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31st January 2019

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Front cover: The established *Anolis* community of Miami, FL. From top; Jamaican giant anole (*Anolis garmani*), Cuban knight anole (*A. equestris*), [right] Hispaniolan bark anole (*A. distichus*), [left] American green anoles (*A. carolinensis*), Puerto Rican crested anole (*A. cristatellus*), Cuban brown anole (*A. sagrei*). Illustration generously provided by Gabriel Ugueto, Gabriel is a scientific illustrator and paleoartist whose work is second to none; contact him for commissions! <u>www.GabrielUgueto.com</u>

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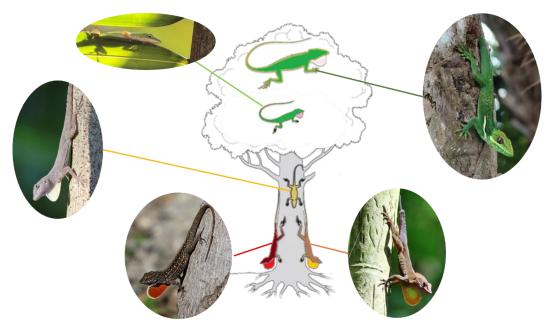
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The attendees of the 7th Anolis Symposium. Fairchild Tropical Botanic Gardens, Miami FL. 17-18th March 2018.

Preface

It had been nearly a decade since the previous *Anolis* symposium was held in Cambridge, MA, at the Museum for Comparative Zoology, Harvard. A reunion of anole biologists en masse was long past due and it was decided that this symposium would be slightly different – we were going to hold it somewhere with anoles! And so, on the weekend of 17-18th March, 2018, nearly 70 anole biologists traveled to sunny south Florida to attend the 7th *Anolis* Symposium held at the beautiful Fairchild Tropical Botanic Gardens in Miami. In the grounds of the botanical gardens, attendees were presented with a diverse community of six (!) species of anole, both native and non-native, representing four distinct ecomorphs.



The anole community of Fairchild Tropical Botanic Gardens, clockwise from top right; Cuban knight anoles (*Anolis equestris*; Crown-Giant), Puerto Rican crested anoles (*A. cristatellus*; Trunk-Ground), Cuban brown anoles (*A. sagrei*; Trunk-Ground), Hispaniolan bark anoles (*A. distichus*; Trunk), and – the sole native – American green anole (*A. carolinensis*; Trunk-Crown). Photos: James Stroud.

The early Spring timing of the symposium was chosen for two reasons, (i) Miami's famous, yet unforgiving, heat is particularly sweltering in the Summer period when conferences and symposia are usually held, but more importantly, (ii) March marks the commencement of the anole reproductive season in Miami! Attendees gathered just as anoles were jostling for societal positions in the early Spring sunshine and were rewarded with a plethora of showy dewlap displays and behavioral interactions. As true royalty passed within earshot¹, attendees were

¹At one point on Saturday, all attendees were locked inside the symposium room while personnel from both the US and Japanese Secret Service escorted the Crown Prince of Japan on a private tour of the garden.... seriously!

regaled with 34 research presentations spanning a broad range of topics on anole biology, from insightful natural history to the latest advances in genome editing.

So, what's changed in anole biology since the 6th symposium in 2009? Well, the field continues to grow at an explosive rate! Web of Science returns 1,345 "*Anolis*" articles from 2009-2018. Most notably, a lot of recent research has focused on how human stressors, such as urbanization and contemporary climate change, are affecting the lives of anoles. Similarly, the human-assisted dispersal of anoles to areas outside of their native ranges continues to yield exciting developments in ecology and evolution. Anole invasion biology led the charge in uncovering evidence for rapid evolutionary change driven by species interactions, after the introduction of brown anoles (*A. sagrei*) to spoil islands in central Florida drove native green anoles (*A. carolinensis*) to evolve larger toepads in response to an increased arboreal lifestyle; findings first presented in *AN VI*. Back in 2009 we were also excited to announce that the newest direction of anole biology was upon us; the sequencing of the *Anolis carolinensis* genome. Now, a decade later, three more species have faced the same fate, with many more underway! These accessions will continue to fuel a swathe of studies of anoles and further cement their position as a model system in ecology and evolution.

There are also now many new anoles to enjoy! A recent study, providing the most comprehensive review of *Anolis* systematics to date, put the number of species at 379, a number which might yet change as anole systematics continues to be a hotly debated topic.

While technological advances are expanding the breadth of research on anoles, we continue to echo the previous newsletter in saying that some of the most exciting results still stem from observations of basic natural history. Who knew that natural selection can act on behavior (see contribution from Lapiedra)? Or, that anole eggs hatch early when they're tickled (see contribution from Doody)? Just how important is it to still study anole behavior (see contribution from Johnson)? And what of those remarkable diving anoles, able stay submerged for up to 15 minutes while appearing to re-circulate oxygen from air bubbles attached to their nostrils (see contribution from Swierk)?

As with previous editions, we reiterate the underlying ethos of the *Anolis* Newsletter, "this newsletter is an informal forum for the presentation of data and discussion of theory relevant to anoles. It serves three functions: to allow investigators to inform others of their current and future research; to provide an outlet for speculation and theoretical musings perhaps inappropriate for publication in more formal venues; and to give an opportunity to present data and ideas that otherwise might never be distributed. As with previous newsletters, there is a general request that nothing said herein be quoted without the authors' express permission."

> James T. Stroud, Anthony J. Geneva, and Jonathan B. Losos Washington University St. Louis, MO January 31, 2019

Fairchild's anole (Anolis fairchildi)

Hosting the *Anolis* meeting at Fairchild Tropical Botanic Garden's had an added special significance to anole biologists. On a 1930 expedition to the tiny island of Cay Sal, a small remnant from a once-larger Cay Sal Bank that sits in the ocean passage between Cuba and the southern tip of Florida, malacologist Paul Bartsch came across two anoles; the ubiquitous brown anole (*A. sagrei*) and a curiously large green anole, found to sport white speckling along its flanks. Bartsch collected specimens and passed them on to the famous Caribbean herpetologist, Thomas Barbour. Upon investigating the specimens, Barbour noted that differences in dorsal and temporal scales separated this island population from two morphologically similar species; the Cuban green anole (*A. porcatus*) and the Bahamian green anole (*A. smaragdinus*). In 1935, Barbour, along with a fellow herpetologist Benjamin Shreve, published their description of this curious new lizard. The authors chose to patronize the species *Anolis fairchildi*, in honor of their good friend, expedition companion, and occasional financier, David Fairchild. Aboard a legendary research vessel owned by Allison Armour, the 1315-ton steamer *Utowana*, Barbour and Fairchild, himself a prolific botanist, had explored the flora and fauna of the Caribbean throughout much of the early 20th century.



Fairchild's anole (*Anolis fairchildi*). Cay Sal, 30 May 2012. Courtesy of Michael Sorenson.

And so, by hosting the VII *Anolis* Symposium at the Fairchild Tropical Botanical Garden, the former private botanical collection of David Fairchild – including many original collections from his Caribbean expeditions, we provided a 21st century update to the ongoing *Anolis*- Fairchild relationship. We would like to thank the current Director of Fairchild's Gardens, Dr. Carl Lewis, for his enthusiastic support of both *Anolis* research in the gardens themselves, and for providing such an exciting and historic venue for the VII *Anolis* Symposium.

Graham Reynolds provides a charming and

more detailed account of the history of Fairchild's anole on *Anole Annals* and in his recent *Breviora* paper, in which he and colleagues document their own exploration of Cay Sal and, for the first time, explore the genetic relationship of *A. fairchildi* to the rest of the *carolinensis* green anole clade.

http://www.anoleannals.org/2018/06/24/anole-outpost-the-cay-sal-bank-part-ii/

Reynolds, R.G., Puente-Rolón, A.R., Castle, A.L., Van De Schoot, M. and Geneva, A.J., 2018.
Herpetofauna of Cay Sal Bank, Bahamas and Phylogenetic Relationships of *Anolis fairchildi*, *Anolis sagrei*, and *Tropidophis curtus* from the Region. *Breviora*, 560(1), pp.1-19.

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Role of a sweet-toothed anole (Anolis conspersus) in orchid pollination

Abstract

Fruit and nectar feeding is characteristic of a large number of island lizards leading to pollination and seed dispersal mutualisms and the potential for lizard-driven evolutionary change in island plants. Oceanic islands, in particular, are recognized as potent sources of pollinator novelty. Unusually, the Cayman Islands endemic orchid, *Myrmecophila thomsoniana*, is pollinated by deceiving cetoniid flower chafer beetles to penetrate under the column, thereby extracting and depositing pollinia. The flowers are non-rewarding other than to produce some nectar on the exterior surfaces of the sepals and ovary which is collected by ants and *Anolis conspersus*. Direct observation of flower visitors shows that Blue-throated Anoles may visit orchid inflorescences between 0.4 - 1.5 times per hour and lick nectar up to 0.8 times per hour. Observed anole influences on pollination are threefold. Anoles jumping into and climbing within the flowers can disrupt beetles from approaching and entering flowers or cause them to fly after pollinia extraction. Rarely an anole may extract pollinia itself. Depending on the timing, the



F ig. 1 Male *Anolis conspersus* licking extrafloral nectaries at base of tepals of Myrmecophila thomsoniana on 8 June 2016 at 16:17, in the Ponciana genet, Lower Valley, Grand Cayman.

anoles can thus affect fitness by decreasing pollination opportunities or increasing outcrossing among genets.

Introduction

Oceanic islands are recognized as potent sources of pollinator novelty (Mayer *et al.* 2015). An outstanding example is Reunion Island's *Angraecum cadetii*, whose main pollinator, a raspy cricket, represented an entire new Order of orchid pollinator when discovered (Micheneau *et al.* 2010). It is also sometimes pollinated by a nectar-feeding day gecko (Begue *et al.* 2014). In the Caribbean, anoles are well-known for fruit and nectar feeding (e.g. Losos, 2009; Losos, 2012; Ríos-Lopez, *et al.* 2016). West Indian anoles are even partial to banana sap (Norval and Mao 2013). It has been argued that such behaviours may lead to pollination and seed dispersal mutualisms, and the potential for lizard-driven evolutionary change in island plants (Olesen and Valido 2003).

For Anolis Symposium VII I described some of the data from ongoing research that show how nectivory by the Grand Cayman Blue-throated Anole, *Anolis conspersus*, could play a role, via both positive and negative disruption of pollinator behaviour, in the evolution of *Myrmecophila thomsoniana* var *thomsoniana*, a Grand Cayman, endemic, epiphytic orchid. *A. conspersus* is also a Grand Cayman endemic. Both plant and reptile have evolved in the 2-3 million years since the low-lying carbonate island last emerged from the sea.

Like all orchids, the male and female reproductive parts of the *M. thomsoniana* flower are fused into a column. The stigma is separated from the anther by a rostellum which prevents autogamy. *M. thomsoniana* is however self-compatible if pollinia are transferred to the stigma by external forces. Isolated observations of anoles visiting the extrafloral nectaries were first reported by Echternacht *et al.* (2000).

Methods

In 2015 and 2016, orchid genets within three phorophytes were monitored daily, in detail, for pollinators from a central location within a 35 by 50 m plot in a mid-island location in Lower Valley, where A. c. conspersus is the relevant subspecies present. I used intensive direct observation paired with time-lapse video to conclusively identify and record behaviours of pollinators and other visitors to the flowers. Anole observations focused on a genet in a Ponciana tree which provides the core of a home range of a male *A. conspersus*. This genet produces up to ten inflorescences in the flowering season, between May and early July. Additionally a minimum of one still image and one 30 second video were captured every five minutes on two Bushnell NatureView HD Max field cameras fitted with f460mm close-up lenses and set up on other inflorescences within the site.

Pollinators

Unusually, the principal pollinator is a flower chafer beetle, *Gymnetis lanius* (Coleoptera: Cetoniinae) (Rose-Smyth, in press). *G. lanius* is limited in distribution to Grand Cayman and Jamaica (Ratcliffe, in press). There are only a handful of orchids known to be pollinated by cetoniids: in South Africa, Asia and Argentina (Singer and Cocucci 1997; Johnson *et al.* 2007; Pedersen *et al.* 2013; Peter and Johnson 2014; Arakaki *et al.* 2016). Additionally, I discovered the Asian Mango flower beetle, *Protaetia fusca* (Coleoptera: Cetoniinae), a first record for this adventive species in Cayman, and an equally effective pollinator of *M. thomsoniana*. Although both species of beetle crawl over the extrafloral nectaries they do not appear to be obviously attracted to them and can spend long periods crawling back and forth on the pedicels and stems and around the outside of the corollas, never visibly feeding. *G. lanius* actually feeds on the flowers of a wide variety of trees and shrubs, most having dense white-flowered inflorescences.

The exact mechanism by which the beetles are deceived to enter the nectarless lip is not yet clear. During the first leg of pollination all eight pollinia are extracted from the anther and glued to the visitor's body. Deposition of pollinia is variable; as few as one, or all eight may be delivered to the stigma.

In 2016, a sample of 19 inflorescences on 5 orchid genets, produced 316 flowers, of which 31% experienced pollinia extraction only, a further 11% experienced pollinia extraction and deposition, and fruit set was 9% (Rose-Smyth, in press). The effective pollinators were the two beetles and to a lesser extent, feral honeybees. Additionally, the Bananaquit, *Coereba flaveola*, and on a single occasion, *A. conspersus*, contributed to extractions-only of pollinia.

Anole behaviour

During the 4-6 weeks that *M. thomsoniana* is in bloom anoles with home ranges encompassing the orchid visit the nectaries at the base of the flower (Fig. 1) and also at the tips of unopened buds, as do a number of ant species. Anoles may creep up the stems, run, and leap from the tree limbs into the flowers. Females sometimes perch, effectively camouflaged, on the brown, persistent, prior year stems. Importantly, anoles do not dislodge the pollinia-containing anther when climbing on the flowers.

In both 2015 and 2016 the Ponciana tree had a resident male and two-three female/subadults. In 2015 the orchid was observed for a total of 57.3 hours over 11 days in June, from as early as 7:20 and up to 18:00. Anole events were observed within the flower clumps 60 times (Fig. 2). Visits equated to between 0.4 - 1.5 times per hour and nectar-licking visits occurred up to 0.8 times per hour. Events ranged in duration from almost instantaneous jumps on and off, to periods of several minutes foraging within the flowers. Forty-four were events where either there was no nectar licking or I could not see the anole's mouth clearly; 16 included confirmed nectaring, often at multiple flowers. Female/sub adults seemed more active than the male even taking into account that they outnumbered the male at least 2:1. Lastly, three of the events occurred when beetles were present; one caused the beetle to fly, the other two anole interventions did not overtly affect the beetle's behaviour (Fig. 2, starred).

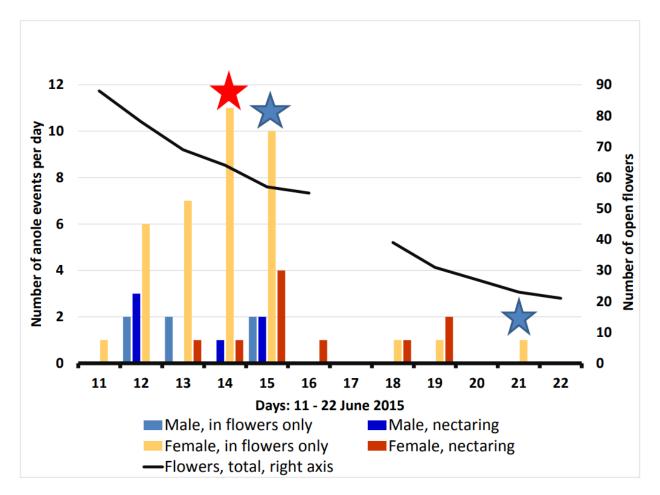


Fig. 2 Anolis conspersus activity in the Ponciana genet, Lower Valley, Grand Cayman from 11^{th} to 22^{nd} June 2015. Left axis = number of anole events per day, total n = 60. Right axis = number of open flowers. No data were collected on 17^{th} June. Blue stars = anole activity on flowers in presence of beetle pollinator having no apparent effect on the beetle; red star = anole activity causing a *Protaetia fusca* beetle with pollinia load to fly away before entering any other flower.

As well as consuming nectar from flowers anoles predate the ants that also visit the nectaries. (See supplemental data video on YouTube: https://youtu.be/rvVHkj7UQz4). Although licking the extrafloral nectaries was never observed to involve the anole putting its head inside the labellum of the flower, when pursuing ants, an anole could be led to do so by an ant running into the tubular cavity of the lip. Based on these behavioural factors, I conclude that a single example of pollinia extraction by a female anole in 2016 (Fig. 3) was most likely the result of the anole snatching at an ant. In this instance the anole did not go to perform pollination. The only

pollinia deposition in the entire genet after she acquired the pollinia was directly observed to be by a *Protaetia* beetle.



Fig. 3 Female *Anolis conspersus* in the flowers of *Myrmecophila thomsoniana* in the Ponciana genet, Lower Valley, Grand Cayman on 8 June 2016 at 17:05. During the course of the day she was observed in the flowers and without pollinia between 09:24 and 09:32; the first confirmed sighting with eight pollinia attached to her head occurred at 15:41 and last at 17:56, shortly before data recording ceased at 18:00 and approximately one hour before sunset. She had lost, or groomed off, all but two of the eight pollinia by the next morning and was observed later in the day with only a yellow smudge remaining.

Discussion

Anolis conspersus has a role in a pollination network that includes an orchid, two beetles, the honeybee, a flower-visiting bird and ants. By extracting pollinia, the behaviour of the anole is confirmed to, albeit rarely, contribute to floral male reproductive fitness and could, conceivably, evolve towards more effective pollinator status. Floral deception is considered to be the ancestral state in orchids and has been shown to have evolved to nectar rewards at least nine times in the large South African genus, *Disa* (Johnson *et al.* 2013). *Myrmecophila thomsoniana* has

apparently undergone one pollinator shift already. The nearest Central America congener of *M. thomsoniana* is pollinated by solitary bees (Parra-Tabla and Vargas 2007).

Currently, *A. conspersus* affects the consistent pollinators both positively and negatively in terms of floral reproductive success. Depending on whether it disturbs beetles before or after pollinia extraction, anole activity can lead to decreased pollination opportunities, or potential for increased outcrossing among genets, respectively. Further, the pollinia extraction, deposition, and natural fruit set rates observed in 2016 are consistent with a degree of pollinator limitation, thus increasing the relative impact of other visitors on pollination success. Importantly, even rare events that promote outcrossing can be significant in an orchid that can produce tens of thousands of seeds in a single fruit.

My future aims include: (a) integrate and analyse all of the 2015 and 2016 data; (b) gather additional quantitative data at the primary site with expanded camera capabilities; and (c) extend the project to assess whether there are any differences in *Anolis conspersus lewisi* behaviour in the eastern districts of Grand Cayman, where the potentially invasive Mango flower beetle is not yet established and pollination rates appear to be lower than at the mid-Island site.

I am pleased to report that the addition of the second field site is paying dividends already. On 15 June 2018 a second occurrence of an anole with pollinia on her head (three) was observed there, within 3 m of the only pollination events of that, or the prior two days, on adjacent inflorescences. These were one extraction-only and one extraction/deposition of four pollinia which implies, at minimum two pollinators and are not inconsistent with the anole causing the pollination. However, actual pollination by *Anolis conspersus* remains to be definitively confirmed.

Acknowledgements

I am grateful to the organisers and participants at Anole Symposium VII for the warm welcome. I also thank my Cayman Islands colleagues, Stuart Mailer and the late Vanessa Block for assistance in the field, and the National Trust for the Cayman Islands for permission to work in its eastern reserve.

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