemental
390 materials).

391 Primarily shorter front limbs could shorten the swing time, thereby aiding in maintaining speed
392 and stance in downward movements (Birn-Jeffery and Higham 2016). Our finding of shorter front to
393 hindlimbs in *H. mabouia* are consistent with expectations of selection for locomotion on steeply inclined

394 surfaces such as walls that is coupled with large hindlimbs for sprinting. But, the significant negative
395 scaling relationship between forelimb length and body size for *P. martini* also highlights the potential that
396 additional major differences in locomotor mode and performance between these species exist. Currently,
397 the foraging mode and activity patterns of *P. martini* remain little studied, as do those of *H. mabouia* in
398 their native range. As comparative studies of gecko functional locomotor morphology and performance
399 continue to illuminate the role of forelimbs in gecko locomotor morphology, future comparisons of
400 locomotor morphology and performance between and within these species offers a promising and exciting
401 research frontier.

402

403 *The role of predation in Hemidactylus invasions?*

404 Superiority in food resource competition has repeatedly been hypothesized as a major factor
405 facilitating the establishment of *H. mabouia* at the expense of native geckos (Petren and Case 1996;
406 Hoskin 2011; Hughes et al. 2015). Our stomach content analyses revealed a significant overlap of major
407 invertebrate prey resources, thereby supporting expectations of food resource competition (Table 1; Fig. 2
408 & 3). However, our study additionally provides direct evidence from stomach contents and indirect
409 evidence from the analysis of $\delta^{15}\text{N}$ isotopes that *Hemidactylus mabouia* acts as an opportunistic
410 vertebrate predator. These provide a broader context to previously reported single instances of predation
411 by *Hemidactylus mabouia* on *Phyllodactylus martini* (Dornburg et al. 2016) and *Gonatodes antillensis*
412 (Dornburg et al. 2011), as well as observations of opportunistic cannibalism (Bonfiglio et al. 2006). We
413 additionally report the first instance of ophiophagy in *H. mabouia* (Table 1), suggesting that this species
414 readily consumes smaller vertebrate prey. This raises a question: How frequent are such predation events?

415 Our isotopic analyses provide some insights to this question, indicating numerous individual *H.*
416 *mabouia* are feeding at a trophic level higher than *P. martini*. As vertebrates represent the only consumers
417 of a higher trophic position in Curaçao, $\delta^{15}\text{N}$ values suggest that predation of vertebrates by *H. mabouia*
418 may not be rare events. Investigations of feeding ecology of the closely related *H. frenatus* have also
419 reported interspecific juvenile predation (Hunsaker 1966; Bolger and Case 1992; Case et al. 1994),
420 suggesting *H. mabouia* to be similarly opportunistic. Juvenile *H. mabouia* are known to avoid predation
421 by larger adults by foraging low to the ground (Howard et al. 2001). It is likely that our results reflect a
422 signature of juvenile mortality of *P. martini* as juveniles of this species will readily forage across a range
423 of wall elevations including those that are occupied by *H. mabouia* (van Buurt 2004). In addition to
424 lowering recruitment, predation on juvenile *P. martini* could offer a competitive advantage for juvenile *H.*
425 *mabouia*. By reducing the density of interspecific competitors at the juvenile stage, more juvenile *H.*
426 *mabouia* would be able to transition to adult and more swiftly increase overall population sizes. As *H.*
427 *mabouia* readily achieves high carrying capacities that can exceed those of other *Hemidactylus* species
428 (Short and Petren 2011), this in turn could greatly increase the pressure of additional density dependent
429 effects on the persistence of native species.

430 Evidence for opportunistic predation of smaller vertebrates by *H. mabouia* raises the concern that
431 in addition to displacing populations of native geckos, the presence of *H. mabouia* can negatively impact
432 overall population structure. Although demographic studies of geckos impacted by *H. mabouia* have been
433 limited, analyses of *Phyllodactylus tuberculosis* in Mexico have implicated the presence of *H. mabouia* in
434 severe contractions of effective population size and recent genetic bottlenecks (Blair et al. 2015). We
435 argue that further assessing the role of *H. mabouia* in juvenile survivorship represents an important, but
436 currently neglected aspect of this species invasion biology. These studies are of particular importance as
437 *H. mabouia* is increasingly being found in non-urban areas throughout its invaded range (Rocha et al.

2011), challenging the assumption that this invasion is limited to urbanizing areas. Fortunately for Curaçao and other similar desert habitats, invasion into the native bush habitat may not be possible due to mechanical properties of *H. mabouia* toe pad adhesion. *Hemidactylus* geckos all possess a basal toe pad system that may not be capable of successfully gaining traction on the loose, and dusty, rocky soil of the island (Russell and Delaugerre 2017). This hypothesis remains to be tested, but if it is supported, the impact of predation and competition on native gecko population sizes in dusty, arid environments could be mitigated by integrating continual corridors of native habitat into urban planning efforts. Such efforts would yield ‘enemy-free’ space and thereby increase the probability of the long-term persistence of native gecko species (Cole et al. 2005).

447

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458

459 **Authors’ Contributions**

460 AD, AJ, AL, DW, GWC, MCB, and TI conceived of the project. AD, AJ, DW, MCB, and TI
461 conducted fieldwork. CL analyzed stomach contents. AD and MCB collected morphometric data. AL
462 prepared isotopic samples. AD, AJ, AL, DW, and CN performed analyses. AD, AL, and CN wrote the
463 initial draft of the manuscript. All authors contributed to subsequent revisions.

464

465 **Figure Legends**

466

467 **Fig. 1 | Violin plots of isotopic data.** **A.** Estimated trophic position for *Phyllodactylus martini* (n=17) and
468 *Hemidactylus mabouia* (n=21) using Nitrogen. **B.** Carbon. Raw nitrogen and carbon isotopic values were
469 corrected using average baseline values across all sites.

470

471 **Fig. 2 | Visualization of stomach content data.** **A.** Data from analyzed *Phyllodactylus martini* (n=72).
472 **B.** *Hemidactylus mabouia* (n=59). Columns in sphere correspond to the relative frequency of an
473 individual’s prey items. Colors correspond to matching prey categories in legend.

474

475 **Fig. 3 | Non-metric multidimensional scaling analysis contrasting stomach contents.** Data from
476 analyzed *Phyllodactylus martini* (n=79) and *Hemidactylus mabouia* (n=57). Ellipses encompass the 95%
477 confidence interval around the centroid of each species, and prey labels indicate location of prey
478 categories within the diet space.

479

480

481 **Fig. 4 | Analysis of morphometric traits.** A. Raincloud plots visualizing SVL differences between
 482 *Phyllodactylus martini* (yellow) and *Hemidactylus mabouia* (brown), depicting the probability
 483 distribution through a rotated violin plot (top), box plot summary of quartiles (middle), and raw data
 484 (bottom) for each species. B-D. Principal components analysis showing overlap of morphological traits
 485 between species. Principal component scores are visualized for each axis and species with background
 486 shading representing fitted convex hulls of the morphospace occupied by each species.

487
 488

489 **Tables**

490

491 **Table 1 | Relative frequency of prey stomach content items across all sampled individual**
 492 ***Hemidactylus mabouia* (total items = 72) and *Phyllodactylus martini* (total items = 115).** Bold values
 493 indicate sums of prey items within major categories (i.e., Insecta).

494

	<i>Hemidactylus mabouia</i>	<i>Phyllodactylus martini</i>
Prey	Relative Frequency	Relative Frequency
Arachnida	0.141	0.191
Scorpiones	---	0.052
Araneae	0.14	0.139
Chilopoda	---	0.009
Insecta	0.507	0.583
Blattaria	0.042	0.00
Coleoptera	0.127	0.235
Diptera	0.056	0.078
Ephemeroptera	0	0.009
Hemiptera	0.056	0.017
Hymenoptera	0.099	0.061
Lepidoptera	0.099	0.096

Orthoptera	0.028	0.087
Isopoda	0.282	0.087
Skin Shed	0.014	0.009
Vertebrata	0.042	---
<i>Gonatodes antillensis</i>	0.014	---
<i>Phyllodactylus martini</i>	0.014	---
<i>Ramphotyphlops braminus</i>	0.014	---
Other	0.014	0.128

495

496 **Table 2 | ANCOVA results testing the effect of snout-vent length (SVL), species, and their**
497 **interaction on measured morphological characters.** Bolded values indicate significant effects. * stands
498 for *P*-values ranging from 0.05 to 0.01, ** for *P*-values ranging from 0.01 to 0.001 and *** for *P*-values
499 smaller than 0.001

500

Trait	log(SVL) (F/P)	Species (F/P)	Species:log(SVL) (F/P)
Post Orbit Width	121.82/***	5.98/*	0.07/0.78
Temporalis Width	1151.42/***	32.45/***	0.07/0.78
Head Length	1298.73/***	101.84/***	0.07/0.78
Jaw Length	526.77/***	86.16/***	0.18/0.66
Head Height	358.09/***	3.23/0.07	0.35/0.55
Humerus Length	163.53/***	43.52/***	8.30/**
Radius Length	464.95/***	54.76/***	0.09/0.76

Femur Length	307.27/***	59.16/***	2.19/0.14
Tibia Length	140.64/***	20.94/***	0.08/0.76

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