Introduction

The development and application of appropriate conservation measures for threatened species depend heavily on an assessment of current population status, to include information about ecology, natural history, and geographic distribution (IUCN, 2001). For species where such information is lacking or entirely absent, collection of data is essential for creation of species action plans and for the procurement and appropriate application of conservation resources (Traill et al., 2007).

Phyllodactylus pulcher Gray, 1828, commonly known as the Barbados leaf-toed gecko, is a nocturnal lizard endemic to the Lesser Antillean island of Barbados (area 431 km²; Fig. 1). It was the first species of the genus to be described and is the only Phyllodactylid known from the Lesser Antilles (Dixon, 1962; Dixon and Huey, 1970; Schwartz, 1979).

Since the original description of Phyllodactylus pulcher was validated by Dixon (1962), only limited supposition of the species’ ecology as a nocturnal, arboreal, and insectivorous predator has been published (Dixon, 1962; Schwartz and Henderson, 1991; Powell and Henderson, 2005). This lack of information, for such a unique species amongst the Lesser Antillean reptile fauna, appears perhaps to be largely due to a historical scarcity of the species on Barbados. Schwartz (1979) alluded to the possible extinction of the gecko, stating that “Phyllodactylus pulcher … occurs (or occurred) on the Lesser Antillean island of Barbados. I know of no recent specimens of P. pulcher collected on Barbados, and on several visits to Barbados have myself been unsuccessful in securing specimens.” (Schwartz, 1979:419). Several other authors have also reported on the scarcity of P. pulcher and uncertainty
of its conservation status (Corke, 1992; Powell and Henderson, 2005; Weiss and Hedges, 2007). Henderson and Breuil (2012), however, listed the species as present on Barbados, presumably based on the only confirmed sighting from the early 1990s (by J. Horrocks) of two individuals seen in the southeast of the island. Given the uncertainty surrounding the conservation status of the species, the need for a systematic investigation of its range and specific distribution has long been recognised (Corke, 1992; Barbados Government, 2002; Powell and Henderson, 2005), and when confirmed sightings of the gecko were made in October 2011, by Damon Corrie of the Caribbean Herpetological Society, a rapid response to assess the species’ conservation needs was put into action. This article reports on previously unpublished data and natural history observations arising from three *P. pulcher* surveys conducted between 2012 and 2014.

**Material and methods**

**Study area.**—Barbados (Fig. 1) is the most easterly of the Caribbean islands (13°N, 59°W). With a total area of 431 km², the coal limestone island rises to a maximum elevation of only 340 m, creating largely xeric conditions (Corke, 1992). Original vegetation on Barbados has become reduced from close to 100% to around 2% (ca. 800 ha remain) since European settlement, with indigenous flora largely restricted to gullies and coastal fringes (Government of Barbados, 2005).

Surveys.—Three preliminary surveys of the gecko location identified by D. Corrie were undertaken from 30 August–1 September 2012 between 17:00 and 23:00 hrs. Based on gecko activity and habitat use data collected during these initial surveys, intensive gecko presence/absence surveys were subsequently undertaken in September 2013 (14 survey nights) and during March–June 2014 (55 survey nights) to identify the extent of the species range and distribution. Surveys were carried out between 18:00 and 23:00 hrs by a team of up to four surveyors, who walked slowly searching the coastline, slopes, cliff edges, rock faces, and rock outcrops, paying particular attention to narrow, deep crevices and other features likely to provide gecko refugia (overhanging vegetation, recesses, honeycombed boulders, holes, walls). These surveys focused on coastal habitat within 100 m of the waterline on the southern, eastern, and northern coastline of Barbados, to ensure survey coverage of habitat seen to be used by *Phyllodactylus pulcher* during the initial surveys of 2012. They also incorporated adjacent areas and habitat types not previously searched systematically. The west and south west coasts were not surveyed because the habitat was judged unsuitable to the species due to coastal urbanization (Williams, 2014).

**Population size.**—Ten capture-mark-recapture (C-M-R) trials were conducted within a 625-m² area of known gecko habitat over a 4-week period (18 April–15 May 2014). Based on previous search experience, the size and positioning of the 25-m² quadrat (13°10’57.60”N, 59°27’30.55”W) was considered to correspond to the seaward and inland boundaries of typical *Phyllodactylus pulcher* habitat on the cliff edge (Williams, 2014). The quadrat was searched for two man-hours between 18:00 and 23:00 hrs during each trial. Attempts were made to capture by hand all geckos encountered (unless...
previously marked), and captured individuals were retained in soft cloth bags until the end of the search (for a maximum of 1 h). Locations of all gecko captures and sightings were temporarily flagged and then recorded on a hand-held GPS (Garmin eTrex 10; Garmin, Olathe, Kansas, U.S.A.; garmin.com). Morphometric data (see below) were obtained from captured geckos, which were then numbered sequentially prior to release at point of capture. Numbers were painted in a dorsal position above the sacrum using nontoxic nail varnish (Case et al., 1994). The data were subsequently analysed using Begon’s weighted mean estimator of population size. The model assumes that the population was geographically and demographically closed for the duration of the study and all individuals were equally likely to be caught (Daltry et al., 2001). We considered the gecko population within the quadrat effectively geographically closed over the sampling period due to the small size of *P. pulcher* and its limited vagility. No deaths were presumed during the trial period and juvenile geckos were excluded from the estimate thus satisfying the assumption of a demographically closed population. Because previously caught animals can remain at the point of release for some time and become biased to recapture (Daltry et al., 2012) we also excluded geckos caught less than 48 h since previous capture from the estimate.

Morphometric data.—Morphological data were collected from 102 individual geckos (ten in 2012, 14 in 2013, 78 in 2014). Age class was determined by visual assessment of secondary sexual features, with geckos < 45 mm SVL classed as juveniles due to lack of obvious features indicating sexual maturity. Weight was determined to the nearest 0.5 g using a 60-g Pesola spring balance, and snout–vent length (SVL) and tail length (TL), were measured to the nearest 0.5 mm using digital Vernier calipers. Length of regenerated tail (TR) growth following autotomy was also recorded, as the frequency of tail loss within a population can be indicative of the degree of exposure to predatory attacks and agonistic inter- and intraspecific interactions (Bateman and Flemming, 2008).

Diet.—The contents of eight faecal samples collected from adult geckos were examined under a microscope and attempts made to identify prey items.

Results

Distribution.—Based on the results of our surveys, the range of *Phyllodactylus pulcher* extends from the cliffs of the southeast along the windward coast to the northern tip of Barbados (Fig. 1). The species distribution on the east coast appears limited by the transition from coral rock cliff habitat to the sandstones, mudstones, and geological formations of the Scotland District (see Donovan and Harper, 2005), where the species was not recorded.

Population estimate.—A total of 29 individual *Phyllodactylus pulcher* were caught and marked during the trials, including six juveniles that were not included in the final population estimate in order to meet assumptions of a closed population. There were 18 recaptures over the sampling period. Since one of these occurred less than 48 h after the original capture of the gecko, it was also excluded from the calculation of the estimate so as not to violate the assumption of all individuals being equally likely to be caught (Table 1). Calculations using Begon’s weighted mean showed that the estimated population size in the quadrat was 33 ± 8.2 individuals of *P. pulcher*. In relation to the study site, the population estimate equates to a density of 0.05 *P. pulcher* per m².

A major consideration of this population size estimate is the potential for overestimation due to the capture (and remarking) of individuals that may have lost their previous mark during the process of shedding skin. In an effort to minimise the potential for lost markings to affect the estimate, the calculation of Begon’s weighted mean was re-run to include only data from the last five sessions. These sessions included more gecko captures (26 captures, 7 recaptures) than the first five (17 captures, 7 recaptures), and were thus considered likely to provide the more accurate estimate. The reduced data resulted in an estimated population size of 25 ± 10, or 0.04 individuals of *Phyllodactylus pulcher* per m². If the quadrat sampled was representative of the habitat available (0.31 km²) within the currently known range of *P. pulcher* (Fig.1), this density estimate of 0.04 *P. pulcher* per m² may suggest an estimated population of more than 12,000. However, since extrapolation based on a single sampling location would be inappropriate, further sampling of more quadrats within *P. pulcher’s* range is needed in order to refine this estimate.

Habitat use and behaviour.—*Phyllodactylus pulcher* emerge from diurnal refuges in deep rock crevices at dusk, and are most active between 19:00 and 21:00 hrs (Fig. 2). The species is scansorial, and it is found on the cliff edges where it forages for invertebrate prey amongst the rocks, particularly where trailing seaside
yam (Ipomoea pes-caprae) and other vegetation provides cover. The species displays some arboreal tendencies and on three occasions geckos were found on the trunks of large palms (Cocos nucifera) and white cedar (Tabebuia pallida) that were within 5m of the cliff’s edge. No direct social interactions were noted in the field.

Morphology. — Our morphological data on Phyllodactylus pulcher (n = 102) collected during the surveys are the first reported from live specimens. Mean adult SVL was (54.7 ± 6.2 mm) for males, and (53.2 ± 4.2 mm) for females. The maximum SVL length recorded for a live gecko (67.3 mm) is slightly larger, but comparable, to that described from preserved type specimens (62 mm; Dixon, 1962). This places P. pulcher as one of the larger species of leaf-toed geckos in South America and the Antilles (Fig. 3a; Dixon, 1962; Dixon & Huey, 1970). Mean weight of adult males was (3.9 ± 1.6 g), and of females (3.3 ± 1.0 g). Complete tails were only present on five out of 77 adult geckos caught, all five of which were female. The average length of these complete tails was (60.7 ± 6.9 mm). The smallest gecko caught had an SVL of 23 mm and weighed 0.1 g; it was one of several neonates found during the survey of March–May 2014. Both sexes of P. pulcher exhibited postanal pores at the base of the tail corresponding to openings of the cloacal sacs (Kerster and Smith, 1955; López-Victoria et al., 2013) (Fig. 3b, c).

Diet.—Examination of faecal samples provided evidence for predation on spiders, crickets, and the alates of West Indian drywood termites (Cryptotermes brevis). Fragmented wing casings of cockroaches (Periplaneta americana) were also found, and one direct field observation revealed that these geckos prey on even relatively large (~ 55 mm) cockroaches. Housed in temporary captivity as part of research into diurnal

Figure 2. The nocturnal activity of P. pulcher (n = 183), as illustrated by frequency of encounters per time period. Geckos hidden were found immotile under rock refugia.

Table 1. Record of Phylloactylus pulcher captures within a 625-m² quadrat during ten C-M-R trials conducted in 2014.

<table>
<thead>
<tr>
<th>Date</th>
<th>Number of geckos caught</th>
<th>Number of marked geckos caught</th>
<th>Number of marked geckos released</th>
<th>Number of marked geckos at large</th>
<th>Number of marked geckos at large x Number of marked geckos caught</th>
</tr>
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<tr>
<td>18 April</td>
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<td>3</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
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<td>2</td>
<td>5</td>
<td>10</td>
</tr>
<tr>
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<td>5</td>
<td>2</td>
<td>2</td>
<td>7</td>
<td>35</td>
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<tr>
<td>26 April</td>
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<td>0</td>
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<td>9</td>
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<tr>
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<td>2</td>
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<td>104</td>
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<td>3 May</td>
<td>5</td>
<td>4</td>
<td>1</td>
<td>19</td>
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</tr>
<tr>
<td>7 May</td>
<td>6</td>
<td>3</td>
<td>3</td>
<td>20</td>
<td>120</td>
</tr>
<tr>
<td>10 May</td>
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<td>3</td>
<td>0</td>
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</tr>
<tr>
<td>15 May</td>
<td>3</td>
<td>2</td>
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<td>23</td>
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</tr>
<tr>
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<td>43</td>
<td>17</td>
<td>22</td>
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<td>597</td>
</tr>
</tbody>
</table>
Figure 3. Images of Phylodactylus pulcher in life. (a) Complete view of adult (SVL = 56.4 mm). (b) Cloacal region of male showing openings of cloacal sacs. (c) Cloacal region of female. (d) Single egg laid in temporary vivarium. Scale = 10 mm. (e) Hatchling (SVL = 23 mm).
refuge selection (Williams, 2014), geckos readily accepted sphingid moths (*Erinyis ello*), although neither ants nor non-winged termites were accepted.

Reproduction.—No gravid females were observed in surveys undertaken during September 2012 and 2013, but six of 39 females caught during surveys of March-May of 2014 showed signs of advanced egg development. A gravid female taken into short-term captivity during this time deposited a single egg by adhering it to the substrate and partially covering it with fine sand (Fig. 3d); the egg measured 11 mm x 9.5 mm. Intact eggs were also occasionally seen during this survey period, in small rock crevices with openings no wider than 10 mm. In most cases more than one egg was present in a single crevice along with shell fragments of previously hatched eggs, regardless of an abundance of unused and apparently suitable deposition sites close by.

**Discussion**

Primarily scansorial, *Phyllodactylus pulcher* shows preference for structurally diverse, rock habitat with an abundance of natural crevices (Williams, 2014). Such habitat specialisation is known for other *Phyllodactylus* species, and with its enlarged terminal lamellae, dorsoventrally compressed body and head, and laterally placed nostrils, *P. pulcher* fits the morphological profile of a boulder and rock specialist (Dixon & Huey, 1970). On Barbados, this habitat was synonymous with the exposed Middle Coral Rock (MCR) cliffs of the south, east, and north coasts (Fig. 1). Morphological adaptation to this habitat type could explain the apparent absence of *P. pulcher* along a large section of the east coast, where the Tertiary sedimentary rocks of marine origin and siliceous sand soils of the Scotland District configure a very different habitat to the Pleistocene limestone cliffs (Randall, 1970; Donovan and Harper, 2005) and offer little in the way of diurnal refugia (Williams, 2014). Phyllodactylid geckos are also noted as being species largely of arid or semi-arid environments (Dixon, 1962). Therefore, considerable variation in rainfall and evaporation along the coast may also account for the patchy distribution of *P. pulcher*, with the cliff tops of the north and south being drier and of mostly saline and xeric scrubland vegetation, compared to the wetter, central parts of the east and west coast (Randall, 1970).

The nocturnal habits of *Phyllodactylus pulcher* are in keeping with those of other *Phyllodactylus* species (Dixon and Huey, 1970; Huey, 1979; López-Victoria et al., 2013), and this has afforded the exploitation of invertebrate prey resources not readily available to the other native and diurnal species (i.e., Barbados anole, *Anolis extremus* and, historically, Barbados skink, *Alinea lanceolata*).

The high percentage of tail regeneration observed in the adult gecko population (94%) indicates a strong pressure from agonistic interactions and/or predation attempts (Bateman and Flemming, 2009). This high frequency of tail loss is unlikely to be a result of intraspecific aggression, particularly considering the many potential fitness costs associated with autotomy such as reduced locomotor performance, social status, growth, fecundity, and loss of fat reserves (reviewed in Bateman and Fleming, 2009; McElroy and Bergmann, 2013). Captive trials investigating the communication signals involved in gecko social behaviour have shown that tails also have an important role in visual signalling, and that tail loss does not commonly occur as result of interactions with conspecifics (Regalado, 2003). Interspecific aggression between *Phyllodactylus pulcher* and the introduced *Hemidactylus mabouia* is also an unlikely explanation given evidence of significant differences in habitat use, and lack of agonistic behaviour between the two in experimental trials (Williams, 2014). Attempted predation from introduced mammalian predators, and potentially cane toads (*Rhinella marina*), is thus the most plausible explanation for the high levels of tail loss observed. Several species introduced to Barbados since the 17th century (Grant, 1959) do pose a serious risk of predation to *P. pulcher*, which, having historically few natural vertebrate predators, could be considered predator-naive and thus more vulnerable to predation by introduced species (Case and Bolger, 1991). Scolopendrid centipedes (*Scolopendra* spp.) are also likely to prey upon *P. pulcher*, although other gecko species have displayed a mediated behavioural response in the avoidance of potentially fatal encounters with scolopendrid centipedes (Pike et al., 2010). Introduced cats (*Felis catus*) and rats (*Rattus* spp.) have caused catastrophic declines and extinctions of endemic island reptiles (Iverson, 1978; Case and Bolger, 1991; Daltry et al., 2001; Powell and Henderson 2005). The presence of both cats and rats along the coastal cliffs of Barbados (R. Williams, pers. obs.) is therefore a serious threat to *P. pulcher*, where the gecko is likely one of the most accessible vertebrate prey species on the cliff edges, along with the Lesser Antillean whistling frog, *Eleutherodactylus johnstonei*. The global impact of mongoose (*Herpestes javanicus*) introductions on diurnal, terrestrial ground
lizards and snakes has also been devastating (Case and Bolger, 1991), and their introduction to Barbados is likely to have played a significant role in the elimination of Erythrolampus perfuscus and Alinea lanceolata (Powell and Henderson, 2005). However, the continued persistence of P. pulcher despite the long-term presence of mongoose suggests the nocturnal gecko may not be a significant prey item of this diurnal predator. The predatory impact of cane toads on native species is not well studied, and although primarily insectivorous, they are also known to be voracious, opportunistic predators of small vertebrates, including geckos (Grant, 1996). The potential impact of cane toads on P. pulcher, as both a competitor for insect prey and a predator, should therefore not be underestimated. Further work, through trapping and dietary analysis of non-native predators on Barbados, is needed to quantify the impact of predation on P. pulcher.

A clutch size of one single egg as seen in Phyllodactylus pulcher is typical for most species of Phyllodactylus (Dixon and Huey, 1970; López-Victoria et al., 2013). Communal egg-laying is also common (Dixon and Huey, 1970), and observations of multiple eggs and shell fragments in single rock crevices would suggest communal egg-laying is also the habit of P. pulcher. It is not certain if P. pulcher utilises deposition sites on multiple occasions, although López-Victoria et al. (2013) reason that extensive use of deposition sites of optimal conditions (i.e., temperature and humidity), is likely for P. transversalis. Extended reproductive season and multiple clutches are known for several Phyllodactylus species from Mexico, as well as for P. kofordi and P. reissii from Perú (Dixon and Huey, 1970; Goldberg, 2007). Gravid females and neonates of P. pulcher (Fig. 3e) have so far only been observed during surveys of March–May, and further observations are required to determine what the precise period of reproductive activity is for the species.

Data collected during the C-M-R trials allowed a first approximation of the Phyllodactylus pulcher population for a given area of suitable habitat. Comparative population data for other Phyllodactylus species is scarce in the literature and could only be sourced for the Colombian leaf-toed gecko (P. transversalis) on 1.2-km² Malpelo Island (Eastern Tropical Pacific; López-Victoria et al., 2013) and for the Dutch leaf-toed gecko (P. martini) on Curaçao (Hughes et al., 2015). The comparisons are useful in putting the estimated P. pulcher density into some perspective; with average density of P. transversalis (0.12 per m²) being three times that of the estimate for the P. pulcher sample population (0.04 per m²). Furthermore, P. transversalis shares the island with two other lizard species (the dotted galliwasp, Diploglossus millepunctatus, and the anole Anolis agassizi) that occur at similar densities to the gecko (López-Victoria, 2006). The higher density of geckos (and other lizards) on Malpelo Island is most likely due to the island being free from invasive predators and relatively undisturbed by human activity (López-Victoria, 2006; López-Victoria et al., 2013). Conversely, P. pulcher density is twice that recorded for P. martini (0.02 per m²; Hughes, et al., 2015). However, the data collection by Hughes et al. (2015) was focused on a gecko population occupying potentially sub-optimal habitat (buildings), where there is also evidence for significant competition from introduced house geckos (Hemidactylus mabouia).

Further surveys throughout the range of Phylodactylus pulcher are required to obtain estimates of population size for future monitoring. It is important to note that the quality of suitable habitat is likely to be variable across the species range, producing significant localised variation in gecko densities (Williams 2014). Following IUCN Red List categorisation of threat (IUCN, 2001), a proposal for a status of ‘Critically Endangered’ is justifiable based on the current data in relation to criteria pertaining to extent of occurrence (criterion threshold; extent of occurrence estimated to be less than 100 km², current estimated P. pulcher range 0.3 km²), and inferred or projected declines in the size of population, range or quality of habitat.

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References


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