ORIGINAL ARTICLE

Out-competed by an invader? Interference and exploitative competition between Tropical House Gecko (*Hemidactylus mabouia* Moreau de Jonnès, 1818) and Barbados Leaf-Toed Gecko (*Phyllodactylus pulcher* Gray, 1828) for diurnal refuges in anthropogenic coastal habitats

Robert Williams[1],* Angelo P. Pernetta[2], and Julia A. Horrocks[3],

1. Robert Williams, Ecology and Conservation Research Group, School of Pharmacy and Biomolecular Sciences, University of Brighton, Huxley Building, Lewes Road, Brighton, BN2 4GJ, United Kingdom. robertjwilliams76@gmail.com

2. Angelo P. Pernetta, Ecology and Conservation Research Group, University of Brighton, Priory Square, Priory Street, Hastings, TN34 1EA, United Kingdom

3. Julia A. Horrocks, Department of Biological and Chemical Sciences, University of the West Indies, Cave Hill, Barbados, West Indies.

*Corresponding author: robertjwilliams76@gmail.com

Abstract.

House Geckos in the genus *Hemidactylus* are highly successful colonizers of regions beyond their native range, often resulting in displacement of native gecko species through competitive interactions for daytime refuge (crevices) and prey resources. We report on data collected from night time surveys undertaken in April-May 2014 on Barbados, West Indies, that focused on the distribution and abundance of the endemic Barbados Leaf-Toed Gecko (*Phyllodactylus pulcher*) and the introduced Tropical House Gecko (*Hemidactylus mabouia*) along unlit coastal walls and among boulders in the grounds of a hotel resort. In contrast to patterns of displacement of native species by *H. mabouia* seen elsewhere, *P. pulcher* was more abundant than *H. mabouia* on coastal walls, whereas the latter was found in greater numbers using boulders at this site. Walls and boulders differed with regard to availability of diurnal refugia suitable for geckos; with the walls having high frequency of small

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crevices with openings < 20 mm, and boulders offering very little cover other than the underside of the boulder itself. To investigate if this niche separation was a result of differences in diurnal refuge use between the species, we conducted experimental trials in which geckos were allowed to select between refugia with different characteristics. Both species selected for narrower and warmer refugia, and refugia that had been previously occupied by the other species. These shared preferences for refugia type suggest that other factors underlie the niche separation observed in the field. In supporting high densities of *P. pulcher*, coastal walls could offer important secondary habitat by augmenting the natural cliff side habitat of this endemic gecko, a finding that could be exploited for the conservation of this candidate species for Critically Endangered classification.

Keywords.

Barbados; Hemidactylus; Island endemic; Leaf-Toed Gecko; Phyllodactylus; Tropical House Gecko

Introduction

Habitat use by ectotherms is often primarily influenced by specific thermal requirements of the species and opportunities for thermal regulation (Adolph 1990; Singh *et al.* 2002). For diurnal species this involves selection of habitat that offers thermal heterogeneity that can be exploited using a suite of behavioral mechanisms such as varying activity time, shuttling between sun and shade, and adjusting posture and perch types (Huey 1982; Diaz 1994). In the case of nocturnal squamates opportunities for thermoregulation are afforded by the selection of diurnal retreat sites with suitable thermal characteristics (Webb & Shine 1988; Kearney & Predavec 2000; Kearney 2002). However, habitat use can also be influenced by biotic determinants such as inter- and intra-specific competition, and predator avoidance (Schlesinger & Shine 1994; Shah *et al.* 2004; Allen *et al*. 2015), which creates conflicting priorities and trade-offs for habitat selection (i.e., thermal preference, safety, or solitude) (Downes & Shine 1998). Habitat use in response to such pressures has significant implications for the fitness of individuals, as habitats determine the microclimates that an animal experiences, which in turn influence an animal's physiological capacities and ultimately its demographic and ecological performance (Huey 1991).

House Geckos in the genus *Hemidactylus* are amongst the most successful colonising invasive species, and are reported to be negatively impacting native gecko species on a global scale (Bomford *et al.* 2008; Rodder *et al.* 2008; Rocha *et al.* 2011). Rapid displacement of species has been shown to occur following the introduction of *Hemidactyus* spp. For example, field studies in Florida recorded complete displacement of resident *H. garnotii* at several locations of study within seven years of the arrival of *H. mabouia* (Meshaka 2000; Short & Petren 2012). Both direct behavioral interference and exploitation competition for food resources may be the fundamental cause of competitive displacement and widespread declines of native geckos by *H. frenatus* introduced onto Pacific islands (Case & Bolger 1992; Petren *et al.* 1993; Case *et al.* 1994; Petren & Case 1996; 1998). The introduction of *H. frenatus* to the Mascarene Islands in the Indian Ocean has also caused devastating declines and extinctions of endemic *Nactus* gecko populations, with native geckos outcompeted for diurnal refuges, rendering them more vulnerable to introduced mammalian predators, and adverse climatic conditions (Cole *et al.* 2005).

Displacement of native gecko species by *Hemidactylus* spp. has been mostly reported for urban environments (although see Cole *et al.* 2005; Cole & Harris 2011), although the incidence of invasive *Hemidactylus* spp. transition into natural habitats is garnering warranted attention (Hoskin 2011; Rocha *et al.* 2011). On small tropical islands with increasing development, anthropogenic structures are likely to have provided a secondary habitat for native geckos, partly due to loss of natural habitat, but also through creation of novel opportunities for foraging, such as the concentration of invertebrate prey around artificial light sources (Petren & Case 1996), diurnal refugia, and egg deposition sites (Henderson & Powell 2001). Displacement of native geckos from these secondary habitats following the introduction of *Hemidactylus* spp., as evidenced by the historical abundance and subsequent decline of the Dutch Leaf-Toed Gecko (*Phyllodactylus martini*) around buildings on the islands of Curaçao and Bonaire, Dutch Antilles following the invasion of *H. mabouia* (Powell *et al.* 2011; Hughes *et al.* 2015), emphasizes the great importance of conserving natural habitats for native species on invaded islands (Hughes *et al.* 2015).

In light of the negative impact of invasive *Hemidactylus* spp. on native geckos elsewhere, we investigated the distribution and abundance of introduced *H. mabouia* and the endemic Barbados Leaf-Toed Gecko, *Phyllodactylus pulcher* Gray, 1828, on unlit coastal walls and ornamental boulders on the island of Barbados, West Indies. *Hemidactylus mabouia* is well established in the wider Caribbean, (Henderson & Breuil 2012), and earliest reports of the species being present on Barbados date back to the 1700's (Grant 1959), where it is now ubiquitous around lit buildings and in urban habitats. The native and recently rediscovered *P. pulcher* is rarely observed around lit buildings and appears to primarily utilise cliff side habitat (Williams *et al*. 2015).

Man-made cliff side structures therefore represent a secondary habitat for both species. In addition to field surveys, we conducted experimental trials to investigate if behavioral differences in preferences for diurnal refuge qualities, and refuge availability in the field, could explain observations of niche separation between the two species.

Materials and Methods

To quantify gecko usage of man-made coastal cliff edge structures we carried out targeted surveys during April - May 2014 of four coastal, coral limestone block walls, and a series of large natural stone boulders edging the lawn of The Crane Resort, Barbados (all situated within Crane Bay, the parish of St Phillip; 13° 6'14.71"N - 59°26'41.84"W). Each wall ran parallel with the cliff edge at an average height of one meter, leaving a maximum of three meters horizontal natural cliff edge habitat on the seaward side (Fig 1a). Habitat of the landward side of the walls at The Crane Resort was well-maintained lawn (Fig 1b). Boulders were situated within the lawn amongst a shrub border (Fig 1c). Planted ornamental vegetation was on the landward side (Fig 1d) of the wall surveyed at Stonehaven property, and rough pasture on the landward side of the wall at a neighbouring neglected residential lot.

Wall searches were conducted between the hours of 18:00 and 20:00 to incorporate the period where geckos are first becoming active and likely to be encountered close to diurnal refuges. Searches involved two surveyors searching both sides of the entire length of each structure by starting at opposite ends and meeting in the middle. Using flashlights, gecko species could be easily identified by body shape, posture, patternation, and toe form. Counts were made of all geckos of each species encountered on both sides of the wall structure. Geckos seen on cliff edges were not counted. Similarly, counts were made of all geckos seen on the boulders during one transect (~154 m) of the lawn edge. Boulders and walls were surveyed on multiple nights during the survey period to achieve an estimate of density for each species (Table 1). Survey effort was not equal across sites due to occasional access restrictions. We compared our density data with that published on *H. mabouia* on buildings in Anguilla (Howard *et al*. 2001) and *H. mabouia* and *Phyllodactylus martini* on Curaçao (Hughes *et al*. 2015). The average abundance of large, medium, and small crevices per m^2 on wall faces (landward and seaward) was measured by counting the number of crevices offering full concealment found within 0.5 m^2 quadrats. Crevice size was determined by measuring the size of openings with homemade diameter gauges, with small crevices equalling < 20 mm (small relative to gecko head depth ~ 5 mm), medium 20-40 mm, and large > 40 mm. To account for variance in character between landward and seaward faces of each wall (i.e., amount of cement render, full mortar joints, and erosion) one quadrat was sampled on each side (directly opposite) of the walls, at 5 meter intervals and at half the height of the wall.

Husbandry and housing**-** Experimental procedure and husbandry methods were reviewed and approved by the ethics committee of the University of Brighton and the University of West Indies. A total of 29 adult *P. pulcher* and 29 adult *H. mabouia* were caught for inclusion in captive trials of refuge selection running in conjunction with the night time surveys (Table 2). Geckos were collected opportunistically from several locations away from the survey walls and boulders where sufficient numbers of geckos could be reliably caught to form groups. Groups were comprised of five (Group A), or six (Groups B, C, D, E), individuals of each species, with only one group held at a time.

Geckos were kept in a dedicated facility at the research base and housed individually in small (210 mm x 150 mm x 95 mm), clear plastic containers with tight fitting net covers. Unglazed ceramic tile formed the substrate of the housing with another raised piece of tile forming a refuge in one half of the enclosure. Geckos experienced natural light cycles with ambient temperature and humidity ranging between 24 ˚C – 28 ˚C and 70% – 87%, respectively. Water was provided *ad libitum* and live invertebrate food items such as moths, termites, spiders, and instar crickets collected from field sites were offered every other day. Uneaten prey was removed from enclosures after one day.

Diurnal refuge choice trials procedure**-** The methodology for experimental trials of refuge selection was adapted from several studies involving the Velvet Gecko *Oedura lesueurii* (Duméril & Bibron, 1836; Schlesinger & Shine 1994; Downes & Shine 1998; Pike *et al*. 2010b).Trials took place in large (620 mm x 390 mm x 410 mm), clear plastic containers with a secure, well ventilated lid and substrate of unglazed ceramic tile. During the day, trial containers were set up providing two refugia of differing character at opposite ends of the container. Refugia characteristics simulated variation in thermal and perceived safety qualities that have shown to elicit refugia preference choice in other geckos (see Downes & Shine 1998). All refugia were constructed in identical fashion using ceramic tiles with small squares of tile as spacers. The five trial conditions tested were as follows:

- Vertical vs. horizontal. One vertical refuge constructed with two ceramic tiles (165 mm x 330 mm x 3 mm) separated by 6 mm. One horizontal refuge (165 mm x 330 mm x 3 mm) raised 6 mm from substrate. Both refugia were open on three sides.
- Large vs. small. Two horizontal refugia, one full size (165 mm x 330 mm x 3 mm) and one half-sized (165 mm x 165 mm X 3 mm), both raised 6 mm and with a single opening (165 mm)
- Narrow vs. wide. Two horizontal refugia (165 mm x 330 mm x 3 mm) one raised 6 mm from the substrate, the other 30 mm. Both refugia had single openings of 165 mm.
- Heated vs. unheated. Two horizontal refugia (165 mm x 330 mm x 3 mm) raised 6 mm and open on one side only. A 5 watt heat mat affixed to the underside of the top of one refuge was turned on for the period 18.00 in the evening until 10.00 the following morning, elevating the temperature of the refuge to a consistent 30˚C - 31˚C. Unheated refugia remained between 26.8˚C - 28˚C.
- Scent of potential competitor vs. unscented. Two horizontal, large, refugia (165 mm x 330 mm x 3 mm) raised 6 mm and open on one side. One side of the trial container and associated refuge were allowed to be utilised by an individual gecko for a minimum of seven daylight hours. Geckos were then switched to containers previously occupied by the opposing species and allowed to select either the used or the unused refugia during the nocturnal activity period.

Geckos were introduced to individual trial containers between 18:00 and 19:30 each evening. After being placed in the centre of the trial container with minimal handling, geckos were allowed to explore their surroundings during the night. Final diurnal refuge selection was recorded between 10:00 and 11:00 the following morning, at which time the geckos were returned to their individual housing containers. All refugia and trial containers were thoroughly soaked, scrubbed, and allowed to air dry prior to being set up for the following trial. Geckos were tested with a different treatment each night. Individuals were returned to their location of capture after the completion of all treatments. The procedure was then repeated with the subsequent groups.

Data analysis- A confidence level of 95% (p - value <0.05) was used to infer any significant statistical association. Non-parametric tests were used to analyse data that did not meet assumptions of normality and homogeneity of variance. Analysis of data was performed using SPSS (v.18).

Results

Focused surveys: Geckos and coastal walls – The distance of walls from a building lit with artificial lighting are shown in Table 1. Stonehaven was in closest proximity (6 m), whilst the derelict wall was furthest away from a lit building (32 m). *Phyllodactylus pulcher* encounters were 6.7 times more frequent than *H. mabouia* along the four coastal walls surveyed, with median *P. pulcher* density (0.06 geckos/m^2) significantly greater than *H. mabouia* density (0.01 geckos/m^2) (Wilcoxon Signed Ranks test, $Z = -3.52$, $P < 0.001$). By contrast, *Hemidactylus mabouia* occurred at a significantly higher mean density (0.05/m^2 ± StDev 0.005) than *P. pulcher* (0.01/m^2 ± StDev 0.005) on the resort boulders (Two sample *t*- test, $t = 10.3$, df = 6, $P < 0.001$) (Table 1).

The highest density of *H. mabouia* recorded from a wall in the current study (0.03 geckos/m^2, Stonehaven) was only comparable to the lowest densities recorded by Howard *et al.* (2001) for the species from buildings on Anguilla (0.04 geckos/m^2). On buildings in Curaçao, Hughes (2015) recorded a higher average density of *H. mabouia* (0.16 geckos/m^2) than the average density observed on coastal walls of Barbados (0.01 ± 0.01 geckos/m^2). Conversely, the average density of *P. pulcher* on the coastal walls (0.79 ± 0.06 geckos/m^2) was greater than the average density of *P. martini* on buildings in Curaçao (0.02 geckos/m^2) (Hughes *et al*. 2015).

There was a statistically significant difference in the frequency of large, medium and small crevices on the survey walls as determined by a Kruskal-Wallis test for independent samples, ($H(2) = 62.3$, $p = <0.001$). Post hoc pairwise comparison indicated that small crevices with openings < 20 mm were significantly ($p = <0.001$) more frequent (5.34/m^2 ± StDev 3.64) on the survey walls than medium (1.94/ m^2 ± StDev 2.02) and large crevices (0.340/ m^2 ± StDev 0.635). Medium sized crevices were significantly ($p = <0.001$) more frequent than large crevices. The individual boulders bordering the resort lawns provided refuge only underneath the boulders themselves.

Diurnal refuge choice results - All geckos made a selection in the diurnal refuge experiments in all 58 trials (Fig. 2). There was no evidence for an association between refuge selection and sex for either species (Chi squared test, *P. pulcher*, $\chi2 = 1.54$, df = 1, $p = 0.214$; *H. mabouia*, $\chi2 = 2.07$, df = 1, $p = 0.150$), therefore observed responses from both sexes were combined in the following analyses.

Phyllodactylus pulcher were selective in four of the five trial conditions, displaying statistically significant preference for narrow rather than wide crevices ($\chi^2 = 5.827$, df = 1, $p = 0.01$); horizontal rather than vertical crevices ($\chi^2 = 4.173$, df = 1, $p = 0.04$); warmer rather than cool refuges ($\chi^2 = 7.758$, df = 1, $p = 0.005$), and for refuges previously occupied by *H. mabouia* ($\chi^2 = 15.206$, df = 1, $p = <0.001$). No preference in crevice size (i.e. Large versus Small) was evident ($\chi^2 = 0.310$, df = 1, $p = 0.57$) (Fig. 1).

Hemidactylus mabouia exhibited selection in three of the five trials, with statistical evidence for preference for narrow crevices ($\chi^2 = 7.758$, df = 1, $P = 0.005$); warmer rather than cool refuges ($\chi^2 = 7.758$, df = 1, $P = 0.005$); and refuges previously occupied by *P. pulcher* ($\chi^2 = 4.172$, df = 1, $P = 0.04$). No preference in crevice orientation was exhibited ($\chi^2 = 0.310$, df = 1, $P = 0.57$), or crevice size ($\chi^2 = 0.862$, df = 1, $P = 0.35$) (Fig. 1).

Discussion

The results of our gecko survey on unlit coastal walls show a marked contrast to previously published patterns of displacement of native gecko species following the introduction of *Hemidactylus* spp. The most pertinent comparison to make is with the *H. mabouia* invasion on Curaçao (Hughes *et al.* 2015). On Barbados the observed densities of *P. pulcher* and *H. mabouia* on coastal walls were virtually a reversal of the density relationship observed between *H. mabouia* and *P. martini* on buildings in Curaçao. Although our survey was limited to unlit coastal edge walls, the comparison to the Curaçao data suggests that *H. mabouia* has not achieved the same numerical dominance over the native gecko in the coastal cliff habitats where *P. pulcher* still remains (Williams *et al*. 2015). By contrast, native *P. martini* did not outnumber *H. mabouia* at any of the 11 sites in Curaçao where they occurred in sympatry (Hughes *et al.* 2015). It is important to note that rather than present a drastic departure from the species' known natural habitat, the location and characteristics of the coastal walls surveyed may have potentially acted to augment the adjacent natural cliff edge habitat of *P. pulcher* (Williams *et al*. 2015) with increased protection from predators, abundance of small crevices, egg deposition sites, enhanced foraging opportunities, and favourable thermal properties. Although *P. pulcher* occurs at higher densities on these walls than in other habitats previously surveyed (Williams 2014), further data are required to determine how the coastal walls may be of benefit to the species. Hughes *et al*. (2015) also found that *P. martini* remained most abundant on structures closest to natural forest habitat, including an unlit wall.

Our survey highlighted a marked separation in gecko habitat use in the grounds of The Crane Resort, with *H. mabouia* predominantly using the individual boulders bordering the lawn area that separates the North and South walls where *P. pulcher* is most abundant. Of note was the fact that the coastal walls provided much opportunity for gecko diurnal refuge, in the form of a high frequency of crevices of various sized openings. Conversely, the only refuge provided by the boulders was underneath the boulders themselves. Because both species were utilising microhabitats offering very different resources for diurnal refuge, we investigated if differences in selection preference for diurnal refuge may explain this observed niche separation between the two species.

Diurnal refuge selection- Several studies have demonstrated that gekkonid lizards are highly selective in regards to the attributes of their diurnal retreat sites (Schlesinger & Shine 1994; Downes & Shine 1998; Shah *et al.* 2004). In our experimental trials, *P. pulcher* and *H. mabouia* also exhibited non-random preference choices for retreat site based on evaluation of criteria such as crevice height, orientation, thermal properties, and previous occupancy by a potential competitor. Furthermore, *H. mabouia* and *P. pulcher* had the same preference in regard to three of the five refuge characteristics trialled, suggesting potential for considerable niche overlap and contest for preferred refugia in the wild. Two of these three preferences shared by *H mabouia* and *P. pulcher*, narrow refugia and warmer refugia, have obvious benefits for fitness.

Selection for narrow refugia is common across taxa as a means to limit vulnerability to predators (Schlesinger & Shine 1994), and our results are consistent with those from trials with other saxicolous gecko species (Schlesinger & Shine 1994; Doughty & Shine 1995; Shah *et al.* 2004). Preference for warmer refugia was also expected considering the importance of thermoregulation to key physiological and behavioral processes in ectotherms. Selection of diurnal retreat site is one mechanism by which rock dwelling nocturnal lizards can thermoregulate and maintain optimum temperatures (Downes & Shine 1998; Schlesinger & Shine 1994; Shah *et al*. 2004; Kearney & Predavec 2004).

Our result showing that both *P. pulcher* and *H. mabouia* have preference (78% of all subjects) for refugia previously occupied by the other species was less expected. Chemoreception in squamates has an important role in identification of conspecifics and subsequent social behavior responses (i.e., mate selection, kin recognition, and territorial behavior) (Cooper & Pèrez-Mellado 2002; Regaldo 2003; Pernetta *et al.*2009; Mason & Parker 2010). It has also been shown that gecko habitat use can be mediated through chemical signals, as demonstrated by avoidance of refuges bearing only the scent of potential predators (Dial *et al.* 1989; Downes & Shine 1998; Shah *et al.* 2004; Webb *et al*. 2010a) and socially dominant conspecifics (Kondo *et al*. 2007). Our results however suggest a direct attraction response to chemical cues laid down by a potential competitor, which is counter-intuitive to the notion that failure to discriminate conspecific from heterospecific pheromones, and mediate behavior accordingly, has the potential to result in interspecific fighting, and interfere with courtship and mating, all of which are likely to have associated costs to fitness (Cooper & Vitt 1987; Cooper & Pèrez-Mellado 2002). We speculate that there are three possible explanations for this response. Firstly, neither *P. pulcher* nor *H. mabouia* was able to detect chemical exudes from each other, in which case refuge selection was based on an unforeseen artifact in the experimental procedure. This is unlikely considering that geckos are known to be highly specialised in olfactory chemoreception (Schwenk 1993). Second, both species could detect the recent presence of another individual but could not distinguish cues as being from another species. The ability to discriminate and respond to cues from heterospecifics has been demonstrated in geckos. When housed in enclosures previously occupied, and thus scented by invasive *H. frenatus* males, the unisexual Mourning Gecko (*Lepidodactylus lugubris*) required more time for egg development and laying than geckos housed in enclosures previously occupied by another *L. lugubris* (Brown *et al.* 2002). Lastly, both species could distinguish the recent presence of the other but have a diminished response since fitness costs associated with avoidance behaviour (i.e., exposure to predators) are judged to outweigh those of any potential interaction with the other gecko species. This outcome draws parallels with the threat sensitivity hypothesis, where in the absence of other cues, individuals should show stronger responses to chemical cues associated with dangerous predators, but should show weaker responses to cues from less threatening species (Webb *et al.* 2010b). If chemosensory recognition of congeners was influencing selection for previously occupied refugia, this could indicate that there was perceived safety associated with the conditioned refuge in an otherwise novel and unfamiliar environment. A similar outcome has been observed in laboratory trials where garter snakes of the genus *Thamnophis* trailed the immediately preceding snake, regardless of species in a Y-maze experiment (Heller & Halpern 1981). Similarity in the chemical constituents of scent profiles between reptile species may explain these results (Mason & Parker 2010; Khannoon 2012), and identification with common compounds in species' scents may have driven refuge choice in the present study.

Phyllodactylus pulcher and *H. mabouia* differed in their response to refugia orientation, with *P. pulcher* displaying preference for horizontal (n = 20) rather than vertical (n = 9) refugia. No clear preference was shown by *H. maboui*, although more (n = 16) selected vertical refugia than horizontal (n = 13). This lack of preference by *H. mabouia* could reflect a greater ability to cling to vertical surfaces (owing to differences in toe morphology), as befitting an edificarian generalist. The preference of *P. pulcher* for horizontal refugia may therefore be due to specialisation to a more ground dwelling, saxicolous lifestyle in its natural cliff habitat (Williams *et al*. 2015).

The general overlap in refuge preference displayed between *P. pulcher* and *H. mabouia* in our experimental trials, and the tendency for both species to actively select for refugia previously occupied by a potential competitor, do not explain the niche separation observed in our survey of man-made coastal features. The most likely explanation for the observed disparity in habitat use between the species is therefore a competitive advantage of *P. pulcher* in exploitative contest for a particular resource synonymous with the coastal walls, or, that as yet unidentified structural and microclimate properties of the walls themselves are favourable to *P. pulcher* whilst excluding *H. mabouia*. Further investigation is required to distinguish which of these mechanisms best explains the pattern of habitat use observed. We propose that further investigation qualifying correlates between properties of coastal walls and gecko use could lead to interesting possibilities for the preservation and creation of similar structures to enhance habitat for *P. pulcher* (and congeners on other islands), and also as a means of mitigation against habitat loss and displacement by *H. mabouia*.

Conflict of Interest: The authors declare that they have no conflict of interest.

All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted

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References

Adolph SC (1990). Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. *Ecology* **71**, 315–27

Allen EK, Avilés Rodríguez KJ, Eifler DA, Powell R (2015). Social and environmental factors influence microhabitat selection in the Brown speckled sphaero, *Sphaerodactylus notatus* (Squamata: *Sphaerodactylidae*). *Journal of Herpetology* **49**, 165–169

Bomford M, Kraus F, Barry SC, Lawrence E (2008). Predicting establishment success for alien reptiles and amphibians: A role for climate matching. *Biological Invasions* **11**, 713–724

Brown SG, Lebrun R, Yamasaki J, Ishii-Thoene D (2002). Indirect competition between a resident unisexual and an invading bisexual gecko. *Behavior* **139**, 1161–73

Case TJ, Bolger DT (1992). The role of introduced species in shaping the distribution and abundance of island reptiles. *Evolutionary Ecology* **5**, 272–290

Case TJ, Bolger DT, Petren K (1994). Invasions and competitive displacement among House Geckos in the tropical Pacific. *Ecology* **75**, 464–477

Cole NC, Harris S (2011). Environmentally-induced shifts in behavior intensify indirect competition by an invasive gecko in Mauritius. *Biological Invasions* **13**, 63–75.

Cole NC, Jones CG, Harris S (2005). The need for enemy-free space: The impact of an invasive gecko on island endemics. *Biological Conservation* **125**, 467–474.

Cooper WE, Pèrez -Mellado V (2002). Pheromonal discriminations of sex, reproductive condition, and species by the lacertid lizard *Podarcis hispanica*. *Journal of Experimental Zoology* **292**, 523–527

Cooper WE, Vitt LJ (1987). Ethological isolation, sexual behavior and pheromones in the *fasciatus* species group of the lizard genus *Eumeces. Ethology* **75**, 328–336.

Dial BE, Weldon PJ, Curtis B (1989). Chemosensory identification of snake predators (*Phyllorhynchus decurtatus*) by Banded Geckos (*Coleonyx variegatus*). *Journal of Herpetology* **23**, 224–229

Diaz JA (1994). Ecological correlates of the thermal quality of an ectotherm's habitat: A comparison between two lizard populations. *Functional Ecology* **11**, 79–89

Doughty P, Shine R (1995). Life in two dimensions: Natural history of the southern Leaf-Tailed Gecko, *Phyllurus platurus*. *Herpetologica* **51**, 193–201

Downes S, Shine R (1998). Heat, safety or solitude? Using habitat selection experiments to identify a lizard's priorities. *Animal Behavior* **55**, 1387–96

Grant C (1959). Herpetology of Barbados, B.W.I. *Herpetologica* **15**, 97 –101

Heller S, Halpern M (1981). Laboratory observations on conspecific and congeneric scent trailing in garter snakes (*Thamnophis*). *Behavioral and Neural Biology* **33**, 372–377

Henderson RW, Breuil M (2012). Lesser Antilles, pp. 148–159. In: Powell R, Henderson RW, eds. Island lists of West Indian amphibians and reptiles. *Bulletin of the Florida Museum of Natural History* **51**, 85–166

Henderson RW, Powell R (2001). Responses by the West Indian herpetofauna to human-influenced resources. *Caribbean Journal of Science* **37**, 41–54

Hoskin CJ (2011). The invasion and potential impact of the Asian House Gecko (*Hemidactylus frenatus*) in Australia. *Austral Ecology* **36**, 240–51

Howard KG, Parmerlee JS, Powell R (2001). Natural history of the edificarian geckos *Hemidactylus mabouia, Thecadactylus rapicauda,* and *Sphaerodactylus sputator* on Anguilla. *Caribbean Journal of Science* **37**, 285–288

Huey RB (1982). Temperature, physiology, and the ecology of reptiles. *Physiology C: Physiological Ecology* **12**, 25–91.

Huey RB (1991). Physiological consequences of habitat selection. *The American Naturalist* **137**, 91–115

Hughes DF, Meshaka WE, van Buurt G (2015). The Superior colonizing gecko *Hemidactylus mabouia* on Curaçao: Conservation implications for the native gecko *Phyllodactylus martini. Journal of Herpetology* **49**, 60–63

Kahnnoon ERR (2012). Secretions of pre-anal glands of house-dwelling geckos (Family: Gekkonidae) contain monoglycerides and 1,3-alkanediol. A comparative chemical ecology study. *Biochemical Systematics and Ecology* **44**, 341–346

Kearney M (2002). Hot rocks and much-too-hot rocks: Seasonal patterns of retreat-site selection by a nocturnal ectotherm. *Journal of Thermal Biology* **27**, 205–218

Kearney M, Predavec M (2000). Do nocturnal ectotherms thermoregulate? A study of the temperate gecko *Christinus marmoratus*. *Ecology* **81**, 2984–2996

Kondo J, Downes SJ, Keogh SJ (2007). Recent physical encounters affect chemically mediated retreat-site selection in a gecko. *Ethology* **113**, 68–75

Mason RT, Parker MR (2010). Social behavior and pheromonal communication in reptiles. *Journal of Comparative Physiology* **19**,729–749

Meshaka WE, JR (2000) Colonization dynamics of two exotic geckos (*Hemidactylus garnotii* and *H. mabouia*) in Everglades National Park. *Journal of Herpetology* **34**, 163–168

Pernetta AP, Reading CJ, Allen JA (2009). Chemoreception and kin discrimination by neonate smooth snakes, *Coronella austriaca. Animal Behavior* **77**, 363–368

Petren K, Bolger DT, Case TJ (1993). Mechanisms in the competitive success of an invading sexual gecko over an asexual native. *Science* **259**, 354–358.

Petren K, and Case TJ (1996). An experimental demonstration of exploitation competition in an ongoing invasion. *Ecology* **77**, 118–132

Petren K, Case TJ (1998). Habitat structure determines competition intensity and invasion success in gecko lizards. *Proceedings of the National Acadamy of Science. U.S.A*. **95**, 11739–11744

Pike DA, Croak BM, Webb JK, Shine R (2010). Context-dependent avoidance of predatory centipedes by nocturnal geckos (*Oedura lesueurii*) *Behavior* **147**, 397–412

Powell R, Henderson RW, Farmer MC, Breuil M, Echternacht AC, van Buurt G, Romagosa CM, Perry G (2011). Introduced amphibians and reptiles in the greater Caribbean: Patterns and conservation implications. *Conservation of Caribbean Island Herpetofaunas* **1**, 63–144

Regaldo R (2003). Roles of visual, acoustic, and chemical signals in social interactions of the Tropical House Gecko (*Hemidactylus mabouia*) *Caribbean Journal of Science* **39**, 307–320

Rocha CFD, Anjos LA, Bergallo HG (2011). Conquering Brazil: The invasion by the exotic gekkonid lizard *Hemidactylus mabouia* (Squamata) in Brazilian natural environments. *Zoologia* **28**, 747–754

Rodder D, Sole M, Bohme W (2008). Predicting the potential distribution of two alien invasive House Geckos (*Gekkonidae: Hemidactylus frenatus, Hemidactylus mabouia*). *North-Western Journal of Zoology* **4**, 236–246

Schlesinger CA, Shine R (1994). Selection of diurnal retreat sites by the nocturnal gekkonid lizard *Oedura lesueurii. Herpetologica* **50**, 156–63.

Schwenk K (1993). Are geckos olfactory specialists? *Journal of Zoology* **229**, 289–302

Shah B, Shine R, Hudson S, Kearney M (2004). Experimental analysis of retreat-site selection by Thick-Tailed Geckos *Nephrurus milii*. *Austral Ecology* **29**, 547–552

Short KH, Petren K (2012). Rapid species displacement during the invasion of Florida by the Tropical House Gecko *Hemidactylus mabouia. Biological Invasions* **14**, 1177-1186.

Singh S, Smyth AK, Blomberg SP (2002). Thermal ecology and structural habitat use of two sympatric lizards (*Carlia vivax* and *Lygisaurus foliorum*) in subtropical Australia. *Austral Ecology* **27**, 616–623

Webb JK, Pike DA, Shine R (2010a). Olfactory recognition of predators by nocturnal lizards: Safety outweighs thermal benefits. *Behavioral Ecology* **21**, 72–77

Webb JK, Weiguo DU, Pike DA, Shine R (2010b). Generalization of predator recognition: Velvet Geckos display anti-predator behaviors in response to chemicals from non-dangerous elapid snakes. *Current Zoology* **56**, 337−342

Webb JK, Shine R (1988). Using thermal ecology to predict retreat site selection by an endangered snake species*. Biological Conservation* **86**, 233–242

Williams RJ (2014). Ecology of the endemic Barbados Leaf-Toed Gecko (*Phyllodactylus pulcher*) and the competitive interaction with the non-native Tropical House Gecko (*Hemidactylus mabouia*): Implications for conservation. MRes thesis, University of Brighton, Brighton.

Williams RJ, Horrocks J, Pernetta AP (2015). Natural history, distribution, and conservation status of the Barbados Leaf-Toed Gecko*, Phyllodactylus pulcher* Gray, 1828 (Squamata, Gekkonidae). *Herpetology Notes* **8,** 197–204

Table 1 Summary of proximity to nearest lighted building, gecko encounters, and gecko densities of four coastal walls and boulders bordering lawns of The Crane Resort, St Philip. Numbers of surveys undertaken at each location are in parenthesis. Mean values displayed ± standard deviation.

Location	**Distance to nearest lighted building (m)**	**$\bar{x}$ *P. pulcher* seen**	**$\bar{x}$ *H. mabouia* seen**	**Surface area surveyed (m^2)**	**$\bar{x}$ *P. pulcher* density (m^2)**	**$\bar{x}$ *H. mabouia* density (m^2)**
Derelict wall (6)	32	2.5 ± 2.1	1.5 ± 2.3	94	0.027 ± 0.02	0.016 ± 0.02
North lawn wall (5)	10	5.2 ± 1.4	1.6 ± 1.1	160	0.033 ± 0.00	0.010 ± 0.00
South lawn wall (8)	18	12.3 ± 1.7	0.5 ± 0.7	110	0.112 ± 0.01	0.005 ± 0.00
Stonehaven wall (2)	6	11 ± 0.0	1.5 ± 0.5	50	0.220 ± 0.00	0.030 ± 0.01
Boulders (4)	10	1.75 ± 0.9	8.7± 0.9	154	0.011 ± 0.00	0.056 ± 0.00

Table 2 Summary of sex ratio and body size of both gecko species used in controlled refuge selection trials. Mean values displayed ± standard deviation.

Species	**Sex ratio (Male:Female)**	**Mean body size**
Phyllodactylus pulcher	13:16	52.9 ± 6.1
Hemidactylus mabouia	15:14	55.8 ± 3.3

Figure legends

Fig. 1 Habitat at The Crane Resort on the seaward side cliff edge of the north wall **A**; landward side of the south wall, **B**; and boulders bordering the lawn, **C**. **D**, Habitat on seaward side of coastal wall at Stonehaven residence.


A
B
C
D

Fig. 2 Refugia selection of *P. pulcher* and *H. mabouia* under controlled conditions. Dashed horizontal line at n = 14.5 shows the expected frequency if no selection was apparent.