Title: Reassessing a Holocene extinction: multiple lines of evidence do not support the historical presence and recent extirpation of a protected anole on the island of Anguilla

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Abstract

Accurate assessment of historical species ranges is important for conservation science and management. Inaccurate historical species ranges can lead to incorrect assumptions about local extinctions, population trends, and potential sites for reintroductions. Yet, historical knowledge is often lacking for many species. Here, we examine the case of the bearded anole, *Anolis pogus*, which has long believed to have been recently extirpated from the island of Anguilla. We addressed the evidence for the historical presence and recent local extinction of *A. pogus* on Anguilla using species abundance modeling, fossil and extant morphological data, and archival DNA sequencing from museum specimens. We found that although viable habitat remains on Anguilla, it is highly fragmented. We also falsified the prior characterization of two size classes of anoles in Anguilla's fossil deposits as evidence for two species (*A. gingivinus* and *A. pogus*) by comparing with the size distribution of both species on neighboring St. Martin. Instead, our data indicate that fossil deposits on Anguilla likely correspond to males and females of the larger anole species, *A. gingivinus*, with no fossil evidence for *A. pogus*. Finally, we sequenced all known museum specimens of *A. pogus* from Anguilla and demonstrate that these specimens were incorrectly identified. Together, our results show that there is no evidence for the historical presence, and thus no evidence for the local extinction, of *A. pogus* on Anguilla. These data are vital for the appropriate management of this species of conservation concern. Furthermore, our study provides a case study for the critical assessment of historical species ranges and narratives of extinction.

Résumé

Une évaluation précise des aires de répartition historiques des espèces est importante pour la conservation et la gestion des ressources naturelles. Des aires de répartition historiques inexactes des espèces peuvent entraîner à des hypothèses erronées sur les extinctions locales, les tendances démographiques et les sites potentiels de réintroduction. Pourtant, les connaissances historiques font souvent défaut pour de nombreuses espèces. Nous examinons ici le cas de l'anole barbu, *Anolis pogus*, qui a longtemps été considéré comme ayant récemment disparu de l'île d'Anguilla. Nous avons examiné les preuves de la présence historique et de la récente extinction locale d'*A. pogus* à Anguilla en utilisant la modélisation de l'abondance des espèces, des données morphologiques des lézards fossiles et actuels, et le séquençage d'ADN à partir de spécimens de musée. Nous avons constaté que bien qu'un habitat viable subsiste à Anguilla, il est très fragmenté. Nous avons falsifié la caractérisation précédente de deux catégories de tailles d'anoles dans les gisements fossiles d'Anguilla comme preuve de la présence de deux espèces (*A. gingivinus* et *A. pogus*) en comparant avec la distribution de taille des deux espèces sur l'île voisine de Saint-Martin. Nos données indiquent que les gisements fossiles d'Anguilla correspondent probablement aux mâles et aux femelles de la plus grande espèce d'anoles, *A. gingivinus*, sans preuve fossile d'*A. pogus*. Enfin, nous avons séquencé tous les spécimens de musée connus d'*A. pogus* d'Anguilla et démontré que ces spécimens ont été incorrectement identifiés. Dans l'ensemble, nos résultats montrent qu'il n'existe aucune preuve de la présence historique, et donc aucune preuve de l'extinction locale, d'*A. pogus* à Anguilla. Ces données sont essentielles pour la gestion appropriée de cette espèce dont la conservation est préoccupante. En outre, notre étude fournit une étude de cas pour l'évaluation critique des aires de répartition historiques des espèces et des récits d'extinction.

Introduction

Conservation biology is often complicated by a lack of historical baseline knowledge (Bonebrake *et al.*, 2010; McClenachan, Ferretti & Baum, 2012; Böhm *et al.*, 2013). A prevalent issue is the lack of definitive records on a species' historical range, and by inference, where they have since been extirpated (Carlton, 1996; Wingard, Bernhardt & Wachnicka, 2017; Claude *et al.*, 2019). Anthropogenic activity has been responsible for myriad extinctions throughout the Holocene (Diamond *et al.*, 1997; Ceballos *et al.*, 2015); yet, the specific extinction narratives of several taxa are uncertain or controversial. For example, little is known of the historical distributions of declining turtles throughout Thailand (Claude *et al.*, 2019); the existence of and subsequent Holocene extinction of some *Ara* macaws throughout the Caribbean has been questioned (Olson & López, 2008); and molecular evidence suggests that the Barbados racoon was an extirpated introduced species rather than an extinct endemic (Helgen & Wilson, 2003). Accurate assessment of recent local extinctions provides important context for current and future conservation management, and also for our understanding of fundamental questions of biodiversity science.

The Caribbean is a biodiversity hotspot (Smith *et al.*, 2005) and a source of major insights in ecology and evolutionary biology (e.g., Rosen, 1975; Ricklefs & Lovette, 1999; Losos, 2009; Papadopoulou & Knowles, 2015; Pringle *et al.*, 2019). Yet, the long history of anthropogenic interconnectivity between islands and lack of reliable records means that the issue of inaccurate historical ranges and extinction narratives is particularly prevalent in the Caribbean (e.g., Kaiser, 1992, 1997; Helgen *et al.*, 2008; Olson & López, 2008; Camargo, Heyer & de Sá, 2009; Giovas, 2019; Yuan *et al.*, 2022, 2023). This poses a challenge not only for regional conservation management, but also for biodiversity science. On the other hand, the Caribbean also provides a compelling system in which to build case studies for resolving difficult issues of historical range uncertainty, which may be applied broadly to other taxa around the world.

Anolis pogus is a species of conservation concern currently restricted to a single island in the Lesser Antilles: St. Martin (Powell, Henderson & Parmerlee, 2005; Powell *et al.*, 2020). Conservation protections are largely based on the small size of its present range and because the species was thought to have been recently extirpated from the neighboring island of Anguilla (Lazell, 1972; Roughgarden *et al.*, 1989). Like many island systems around the world (Wilmshurst *et al.*, 2014; Graham *et al.*, 2017), the Anguilla Bank Islands (i.e., Anguilla, Saint Martin, Saint Barthélemy, and their satellites) were altered by initial human settlement predating detailed written records (Napolitano *et al.*, 2019). Thus, there is limited information on the historical status of *A. pogus*. Circumstantial evidence for the local extinction of *A. pogus* on Anguilla during the Holocene are based on fossil deposits (Roughgarden *et al.*, 1989; Pregill, Steadman & Watters, 1994; Roughgarden, 1995) and land connectivity across the Anguilla Bank islands during low sea levels (Christman, 1953). However, molecular evidence indicates at least some fossil deposits on Anguilla are singularly *Anolis gingivinus* (Kemp & Hadly, 2016), a widespread species that is extant across the Anguilla Bank Islands. Only two alleged specimens of *A. pogus*, both collected in 1922, have been reported from Anguilla despite extensive surveys. Neither specimen was originally identified as *A. pogus* and both were subsequently re-identified in collection (Lazell, 1972) (S. Kennedy-Gold, personal communication). Some authors have speculated that the species may have also been historically present and subsequently extirpated from the island of St. Barthélemy (Lazell, 1972). However, no fossil or extant records indicate *A. pogus* has any historical presence on Saint Barthélemy (Lazell, 1972). Consequently, the historical presence of *A. pogus* beyond the island of St. Martin remains unclear.

Whether *A. pogus* was extirpated from Anguilla matters not only for conservation assessments and management of the species, but also for our understanding of regional biogeography and the distribution of biodiversity. To address this uncertainty, our study asked three questions. First, do Holocene fossil records reflect two-species anole communities on Anguilla? Second, is there suitable habitat remaining for *A. pogus* on Anguilla and Saint Barthélemy? Third, can we use genetic sequences of historical specimens to confirm the presence of *A. pogus* on Anguilla? We discuss our results clarifying the history of local extinction in *A. pogus* as well as its implications for using integrative datasets to better assess conservation-relevant species histories.

Methods

Assessing fossil evidence of two-species communities

Fossil records of Anguillan anoles come from three archeological sites: Katouche Bay (Roughgarden *et al.*, 1989; Roughgarden, 1995; Kemp & Hadly, 2016), Center Cave, and The Fountain (Pregill *et al.*, 1994). Pregill et al. (1994), argued that the bimodal size distribution of anole fossils found at Center Cave and The Fountain were evidence of a two-species anole community: *A. pogus* and *A. gingivinus*. To confirm this assessment, we compared the size data from Pregill et al. (1994) with both field-collected and museum data from *A. pogus* (43 male; 27 female) and *A. gingivinus* (90 male; 49 female). Field surveys occurred intermittently between 2020 and 2023. Museum specimens were from the collections of the California Academy of Sciences (San Francisco, CA) and the National Museum of Natural History (Washington, DC). All size data was taken as snout-vent length (SVL).

Abundance modeling on Anguilla and Saint Barthélemy

It has been suggested that deforestation may have contributed to the extinction of *A. pogus* on Anguilla (Pregill *et al.*, 1994). The island of Anguilla was largely deforested for charcoal production during WWI (Howard & Kellogg, 1987) and it has been demonstrated that *A. pogus* is more abundant in closed canopy sites on St. Martin (Jesse *et al.*, 2018; Yuan et al. 2024). However, we lack empirical data on the present day habitat suitability of Anguilla. We used the random forest model built from abundance surveys on St. Martin (Yuan et al. 2024) to predict abundance-based habitat suitability on the islands of Anguilla and Saint Barthélemy. These models were fit using 100 survey plots distributed throughout St. Martin and 1 arc-second resolution environmental rasters. As predictor variables, we downloaded the same raster layers as the original model, but for Anguilla and St. Barthélemy. Specifically, these were global canopy cover (Hansen *et al.*, 2013), land use (WorldCover2.1; Zanaga *et al.*, 2022), and elevation (SRTM; Farr & Kobrick, 2000) resampled to 1 arc-second resolution. Analyses were performed in R v4.3.2.

Sequencing historical specimens

Only two *A. pogus* have ever been reported from Anguilla and none from St. Barthélemy. Both specimens were originally collected in 1922 as *A. gingivinus* and subsequently identified as *A. pogus* (Lazell, 1972). We physically examined both specimens, R-16596 and R-16597, from the collections of the Museum of Comparative Zoology (Cambridge, MA) to resolve this discrepancy in their identification. We then performed WGS on excised liver samples. As the original preservation conditions of these specimens is unknown, we performed a 100°C heat treatment for 20 minutes to break potential cross-links (Hykin, Bi & McGuire, 2015). We then extracted whole genome DNA using the QIAmp DNA Mini kit. We performed whole genome sequencing using a NEBNext FS Ultra Express Kit. Because the resulting historical DNA was highly fragmented, we shortened enzymatic fragmentation to 5 minutes, but otherwise followed the manufacturer's protocols. Libraries were 150 bp paired end sequenced by Novogene Corporation using an Illumina NovaSeq X.

Our recovered sequences were predominantly mitochondrial (~65% across both specimens). Thus, we opted to map our reads to an *A. pogus* mitochondrial reference genome (Yuan et al. 2024) following QC and adapter trimming. We performed read mapping using BWA-MEM (Li, 2013). We then hard called genotypes by exporting the overall consensus sequence for each specimen. We extracted cytochrome b sequences and used BLAST to confirm species identification. Based on our BLAST results, we selected species for phylogenetic analyses. We generated a maximum-likelihood tree using IQ-TREE 2 (Minh *et al.*, 2020) using both MCZ specimens, 53 *A. pogus* mitogenomes from Yuan et al. (2024), and 35 *A. schwartzi* mitogenomes. Reference mitogenomes for *A. schwartzi* were assembled *de novo* from WGS data using MITObim (Hahn, Bachmann & Chevreux, 2013) with a cytochrome b sequence as a bait. WGS data for *A. schwartzi* were generated for another study (M.L. Yuan, unpublished data).

Results

Assessing fossil evidence of two-species communities

The estimated SVLs from Center Cave and The Fountain are 55–65 mm and 39–50 mm (Pregill *et al.*, 1994). These ranges overlap with male *A. gingivinus* (median = 56, IQR = 53.6–59.5) and *A. pogus* (median = 41.2, IQR = 40.3–42.2) (Fig 2A). However, the distribution of estimated fossil SVLs better matched a single species community of male and female (median =

45, IQR = 42.5–46) *A. gingivinus* because the size range of female *A. pogus* (median = 35.9, IQR = 34.5–37.5) was not represented in the fossil deposits.

Abundance modeling on Anguilla and Saint Barthélemy

When our random forest models (canopy cover + elevation + urbanization) were projected onto Anguilla and Saint Barthélemy, we found that suitable habitat for *A. pogus* persists on both these islands (Fig 1). However, the highest quality habitat was highly fragmented on both Anguilla and Saint Barthélemy.

Sequencing historical specimens

We confirmed that both R-16596 and R-16597 belonged to the *A. wattsi* species group (which includes *A. pogus*) based keeled midventral scales, which are lacking in the co-distributed *A. bimaculatus* species group including *A. gingivinus* (Lazell, 1972). However, we could not morphologically differentiate between the members of the *A. wattsi* group due to a lack of identifying characteristics in preservation (Lazell, 1972). Our historical DNA sequencing resulted in 102,529,039 reads for R-16596 and 84,411,475 for R-16597. We successfully assembled a mean of 63.5% of the mitochondrial genome at an average depth of 199,620X and 223,521X respectively. We re-identified both R-16596 (best match = PP195496: E = 0.0; 99.8% identity) and R-16597 (best match = PP195494: $E = 2.0 \times 10^{-84}$; 98.9% identity) as *A. schwartzi* (another member of the *A. wattsi* species group) from St. Eustatius based on extracted cytochrome b sequences. Our maximum-likelihood tree confirms that R-16596 and R-16597 were nested with *A. schwartzi* from St. Eustatius rather than *A. pogus* (Fig 2B).

Discussion

Our findings did not support the historical presence of *A. pogus* on Anguilla. We falsify both fossil (Pregill *et al.*, 1994) and museum specimen (Lazell, 1972) based evidence previously used to argue to for the recent presence and extinction of *A. pogus* on Anguilla. Specifically, we found the bimodal size distribution of fossils described by (Pregill *et al.*, 1994) better fits sexual dimorphism in *A. gingivinus* rather than a two anole species community (Fig 2A). Previous work by (Kemp & Hadly, 2016) also did not find support for two species in Anguillan fossils based on evidence from their size distribution and ancient DNA sequencing. Paleontological evidence can play an important role in conservation particularly as a tool for assessing historical ranges (Burney & Burney, 2007; Wingard *et al.*, 2017; Claude *et al.*, 2019). Yet, the case of *A. pogus* highlights the importance of interpreting fossil records correctly. As for the two specimens of *A. pogus* collected on Anguilla, our results indicated that they were misidentified. Although we confirmed that they morphologically belong to the *A. wattsi* species group, our genetic evidence indicated that they are *A. schwartzi* rather than *A. pogus*. Specifically, both MCZ R-16596 and R-16597 best matched with *A. schwartzi* from the island of Sint Eustatius (Fig 2B). It is likely that these specimens were not collected on Anguilla at all, but were missorted specimens that were collected as part of the same expedition to both Sint Eustatius and Anguilla (S. Kennedy-Gold, personal communication). Thus, neither St. Barthélemy (Lazell, 1972) nor Anguilla appear to have been recently inhabited by *A. pogus*.

It should be noted that both Center Cave and The Fountain fossil deposits predate European colonization, but not human arrival on Anguilla (Pregill *et al.*, 1994). However, the Katouche Bay deposit does predate human habitation of the island and dates back over 10,000 years before present (Roughgarden, 1995; Kemp & Hadly, 2016). This latter deposit supports the conclusion that *A. pogus* did not occur on the island during the period of human inhabitation. Nevertheless, we cannot draw definitive conclusions about the presence of *A. pogus* on Anguilla prior to the Holocene. The three islands of Anguilla, St. Martin, and St. Barthélemy have been connected as a single landmass during periods of lower sea levels (Christman, 1953) and molecular clock dating of *A. pogus* from St. Martin suggests that extant *A. pogus* last shared a common ancestor in the Pleistocene, 1.80 Ma [1.62-1.98 Ma] (Yuan et al. 2024). Our models also predicted suitable, albeit fragmented, habitat on both islands (Fig 1). Thus, it remains possible that the historical distribution of *A. pogus* extended into Anguilla and St. Barthélemy prior to their separation from St. Martin. Nonetheless, we found no evidence that the species persisted on these islands into the Holocene. If *A. pogus* did occur on these islands, their local extinction was more likely caused by environmental pressures associated with changing Pleistocene climate and sea levels. Extinctions of native species following initial human arrival and subsequent European colonization have clearly occurred in the Caribbean (Fitzpatrick & Keegan, 2007; Bochaton *et al.*, 2021) and on islands around the world (Olson, 1989; Steadman, 1995; Martin & Steadman, 1999). However, despite the prevailing narrative, it does not appear that *A. pogus* on Anguilla was one such case.

The lack of clarity for species historical native ranges is a common problem in the Caribbean (Helgen *et al.*, 2008; Olson & López, 2008; Camargo *et al.*, 2009; Giovas, 2019; Yuan *et al.*, 2022, 2023). Other Caribbean taxa whose historical extinctions are controversial include *Ara* macaws (Olson & López, 2008) and *Iguana* lizards (Martin *et al.*, 2015; Breuil *et al.*, 2018). Incomplete or incorrect information on a species historical distribution can have important consequences for biodiversity science and conservation management (Carlton, 1996; Wingard *et al.*, 2017). For example, conservation efforts have been inadvertently extended toward introduced species such as racoons on Guadeloupe (Pons *et al.*, 1999; Helgen *et al.*, 2008). A lack of empirical data has long posed an issue for conservation questions regarding *A. pogus* beyond the Anguilla question address by our study. The species has historically been considered an obligate of upland forest (Lazell, 1972). However, evidence now shows that the species is actually widespread throughout St. Martin across all habitats (Powell *et al.*, 2005; Jesse *et al.*, 2018; Yuan et al. 2024). The species was also originally thought to be declining despite lack of demographic data (Powell *et al.*, 2020). Again, recent evidence has shown strong census numbers for the species (Jesse *et al.*, 2018) and genomic evidence indicates recent demographic expansion (Yuan et al. 2024). Therefore, it does not appear that anthropogenic activity has meaningfully threatened *A. pogus*. Taken together, work on *A. pogus* demonstrates the importance of multiple lines of empirical evidence for the accurate assessment of a species conservation status. Controversy regarding the conservation status and historical distributions of Caribbean species is likely to continue given the region's complicated anthropogenic and biogeographic history (Kaiser, 1997; Olson & López, 2008; Giovas, 2019; Napolitano *et al.*, 2019; Nägele *et al.*, 2020) combined with a lack of data for many species (Böhm *et al.*, 2013). Substantial further work is required to build a better conservation and biodiversity science framework for regions like the Caribbean with high uncertainty for historical baselines. Our study provides a case study for integrative assessment of historical species ranges and local extinctions relevant for biodiversity science and conservation.

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Author Contributions

MLY conceived of the study and analyzed the data. MLY, RCB, EAM collected the data and designed the methodology. MLY and RCB funded and supervised the study. MLY wrote the manuscript. All authors edited the manuscript and approved of its publication.

Data Availability

The following statement will be included if the manuscript is accepted: Raw sequence data have been accessioned in SRA (no. ####). All other data are accessioned in Dryad (doi:###).

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Fig 1 Predicted abundances for *A. pogus* on the islands of (A) Anguilla and (B) St. Barthélemy using random forest models (urbanization + canopy cover + elevation) fit to survey data from St. Martin.

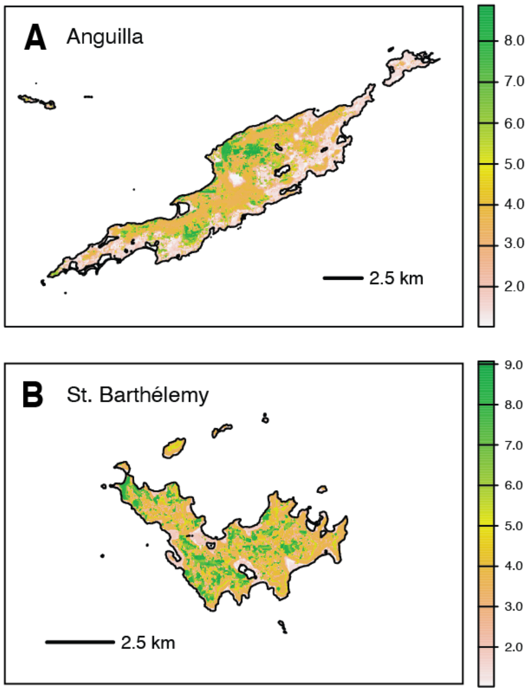

Fig 2 (A) Density plot of *A. gingivinus* and *A. pogus* SVLs collected from specimens and live samples on St. Martin. Males and females are shown separately for each species. Grey blocks represent reported size ranges of *Anolis spp.* fossils from Anguilla reported in Pregill et al. 1994. Female *A. pogus* do not fall within size ranges of Anguillan fossils. (B) Mitochondrial maximum likelihood tree of *A. schwartzi* and *A. pogus* with MCZ samples (R-16596 and R-16597) from Anguilla included. Nodes with bootstrap values above 90 are noted. Note that both MCZ samples, denoted by a star, are nested within *A. schwartzi* from St. Eustatius.