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INVESTIGATING THE POLLINATION BIOLOGY OF A LONG-LIVED ISLAND ENDEMIC EPIPHYTE IN THE PRESENCE OF AN ADVENTIVE ALIEN POLLINATOR

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Myrmecophila thomsoniana (Laeliinae), though widespread and locally abundant, is endangered through habitat destruction. Pollination biology and phenology of the nominate variety were examined using intensive direct observation and time-lapse videography in Grand Cayman. *Myrmecophila thomsoniana* var. *thomsoniana* is self-compatible and non-rewarding other than via extrafloral nectaries, which attract ants and *Anolis conspersus* (Squamata: Dactyloidae). The orchid is primarily pollinated by native *Gymnetis lanius* (Coleoptera: Cetoniinae). The adventive, alien cetoniid, *Protaetia fusca,* was first recorded in 2015. In 2016, *P. fusca* and non-native, feral *Apis mellifera* accounted for almost half of all pollination events that were identified to species. Blooming was from late May to early July, coincident with the onset of the rainy season. In the sample reported, receptive flowers totaled 316, mean per inflorescence 16.63(± s.d. 6.17).

The flowering maximum was negatively correlated with pollination events. Pollinarium removal was 42%, depositions 10.7%, and successful fruit set 9.2%. These data are valuable for development of a species conservation plan *for* M. *thomsoniana* var. *thomsoniana* and indicate that this orchid can be an important tool for the study of effects of alien species on reproductive success and evolutionary trends.

Although rediscovery of the type specimen of *Myrmecophila thomsoniana* (Rchb.f.) Rolfe (Laeliinae, Orchidaceae) has dispelled confusion as to the nomenclature of the species and its varieties (Rose-Smyth 2016), the life-history traits of the national flower of the Cayman Islands are largely unknown. As one of only a handful of endemic species in the Cayman flora, M. *thomsoniana* is rated as EN A3bc on the IUCN Red List because habitat destruction threatens the primary habitats in which it is widespread and locally abundant (Barrios and Burton 2014). *Myrmecophila thomsoniana* is also protected under the National Conservation Law 2013 of the Cayman Islands. The law requires that a species conservation plan be prepared and approved through a process of public consultation. In addition to the value of autecology to inform conservation efforts, data for M. *thomsoniana* may contribute to the body of data for species recently evolved on oceanic islands, often a source of pollination biology novelty (Mayer *et al.* 2011).

Casual observation confirms that M. *thomsoniana* var. *thomsoniana* (hereinafter simply referred to as M. *thomsoniana)* blooms in Grand Cayman in the early part of the rainy season and produces seed capsules that mature and disperse seeds within two to three months of first flowering. Pollinator-exclusion and hand-pollination experiments show that M. *thomsoniana* is self-compatible but not autogamous. *Gymnetis lanius* L. (Coleoptera: Scarabeidae: Cetoniinae) is a medium (length 16-20mm) flower chafer that flies, coincidentally, from May to July in Grand Cayman. Occasional sightings of G. *lanius* in the vicinity of blooming orchids and a close encounter in which the beetle clumsily bounced off a plant led to speculation that it could be a pollinator.

This paper reports preliminary results based primarily on intensive direct observation and time-lapse videography conducted in 2016 aimed at describing the flowering phenology and pollination biology of this orchid. Supplemental observations of floral visitors from

2012, 2014, 2015, and 2017 are included to provide a complete list of observed visitors. The behavior of selected floral visitors in the early part of the flowering season is described. Two cetoniid flower chafer beetles (one an adventive alien), an endemic curculionid weevil, and non-native feral honeybees were identified as legitimate pollinators.

Material and methods

Observations were carried out in and adjacent to natural and regenerating dry forest at Lower Valley in central Grand Cayman, 19.274N, 81.290W, in which *in situ* and re-established orchid genets occur epiphytically on native and naturalized trees in a plot measuring approximately 35×50 m. Flowering phenology of 19 inflorescences among five genets and direct observation of flower visitors and pollinators of 16 inflorescences on three genets were coupled with time-lapse photography of two inflorescences per day from among the 19, using two Bushnell NatureView HD Max field cameras fitted with f460mm close-up lenses. Time-lapse was set to capture one still image and one 30-second video every five min. Movement in the field of view could also trigger image capture. Data were collected from 27 May to 11 July 2016; daily observation periods were from pre-dawn to sunset with limited exceptions.

The phorophytes on which the three focal genet were established were located in a 180° arc such that direct visual observations could be conducted from an observation post at a distance of 5-10m. Genets were labeled according to phorophyte and inflorescences tagged individually. Position of nectaries, production of nectar, and presence or absence of scents were noted.

Behaviors of arthropod, avian, and herpetofauna visitors were recorded manually and/or photographed from as close as the specimens permitted without interfering with the plant-animal interactions. Supplemental observations of floral visitors, including food plants of the herbivorous beetles, were made at the same study site at the Queen Elizabeth II Botanic Park, Colliers Wilderness Reserve, East End, and in the author's rural garden in Lower Valley.

Phenological data collected were total flowers per inflorescence, dates of anthesis, pollinia extraction, pollinia deposition, seed-capsule formation, and commencement of natural senescence.

The *M. thomsoniana* pollinarium is composed of eight pollinia enclosed in a compartmentalized anther cap. While the entire pollinarium is invariably extracted when the anther is dislodged, deposition may vary from 1-8 of the individual pollinia. Ne'eman *et al.* (2009) and King *et al.* (2013) advocated single-visit deposition (SVD), defined as number of pollen grains delivered by a given pollinator to the stigma of a flower in a single visit as the preferred metric of pollen-deposition effectiveness. In orchid species in which microscopic pollen grains are packaged in more than one discrete pollinium, the number of pollinia deposited is a practical simplification of the concept.

Numbers of pollinia deposited per stigma (and on any other part of the flower) were recorded; however, for the purposes of this paper, SVD is defined as deposition of any number of pollinia on the stigma. Pollination event refers to either a pollinarium extraction or deposit of pollinia.

Results

Floral visitors

Nectaries on *M. thomsoniana* are located extraflorally on the dorsal tips of the sepals, at the distal end of the ovary above the proximal ends of the sepals and petals (here termed basal nectaries), and at the bracts where the pedicels spring from the stem. No nectar is produced within the tube formed by the column and labellum. Nectar production is neither regular nor continuous. The significant species groups visiting *M. thomsoniana* in the flowering seasons 2012-2017 (other than 2013, which was not sampled) were three beetles, four ants, two lizards, two birds, honeybee, paper wasp, and the caterpillar of a day-flying moth (Table 1). These floral visitors may be divided between native and non-native species and according to the nature of their activities and impact on pollination success. From 2015 two of the three beetles and the honeybee were all found to be frequent and effective pollinators. An endemic curculionid weevil, *Lachnopus vanessablockae* Girón & O'Brien, was the first pollinator to be discovered in a single pollination event occurring in June 2012. *Gymnetis lanius* was confirmed to be the primary native pollinator in 2015 (Fig. 1A).

There is some evidence that synchronous emergence may occur in some years. On 9 May 2015 hundreds of beetles were observed at the Queen Elizabeth II Botanic Park swarming over native trees along a service road. Large numbers can also congregate on ripe mangoes that have been opened by other frugivores. The flight behavior of *G. lanius* in the study site consisted of large, looping trajectories in open space with wide to narrowing spirals toward the floral displays, indicating attraction to the floral scent. Flight direction was not correlated with wind direction or speed. Beetles could spend up to several minutes circling in and around a phorophyte before attempting to land or flying away. *Gymnetis lanius* can be exceedingly clumsy, bouncing off twigs, leaves, and flowers before alighting. They rarely landed in an appropriate "approach for pollination" position on the lip of the flower, and even if one did, it often crawled sideways to the outside of the flower. If the beetle did not fly again immediately after landing, it might spend many minutes crawling over the flower, traversing up and down the pedicels, back to the same flower or onto another. Many leave without ever attempting to enter the lip cavity; those that do may back out before penetrating far enough to trigger the removal of the anther. Individuals of *G. lanius* were observed flying and landing on the orchids in the predawn, but no evidence of nocturnal activity was collected by the time-lapse cameras. Flight continued through the morning hours and tapered off from the early afternoon. (Supplemental data video YouTube: https://youtu.be/ONMVVk6nGe8)

Gymnetis lanius that managed to land on orchid flowers paid scant attention to the extrafloral nectaries and did not eat floral parts. Actual food plants for *G. lanius* observed in the course of the study are a range of native species (other than mango) typically having loose to densely paniculate inflorescences of small whitish flowers (Table 2).

Protaetia fusca Herbst (Coleoptera: Scarabeidae: Cetoniinae) (Asian mango flower beetle) was first recorded in 2015 at both Lower Valley sites and has continued to be abundant in the orchid flowering season (Fig. 1B). *Protaetia fusca* is smaller and faster than *G. lanius* and more adept at landing. It also spirals toward floral displays and may zig-zag tightly before alighting. Crawling behavior is similar to *G. lanius*, and these beetles also did not seem to be attracted by nectaries. Individuals may spend up to 24 hours "parked" between the lip and the sepals and petals. *Protaetia fusca* can sometimes penetrate the lip cavity and reverse out without dislodging the anther. Most individuals of *P. fusca* observed on the orchid displayed the characteristic male terminal spines on the elytra. *Protaetia fusca* was not observed flying as early in the morning as *G. lanius* and continued to be more active into the afternoon hours. (Supplemental data video YouTube: https://youtu.be/adT5JZbL0lQ)

The third frequent and effective pollinator was non-native *Apis mellifera* (Hymenoptera: Apidae) (Fig. 1C), which may be feral or domesticated. Single individuals may approach several flowers in succession, occasionally landing at the basal nectaries or may approach the lip tube more directly and probe for rewards within the lip. Bees may exit the lip

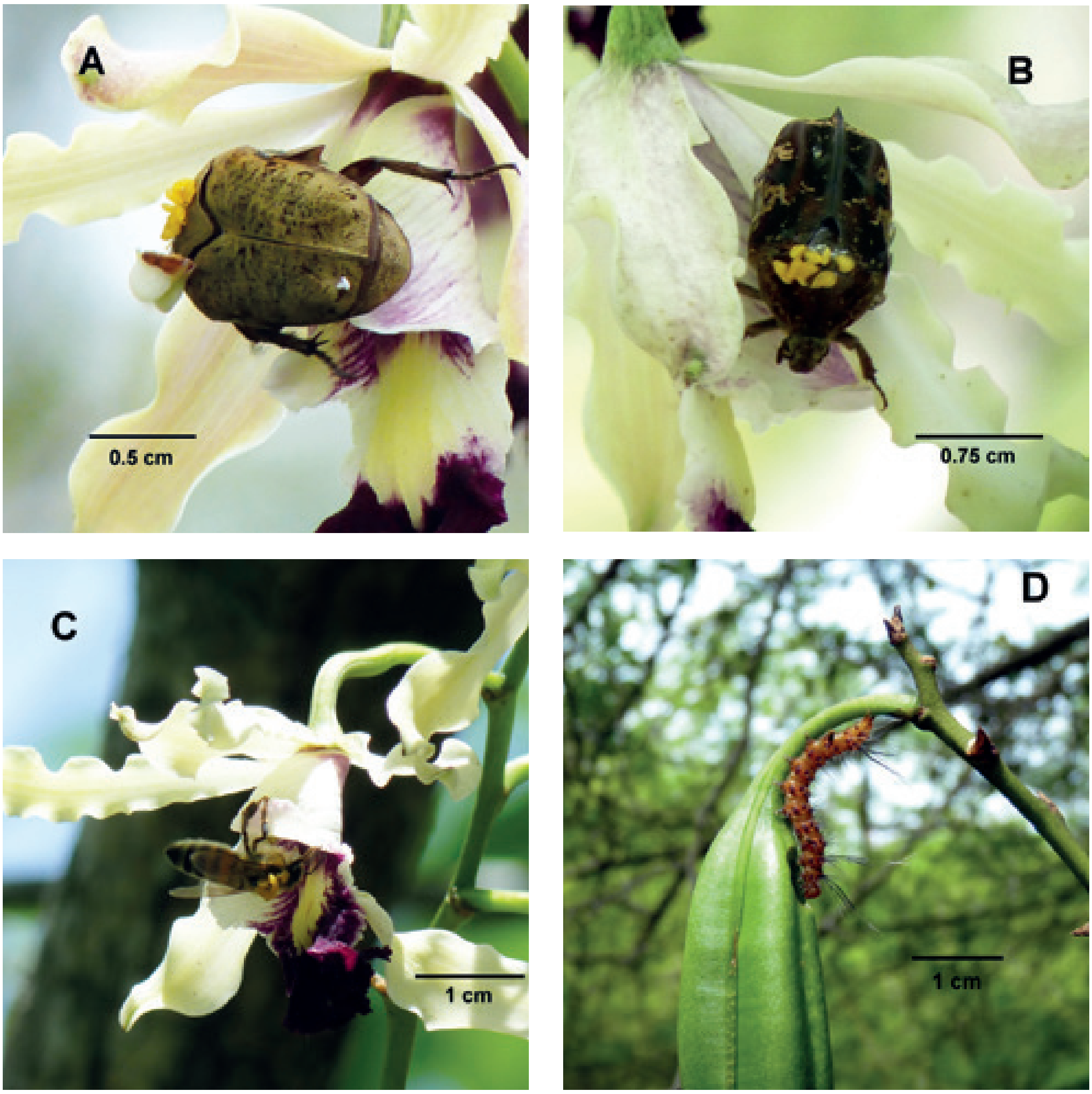

Fig.1. Pollinators and seed predator of *Myrmecophila thomsoniana* in Grand Cayman. (All photographs by the author). A. *Gymnetis lanius*; B. *Protaetia fusca* individual involved in both extraction and deposition of pollinia on 9 June 2016 shortly after the initial extraction. Male elytral terminal spines evident; C. *Apis melifera*; D. Caterpillar of *Empyreuma cf. affinis* attacking immature seed capsule.

in an orderly way or may tumble out and fly erratically, perhaps dependent on whether the pollinarium has attached cleanly to the thorax or not. Bees may fly away immediately, but continuous probing resulting in geitonogamous pollinations have been observed on two occasions (26 June and 1 July 2016). Native solitary bees, *Megachile jerryrozeni* (Hymenoptera: Megachilidae) and *Xylocopa* sp. (Hymenoptera: Apidae), neither of which are abundant, were infrequently observed but not recorded at flowers of M. *thomsoniana*.

Like M. *thomsoniana*, *Anolis conspersus* (Squamata: Dactyloidae) is endemic to Grand Cayman. *Aolis conspersus* is a trunk-crown ecomorph (Losos 2009). Where home ranges include trees with M. *thomsoniana*, both males and females may visit the basal nectaries frequently and may also pursue the ants that frequently traverse the inflorescences. The single example of pollinia extraction by a female anole (8 June 2016) was mostly likely the result of the anole pursuing an ant, as the anoles otherwise do not appear to be at all attracted to probe the interior of the lip.

Table 1. Visitors to flowers of *Myrmecophila thomsoniana* having positive or negative impacts on pollination success. Observations 2012–2017. Y and y = observed, N and n = not observed; capitalized letters indicate multiple observations; lower case = action (or absence of action) confirmed by observation but rare or of limited effect. p = some individuals observed at extrafloral nectaries but no clear evidence of nectar consumption. Nect = Nectivore; Flor = Florivore; Sp = Seed Predator.

Species	Species status	Male fitness	Female fitness	Behavioral interference	Nectivore	Florivore	Seed predator
Gymnetis lanius (Coleoptera: Cetoniinae)	Jamaica and Grand Cayman only	Y	Y	y	Np	N	N
Protaetia fusca (Coleoptera: Cetoniinae)	Non-native	Y	Y	y	Np	N	N
Apis mellifera (Hymenoptera: Apidae)	Non-native	Y	Y	n	Np	N	N
Anolis conspersus (Squamata: Dactyloidae)	Cayman endemic	y	N	Y	Y	N	N
Lachnopus vanessablockae (Coleoptera: Curculionidae)	Cayman endemic	y	y	n	n	y	N
Coereba flaveola sharpei (Aves: Passeriformes)	Cayman endemic	y	N	y	N	N	N
Ant spp. (at least 4 species) (Hymenoptera: Aculeata)	Native	N	N	N	Y	N	N
Pollistes major (Hymenoptera: Vespidae)	Native	N	N	N	y	N	N
Spindalis zena salvini (Aves: Passeriformes)	Cayman endemic	N	N	y	N	y	N
Iguana iguana (Squamata: Iguanidae)	Invasive non-native	N	N	y	N	Y	N
Empyreuma cf. affinis (caterpillars) (Lepidoptera: Noctuoidea)	Native	N	N	N	N	y	Y

Individual paper wasps, *Polistes major* (Hymenoptera: Vespidae), were occasional visitors to the inflorescences of the poinciana genet during 2016; however, once contacting with nectaries, certain individuals spent considerable time moving methodically through the flowers of an inflorescence and then from inflorescence to inflorescence (e.g. 15 minutes from 14:30, 8 June).

The bananaquit, *Coereba flaveola sharpei* (Aves: Passeriformes), is the Cayman Islands endemic subspecies of a widespread Neotropical species that feeds primarily on nectar by piercing the sides of flower tubes and spurs (Bradley and Rey-Millet 2013). Immature bananaquits were the age group most frequently observed interacting with orchid flowers. Naïve birds probed the side lobes of flowers leaving characteristic piercings and shredded tissue. Piercing at the base of the column does not ordinarily result in removal of the anther but usually leads to premature senescence of the flower. In one instance, pollinia removal could reasonably be attributed to aggressive piercings. On 28 June 2016, five of the six remaining open flowers on one inflorescence were found with pollinia extracted; four had pierced and torn lips, whereas the fifth did not. A seventh flower in the course of senescence, having been pollinated on the 27th, was also pierced, and the germinated pollinia were not affected.

Florivory by the non-native green iguana (*Igua-*

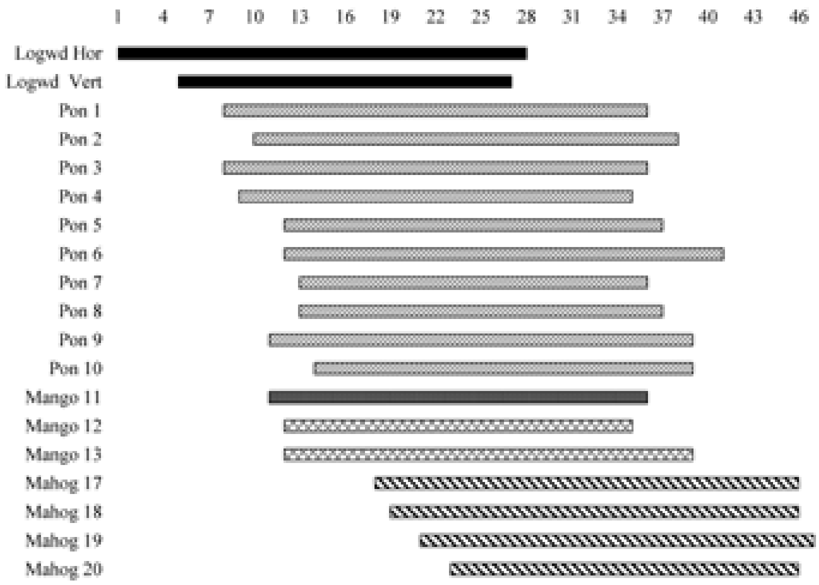

Fig. 2. Flowering periods of 19 inflorescences in five genets between 27 May (Day 1 on the horizontal axis) and 11 July (Day 46). Each genet is represented by a change in bar-hatching.

na iguana) was observed directly in the study site on 22 June 2015 when a medium-size adult paused while ascending the mahogany phorophyte to reach out and draw an inflorescence toward it. The iguana tore off one flower and parts of others before continuing up into the canopy of the tree. In 2017, 49 flowers (including two that had been pollinated) across six inflorescences of a different genet were completely consumed over a period of six days by a smaller juvenile iguana. A further antagonistic actor affecting pollination success is a caterpillar attributed to the day-flying species *Empryeuma affinis* (Lepidoptera: Noctuiodea). Caterpillars of varying sizes were observed feeding on *M. thomsoniana* flowers in both 2015 and 2016. In 2015 large caterpillars were found cutting circular holes in fruits in order to enter the interior and consume the developing seeds (Fig. 1D), resulting in the loss of three seed capsules formed in the study population. Twelve other taxa of visitors to *M. thomsoniana* fell into two broad categories: visiting for nectar or for shelter (Table 3). All were uncommon or rare, and none was seen to have a negative impact on pollination.

Phenology

Though the sample of five genets presented here was not large enough to perform meaningful statistical analysis, these and other field observations in Grand Cayman support the following statements: the number and size of *M. thomsoniana* inflorescences are related to genet size; larger genets produce more inflorescences, and those are more likely to be panicles, whereas smaller inflorescences are simple racemes. Growth is determinate; the abortive terminal buds on the side branches and main axis have usually differentiated by the time the lower buds open.

From first receptive flower to last senescence, the 2016 sample population was in flower for 46 days. Mean individual inflorescence longevity was 26 days. Flowering tended to be synchronous within genets (Fig. 2). Flowering and pollination metrics are presented in Table 4. Receptive flowers totaled 316, and mean, minimum, and maximum flowers per inflorescence were 16.63(± S.D. 6.17), 10, and 33, respectively. Compared to total flowers available, pollinarium removal was 42%, all depositions 10.7%, and successful fruit set 9.2%. Of the five depositions that did not result in a viable seed capsule, three were accounted for by deposition of pollinia onto the edge of the rostellum such that the pollinia did not contact the stigmatic surface. Thus, on the defini-

Table 2. Food plants of *Gymnetis lanius* observed directly in Grand Cayman 2015-2017, other than *Erythoxylum areolatum* which is illustrated in Proctor (2012), from which the flower forms and colors are also drawn.

Species	Common name	Family	Flowers	Color
Petitia domingensis Jacq.	Fiddlewood	Lamiaceae	small in cymose panicles	creamy-white
Chionanthus caymanensis Stern	Ironwood	Oleaceae	small in many flowered panicles	white, fragrant
Erythroxylum areolatum P. Browne	Smokewood	Erythroxylaceae	small, clustered in leaf axils	creamy-white, fragrant
Calyptranthes pallens Griseb.	Bastard strawberry	Myrtaceae	small in sessile clusters in many flowered panicles	light golden
Myrcianthes fragrans (Sw.) McVaugh	Cherry	Myrtaceae	small in dichasia in leaf axils	white
Hypelate trifoliata Sw.	Pompero	Sapindaceae	small in axillary panicles	creamy-white
Smilax havanensis Jacq.	Wire Wiss	Smilacaceae	small, umbellate at leaf axils	greenish white
Croton linearis Jacq.	Rosemary	Euphorbiaceae	small on terminal racemes	white
Passiflora suberosa L.	Passion vine	Passifloraceae	medium, 1-2 in axils	greenish white
Mangifera indica L.	Mango	Anacardiaceae	small in large terminal panicles	variable – greenish white, pinkish golden

tion of SVD adopted above, 31 (9.8%) flowers received effective deposition of pollen. The flowers receiving non-effective depositions of pollinia senesced at the same rate as flowers from which pollinia had been extracted and no depositions made.

The other two failures both followed deposition of a single pollinium into the distal corner of the stigma and apparent germination. Both flowers exhibited slight thickening of the ovary but failed and turned yellow-brown 10 and 12 days after pollinia deposition, respectively. Failure of seed capsules to mature constituted 6.45% of SVD.

Anthesis followed a normal curve, and the flowering maximum of 184 occurred on 20 June (Fig. 3, solid line). Pollinator events showed a distinct bimodal distribution for pollinarium extraction and a similar but less distinct distribution for depositions and fruit set coupled with a rise in late June/early July (Fig. 3, bar chart). Significantly, from the second week, *G. lanius* was to be found feeding on fiddlewood and ironwood, both within the immediate site and surrounding native vegetation. The fiddlewood bloomed in successive flushes, whereas the ironwood trees bloomed in a single flush for about a week.

Forty-two of the 134 (31.3%) pollination events in this subset of the study population were observed directly and/or via time-lapse videography. The difference in observed sources of early- and late-season pollination events can be illustrated by comparing the seven-day periods 4-10 June and 26 June-2 July (Fig. 4). *Gymnetis lanius* and *P. fusca* predominated in the early period and honeybees in the later one. Of all pollination events observed directly, *P. fusca* and *A. mellifera* together accounted for almost half (20 of 42), and *P. fusca* alone represented an increase of 88% compared to *G. lanius* events. Although no *G. lanius* events were observed directly after 15 June, we are

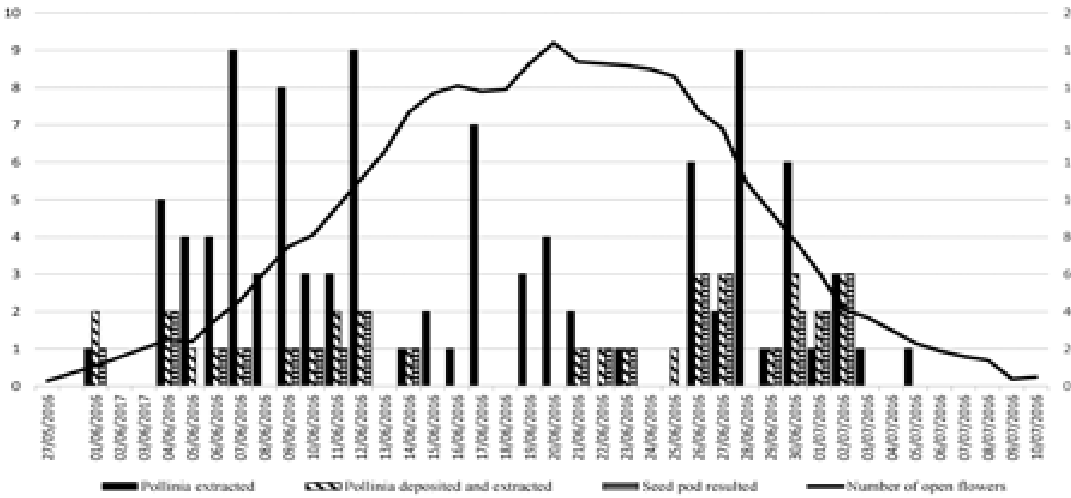

Fig. 3. Gross phenology and pollinator events recorded between 27 May and 5 July 2016 for 19 inflorescences of *Myrmecophila thomsoniana* on five genets. Solid line (right axis): receptive flowers per day, N = 316; the flowering maximum (184) occurred on 20 June. Bar chart (left axis): number of pollinator events. Each event was a single-visit, with one exception that could be interpreted as two deposits onto a stigma (2/7). In five cases of pollinia deposit and extraction seed capsules failed to mature (1/6, 5/6, 11/6, 25/6, and 30/6); in one case no pollinia were extracted, but one pollinium was deposited and did result in a viable seed capsule (30/6).

confident that this species continued to contribute some pollination events based on continued approaches made to inflorescences, though at a reduced frequency.

Discussion

Myrmecophila thomsoniana is deceit-pollinated in the sense that it does not offer meaningful nectar or pollen rewards to pollinators. It is principally pollinated by one near-endemic beetle species (*G. lanius*), which occurs in Jamaica and Grand Cayman but is not recorded from Cayman Brac or Little Cayman (Ratcliffe, 2018). It was seen to be pollinated once by an endemic weevil (*Lachnopus vanessablockae*), and two other endemic visitors (*Anolis conspersus* and *Coereba flaveola sharpei*) to the flowers are potential pollinators, albeit at a low frequency. Two exotic species (*Protaetia fusca* and *Apis mellifera*) are also capable and significant pollinators at the Lower Valley study site.

These observations of *P. fusca* constitute a new record for the Cayman Islands beetle fauna. *Protaetia fusca* is native to Southeast Asia and

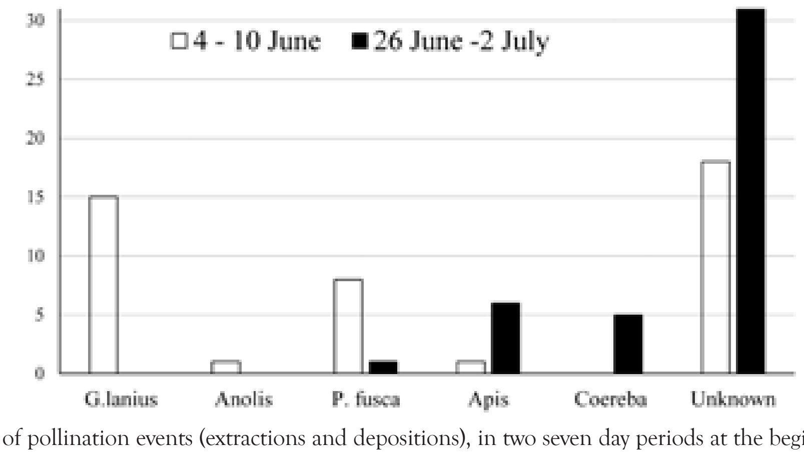

Fig. 4. Distribution of pollination events (extractions and depositions), in two seven day periods at the beginning and end of the flowering season, by five species of actors observed directly and via time-lapse videography (other than Coereba flaveola extractions, which were inferred from characteristic piercings of the labellum) and also events for which no actor was observed. The flower beetles (*Gymnetis lanius, Protaetia fusca*) and honeybee (*Apis mellifera*) were solely responsible for deposition of pollinia and successful seed capsule formation.

Table 3. Visitors to flowers of *M. thomsoniana* 2012-2017 having no apparent effect on pollinators

Species	Activity	Frequency
Sarcophaga sp. (Diptera: Sarcophidae)	Visitor to extrafloral nectaries	Occasional
Blue–black hoverfly (Diptera: Syrphidae)	Visitor to extrafloral nectaries	Uncommon
Gallipeza sp. (Diptera-Micropezidae)	On exterior of flower, at nectaries	Rare
Spider (Aranaea)	Resident in the lip tube, web “door”	Less than one per inflorescence
Osteopilus septentrionalis (Amphibia: Hylidae)	Lodged in lip	Single occurrence 2015
Ladybird (Coleoptera: Coccinellidae)	Lodged in lip	Single occurrence in 2016
Crickets (Orthoptera: Gryllidae)	In lip tube or on tepals	Rare
Cockroaches (Blattodea)	In lip tube or on tepals	Rare
Green lacewing (Neuroptera)	In lip tube or on tepals	Rare
Planthopper (Hemiptera)	In lip tube	Rare
Brown/tan beetle (Coleoptera)	On pedicel of senesced flower	Rare
Polycesta goryii (Coleoptera: Buprestidae)	On flower	Single casual visitor; other observations confirm it is not ordinarily attracted to flowers

Australasia, has invaded numerous Pacific and Indian Ocean islands (Krell and Breidenbaugh 2016), and is known to be adventive in the Bahamas since 1979 and in southeast Florida and Barbados since 1982 (Woodruff 2006), and more recently in the Caribbean Leeward Islands of the Guadeloupe Archipelago and St. Barthélemy (Peck *et al.* 2016). The Lower Valley study sites are adjacent to or within 2.0 km of four horticultural nurseries, including the Department of Agriculture, which all import fruit trees periodically and may have been the source of the importation of *P. fusca*. The date of introduction of *A. mellifera* into Grand Cayman is not known, but the earliest permanent settlements date to the mid-18th century. Individuals of *P. fusca* observed on *M. thomsoniana* closely enough to make the determination exhibited male elytral spines (Fig. 1 B). Interestingly, in Japan, females of *Protaetia pryeri* are never found on *Luisia teres* (Thunb.) Blume, but males are the effective pollinator and sometimes engage in pseudocopulation behavior on the lip (Arakaki *et al.* 2016).

The discovery of another orchid naturally pollinated by beetles adds to a small but diverse collection of species across the Orchidaceae having beetles, often flower chafers, as pollinators (Johnson *et al.* 2007; Pedersen *et al.* 2013; Peter and Johnson 2014; Arakaki *et al.* 2016). One example of a *Gymnetis* sp. exhibiting landing behavior similar to those of G. *lanius* was observed on a member of subtribe

Eulophiinae in central Argentina, the primary pollinator of which is another cetoniid, *Euphoria lurida* (Singer and Cocucci 1997).

Honeybees and bananaquits are distributed across the entire island of Grand Cayman, but *P. fusca* appears to be currently limited in distribution in Grand Cayman to the Lower Valley area. Comparison of the Lower Valley orchid population with populations in which *P. fusca* is absent will assist in calculating the impact of this potential invasive species.

Such extrafloral nectar as is produced is primarily consumed by ants and secondarily by anoles that have learned to recognize its presence. *Anolis conspersus* is a facultative visitor to nectaries and has the propensity to spend significant periods moving within the flowers of *M. thomsoniana* inflorescences throughout the flowering season. It therefore has the capability of being a significant cause of interference with pollination either through preventing pollinators from landing or causing them to flee when the anoles jump onto the inflorescence. Anole disruption after pollinia extraction may, however, be a positive influence for outcrossing. Green iguanas appear to have varying taste for *M. thomsoniana* flowers, but once that taste is acquired it can lead to stripping of entire inflorescenses and genets. This highly invasive species was introduced into the pet trade in Grand Cayman in the 1980s and is now a severe threat to native flora and fauna (Department of Environment, unpubl.). Road-building into primary woodlands present easy entry for the invaders. Pollinarium removal and fruit set as a percentage of total floral display of 42% and 9.2% was considerably higher than the average rates of ~9% and ~3% reported for the Mexican congeneric *M. christinae* Carnevali & Gómez-Juárez, the known pollinators of which are native *Eulaema* (Hymenoptera: Apidae) and *Xylocopa* bees (Parra-Tabla and Vargas 2007).

Figure 3 clearly indicates that pollinator activity declined during the peak of flowering. Coupled with the observations of activity periods of the four main actors (Fig. 4), the flowering season in the sample population for 2016 can be described as follows: 1) an initial period of intensive *G. lanius* presence in the first two weeks with the beetle activity declining to much lower levels due to diversion to rewarding food plants (and also, probably, fewer absolute numbers); 2) emergence of *P. fusca* as a pollinator after the first week and its continuation at moderate levels until the end of flowering; 3) high activity by honeybees and

Table 4. Metrics for 19 inflorescences of *M. thomsoniana* flowering between 27 May and 11 July 2016. Mean ± S.D. and range per inflorescence and as a percentage of total flowers where applicable.

	N	Mean	± SD	Range	As % total flowers
Inflorescence longevity (days)	19	25.95	2.17	23-29	
Maximum flowers open simultaneously*	19	12.89	5.52	7-25	
Longest lived flower* (days)	19	18.37	1.77	15-21	
Total flowers	316	16.63	6.17	8-33	
Total pollinia extractions	133	7.00	3.77	2-14	42.0
Total pollinia extractions not accompanied by deposition	100	5.26	3.02	0-10	31.6
Total pollinia depositions	33	1.74	1.52	0-5	10.4
Total pollinia depositions with no extraction	1	0.05	0.23	0-1	0.3
Total seed capsules matured	29	1.53	1.39	0-5	9.2
Total seed capsules failed	5	0.26	0.56	0-2	1.6

*per inflorescence

extractions attributable to a rare bananaquit interference toward the end of the season. Parra-Tabla and Vargas (2004), in a study of four fragmented populations of M. *christinae* in the Yucatan, found that the orchid showed increased fitness away from the flowering maximum, but intensity varied among years and could be dependent on population density.

Further analysis of the complete dataset generated during 2016 will focus on drawing out the finer details of pollinator effectiveness (visitation rates, number of pollinia deposited onto receptive stigmas per event), efficiency in terms of number of pollinia proceeding to germination and seed set, and the respective contributions to autogamy and geitonogamy versus outcrossing by the different pollinators.

Data collected at other natural sites in the eastern districts and over several seasons will enable the background level of native and long-established pollinators to be assessed against the newly arrived cetoniid. On a practical level, these data will provide a foundation for a species conservation plan for M. *thomsoniana.* In the longer term this orchid could be an important tool for the study of effects of pollinator shifts as a driver of reproductive success and evolutionary trends (Van der Niet *et al.* 2014). For example, pollinator limitation may be couched as a within-season negative that could be overcome by increased investment in pollinator attraction if resource limitation over the orchid's life-time could accommodate it (Tremblay *et al.* 2005). If *P. fusca* persists and spreads in Grand Cayman, it will be a natural experiment in effective increased pollinator attraction. Given the long life span of adult M. *thomsoniana*, if the background rate of pollination by G. *lanius* is an adaptive balance of pollinator and resource availability, then substantial increase in pollinations by introduced *P. fusca* represents a perturbation that may be evident in a change in survival before any phenotypic adaption of flowers can take effect.

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Errata

Literature Cited (additions)

On page 81 Ne’eman *et al* 2009 was cited but omitted from the Literature Cited list.

On page 82 the citation for the weevil pollinator, Girón *et al.* 2018, was omitted.

Girón, J. C., O’Brien, C. W., and Rose-Smyth, C. 2018. On the West Indian weevil genus *Lachnopus* Schönherr, 1840 (Coleoptera: Curculionidae: Entiminae): description of new species, annotated checklist and species groups. Zootaxa 4423: 1-85. https://doi.org/10.11646/zootaxa.4423.1.1

Ne’eman, G., Jurgens, A., Newstrom-Lloyd, L., Potts, S. G., and Dafni A. 2009. A framework for comparing pollinator performance: effectiveness and efficiency. Biol. Rev., doi: 10.1111/j.1469-185X.2009.00108.x. Epub 2009 Dec 9.