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Habitat use by an endemic and a non-native gecko: natural habitat provides a last refuge for the Barbados Leaf-Toed gecko

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ABSTRACT

Island endemic reptiles face many threats that potentially have a negative effect on their conservation status, such as habitat loss, interactions with introduced predators and competitors, and stochastic environmental events. Since confirmation of the continued existence of the Barbados Leaf Toed gecko (*Phyllodactylus pulcher*) on the island of Barbados, West Indies, efforts have been made to increase ecological knowledge of the gecko in order to inform conservation direction and safeguard this critically endangered endemic species. The present study is the first to determine the microhabitat use of *P. pulcher* and that of the non-native gecko *Hemidactylus mabouia* on Barbados, and makes comparison to patterns of displacement of native geckos following *Hemidactylus* spp. invasions seen elsewhere. Factor Analyses of gecko locations and habitat data collected during night-time surveys indicated a strong non-random selection by *P. pulcher* for structurally diverse, rock habitat with an abundance of natural crevices. Where *H. mabouia* is present in natural habitat along the Barbados coast, the species also selected for exposed rocky habitat, albeit to a significantly lesser degree than did *P. pulcher*. Measures of body condition suggest the non-native gecko is less able to exploit such habitats and that its ability to thrive on Barbados is due to utilisation of a broader niche as befitting a habitat “generalist”, rather than competitive displacement of the native gecko from cliff side habitat. Our findings highlight the importance for protection of the remaining natural cliff side habitat and promotion of biosecurity on Barbados as being key to the survival of *P. pulcher*.

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Introduction

Predation from introduced mammalian predators, such as the Asian mongoose (*Herpestes javanicus*), rats (*Rattus* spp.), and cats (*Felis catus*) is undoubtedly the major cause of population declines of many endemic island reptile species [1]. However, there is also growing evidence that competitive interactions between non-native and native reptile species can significantly affect abundance, distribution, and community structure [2–6]. Yet, unlike predation, there are few documented cases where competition has been implicated as the causal mechanism threatening the extinction of reptile species in particular [but see 6,7].

Interspecific competition occurs when ecologically similar species overlap in their utilisation of food, space, or time niches [8]. Interactions caused by this overlap are generally categorised as either direct interference, with one species aggressively displacing the other from a shared resource, or indirect, such as exploitative competition, where the ability of a competitor to acquire a key resource prevents or reduces the other species from obtaining the same resource [9]. The outcomes of conflict arising from such overlap are often asymmetrical, most

demonstrably in relation to body size [8,9], which in time can lead to niche segregation, character displacement, exclusion of inferior competitors from a particular niche, and potentially, extinction [8–12].

Lizards have long been an important model species for research on the occurrence of competition in nature and investigations into its role in shaping ecological communities [10,13–15]. Furthermore, the incidence of introductions of non-native lizard species to island ecosystems has provided opportunities for researchers to observe the mechanisms of competition underlying successful colonization events [2,7,16,17].

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 [18–20], particularly in urban habitats [21,22]. On the islands of Curaçao and Bonaire in the southern Caribbean, the relatively rapid displacement of the Dutch Leaf-Toed gecko (*Phyllodactylus martini*) from otherwise occupied buildings, to structures nearer the forest, has been observed following the introduction of *H. mabouia* to the islands in the late 1980's [23,24]. *Hemidactylus mabouia* is well established in the wider Caribbean

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[25], and earliest reports of the species being present on Barbados, where it is ubiquitous on and in buildings (RW, pers obs), date back to the 1700's [26]. In light of large-scale patterns of negative impacts on native geckos, the long-established presence of *H. mabouia* on Barbados may well have contributed to the displacement, and thus documented scarcity of, the ecologically and morphologically similar Barbados Leaf-Toed gecko (*Phyllodactylus pulcher*) from suitable habitat on the mainland [27].

Endemic to the island of Barbados, *P. pulcher* is unique amongst the region's reptile fauna as being the only species of the genus described from the Lesser Antilles [28]. Rediscovered in 2011, only recently has detailed information on the natural history and limited range of the Barbados Leaf-Toed gecko been published [29]. Owing to its scarcity and restricted range the species now has an IUCN classification of Critically Endangered [30].

Experimental trials testing the diurnal refuge preference of both *P. pulcher* and *H. mabouia*, have shown considerable overlap in refuge preference, and a tendency for both species to actively select for refugia conditioned with scent from the potential competitor, suggesting there may be considerable niche overlap and contest for preferred refugia in the wild [31]. Furthermore, niche separation has been observed in surveys of anthropogenic features in coastal cliff habitats, where in contrast to patterns of displacement of native species by *H. mabouia* seen elsewhere, *P. pulcher* appears more abundant than the non-native on coastal cliff edge walls [31].

Established theory on competition posits that competition is expected to decrease over time as species coevolve or disappear from areas of sympatry by local extirpation [4,14]. Any competitive interaction between *H. mabouia* and *P. pulcher* may therefore have been mediated by time and be reflected in current variations in species distribution, abundance, individual fitness, and microhabitat use [8–10,14].

The aims of the present study were (a) to provide an assessment of the primary patterns of microhabitat use by *P. pulcher* throughout its range and (b) to quantify and compare the spatial patterns of microhabitat use and individual fitness between *P. pulcher* and a potential competitor, *H. mabouia*.

Methods

Study site

This study was undertaken in Barbados, the most easterly of the Caribbean islands (13°N, 59°W). With a total area of 431 km², the coral limestone island rises to a maximum elevation of only 340 m, creating largely xeric conditions [32]. Natural vegetation on Barbados has become reduced to around 2% of its historical

extent prior to European settlement (ca. 800 ha remain), with indigenous flora largely restricted to small patches of woodland, gullies and coastal fringes [33].

Survey method

Fieldwork was conducted in coastal habitat found within 100 m of the waterline in the six island parishes on the south, east, and northern coastline of Barbados. This survey area ensured coverage of habitat seen to be used by *P. pulcher* during targeted surveys of 2012 and 2013 [29]. The west and southwest coasts were not surveyed due to the habitat within 100 m of the waterline being either intertidal or highly urbanized (Figure 1). Urban environments account for 74% of the land use within 100 m of this leeward shore, as opposed to 15% on the east and south east coasts [34].

We used ArcMap ver.10.1 (Environmental Systems Research Institute) to create potential survey points at 25 m spacing in a grid formation throughout the study area. 2249 points were generated by this grid, from which one hundred points were then randomly

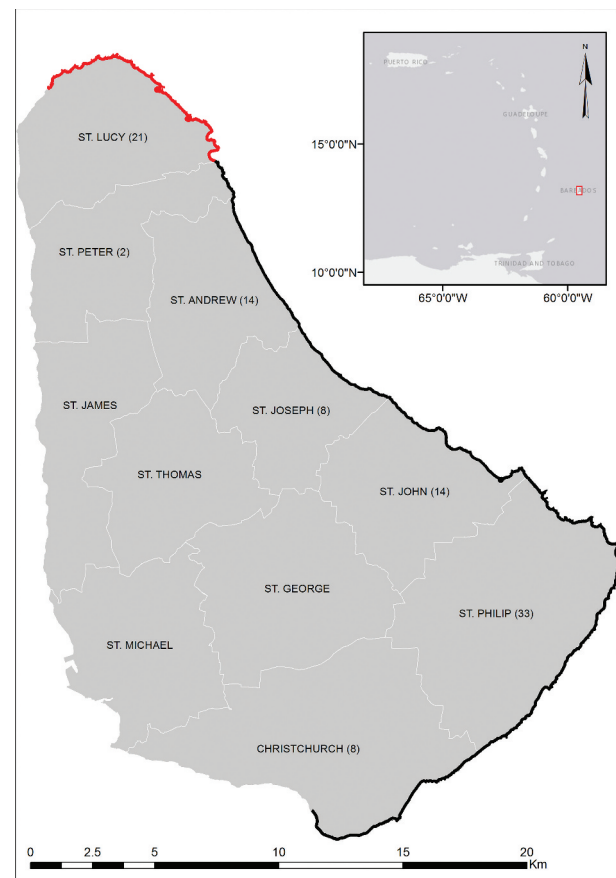


Figure 1. Barbados, its parish boundaries, and extent of the 2014 gecko study area (100 m from waterline shown in black and red). The red area indicates portion of survey area that was also the focus of a separate analysis comparing gecko habitat use on the North coast to elsewhere. Distribution of the number of points surveyed within the study area for each parish is given in parenthesis.

selected (in ArcMap) to form the basis of the habitat use survey. This sample area represented 5% of the potential study area generated. To ensure equal survey effort throughout the study area, we stratified the distribution of the 100 points to be surveyed (during the random selection) by the total number of potential survey points falling within each of the six parishes that comprised the survey area (Figure 1).

All 100 points were surveyed over the course of a four-week period, beginning 4 April 2014. Points were navigated to within ± 1 metre accuracy using hand held GPS (Garmin *etrex 10™*), and upon approach an assessment was made in consideration of safety and accessibility to carry out the survey at that location. In incidences where predetermined points were deemed unsafe or inaccessible, an adjacent (accessible/safe) point on the grid was surveyed instead.

Point surveys entailed the night-time visual search for both gecko species within a 12.5 m radius around each point. We judged this search area to be of a practical size to carry out a comprehensive search for geckos during 30 min of search effort (3×10 surveyor mins), based on previous experience surveying for the species on Barbados [29]. We undertook searches between the hours of 18:00 and 23:30, to coincide with the period of peak activity for both gecko species [29,35]. The search team consisted of three experienced surveyors who searched for a period of 10 minutes using head torches (white light). Surveyors searched immediate habitat by scanning trees, the ground, rock faces, and likely gecko refuges such as crevices, loose rocks, logs, and debris piles. We took care to spread the search effort within the search area, and to not degrade habitat quality by undue disturbance of habitat features and careless interference of potential refugia [36].

We recorded locations (at point of first sighting) of all geckos seen during the 10 min search, and opportunistically en-route to and from survey points, on hand held GPS. In addition, we temporarily marked locations with biodegradable flagging tape. All observed geckos were identified to species by pattern (*P. pulcher* has a distinctive lateral stripe running from the snout through the centre of the eye, and a bolder, more symmetrical dorsal pattern than *H. mabouia*), body shape, and posture. When possible, we caught geckos (by hand) for morphological analysis, placing them in individual breathable cloth bags prior to processing. Following gecko searches, we recorded data on microhabitat variables within a 1 m radius of the first observed location of all gecko encounters, as outlined in Table 1. To establish whether gecko habitat use was non-random, we collected the same microhabitat data from random control points that simulated gecko locations [after 37]. Since habitat structure (e.g. vertical surfaces, raised perches) is important to many geckos, we generated these simulated locations by

releasing a half inflated, untied balloon from the point of every real gecko sighting, taking the point of first impact of the deflated balloon as the location for the control point. This ensured we accounted for structural features in the collection of habitat data. If we didn't find any geckos during the initial search, we took habitat data from two random points generated from the survey point itself (established when optimal GPS proximity to 0 metres was achieved) using the method above. This method therefore resulted in a minimum of two locations where we recorded habitat data around each survey point. Additional habitat data were recorded from point of first sighting of geckos we observed opportunistically, and geckos seen during a separate mark-recapture study undertaken at St Phillip (also in April 2014) [29].

Habitat use data analysis

We explored microhabitat use data by factor analysis to reduce the habitat variables into a smaller number of components that may describe underlying patterns. Data were initially transformed prior to analysis using $\text{Log}_{10} + 1$ for continuous variables and arcsine-square root for percentages. We considered Factors with eigen values ≥ 1 as significant and used them in further analysis. Within factors, we considered variables with loadings greater than 0.4 as important [37,38]. We then applied analysis of variance (ANOVA) to determine whether factor scores varied between gecko microhabitats and microhabitat data from random points (simulated locations), followed by Post-hoc analysis using Fisher's LSD to identify where significant variations lay between groups. We ran two separate factor analyses to ask specific questions about the gecko habitat use data set. The first run was primarily concerned with the entire data derived from the random point survey to determine if geckos were using microhabitat non-randomly, and if variation in habitat use existed between the two species. In the second analysis, we investigated whether *P. pulcher* is potentially being excluded from suitable habitat in the north of the island. We based this investigation on observations of a contrast between the frequency of encounters of *P. pulcher* and *H. mabouia* on the north and south coast, despite similar appearances in macrohabitat at both locations [39]. In this latter analysis, we compared habitat use data collected from *P. pulcher* locations throughout the entire study area to data from random points and *H. mabouia* locations along the coast at North Point, St Lucy (Figure 1). In order to compare the availability and character of naturally formed refuges between these locations in greater detail, we included observed frequencies of various sized crevices (see Table 1), under-rock refuges, and holes/burrows as habitat variables in this second analysis. Due to sand substrate being recorded at only one point, and

Table 1. Summary of habitat variables recorded during random surveys, methods of recording, and equipment used.

Variable	Categories	Method	Equipment
Substrate type	Soil, sand, rock, artificial	Visual assessment of % substrate type within 1 m radius, e.g. soil, sand, rock	N/A
Ground cover	Leaf litter, vegetation < 1 m, artificial, bare soil, bare rock	Visual assessment of % type covering substrate	N/A
Frequency and type of refugia	Under rock, crevice, hole, artificial	Visual count of all refugia classified into types	N/A
Substrate temperature		Recorded at point of gecko sighting/capture/random point	thermohygrometer (TFA™) accurate to ±1°C
Distance to nearest refuge		Measured distance (mm) from point of sighting to nearest feature for retreat that offers full concealment	Measuring tape
Frequency of crevice sizes	(small = < 20 mm, medium 20–40 mm, large > 40 mm)	Visual count of all crevices offering full concealment, classified by size of opening	Diameter gauges in the form of acetate tubes
Canopy cover		Visual assessment of % canopy cover of vegetation > 1 m high affecting 1 m radius of the point	N/A
Perch type and orientation		Visual assessment of substrate on which gecko was seen and vertical/horizontal positioning of the gecko	N/A

an absence of anthropogenic features at these survey locations, associated habitat variables were omitted from the analysis.

Morphometric data analysis

We collected morphological data from geckos encountered during the survey as part of a wider study [39], and used the data to generate body condition scores for all captured animals. Geckos were caught by hand and weighed to 0.5 g using a 60 g Pesola spring balance. Snout-to-vent length (SVL) was measured to 0.5 mm using digital Vernier callipers. All geckos were returned to the point of capture following sampling. We tested for variation in body size (SVL) between species using students *t*-test (with data having met assumptions for parametric tests), and made additional comparison (*z* test) to data reported from other *H. mabouia* populations in the literature [35,40,41]. We tested for variance (ANOVA) in body condition between *P. pulcher* and *H. mabouia*. using an index of body condition created from the residuals of linear regression on log transformed SVL and mass data of individuals [42]

Results

Habitat data were collected from a total of 85 *P. pulcher* locations, 69 *H. mabouia* locations, and 184 simulated control locations This included data obtained from the point surveys, locations of geckos seen opportunistically and en route to/from survey points, and data obtained during mark-recapture sessions (see methods) (Table 2).

Factor analysis 1: microhabitat selection

Factor analysis of 18 habitat variables recorded at gecko locations ($n = 154$) and simulated locations ($n = 184$) produced five significant factors,

cumulatively accounting for 66% of the variance within the data (Table 3). Factor 1 was defined by positive loading values for Percentage of substrate that was soil, Percentage of vegetation ground cover, Perches on ground vegetation, and Increasing distance to the nearest refuge. There were negative loading values for Percentage of rock substrate, Percentage of exposed bare rock, Number of naturally formed crevices, and Vertical orientation on perches. The Factor 1 axis therefore represents the gradient from sites of grassland habitat (highly loading factor scores), where the only available perch is ground vegetation and refuges are sparse (such habitat often provided no refuge within the survey radius); to structurally diverse habitat of exposed rock with naturally formed crevices (negative factor scores; Figure 2(a)). The second factor was defined by positive values for Percentage of sand substrate, Percentage leaf litter cover, Canopy cover, and the Number of refuges other than crevices. These positive scores denote littoral woodland habitat and dune habitat of tall vegetation, where holes and burrows are abundant in the soft substrate. Negative values were for Percentage of artificial substrate and Percentage of ground covered by anthropogenic materials – indicative of habitat features such as walls of residential properties, synthetic debris, or

Table 2. Summary of number of locations at which habitat use data was collected, attributable to species, control points, and survey method. Opportunistic sightings refer to geckos encountered en route to and from random survey points.

Point type	No. recorded during random survey	No. recorded opportunistically during the random survey	No. recorded during mark-recapture survey	Total
<i>P. pulcher</i>	15	18	52	85
<i>H. mabouia</i>	20	12	37	69
Simulated	175	0	9	184
Total	210	30	98	338

Table 3. Factor analysis loadings, eigenvalues, and percentage of variation explained by five significant factors resulting from factor analysis of habitat use variables collected from *P. pulcher* ($n = 85$) and *H. mabouia* ($n = 69$) sightings, and random points ($n = 184$) during surveys of the Barbados coast. Shaded columns indicate factors where significant variation in scores occurred between gecko species and random points. Factor loadings with absolute values ≥ 0.4 (indicated by an asterisk) are considered important [Field, 2000; in Pernetta et al. [37]].

Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5
Substrate - % Soil	0.866*	0.069	0.192	0.113	0.064
Substrate- % Sand	0.073	0.420*	-0.235	-0.492*	-0.033
Substrate- % Rock	-0.858*	-0.151	0.093	0.116	0.039
Substrate- % anthropogenic	0.103	-0.408*	-0.834*	0.073	-0.173
% Vegetation ground cover	0.767*	-0.291	0.355	0.005	-0.225
% Leaf litter ground cover	0.043	0.679*	-0.253	0.484*	0.025
% Exposed bare soil/sand	0.157	0.356	-0.204	-0.523*	0.524*
% Exposed bare rock	-0.846*	-0.146	0.107	0.017	0.116
% Anthropogenic ground cover	0.072	-0.412*	-0.821*	0.083	-0.174
Canopy cover	0.169	0.675*	-0.228	0.446*	0.071
Distance to nearest refuge	0.566*	-0.173	0.069	-0.010	-0.049
Nearest refuge type	0.610*	-0.198	-0.013	0.067	0.481*
Substrate temperature	-0.188	-0.158	-0.073	0.503*	0.410*
Perch type	0.838*	-0.055	-0.094	0.097	0.023
Gecko orientation on perch	-0.509*	-0.214	-0.126	-0.003	0.148
No. Refuges other than crevices	-0.323	0.604*	-0.170	-0.114	-0.366
No. Natural crevices	-0.694*	-0.110	0.056	0.012	0.140
No. anthropogenic crevices	0.136	-0.025	-0.518*	-0.234	0.238
Eigenvalue	5.160	2.211	2.100	1.322	1.045
% Variance Explained	0.287	0.123	0.117	0.073	0.058

construction materials. These anthropogenic features were also the only variables of significance in Factor 3, again with negative loadings, but including Frequency of artificially formed crevices (Figure 2(b)). Factor 4 had positive loading variables attributable to woodland habitat, such as Amount of leaf litter, Percentage of canopy cover and Substrate temperature. Negative loadings were with Percentage of sand substrate and amount of exposed bare soil/sand, both characteristics associated with dunal habitat. The fifth factor defined by positive loadings for Percentage of substrate that was bare soil/sand, Type of nearest refuge (in this case holes/burrows), and Substrate temperature (Table 3).

ANOVA, applied to individual scores of the factor analysis to test for differences in habitat selection between both gecko species, and for comparison with random points, showed significant variation in mean factor scores between *P. pulcher*, *H. mabouia*, and random points, for Factors 1 ($F_{2, 337} = 128.72$, $P < 0.0001$), 2 ($F_{2, 337} = 4.38$, $P = 0.01$), and 3 ($F_{2, 337} = 3.54$, $P = 0.03$). There was no significant variation in mean factor scores between groups for Factors 4

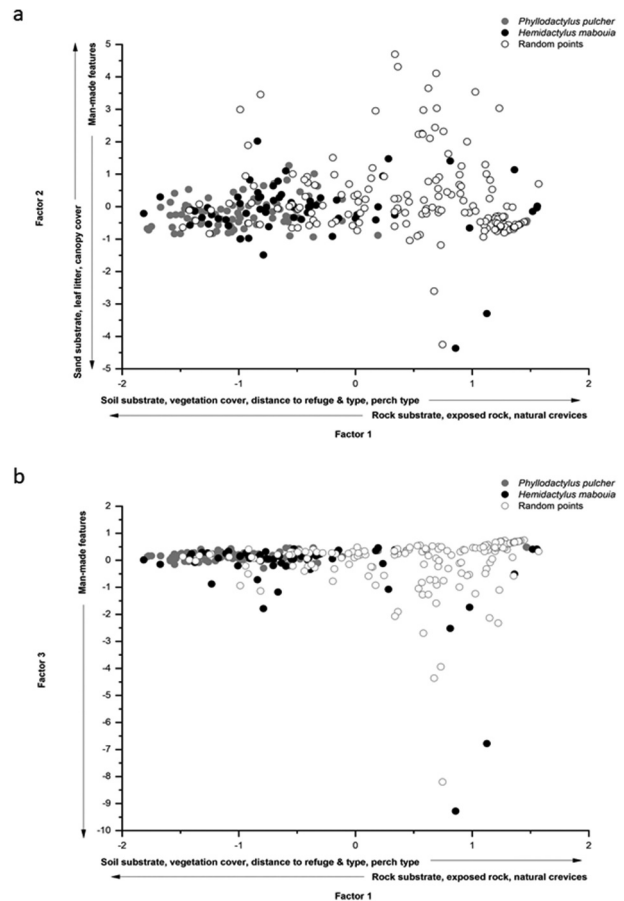


Figure 2. Relationship between factor scores of *P. pulcher* (grey circles; $n = 87$), *H. mabouia* (black circles; $n = 69$), and random habitat points (open circles; $n = 184$) for (a) Factors 1 and 2 and (b) Factors 1 and 3.

($F_{2, 337} = 0.03$, $P = 0.975$) and 5 ($F_{2, 337} = 0.32$, $P = 0.728$). Fisher's LSD post-hoc test indicated where the significant variations lay between groups in regard to Factors 1, 2 and 3 (Table 4).

There was significant variance in mean scores between both gecko species, and with random points, with regard to Factor 1. Although both gecko species scored negatively (*P. pulcher*, $-0.9441 \pm \text{S.E.} = 0.56$; *H. mabouia*, $-0.345 \pm \text{S.E.} = 0.895$), suggesting active selection by geckos for habitats with greater amounts of exposed rock and naturally formed crevices, the significant variation between species scores indicated that this preference was more strongly exhibited by *P. pulcher*. Random points differed significantly from both gecko species in regard to mean scores for Factor 2 (random points, $0.1455 \pm \text{S.E.} = 1.1862$; *P. pulcher*, $-0.1945 \pm \text{S.E.} = 0.4595$; *H. mabouia*, $-0.143 \pm \text{S.E.} = 0.897$), suggesting that woodland habitat and tall scrub habitat featured more significantly in the random samples than at gecko locations. The negative mean score of *H. mabouia* for Factor 3 ($-0.269 \pm \text{S.E.} = 1.490$) was significantly different to the mean scores of both *P. pulcher* ($0.1433 \pm \text{S.E.} = 0.1664$) and random points ($0.0331 \pm \text{S.E.} = 0.9881$), indicating that

Table 4. Results of Fisher's LSD post hoc test identifying variation in mean scores for factors 1, 2, and 3 between groups ($P = P. pulcher$, $H = H. mabouia$, $R =$ random points). Asterisk denotes significant variation in mean scores between groups.

Factor 1					
Grouping	Difference of means	SE of difference	95% CI	T-value	Adjusted P-value
P – H*	0.599	0.122	0.359, 0.838	4.92	<0.001
R – P*	1.521	0.0983	1.3268, 1.7133	15.47	<0.001
H – R*	0.921	0.107	0.712, 1.131	8.64	<0.001
Factor 2					
Grouping	Difference of means	SE of difference	95% CI	T-value	Adjusted P-value
P – H	0.052	0.160	–0.262, 0.366	0.32	0.751
R – P*	0.342	0.129	0.087, 0.593	2.64	0.012
H – R*	0.288	0.143	0.013, 0.563	2.06	0.041
Factor 3					
Grouping	Difference of means	SE of difference	95% CI	T-value	Adjusted P-value
P – H*	–0.412	0.164	–0.727, –0.097	–2.58	0.014
R – P	–0.110	0.129	–0.364, 0.144	–0.85	0.393
H – R*	0.302	0.143	0.026, 0.578	2.15	0.032

more *H. mabouia* were seen in association with anthropogenic features during the surveys (Figure 2(b)).

Factor analysis 2: Phyllodactylus pulcher microhabitat use vs. available microhabitat and Hemidactylus mabouia habitat use at North Point

Seven factors of significance were produced from analysis of the 17 variables; which cumulatively explained 73% of the variation in the data (Table 5). Results from an ANOVA applied to test variance in mean scores between gecko locations and random points for each of these factors indicated significant variation between groups for Factors 1, 4, and 5 (Factor 1, $F_{2, 125} = 23.25$, $P < 0.0001$; Factor 4, $F_{2, 125} = 3.19$, $P = 0.04$; Factor 5, $F_{2, 125} = 4.96$, $P = 0.008$). Factor 1 alone accounted for 24% of the variance in the data. There was no significant variation in mean factor scores between the three groups for Factor 2 ($F_{2, 125} = 1.76$, $P = 0.176$), Factor 3 ($F_{2, 125} = 1.04$, $P = 0.356$), Factor 6 ($F_{2, 125} = 1.42$, $P = 0.247$), or Factor 7 ($F_{2, 125} = 2.74$, $P = 0.068$).

Fisher's LSD post hoc test showed mean scores differed significantly for all three groups with regard to

Factor 1 (Table 6). Only *P. pulcher* locations had a positive mean score (mean (\pm S.E.) = 0.353 ± 0.691), which suggests the species was using habitat with higher Percentage of rock substrate, Exposed rock, and greater Frequency of small crevices than was observed at *H. mabouia* locations and at random points recorded at North Point. The negative mean scores for Factor 1 of *H. mabouia* and random points from North Point (*H. mabouia*, $-0.309 \pm$ S.E. = 1.00; random points, $0.925 \pm$ S.E. = 1.198) suggest that these sites were of increased Soil substrate, Vegetation ground cover, and Perch types other than rock (vegetation, bare soil/sand). However, the significant difference between the two mean scores suggests *H. mabouia* were selecting habitat at a lesser extreme on this gradient than was observed at random points (Figure 3(a)). The positive mean score of *H. mabouia* ($0.350 \pm$ S.E. = 1.280) differed significantly from the negative mean score of *P. pulcher* ($-0.158 \pm$ S.E. = 0.928) with regard to Factor 4 (Table 6). A positive mean score for this factor suggests *H. mabouia* at North Point were using habitat that

Table 5. Factor analysis loadings, eigenvalues, and percentage of variation explained by seven significant factors resulting from factor analysis of habitat use variables collected from all *P. pulcher* ($n = 84$) in natural habitat, and *H. mabouia* locations ($n = 18$) and random points ($n = 26$) from the northern tip of the Barbados coast (North point). Shaded columns indicate factors where significant variation in scores occurred between gecko species and random points. Factor loadings with absolute values ≥ 0.4 (indicated by an asterisk) are considered important [Field, 2000; in Pernetta et al. [37]].

Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7
Substrate – % Soil	–0.845*	0.287	–0.035	0.082	0.206	0.038	0.158
Substrate- % Rock	0.815*	–0.406*	0.131	–0.043	–0.171	–0.003	–0.110
% Vegetation ground cover	–0.805*	–0.174	0.292	0.049	–0.240	0.213	0.124
% Leaf litter ground cover	–0.037	0.341	0.075	–0.731*	0.355	–0.127	0.065
% Exposed bare soil/sand	–0.263	0.342	–0.371	0.344	0.168	–0.485*	–0.111
% Exposed bare rock	0.844*	–0.168	–0.142	0.190	0.055	0.064	–0.102
Canopy cover	0.112	–0.329	–0.073	–0.031	0.082	–0.381	0.634*
No. Hole/burrows	–0.260	–0.046	–0.144	0.450*	0.362	–0.233	–0.255
No. Under rock refuge	0.080	0.477*	–0.516*	0.100	–0.458*	0.225	0.082
No. Large crevices	0.173	0.425*	0.540*	0.171	–0.411*	–0.066	0.042
No. Medium crevices	0.398	0.609*	0.379	0.333	0.083	0.038	0.032
No. Small crevices	0.530*	0.385	0.295	0.240	0.213	0.026	0.291
Distance to nearest refuge	–0.334	–0.274	0.048	0.245	–0.507*	–0.426*	–0.085
Nearest refuge type	–0.129	–0.312	0.663*	0.187	0.340	0.000	–0.232
Substrate temperature	0.129	–0.223	–0.371	0.390	0.289	0.483*	0.114
Perch type	–0.699*	–0.140	0.176	0.185	–0.010	0.282	0.235
Orientation on perch	0.299	–0.190	0.026	0.186	0.030	–0.138	0.520*
Eigenvalues	4.088	1.854	1.693	1.425	1.312	1.073	1.041
% Variance Explained	0.240	0.109	0.100	0.084	0.077	0.063	0.061

Table 6. Factor analysis 3: results of Fisher's LSD *post hoc* test identifying variation in mean scores for factors 1, 4, and 5 between groups ($P = P. pulcher$, $H = H. mabouia$ at North point, $R =$ random points at North point). Asterisk denotes significant variation in mean scores between groups.

		Factor 1				
Grouping	Difference of means	SE of difference	95% CI	T-value	Adjusted P-value	
P – North Point H*	-0.662	0.224	-1.104, -0.219	-2.96	<0.001	
P – North Point R*	-1.278	0.193	-1.660, -0.896	-6.62	<0.001	
North Point R – North Point H*	-0.616	0.264	-1.139, -0.094	-2.34	0.024	
		Factor 4				
Grouping	Difference of means	SE of difference	95% CI	T-value	Adjusted P-value	
P – North Point H*	0.508	0.255	0.003, 1.013	1.99	0.049	
P – North Point R	0.425	0.221	-0.011, 0.862	1.93	0.056	
North Point R – North Point H	-0.083	0.301	-0.679, 0.514	-0.27	0.785	
		Factor 5				
Grouping	Difference of means	SE of difference	95% CI	T-value	Adjusted P-value	
P – North Point H*	0.701	0.252	0.202, 1.200	2.78	0.006	
P – North Point R	-0.192	0.218	-0.623, 0.239	-0.88	0.380	
North Point R – North Point H*	-0.893	0.297	-1.481, -0.304	-3.00	0.003	

had a higher Frequency of holes and burrows, whilst the negative score of *P. pulcher* locations indicated use of habitat with more Leaf litter (Figure 3(b)). *Hemidactylus mabouia* from North Point also scored a positive mean for Factor 5 ($0.641 \pm \text{S.E.} = 0.916$) which was negatively correlated with the Number of large crevices and under rock refuges, as well as the Distance to nearest refuge (Figure 3(b,c)). This score was significantly different to the negative mean scores for both *P. pulcher* ($-0.060 \pm \text{S.E.} = 1.008$) and random points ($-0.251 \pm \text{S.E.} = 0.872$) (Table 6).

Body size and condition

Mean adult body size (SVL) was similar (t-test, $t_{84} = -1.30$, $P = 0.19$) for both *P. pulcher* ($53.5 \pm \text{S.E.} = 0.6$, $n = 55$) and *H. mabouia* ($54.7 \pm \text{S.E.} = 0.6$, $n = 34$). However, mean adult SVL of *H. mabouia* was significantly shorter (Z test, $z = -17.23$, $P = < 0.0001$) than that recorded for the species on Anguilla, Lesser Antilles, ($59.2 \pm \text{S.E.} = 1.4$, $n = 17$) by Howard et al. [40], in Florida ($z = -5.33$, $P = < 0.0001$ ($58.7 \pm \text{S.E.} = 4.3$, $n = 20$) by Meshaka [35], and in Brazil ($z = -152.63$, $P < 0.0001$) ($56.6 \pm \text{S.E.} = 0.07$; $n = 176$) by Anjos and Rocha [41]. When comparing body mass vs length ratios, there were no significant differences between sex for *P. pulcher* (ANCOVA) ($F_1 = 1.67$, $P = 0.20$) or *H. mabouia* ($F_1 = 1.06$, $P = 0.31$). There was significant variation in body condition between the two gecko species in coastal habitat of Barbados, with *P. pulcher* individuals having greater body mass for a given SVL than *H. mabouia* (ANCOVA $F_1 = 38.86$, $P = < 0.0001$) (Figure 4).

Discussion

Through our analysis of the microhabitat variables recorded during the random point surveys, we were able to identify important habitat features conducive to the persistence of *P. pulcher* in its current range. Our

results provide evidence for a strong non-random selection by *P. pulcher* for structurally diverse, rock habitat with an abundance of natural crevices. *Phyllodactylus pulcher* has also been found to occur at high densities in certain anthropogenic habitats; particularly unlit coastal walls made of coral stone and concrete block adjacent to cliff side habitat [31]. The microhabitat selection demonstrated by *P. pulcher* in our results supports the theory that these high densities occur because some walls serve to augment microhabitat features of the connecting cliffs that are important to the species (i.e. increased number of small crevices) [31]. Other Phyllodactylids are known to be habitat specialists, well-adapted to their natural environment [43], and our results, in addition to aspects of *P. pulcher* morphology (i.e. enlarged terminal lamellae, slightly dorsoventrally compressed body and head, large eye diameter to head size, and laterally placed nostrils), strengthen the likelihood of *P. pulcher* being a specialist of cliff side habitat [29]. Our results also lend support to the theory that availability of suitable habitat for *P. pulcher* is inextricably linked to the geological heterogeneity characterising the south, east and north coasts of Barbados, thus limiting the species wider distribution on the island [29].

Overall, our results demonstrate that although there was significant difference in microhabitat use by *P. pulcher* and *H. mabouia*, habitat use was still more similar between species than compared to random control points. We detailed the occurrence of *H. mabouia* in natural habitat along the Barbados coast, with factor analysis revealing that this species also selected for exposed rocky habitat, albeit to a significantly lesser degree than did *P. pulcher*. In one area in particular, the northern cliffs of St Lucy, *H. mabouia* appeared to be the more abundant species in this habitat, with very few *P. pulcher* being found in this area (this study $n = 1$; $n = 5$ Williams (2013) unpublished data). The ability of invasive *Hemidactylus* spp. to displace and cause local

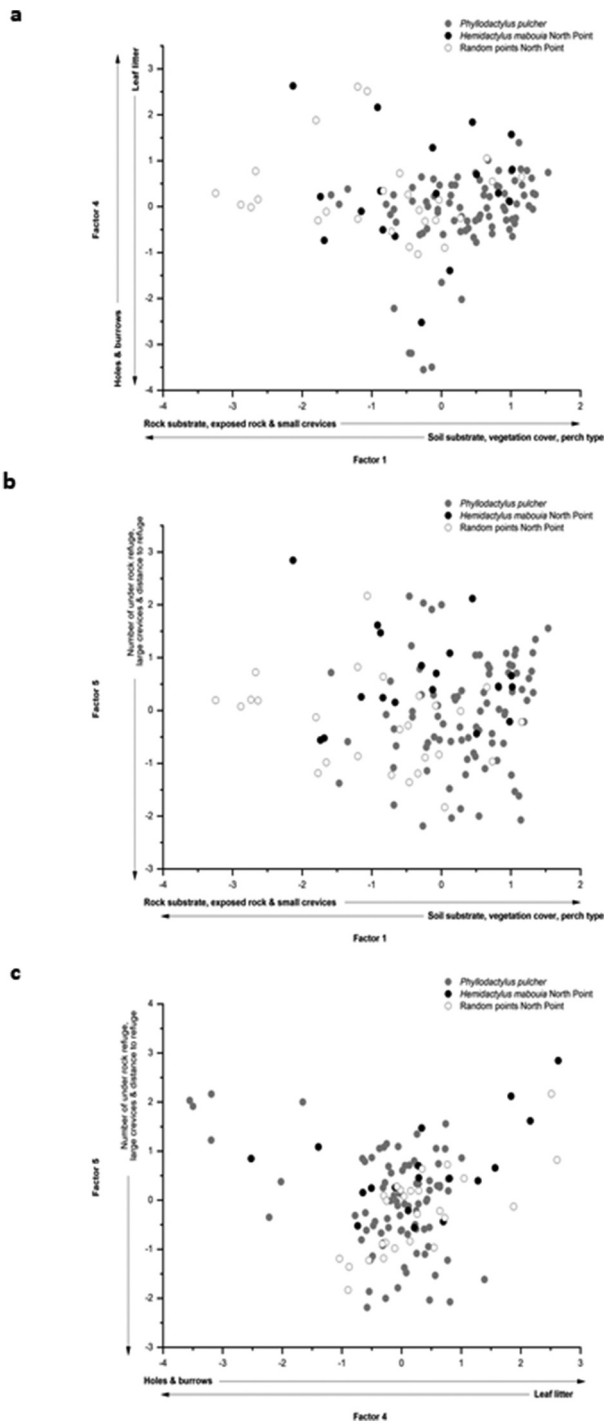


Figure 3. Relationship between factor scores of *P. pulcher* (grey circles; $n = 84$), North point *H. mabouia* (black circles; $n = 18$), and random North point (open circles; $n = 26$) points for (a) Factors 1 and 4, (b) Factors 1 and 5, and (c) Factors 4 and 5.

extirpation of native gecko species has received much attention, most notably in respect to urban and altered environments [3–5,22,44]. In the Pacific Islands, where displacement of native geckos from many urban areas has been complete, the same has not been so pronounced in natural, forested areas of the same islands [5]. The colonisation of *Hemidactylus* spp. into natural habitats is however less well understood [20,21 but see 6]. On Isla de Utila, in the Honduran Bay Islands,

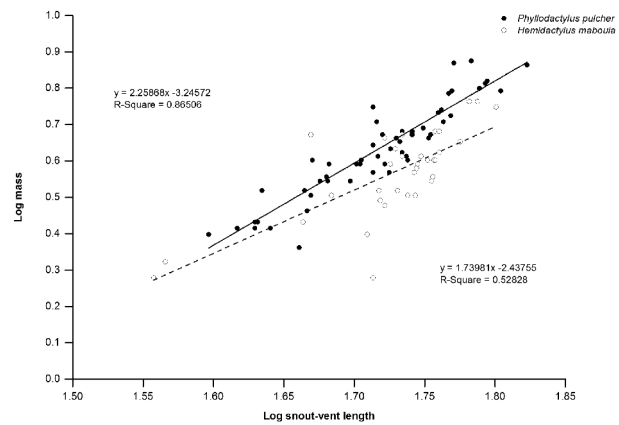


Figure 4. Relationship between snout-vent length and mass of adult *P. pulcher* and *H. mabouia* caught in natural habitat on the island of Barbados.

introduced *Hemidactylus frenatus* are more commonly found than the native *Phyllodactylus palmeus* in natural forested areas of the east coast [45]. However, there is no indication given as to how prevalent the native species was in this habitat prior to the invasion of *H. frenatus*. Similarly, with no records of the historical range of *P. pulcher*, it is not known if this species was ever abundant on the northern cliffs (or inland habitats) of Barbados. Characteristics of the rocky habitat used by *P. pulcher* throughout its range, namely high frequencies of small and large crevices, under-rock refuges and increased leaf litter, were not features of the habitat used by *H. mabouia* at North Point (St. Lucy), or of microhabitat sampled at random points in that vicinity. Comparison of current *P. pulcher* habitat use with the available habitat does therefore suggest that the northern cliffs may not be entirely suitable for *P. pulcher*, regardless of the presence of *H. mabouia*. However, some degree of caution is needed in this interpretation considering the length of time *H. mabouia* and non-native predators have been resident on Barbados. *Hemidactylus mabouia* has been present since as early as 1700, and introduction of cane toads and mongoose likely occurred in the 1800s [26]. The currently observed range, and specific habitat use of *P. pulcher*, may therefore be a manifestation of a reduced fundamental niche in a long-term response to combined pressures of predation and competition from introduced species [8,10,11,46,47].

The average size (SVL) of *H. mabouia* on Barbados was significantly less than that recorded for the species in Anguilla [40], Florida [35], and south-eastern Brazil [41]. This discrepancy in size could be largely due to the Anguilla and Florida data being derived exclusively from individuals collected from around lit buildings, a prey rich habitat that the species is well known to exploit [35,44]. Anjos & Rocha [41] did however collect geckos from more natural habitat. Furthermore, we found *H. mabouia* individuals to have lower body

condition than *P. pulcher* in the habitats surveyed on Barbados. Body condition is a direct indicator of individual fitness, representative of the animal's ability to obtain and synthesise food resources [48]. These results therefore suggest that *H. mabouia* may be less efficient in exploiting prey resources in natural coastal habitat on Barbados than *P. pulcher*. This disparity is not surprising considering the affinities of *H. mabouia* to an edificarian lifestyle and as a human commensal [40], as opposed to the apparent specialist cliff side niche of *P. pulcher*. Specifically, differences in foraging tactics appropriate to each species' preferred habitat could well be the underlying cause for variation in body condition observed during this study. *Hemidactylus* spp. are typically ambush predators of invertebrate prey who benefit from structurally simple habitats and aggregations of winged insects around artificial light sources [4,49–51]. Conversely, *P. pulcher* may have a more active approach to encountering dispersed insect prey amongst structurally diverse rock habitat (RW pers obs). In experimental trials, the competitive advantage of *H. frenatus* over native *Lepidodactylus lugubris* in exploitative contest for insect prey was shown to diminish in structurally complex environments, and when prey is dispersed rather than clumped around light sources [4,5]. The smaller body size of *H. mabouia* in natural habitats of Barbados compared to those found in urban areas elsewhere [24,35,40] also supports the theory that the species is foraging less efficiently in natural habitats surveyed during this study. If this is correct, and the potential impacts of the invasive species on the native gecko are alleviated as a result, then the ability of *H. mabouia* to thrive on Barbados may be more a reflection of the successful exploitation of vacant niches (less rocky sites, buildings further from coastal edges) as befitting a habitat "generalist", rather than competitive displacement of the native gecko.

The structurally diverse coastal cliffs with abundant natural crevices on the south east coast of Barbados are the preferred habitat for *P. pulcher*. Much of the habitat currently used by the gecko lies within the Coastal Landscape Protection Zone (OS3), where all new developments must be set back 30 m from the cliff edge (Physical Development Plan 2017 Draft). Although primarily to protect developments from erosion-prone cliff edges, salt spray and storms, the designation is also to ensure access for public use remains along these coastal cliffs. The obligatory set-back should reduce direct impacts of tourism infrastructure on *P. pulcher* habitat. However, new developments will increase the level of artificial light at night preferred by foraging *H. mabouia*, as well as bringing more predatory species like rats and cats into areas utilised by *P. pulcher*. Although *P. pulcher* is found on Barbados' only offshore island, the islet is small (0.15 ha) and only a small part of it provides suitable gecko habitat (Williams, 2012 unpublished data). Options to conserve preferred *P. pulcher* habitat, if

pressure on its natural range from coastal development increases, may therefore be limited to the provision of coastal wall structures that augment key *P. pulcher* resources [31] and/or construction of a biosecure area on the mainland; an expensive and high-maintenance option.

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