

Establishment of *Anolis sagrei* on Bermuda represents a novel ecological threat to Critically Endangered Bermuda skinks (*Plestiodon longirostris*)

James T. Stroud · Sean T. Giery · Mark E. Outerbridge

Received: 20 April 2016 / Accepted: 11 February 2017 / Published online: 17 February 2017
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Abstract Bermuda is an isolated, oceanic island with only one endemic terrestrial vertebrate, the Critically Endangered Bermuda skink (*Plestiodon longirostris*; Squamata, Scincidae). Major declines in *P. longirostris* populations have been caused primarily by habitat loss and mortality via invasive species (e.g., predation from birds and cats) and human waste products (e.g., trapped in discarded bottles). However, biotic interactions and interspecific competition with invasive lizards have also been identified as potentially detrimental to *P. longirostris* populations. Here, we provide the first occurrence records of a highly invasive lizard, the Cuban brown anole (*Anolis sagrei*), on Bermuda. We assess the brown anole's diet, habitat use, morphology, and island-wide distribution for comparison to the native skink, *P.*

longirostris. Results of this study indicate that *A. sagrei* in Bermuda are highly terrestrial (>60% of all lizards observed on the ground vs. in trees) and forage primarily on terrestrial invertebrates. These data indicate substantial ecological overlap with the exclusively-terrestrial *P. longirostris*. This is in contrast to the other established non-native lizards on Bermuda, which are principally arboreal and have successfully coexisted with *P. longirostris* for >60 years. At present, the geographic distributions of *A. sagrei* and *P. longirostris* do not overlap. However, all extant skink populations are within several kilometers of brown anole populations (with the nearest being <0.5 km). The extensive overlap in ecological niche between the Bermuda skink and the invasive brown anole will likely present a serious conservation threat if contact is made. This study is exceptional in providing clear in situ ecological data which predict a conservation threat of an established invasive species to a Critically Endangered island endemic prior to coexistence. Continued monitoring of this situation as *P. longirostris* and *A. sagrei* inevitably come into contact will allow these a priori hypotheses of conservation risk via ecological overlap to be tested.

J. T. Stroud (✉)
Department of Biological Sciences, Florida International
University, Miami, FL 33199, USA
e-mail: jamesTstroud@gmail.com

J. T. Stroud
Fairchild Tropical Botanical Gardens, Coral Gables,
FL 33156, USA

S. T. Giery
Department of Applied Ecology, North Carolina State
University, Raleigh, NC, USA

M. E. Outerbridge
Department of Environment and Natural Resources, 17
North Shore Road, Hamilton Parish FL04, Bermuda

Keywords *Anolis* · Invasive species · Oceanic island · Endemic · Endangered · Competition · Niche

Introduction

Understanding how introduced species interact with native species is a primary conservation issue (Powell et al. 2011). The introduction of non-native species can increase the extinction vulnerability of native species if they represent novel sources of competition, predation, or disease. These biotic interactions are particularly concerning for native species already considered vulnerable to extinction due to other factors. Many island endemics, in particular, face heightened extinction risks due to a combination of threats such as low genetic diversity, overexploitation, and habitat loss and fragmentation (Sodhi et al. 2009). From an evolutionary perspective, island endemics are at a further disadvantage as they are often considered to be competitively inferior relative to invasive species derived from more diverse communities (Simberloff 1995).

Here we report the first official records of a highly invasive vertebrate, the Cuban brown anole (*Anolis sagrei*; Fig. 1) on Bermuda. In addition to documenting the establishment of this invasive species, the purpose of this study was to estimate the potential impact of the *A. sagrei* invasion on the Critically Endangered Bermuda skink (*P. longirostris*), prior to contact between the two species. Risk assessments of newly established non-native species is an integral yet often overlooked aspect of invasion biology (Andersen et al. 2004). Commonly, invasive species management is reactionary with risk management being



Fig. 1 Adult male Cuban brown anole (*A. sagrei*) in Bermuda with an extended dewlap during a signal display: this species is easily distinguishable from other established *Anolis* lizards on Bermuda by a brown dorsal pattern and red coloration of the dewlap. Photo: JStroud

used in place of risk assessment. Management protocols are only implemented following perceived or observed negative effects of invasives on native species or ecosystems. However, reactive management can be expensive, ineffective, and extremely difficult to successfully complete (Davies and Johnson 2011). Because we have detected this invasion in its initial stages, whereby a non-native species is established but contact with a vulnerable endemic has not yet been made, we designed our study to capitalize on this opportunity.

First, we estimate the degree of potential competitive interference between *A. sagrei* and *P. longirostris* by assessing ecological overlap in structural habitat use and diet. To estimate the uniqueness of the threat posed by *A. sagrei* we compare these same ecological niche axes between *A. sagrei* and the three other established non-native *Anolis* on Bermuda. We then examine the degree of morphological overlap between *A. sagrei* and *P. longirostris* as a proxy of both competitive and predatory interaction potential. Finally, we use ecological theory and published data to develop predictions regarding the likely conservation threat *A. sagrei* poses to *P. longirostris* if spread continues and contact is made.

Methods

Bermuda is a small, isolated oceanic island (32.30°N, –64.78°W; 5500 ha total land area) located in the western North Atlantic, ca. 960 km east of North Carolina, USA, with only one endemic terrestrial vertebrate, the Critically Endangered Bermuda skink [*Plestiodon* (syn *Eumeces*) *longirostris*] (Bacon et al. 2006; IUCN 2015). Bermuda does, however, have a rich and well-documented history of non-native lizard introductions. In 1905, Graham's anoles (*A. grahami*) were purposefully introduced from Jamaica as a biological control of crop-destroying scale insects (*Carulaspos minima*) (Wingate 1965). Despite the quick establishment, high population density, and rapid expansion of *A. grahami* in Bermuda, biological control of the pest insect was unsuccessful as they were rarely eaten. Great kiskadee flycatchers (*Pitangus sulphuratus*) were subsequently introduced in 1957 to control *A. grahami* populations, and in a classic case of conservation mismanagement, both species (Great kiskadees and Graham's anoles) have

subsequently flourished and have been observed predated native fauna, including Bermuda skinks (Davenport et al. 2001; Bacon et al. 2006). In the 1940's two additional *Anolis* species were introduced, albeit this time unintentionally: first, the Antigua marbled anole (*A. leachii*; known locally as “the Warwick lizard”) was observed in Central Bermuda, and second, the Barbados painted anole (*A. extremus*) was recorded from Sandy's Parish in north-west Bermuda (Losos 1996). All three anoles are successfully established on Bermuda and, as of 2015, at least two species (*A. grahami* and *A. leachii*) are found throughout the island. A fifth species, the American green anole (*A. carolinensis*), has also been recently recorded but only comprised of a single individual found in a cargo dock, and is therefore not considered established (Stroud et al. 2016).

Anolis sagrei is a small [~ 40 – 60 mm snout-vent length (SVL)], predominantly terrestrial lizard with a generalist invertebrate diet (Schoener 1968; Giery et al. 2013). Native to Cuba and the Bahamas, *A. sagrei* is also an extremely successful and aggressive invasive species with long-established, rapidly expanding populations in the USA (Florida, Georgia, Alabama, Louisiana, Texas, and California), the Caribbean (Grand Cayman, Grenada, Barbados, Turks and Caicos, and Jamaica), Pacific islands (Hawaii and Taiwan), Costa Rica, and Singapore (Kolbe et al. 2007). In its non-native range *A. sagrei* competes with native lizard species leading to substantial population declines, as well as shifts in resource use and spatial ecology, of the native species (Stuart et al. 2014).

Suspected populations of *A. sagrei* were known to the Bermuda Department of Environment and Natural Resources since 2013 (J. Macedonia *pers. comms*). On 16 August 2014 we confirmed the presence of *A. sagrei* in Paget Parish (hereafter Site A: 32.290°N , -64.771°W). Subsequently, from 17 to 31 Aug 2014 and 17 to 30 Aug 2015 we conducted extensive visual surveys of 114 sites including several offshore islands in order to map the distribution of *A. sagrei* throughout Bermuda. We recorded microhabitat use, specifically perch height (cm) (i.e. the vertical distance from ground of the observed lizard), to provide ecological comparisons between *A. sagrei* and other introduced *Anolis* lizards. To do this we haphazardly collected data on all other species throughout both 2014 and 2015 research trips at multiple sites across Bermuda. In 2015 we discovered an additional geographically

distinct population of *A. sagrei* in Pembroke Parish (hereafter Site B: 32.299°N , -64.792°W ; 22 August 2015). A distance transect survey was conducted at site A in 2015 whereby the distance of all observed lizards from the transect allows estimations of population density and size to be calculated. The transect totaled 466 m in length and covered both core and peripheral areas of the *A. sagrei* population. Estimates of population density and size using this method were calculated using the program Distance (Thomas et al. 2010).

To assess morphology and diet of *A. sagrei*, we collected 63 individuals from Site A (32 males, 31 females), and 25 individuals from Site B (20 males, 5 females) during August 2015 (total $N = 88$). Lizards were caught using dental floss nooses attached to Cabela's panfish poles and euthanized. Stomach contents were analyzed under a dissection microscope (10 – $60\times$ magnification) and identified to the lowest taxonomic level possible. Reproductive state (gravidity) of mature females (SVL > 34 mm; Norval et al. 2010) was assessed during dissection. *Plestiodon longirostris* specimens were not collected for diet analysis as populations are vulnerable and highly protected (Level 1, Bermuda Protected Species Act 2012); diet data for *P. longirostris* were supplied by the Bermuda Department of Environment and Natural Resources, and morphology data taken from Raine (1998). General body size comparisons of *A. sagrei* versus *P. longirostris* were assessed by regressing SVL (mm) to mass (g).

Results

During island-wide surveys, we identified two geographically distinct populations of *A. sagrei* in Bermuda (Fig. 2). At both sites, *A. sagrei* occurred at high densities and individuals of all age classes were recorded (i.e. hatchlings and reproductively-mature adults). Conversations with a resident of Site A revealed the population has been established and reproducing since at least 2011 and has grown substantially (Trent Garner *pers. comms*). All adult female *A. sagrei* collected from both sites in this study ($n = 36$) were gravid (smallest gravid female = 37.5 mm SVL). We recorded range expansion of *A. sagrei* at Site A of ~ 50 m between 2014 and 2015 sampling expeditions. Distance transect data

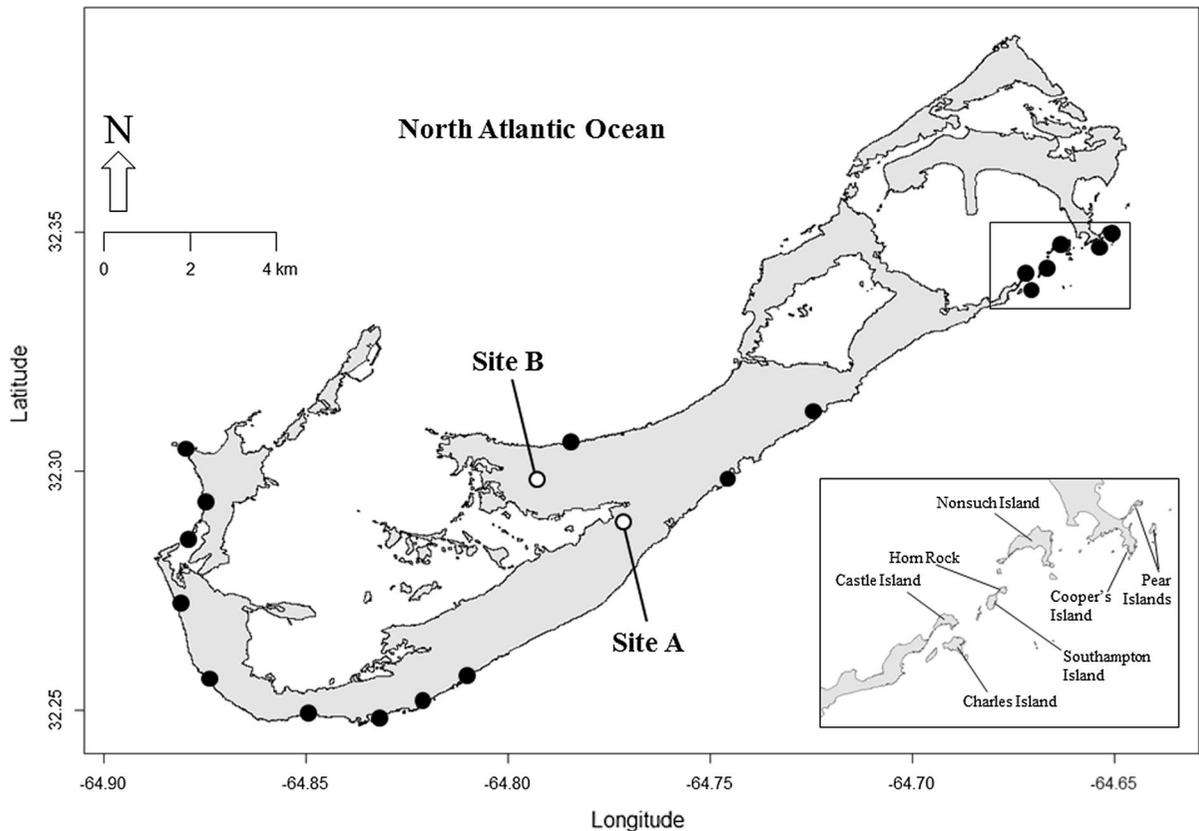


Fig. 2 The current distribution of Bermuda skinks (*P. longirostris*; black circles) and the recently discovered Cuban brown anole (*A. sagrei*; white circles) populations. All islands

labelled in the inset have established *P. longirostris* populations. Skink population data are the most up-to-date available from the Bermuda Department of Environment and Natural Resources

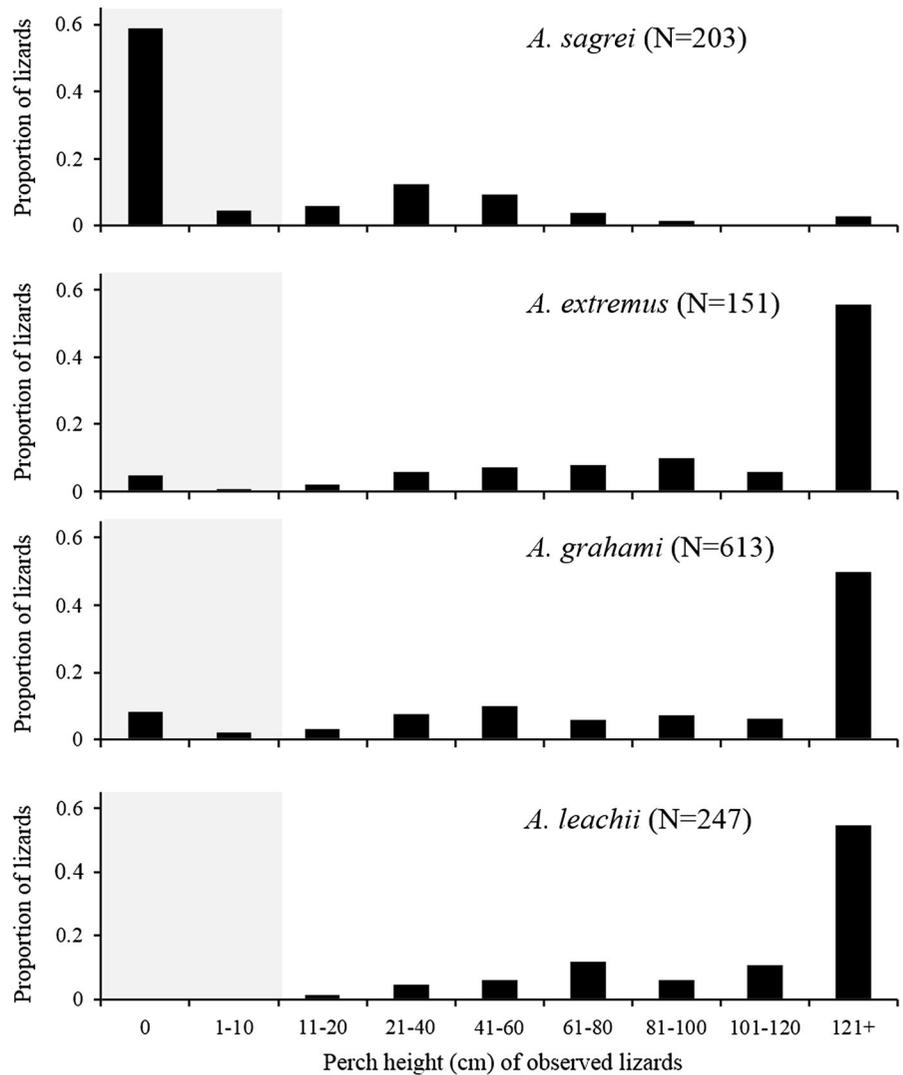
generated an estimated population density of 1 individual per 10 m² (SE = -0.06) which, given the current distribution of *A. sagrei* at Site A (~2.27 ha), results in a population estimate of 2274 ± 134 individuals. If our density estimate of Site A is representative of the population at Site B (as suspected based on personal observations), then we estimate that population B (~2.5 ha) also supports >2000 individuals. Taken together, a coarse but conservative estimate of the total number of *A. sagrei* on Bermuda is therefore ca. 4000–5000 individuals.

Our assessment of structural habitat use of *A. sagrei* on Bermuda revealed that they are highly terrestrial (>60% of individuals observed on the ground), especially compared to other *Anolis* species established on Bermuda which are all predominantly arboreal (Fig. 3). Adult male *A. sagrei* perched higher (mean = 32.2 cm, SE = 4.7 cm, n = 92) than both

adult females (mean 14.2 cm, SE = 3.0 cm, n = 63) and juveniles (mean = 3.9 cm, SE = 1.4 cm, n = 42). *Plestiodon longirostris* are almost exclusively terrestrial but will occasionally perch on substrates low to the ground (i.e. <10 cm) (Wingate 1965; Bacon et al. 2006). These results suggest a high structural habitat overlap of *A. sagrei* with *P. longirostris* of all age and size classes, and detailed assessments of morphology reveal a considerable size overlap of adult *A. sagrei* with young *P. longirostris* (Fig. 4).

Plestiodon longirostris primarily consume terrestrial and leaf-litter arthropods (L. Kitson unpub. data). Wingate (1965) and Verill (1902) noted that ants (Formicidae)—specifically *Pheidole megacephala*—and woodlice (Isopoda) comprised the greatest proportion of the skink's diet. The marine amphipod *Platorchestia platensis* (formerly *Orchestia agilis*)

Fig. 3 Proportional habitat use of *Anolis* lizards established on Bermuda. Grey areas indicated high terrestriality (lizards observed 0–10 cm from the ground) which Bermudian skinks (*Plestiodon longirostris*) solely utilize. Data are combined for all mature individuals of both sexes



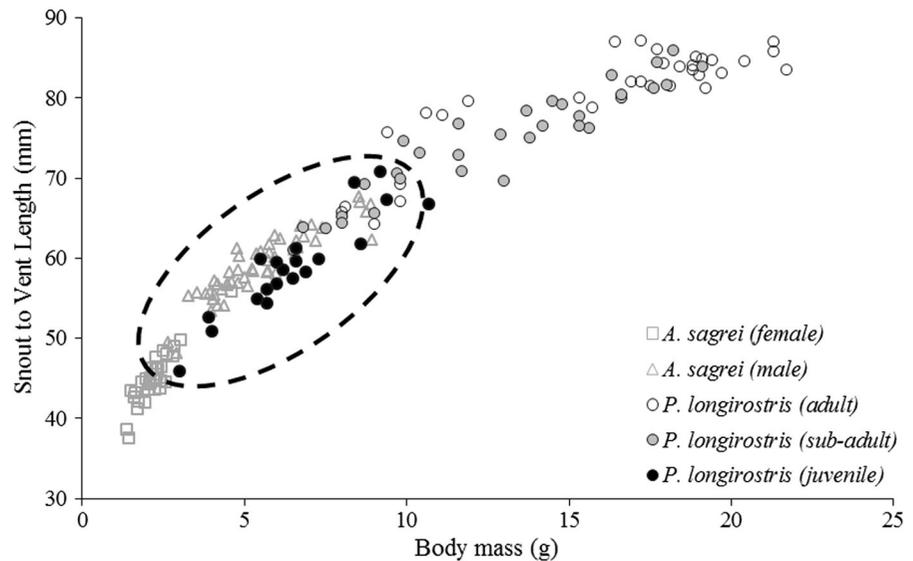
were observed in the stomachs of skinks collected near the coast (Verill 1902). Additionally, *P. longirostris* opportunistically scavenge on a variety of non-arthropod food items [e.g., broken seabird eggs, carrion, cactus fruit (*Opuntia* sp.)] (Davenport et al. 2001).

We identified 558 individual food items of 17 different Orders in the stomachs of 63 *A. sagrei* (Table 1). Our results show that *A. sagrei* on Bermuda are generalist consumers of terrestrial arthropods. Ants (Formicidae) contributed a substantial proportion (71.3%) of total prey items, but lepidopterans (5.9%), homopterans (5.0%), coleopterans (4.3%), and hemipterans (4.3%) were also frequently recorded. Both *Pheidole megacephalus*

and *Platorchestia platensis*—the only prey items of Bermuda skinks identified to species in previous studies (Verill 1902; Wingate 1965)—were found in the stomachs of *A. sagrei*. There were no major differences in diet between adult males and females. Two cases of cannibalism by *A. sagrei* were recorded; once by an adult male (found perched 1.9 m from the ground) and once by an adult female (found on the ground).

Overall there was an extremely high dietary overlap between the *A. sagrei* investigated in this study and published stomach contents of *P. longirostris*. Specifically, 80.8% of Arthropod Orders recorded in the stomach of *A. sagrei* in this study are known prey items of *P. longirostris* (Table 1).

Fig. 4 General body size overlap between *P. longirostris* (juveniles $n = 20$, subadults $n = 32$, adults $n = 33$) and *A. sagrei* (males $n = 52$, female $n = 36$). Circled area indicates body size overlap. *P. longirostris* snout-vent length and mass data taken from Raine (1998)



Discussion

While the origin of *A. sagrei* populations on Bermuda is unknown, these populations are established (reproducing for at least 5 years), large (our estimate of ca. 4000–5000 individuals already exceeds the total global population of *P. longirostris* with ca. 3500 individuals; Edgar et al. 2010), and expanding. Firstly, we identify a substantial ecological overlap between *A. sagrei* and *P. longirostris*—both species are highly terrestrial (Fig. 3) and feed primarily on ground-dwelling arthropods (Table 1). Secondly, we demonstrate that *A. sagrei* broadly overlap in body size with *P. longirostris* (Fig. 4), meaning competitive interactions may be likely, and that Bermudian *A. sagrei* consume smaller lizards. And thirdly, that the ecological threat posed by *A. sagrei* to *P. longirostris* is unique compared to those posed by all other non-native *Anolis* lizards on Bermuda.

Based on our observed range expansion at Site A from 2014 to 2015 (0.05 km/year), we estimate that contact between *A. sagrei* and *P. longirostris* may occur in ~ 10 years (0.5 km linear distance). It is highly likely, however, that contact between the two species will occur sooner. Indirect dispersal via human transport is commonly observed in *A. sagrei*; adults stowaway in nursery plants, on cars, and inside garbage waste, while eggs are easily transported in soil (Lee 1985; Goldberg et al. 2002; Kolbe et al.

2016). Site A is a plant nursery which could greatly expedite the spread of *A. sagrei*.

If contact is made between *A. sagrei* and *P. longirostris*, the possibility of extended coexistence is unclear. In islands across the Caribbean, establishment success of introduced *Anolis* lizards has a strong negative relationship with the degree of ecological similarity they have with native lizards (Losos et al. 1993). This relationship suggests that priority effects—the prior establishment of a species in an area (Fukami 2015)—may be particularly important for assembly patterns of introduced *Anolis* lizards on Bermuda (Wingate 1965; Losos 1996). The prior establishment of *P. longirostris* in areas devoid of *A. sagrei* may provide a demographic advantage rendering *A. sagrei* expansion attempts unsuccessful. This is a hypothesis that can be tested by continued monitoring of species distributions.

If coexistence does occur, we predict that there will be strong interspecific competition for habitat, prey, or both. Given that *A. sagrei* achieves extremely high densities once established (4900–12,000 individuals/ha; Campbell and Echternacht 2003), space and food may become limiting. Our estimates of *A. sagrei* population densities in Bermuda are high (ca. 1000 individuals/ha), however it is likely that these populations are in an initial stage of invasion, and prior to exponential growth—a lag time pattern commonly recorded in invasive species (Sakai et al. 2001). High density populations of invasive *A. sagrei* in Taiwan

Table 1 Stomach contents analysis of two independent populations of Cuban brown anoles (*A. sagrei*) (Site A, Site B) and a combined species total

Order	Family	<i>Anolis sagrei</i> diet						Skink diet
		No. of prey items			Proportional no. prey items (%)			
		Site A	Site B	Combined	Site A	Site B	Combined	
ARANAEA		1	1	2	0.4	0.3	0.4	X
	<i>Araneidae</i>	1	1	2	0.4	0.3	0.4	
GASTROPODA		4	0	4	1.7	0	0.7	X
BLATTODEA		0	1	1	0	0.3	0.2	X
	<i>Blattidae</i>	0	1	1	0	0.3	0.2	
COLEOPTERA		17	7	24	7.3	2.2	4.3	X
	<i>Chrysomelidae</i>	2	1	3	0.9	0.3	0.5	
	<i>Coccinellidae</i>	2	0	2	0.9	0	0.4	
	<i>Curculionidae</i>	1	2	3	0.4	0.6	0.5	
	<i>Elateridae</i>	1	2	3	0.4	0.6	0.5	
	<i>Scarabaeidae</i>	7	2	9	3	0.6	1.6	
	<i>Scolytidae</i>	4	0	4	1.7	0	0.7	
DERMAPTERA		14	1	15	6	0.3	2.7	
	<i>Anisolabididae</i>	14	1	15	6	0.3	2.7	
DIPTERA		4	1	5	1.7	0.3	0.9	X
HEMIPTERA		11	13	24	4.7	4	4.3	
	<i>Aphididae</i>	1	6	7	0.4	1.9	1.3	
	<i>Blissidae</i>	8	7	15	3.4	2.2	2.7	
	<i>Cydnidae</i>	2	0	2	0.9	0	0.3	
HOMOPTERA		20	8	28	8.6	2.5	5	
	<i>Cicadellidae</i>	20	8	28	8.6	2.5	5	
HYMENOPTERA		122	277	399	52.1	85.5	71.5	X
	<i>Apidae</i>	1	0	1	0.4	0	0.2	
	<i>Formicidae</i>	121	277	398	51.7	85.5	71.3	
ISOPTERA		0	1	1	0	0.3	0.2	
LEPIDOPTERA		28	5	33	12	1.5	5.9	X
	<i>Hesperiidae</i>	16	0	16	6.8	0	2.9	
	<i>Nymphalidae</i>	1	3	4	0.4	0.9	0.7	
	<i>Pieridae</i>	11	2	13	4.7	0.6	2.3	
ORTHOPTERA		1	1	2	0.4	0.3	0.4	X
	<i>Gryllidae</i>	1	0	1	0.4	0	0.2	
	<i>Acridae</i>	0	1	1	0	0.3	0.2	
THYSANOPTERA		1	0	1	0.4	0	0.2	
	<i>Thripidae</i>	1	0	1	0.4	0	0.2	
AMPHIPODA		1	0	1	0.4	0	0.2	X
	<i>Talitridae</i>	1	0	1	0.4	0	0.2	
ISOPODA		7	6	13	3	1.9	2.3	X
	<i>Porcellionidae</i>	7	6	13	3	1.9	2.3	
CHILOPODA		1	0	1	0.4	0	0.2	
	<i>Geophilidae</i>	1	0	1	0.4	0	0.2	
SQUAMATA		2	2	4	0.9	0.6	0.7	

Table 1 continued

Order	Family	<i>Anolis sagrei</i> diet						Skink diet
		No. of prey items			Proportional no. prey items (%)			
		Site A	Site B	Combined	Site A	Site B	Combined	
	<i>Dactyloidae</i>	2	2	4	0.9	0.6	0.7	

Data are presented as raw stomach contents and as proportion of total stomach contents. Taxonomic Orders are highlighted in bold, with a breakdown to family where possible highlighted underneath in italics. Orders known to be consumed by Bermudian skinks (*P. longirostris*) are marked with an 'X' in the final column

(1275–2900 individuals/ha; Huang et al. 2008) were such a robust predatory force that ground arthropod diversity and structure were dramatically altered. Furthermore, the communities most affected by Taiwanese *A. sagrei* were ant communities, the primary prey resource of *P. longirostris* (Wingate 1965). If sites of coexistence are identified, rapid monitoring of the arthropod community will help to understand the extent of *A. sagrei* effects on food resources, and provide further insight into potential conservation risks for *P. longirostris* via dietary overlap.

Predation is the most common interaction through which invasive species negatively affect endemic species (Sodhi et al. 2009). Although *P. longirostris* experience predation from several non-native predators, all have coexisted with *P. longirostris* for at least 40 years (Davenport et al. 2001; Bacon et al. 2006). It has been suggested, following direct observations of *P. longirostris* predation by *A. grahami*, that exceptionally high population densities of *P. longirostris* on islands devoid of *Anolis* lizards provides evidence for a predator–prey interaction (Wingate 1998). While this may be true, this could also be explained by a competitive relationship. Whether *A. sagrei* poses a significant predatory risk is difficult to predict; adult *P. longirostris* are much larger than *A. sagrei*, but skink hatchlings and juveniles are small enough to be considered viable prey items for adult *A. sagrei*, particularly adult males (hatchling SVL 35 mm, mass 1.1 g; juvenile SVL 49.5 mm; mass 4.1 g; L. Kitson unpubl. data). Although adult males are the most arboreal age/sex class of *A. sagrei* on Bermuda and therefore encounter rates with skinks may be lower, the majority of individuals were found on or near to the ground, which is typically where most foraging activity occurs (Giery et al. 2013). Therefore, during periods of active foraging, *A. sagrei* will experience a high

habitat overlap with *P. longirostris*. Adult *Anolis sagrei* of both sexes on Bermuda are saurophagus (Table 1), and therefore the conservation threat to *P. longirostris* from *A. sagrei* may include predation on hatchlings.

Our assessment of niche overlap between Bermudian *A. sagrei* and *P. longirostris* suggests that the *A. sagrei* invasion could pose a unique and substantial conservation threat through competition for space and food. However, native species extinctions resulting from interspecific competition with invasive species are extremely rare (Sax et al. 2007), suggesting that estimates of ecological overlap may not predict extinction risk in cases like this. Predation by invasive species, however, does drive native species to extinction. Given the saurophagous nature of Bermudian *A. sagrei*, and the small size of *P. longirostris* hatchlings, we believe a predatory interaction is possible, although as coexistence does not yet occur this remains undocumented.

The situation on Bermuda provides an exceptional opportunity to test further a priori predictions about how ecological interactions, specifically competition and predation, between an invasive and a vulnerable endemic may pose a conservation risk when the species come into contact. Future monitoring of the distribution, population demographics, and ecology of *A. sagrei* on Bermuda is critically important to maintain effective conservation and management of the few remaining natural *P. longirostris* populations in the world.

Acknowledgements This is contribution #246, Bermuda Biodiversity Project (BBP), Bermuda Aquarium, Natural History Museum and Zoo, Department of Environment and Natural Resources. We thank the Bermuda Zoological Society (Eric Clee Fund) for financial research support, as well as to Thad and Evan Outerbridge for providing accommodation. We thank Kenneth Feeley, Evan Rehm, Rachel Hillyer, Catherine

Bravo-Avila, Jason Kolbe, Joe Macedonia, and one anonymous reviewer for providing important and insightful comments on previous versions of this manuscript. JS was supported by the FIU Judith Evans Parker Travel Fund and an FIU Dissertation Evidence Acquisition Fellowship. STG was supported by NSF DEB #1406399.

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