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ORIGINAL PAPER

Mortal combat between ants and caterpillars: an ominous threat to the endangered Schaus swallowtail butterfly (*Heraclides aristodemus ponceanus*) in the Florida Keys, USA

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Abstract The federally endangered Schaus swallowtail butterfly (*Heraclides aristodemus ponceanus*) has reached critically low numbers. Exotic ants are a potential threat to *H. a. ponceanus* and other rare butterflies as they can attack immature stages. Ant surveys conducted in subtropical dry forests in Biscayne National Park documented ant species diversity and relative abundance. A caterpillar predator exclusion experiment using physical barriers in different combinations evaluated caterpillar survivorship of both early and late instar caterpillars exposed to different threats. Ant-caterpillar interactions were also documented by placing caterpillars on plants and observing physical interactions between caterpillars and ants. A total of 1418 ants comprising 25 ant species was captured and identified. In canopies of *H. a. ponceanus* host plants, 243 ants comprising 12 species were found. The four most common ants collected in the host plant canopies were *Pseudomyrmex gracilis, Camponotus planatus, Cremastogaster ashmeadi*, and *Camponotus floridanus*. The predator exclusion experiment revealed survivorship was significantly lower for early and late instar caterpillars without any physical barrier, as well as for early instars not protected by a mesh cage. *Pseudomyrmex gracilis* and *C. floridanus* were more aggressive towards caterpillars in comparison to other ant species; these two species ranked first and second in the "ant danger index" ranking predatory abilities of the four most common ant species. *Pseudomyrmex gracilis* is a common arboreal exotic ant in Biscayne National Park and presents a major threat to caterpillars during their earliest life stages.

Keywords Formicidae · Florida keys · Invasive species · Papilionidae · Predator–prey interactions · Subtropical dry forests

Introduction

Mortality at every life history stage is common for most invertebrates, but for species whose numbers are reduced or reproduction limited to a short time period, heavy predation on immatures can severely threaten their continued existence (Schoener et al. 2001; Beuzelin et al. 2009; Wagner and Van Driesche 2010). The federally endangered Schaus swallowtail butterfly (*Heraclides aristodemus ponceanus*) inhabits subtropical dry forest and is known from a limited number of locations. Its occurrence is associated with clumped distributions of torchwood (*Amyris elemifera*, Rutaceae), the primary larval host plant (Emmel et al. 1988; Jameson 2002; United States Fish and Wildlife Service 2008). Schaus swallowtail populations in Biscayne National Park (BNP) and North Key Largo (NKL) have declined precipitously over the last 15 years (Salvato 2008; United States Fish and Wildlife Service 2008; Fig. 1). In 2012, two projects were implemented to increase *H. a. ponceanus* population: a captive-breeding program at the University of Florida (Daniels 2014) and the National Park Service (NPS) Schaus swallowtail habitat enhancement project in BNP. The Schaus swallowtail habitat enhancement project capitalized upon ongoing projects that required the elimination of invasive plants in particular

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Data Availability The data are in the process of being archived in Dryad Digital Respository.

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Fig. 1 Geographic range of the federally endangered *Heraclides aristodemus ponceanus* in south Florida. The historic ranged is outlined in *yellow*, the current range is outlined in *red*, and the boundary of Biscayne National Park is outlined in *blue*. Map generated by Lydia Cuni

sections within subtropical dry forests at Elliott and Adams Keys (Whelan 2011; Whelan and Atkinson 2015); over 3000 host plants for the *H. a. ponceanus*, mostly *A. elemifera* and *Zanthoxylum fagara* (Rutaceae), were planted and nurtured in restoration sites at Elliott and Adams Keys. Despite a bottom-up approach (increased food source) to bolster *H. a. ponceanus* populations (Jameson 2002; Dennis et al. 2004; Mathew and Anto 2007), investigations of top-down effects on a rare butterfly concentrated in BNP and NKL are nonexistent (Didham et al. 2007; Salvato 2008; United States Fish and Wildlife Service 2008). Predation by invertebrates, such as ants, can thwart the recovery process (Schoener et al. 2001; Wagner and Van Driesche 2010; Lach et al. 2016). Specifically, most ants are generalist and opportunistic foragers, numerically dominant in subtropical and tropical ecosystems, and active day and night foragers (Carroll and Janzen 1973; Jeanne 1979; Brown 2000; Floren et al. 2002). The ecological impacts of exotic ants inhabiting the islands are unknown, despite their ubiquitous presence in the forests (United States Fish and Wildlife Service 2008; Moreau et al. 2014).

Exotic ants can negatively affect other organisms through predation, competition, and alteration of local habitats (Williams 1994; Vitousek et al. 1996; Mack and D'Antonio 1998; Holway et al. 2002; Lach and Hooper-Bùi 2010; Lach et al. 2016). Prolific exotic ants can become invasive in new territories with novel food resources, reduced interspecific and intraspecific competition, release from natural enemies, and enhanced physiologic abilities to thrive in disturbed environments (Holway et al. 2002; Krushelnycky et al. 2010; Lach et al. 2016; Calcaterra et al. 2016). Approximately 37 exotic ant species have been identified in the Florida Keys, including three species on the top 100 world's worst invasive alien species list: the big-headed ant (*Pheidole megacephala*), the little fire ant (*Wasmannia auropunctata*), and the red imported fire ant (*Solenopsis invicta*) (Lowe et al. 2000; Moreau et al. 2014). Few studies have investigated direct and indirect impacts of exotic ants on native flora and fauna in the Florida Keys, with the exception of red imported fire ants; a laboratory study confirmed that red imported fire ants are highly efficient predators of all immature life stages of the giant swallowtail butterfly (*Heraclides cresphontes*), which were used as a surrogate species for *H. a. ponceanus* (Forys et al. 2001).

Solenopsis invicta has been considered a potential threat to *H. a. ponceanus* because of its aggressive nature (Forys et al. 2001). *Solenopsis invicta* displace native species in disturbed environments; they are efficient predators and scavengers, consuming vulnerable organisms including ticks, caterpillars, beetle grubs, and even mosquito larvae in moist substrate (Porter and Savignano 1990; Forys et al. 2002; Zettler et al. 2004; Allen et al. 2004; Beuzelin et al. 2009). *Solenopsis invicta* form large colonies that can monopolize disturbed sites adjacent to subtropical dry forests (Forys et al. 2001, 2002; Tschinkel 2006). In south Florida, they are unlikely to colonize interior parts of subtropical dry forests because they are mainly habitat-restricted to human-modified, disturbed sites (Tschinkel 1988, 2006; King and Tschinkel 2006).

The exotic graceful twig ant (*Pseudomyrmex gracilis*), is arboreal and also poses potential risk to rare butterflies as the ants search for prey on shrubs and trees (Saarinen and Daniels 2006; Wetterer 2010). An opportunistic, solitary forager, *P. gracilis* mainly scavenges for food in its natural range (Mexico, Central, and South America; Whitcomb et al. 1972). In south Florida, its predatory behavior is deleterious to rare and vulnerable invertebrate species because these ants are physically larger than the other native *Pseudomyrmex* ant species in south Florida (Wetterer 2010; Deyrup 2016); years earlier, Deyrup et al. (2000) warned that the graceful twig was a "possible ecological villain" in Florida. *Pseudomyrmex gracilis* is a common pest on shrubs and trees in both urban and natural environments (MacGown and Hill 2010).

The exotic little fire ant (*Wasmannia auropunctata*) is a small stinging ant that can overwhelm invertebrate prey through aggressive recruitment (Wetterer and Porter 2003). In BNP, *W. auropunctata* has been collected on both trees and ground. The little fire ant inhabits both disturbed and intact forests in BNP. *Wasmannia auropunctata* and *P. gracilis* are native to Mexico and Central America (Wetterer and Porter 2003; Wetterer 2010). All three exotic ant species are native to South America (Buren et al. 1974; McGlynn 1999).

The limited range of *Heraclides aristodemus ponceanus*, reduced habitat, and exposure to natural extreme weather events may not allow its immature stages to withstand exotic and native ant predation over time (Schoener et al. 2001; United States Fish and Wildlife Service 2008), limiting the number of adult butterflies of this endangered species. The current government management protocol for *H. a. ponceanus* reported exotic ants as major threats to the eggs and larvae (United States Fish and Wildlife Service 2008). Here we address potential impacts ants may have on caterpillars that use *A. elemifera* and *Z. fagara* as larval host plants. We want to know: (1) What ant species forage in the canopies of *A. elemifera* and *Z. fagara* in BNP?; (2) Are the most common ant species native or exotic?; (3) Are crawling or non-crawling predators greater threats to *Heraclides* caterpillar species?; and (4) How do interactions between the most common ant species and *Heraclides* caterpillar species compare?

Methods

Site description

Biscayne National Park (BNP) became a national park in 1980, with most of its area (95%) comprised of marine environments. The terrestrial area consists of a narrow strip of land on the mainland and 42 islands, most of which is dominated by mangrove forest (2400 ha). Coastal subtropical dry forests, critical habitat for *H. a. ponceanus*, make up only 723 ha (23%) of the terrestrial lands (Whelan et al. 2013). Elliott Key (25°27′12.39″N, 80°11′39.05″W), the largest island, is roughly 7 miles long, and nearly a mile wide, with subtropical dry forests covering 68 percent of the area (Whelan et al. 2013). On Adams Key (25°23′52.34″N, 80°14′05.67″W), subtropical dry forests account for 43% of the area.

South Florida has a distinct wet-dry season: the rainy season typically starts early June and continues through October; however, dry spells can occur in July and part of August (Snyder et al. 1990). The univoltine *H. a. ponceanus* emerges from its chrysalis typically in May with a flight season lasting until mid-June; occasionally, a second emergence happens mid-August and September depending on the amount of rain (Loftus and Kushlan 1984; Emmel et al. 1988; Minno and Emmel 1993). *Heraclides aristodemus ponceanus* have been reported flying as early as April. Currently, the largest population of *H. a. ponceanus* inhabits BNP, particularly Elliott and Adams Keys (Minno 2015).

Ant survey

Ant surveys were conducted for 1 year (December 2013–November 2014) in the subtropical dry forest at Elliott and Adams Keys. Ants were collected using pitfall traps to characterize relative species abundance and diversity (Wang et al. 2001; Andersen et al. 2002); each trap was a 50 mL plastic test tube filled with 20 mL of lemon-scented, soapy water solution, with one hole (1.5 cm diameter) drilled into each screw-on cap to protect against adverse weather conditions (Wang et al. 2001; Ribas et al. 2003; Lubertazzi and Tschinkel 2003). Each sampled area was selected based on the presence of *A. elemifera* and *Z. fagara*, along a North–South gradient at Elliott Key, and an East–West gradient at Adams Key, differing because of the islands' overall shapes. Non-host trees in the forest, 10–15 m away from each *A. elemifera* and *Z. fagara* sampled, were also sampled. Four pitfall traps were placed on or near each tree: one at the base, one on the trunk (2 m above the ground), and two in the canopy. Pitfall traps were dispersed throughout the sampled areas every month, collecting crawling insects for 5 days. Afterwards, collected ants were preserved for subsequent determination. A total of 296 pitfall traps was deployed on 74 trees at Elliott and Adams Keys. One hundred forty-eight traps were placed in tree canopies, 74 were placed on the trunk, and 74 were partially buried in the ground adjacent to the base of each tree. Thirty *A. elemifera*, 14 *Z. fagara*, and 30 non-host trees were sampled during the study.

Caterpillar predator exclusion experiment

A 2×6 factorial design with six treatments was employed to compare the effects of crawling and non-crawling predators against caterpillars of two different sizes (modified from Koptur et al. 1998; Cuautle and Rico-Gray 2003; Mestre et al. 2016). This experiment was conducted from March 2014 to November 2014. Using soft forceps, early (<1.5 cm) and late (>3 cm) instar *H. cresphontes* caterpillars (used as a surrogate for *H. a. ponceanus* caterpillar) were gently placed on *Z. fagara* in the forest at Elliott Key only; logistical constraints did not allow this experiment to be adequately conducted at Adams Key. Despite *H. a. ponceanus* preference for *A. elemifera*, they also utilize *Z. fagara* as a secondary host plant (Jameson 2002; United States Fish and Wildlife Service 2008). The majority of *H. cresphontes* caterpillars, raised in an outdoor nursery at Florida International University for both the caterpillar predator exclusion experiment and ant-caterpillar interaction study, were fed *Z. fagara* leaves, due to both logistical and financial constraints of maintaining an adequate supply of *A. elemifera*.

Treatments applied to caterpillars were: (1) no barriers (no tanglefoot/no cage), (2) tanglefoot present/no cage, (3) no tanglefoot/cage with holes present, (4) tanglefoot present/cage with holes present, (5) no tanglefoot/cage present, and (6) tanglefoot present/cage present. Tanglefoot® is a non-toxic, non-drying, sticky resin that creates a barrier and deters crawling insects from crossing it. Cages were made from recycled 32 oz sports drink bottles that were cut open, shaped into a frame, and placed over a wild lime branch. Ultra-fine cotton cheesecloth was placed over the sports drink bottle frame and sealed with staples and white zip ties. One caterpillar was placed on a branch inside the cage or without a cage; for early instar caterpillars, each treatment had 16 replicates; for late instar caterpillars, each treatment had 15 replicates. Some treatments required holes in the mesh cage; therefore, six holes ($r = 1.5$ cm) were cut into the mesh. Each individual *Z. fagara* tree received a randomly assigned assortment of 6–8 treatments spread across different branches. Each *Z. fagara* tree was thoroughly scrutinized for caterpillar presence or absence after 5 days and recorded to determine survivorship for each treatment. No *Z. fagara* tree was used more than once during the experiment.

Ant-caterpillar interaction study

Ant interactions with both early (<1.5 cm in length) and late (>3 cm) instar caterpillars were conducted in the forests at Elliott and Adams Keys from April 2014 to October 2014. *H. cresphontes* caterpillars were again used as surrogate species, as they also use *A. elemifera* and *Z. fagara* as host plants in BNP, and interact with the same ant species. Foraging ant locations were selected based on relative abundance (determined from previous ant surveys) in the canopy of *A. elemifera* and *Z. fagara*. An individual caterpillar was placed on a leaf (*A. elemifera* and *Z. fagara*) and allowed to settle before interacting with ants. Observations ended after 10 min upon first contact, unless the caterpillar was removed before that time (Oliveira et al. 1987; Bächtold et al. 2012; Sendoya and Oliveira 2015). Observers timed each interaction trial from the first contact between ant and caterpillar. The caterpillar's fate was reported after each trial. Caterpillar mortality was defined as removal by ant species or caterpillar leaf abandonment (dropping from the leaf to avoid ant harassment). No caterpillars or ants were used more than once during this study; for early instar caterpillars, 16 trials each were conducted with *Camponotus floridanus* and *Camponotus planatus*, 15 trials with *P. gracilis*, and 10 trials with *Cremastogaster ashmeadi*; for late instar caterpillars, 15 trials each were conducted with *C. floridanus, C. planatus*, and *P. gracilis*, and 11 trials with *C. ashmeadi*.

Data analysis

A generalized linear model (negative binomial with log link to account for overdispersion) was used to model the frequency of *P. gracilis* on trees. The negative binomial model was selected as the best-fit model to account for overdispersion and true zeros. Model comparisons (poisson and negative binomial) were analyzed using the program IBM® SPSS® Statistics 22 (2013).

A contingency table analysis was performed on data collected from the caterpillar predator exclusion experiment. Adjusted standardized residuals (Z-scores) calculated from the contingency table were transformed by squaring them to obtain Chi square values. Afterwards, the Chi square values were used to calculate exact p values with the significance function group in SPSS. Exact p values were compared to the adjusted α-value to determine significance. Adjusted α-values were calculated by dividing the accepted α-value of 0.05 by the total number of factors (12) which equaled 0.004167. Exact p values equal to or less than the adjusted α-value were considered significant.

A Shapiro–Wilk test for normality was performed on the discovery time for the ant-caterpillar interaction study. A one-way ANOVA was performed followed by the Fisher's Least Significant Difference post-hoc test. All data analyses reported above were conducted using IBM® SPSS® Statistics 22 (2013).

An Ant Danger Index (ADI) was generated to rank the predatory abilities of ants against caterpillars. Each ant species was given an ADI score based on relative abundance in tree canopies (*A. elemifera* and *Z. fagara*), average time to first interaction with caterpillar, rate of ant recruitment, and ant-caterpillar interactions leading to caterpillar mortality. The total score for each ant species was divided by 25 (the maximum score an ant species could receive) and then multiplied by 100 (percentage of total possible score) for their final ADI score, which ranged from 0 to 100, allowing the species to be ranked (Possley et al. 2016).

Results

Ants on and around plants

Twenty-five ant species were collected in pitfall traps on trees at Elliott and Adams Keys in BNP (Table 1; Fig. 2), a total of 1418 individual ants. Taxa were determined with help from Mark Deyrup (Archbold Biological Station, Venus, Florida). Twelve ant species (243 total ants) were collected in canopies of torchwood and wild lime (Table 2; Fig. 3); the four most common of these were *P. gracilis, C. planatus, C. ashmeadi*, and *C. floridanus*. The most abundant ant collected in canopies of *A. elemifera* and *Z. fagara* was *P. gracilis*, representing 35% of the total ants collected;

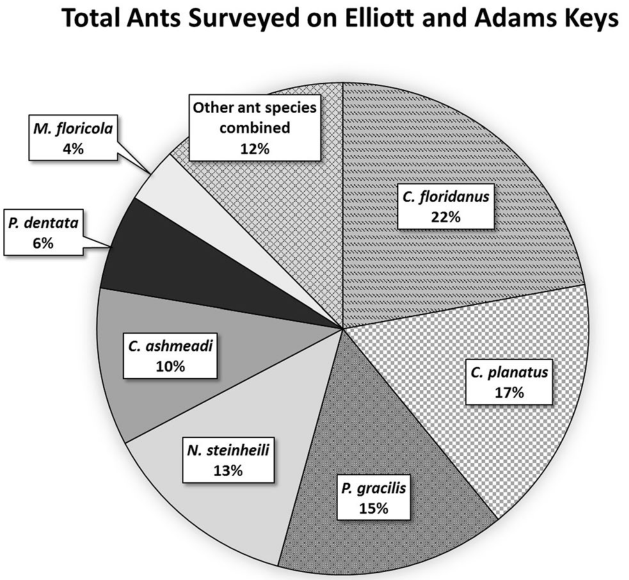

Fig. 2 Percentage of ant species captured in pitfall traps at Elliott and Adams Keys (tree canopy, trunk, and base). Overall, 1418 total ants comprising 25 ant species were captured and identified from pitfall traps

Table 1 Ants collected in pitfall traps at Elliott and Adams Keys: number of individuals of each species, and status

	Subfamily	Species	Number	Native or exotic
1	Formicinae	*Camponotus floridanus*	314	Native
2	Formicinae	*Camponotus planatus*	241	Exotic
3	Formicinae	*Camponotus tortuganus*	7	Native (probably)
4	Formicinae	*Nylanderia steinheili*	185	Exotic
5	Formicinae	*Brachymyrmex depilis*	12	Native
6	Formicinae	*Brachymyrmex obscurior*	10	Native (probably)
7	Pseudomyrmecinae	*Pseudomyrmex gracilis*	215	Exotic
8	Pseudomyrmecinae	*Pseudomyrmex elongatus*	12	Exotic (probably)
9	Pseudomyrmecinae	*Pseudomyrmex ejectus*	3	Native
10	Pseudomyrmecinae	*Pseudomyrmex simplex*	1	Native (probably)
11	Myrmicinae	*Crematogaster ashmeadi*	147	Native
12	Myrmicinae	*Pheidole dentata*	90	Native
13	Myrmicinae	*Pheidole floridana*	11	Native
14	Myrmicinae	*Pheidole moerens*	2	Exotic
15	Myrmicinae	*Monomorium floricola*	52	Exotic
16	Myrmicinae	*Temnothorax allardycei*	30	Native (probably)
17	Myrmicinae	*Aphaenogaster miamiana*	24	Native
18	Myrmicinae	*Cyphomyrmex minutus*	16	Native (probably)
19	Myrmicinae	*Solenopsis invicta*	15	Exotic
20	Myrmicinae	*Solenopsis geminata*	13	Native
21	Myrmicinae	*Cyphomyrmex minutior*	3	Exotic
22	Myrmicinae	*Wasmannia auropunctata*	2	Exotic
23	Dolichoderinae	*Tapinoma melanocephalum*	8	Exotic
24	Ponerinae	*Odontomachus brunneus*	4	Native
25	Ponerinae	*Odontomachus ruginodis*	1	Exotic (probably)

Ant species status in south Florida determined by several references (Moreau et al. 2014; Deyrup 2016)

Table 2 Ants collected in pitfall traps in the canopies of *Amyris elemifera* and *Zanthoxylum fagara*: number of individuals of each species, and status

	Subfamily	Species	Number	Native or exotic
1	Formicinae	*Camponotus floridanus*	32	Native
2	Formicinae	*Camponotus planatus*	51	Exotic
3	Formicinae	*Camponotus tortuganus*	2	Native (probably)
4	Formicinae	*Brachymyrmex depilis*	8	Native
5	Formicinae	*Brachymyrmex obscurior*	3	Native (probably)
6	Pseudomyrmecinae	*Pseudomyrmex gracilis*	84	Exotic
7	Pseudomyrmecinae	*Pseudomyrmex elongatus*	3	Exotic (probably)
8	Pseudomyrmecinae	*Pseudomyrmex ejectus*	1	Native
9	Myrmicinae	*Crematogaster ashmeadi*	45	Native
10	Myrmicinae	*Monomorium floricola*	3	Exotic
11	Myrmicinae	*Temnothorax allardycei*	8	Native (probably)
12	Dolichoderinae	*Tapinoma melanocephalum*	3	Exotic

Ant species status in south Florida determined by several references (Moreau et al. 2014; Deyrup 2016)

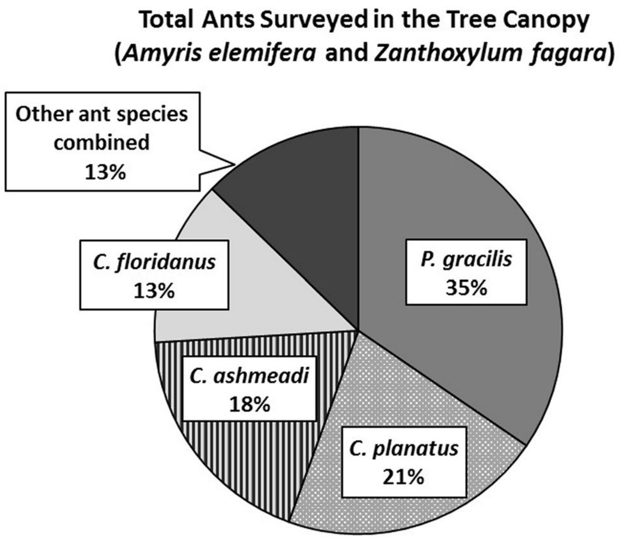

Fig. 3 Percentage of ant species captured in pitfall traps on *Amyris elemifera* and *Zanthoxylum fagara*. Overall, 243 total ants comprising 12 ant species were captured and identified from pitfall traps used in the canopy. The four most common ants collected were *P. gracilis, C. planatus, Crematogaster ashmeadi*, and *C. floridanus*. They represented 87% of all collected ants on *A. elemifera* and *Z. fagara. Pseudomyrmex gracilis* and *C. planatus* are exotic species and represented 56% of the total sampled ants

C. planatus was second at 21%; *C. ashmeadi* was third at 18%; and *C. floridanus* was fourth at 13% (Fig. 3). These four ant species represented 87% of collected ants in canopies of *A. elemifera* and *Z. fagara*. Both *P. gracilis* and *C. planatus* are exotic ant species in south Florida (Moreau et al. 2014; Deyrup 2016).

The frequency of *P. gracilis* individuals collected on three different groups of trees was compared using a generalized linear model (negative binomial with log link). This ant species was most frequent on *A. elemifera* (mean = 1.590, SD = 2.080), followed by *Z. fagara* (mean = 1.450, SD = 1.927), and then non-host trees (mean = 0.990, SD = 1.421). The omnibus test (compares the fitted model against the intercept only model) for the negative binomial model was not significant ($\chi^2 = 4.291$, $df = 2$, p value = 0.117; Table 3). However, individual parameters (tree groups) were investigated to determine significance using non-host trees as the baseline group to compare the frequency of *P. gracilis* collected for each tree group. Only *P. gracilis* collected on *A. elemifera* (the primary host tree for *H. a. ponceanus*) was significantly higher than non-host trees ($\chi^2 = 4.119$, $df = 1$, p value = 0.042; Table 3; Fig. 4).

Caterpillar predator exclusion experiment

Exclusion experiments revealed that early instar caterpillars were vulnerable to both crawling and non-crawling predators. Contingency table analysis revealed that survivorship, defined as caterpillar present on leaf, was significantly lower for early instar caterpillars in treatments with no barriers (18.8%; exact p value = 0.000003 < adjusted α-value = 0.004160), with tanglefoot only (31.3%; exact p value = 0.000465 < adjusted α-value = 0.004160), and for cages with holes and tanglefoot absent (37.5%; exact p value = 0.002700 < adjusted α-value = 0.004160), compared to the other barrier treatments (Table 4; Fig. 5). For the larger caterpillars, survivorship was only significantly lower when there were no barriers at all (33.3%; exact p value = 0.001374 < adjusted α-value = 0.004160; Table 4; Fig. 5).

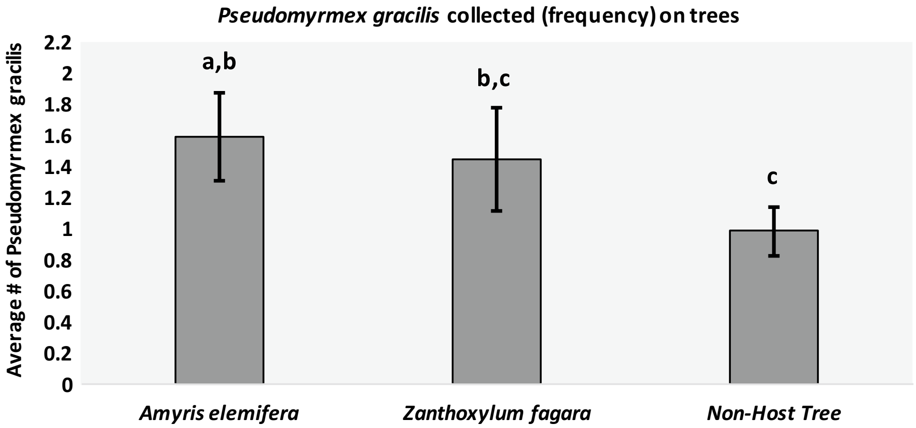

Fig. 4 Graphical representation of *Pseudomyrmex gracilis* collected on three different group of trees at Elliott and Adams Keys in Biscayne National Park, Florida. The *bars* represent averages of count data with standard error bars. *Lowercase letters* reflect statistical significance. Overall, *P. gracilis* was only significantly more frequent on *Amyris elemifera* than non-host trees. *Amyris elemifera* is the primary host tree for the *Heraclides aristodemus ponceanus*

Table 3 Generalized linear model (negative binomial with log link) results of *Pseudomyrmex gracilis* collected on three different groups of trees

Parameter	Mean	SD	SE
Amyris elemifera	1.590	2.080	0.256
Zanthoxylum fagara	1.450	1.927	0.346
Non-host tree	0.990	1.421	0.170

Omnibus test

Chi-square	*df*	*p* value
4.291	2	0.117

Hypothesis test

Parameter	Wald Chi-square	*df*	*p* value
Intercept	8.357	1	0.004
Amyris elemifera	4.119	1	0.042
Zanthoxylum fagara	0.102	1	0.750
Non-host tree	–	–	–

Ant-caterpillar interactions

Pseudomyrmex gracilis (n = 30 trials; mean = 56.533, SD = 32.324, $p < 0.001$) discovered caterpillars significantly faster than did *C. planatus* (n = 31 trials; mean = 115.806, SD = 58.579), *C. ashmeadi* (n = 21 trials; mean = 123.524, SD = 64.697), and *C. floridanus* (n = 29 trials; mean = 122.690, SD = 87.015; Fig. 6). *C. ashmeadi* (n = 21 trials; mean = 0.429, SD = 0.148) and *C. floridanus* (n = 29 trials; mean = 0.345, SD = 0.614) occasionally recruited workers to combat caterpillars; *P. gracilis* and *C. planatus* did not recruit workers when interacting with caterpillars (Fig. 7). Overall, early instar caterpillars had higher rates of mortality compared to late instar caterpillars. Early instar caterpillars suffered the most damage when interacting with *P. gracilis* (n = 15 trials, 86.7% mortality); late instar caterpillars successfully foiled *P. gracilis* advances (n = 15 trials, 0% mortality). Early instar caterpillar mortality was moderately high with *C. floridanus* (n = 16 trials, 56.3% mortality); these were the only ant species tough enough to remove or force some late instar caterpillars to completely abandon the leaf (n = 15 trials, 40% mortality). *Crematogaster ashmeadi* attacked only a few early instar caterpillars during the trials (n = 10 trials, 20% mortality) and were ineffective in harming late instar caterpillars (n = 11 trials, 0% mortality). Finally, *C. planatus* demonstrated no aggressive encounters with either early (n = 16 trials, 0% mortality) or late instar (n = 15 trials, 0% mortality) caterpillars (Table 5).

The Ant Danger Index ranked the predatory abilities of *C. ashmeadi, C. planatus, C. floridanus*, and *P. gracilis* against caterpillars that utilized *A. elemifera* and *Z. fagara* as host plants; since all four ant species represented 87% of the total sampled ants collected in canopies of *A. elemifera* and *Z. fagara*, only these ants were compared. *Pseudomyrmex gracilis* received the highest final score at 52, and *C. floridanus* had the next highest score at 40; both *C. ashmeadi* and *C. planatus* received lower scores of 24 (Table 6).

Discussion

Ants are important predators in tropical forest ecosystems (Jeanne 1979; Smiley 1985; Tobin 1995; Floren et al. 2002). Their abundance and active foraging day and night presents chronic passive and aggressive encounters with caterpillars (Lopez and Potter 2000; Seifert et al. 2016). Many factors, however, determine whether ant species will have beneficial, neutral, or negative effects toward caterpillars (Buckley 1987; Kaminski et al. 2010; Mestre et al. 2016). With the exception of those Lepidoptera whose caterpillars have mutualistic relationships with ants, early instar and small caterpillars are negatively associated with invertebrate predators, especially in subtropical and

Table 4 Results of predator exclusion experiment using *H. cresphontes* larvae on *Amyris elemifera* and *Zanthoxylum fagara*. Z scores (adjusted z-scores) were acquired through the contingency table analysis and then squared to obtain Chi square values

Treatments	#Alive/total # of trials	Adjusted z-score	Chi square	*p* value
Early instar caterpillars				
(1) No barriers (no tanglefoot/no cage)	3/16 = 18.7%	4.70	22.09	0.000003*
(2) Tanglefoot present/no cage	5/16 = 31.3%	3.50	12.25	0.000465*
(3) No tanglefoot/cage with holes present	6/16 = 37.5%	3.00	9.00	0.002700*
(4) Tanglefoot present/cage with holes present	14/16 = 87.5%	−1.60	2.56	0.109599
(5) No tanglefoot/cage present	14/16 = 87.5%	−1.60	2.56	0.109599
(6) Tanglefoot present/cage present	15/16 = 93.8%	−2.20	4.84	0.027807
Late instar caterpillars				
(1) No barriers (no tanglefoot/no cage)	5/15 = 33.3%	3.20	10.24	0.001374*
(2) Tanglefoot present/no cage	11/15 = 73.3%	−0.30	0.09	0.764177
(3) No tanglefoot/cage with holes present	13/15 = 86.7%	−1.50	2.25	0.133614
(4) Tanglefoot present/cage with holes present	15/15 = 100%	−2.70	7.29	0.006934
(5) No tanglefoot/cage present	14/15 = 93.3%	−2.10	4.41	0.035729
(6) Tanglefoot present/cage present	15/15 = 100%	−2.70	7.29	0.006934

Chi square values were used to calculate exact *p* values with the significance function group in SPSS. Exact *p* values were compared to the adjusted α-value to determine significance. The adjusted α-value based on the Bonferroni correction was set at 0.00416 (0.05/12). Exact *p* values equal to or less than the adjusted α-value were considered significant. Asterisk denotes significance. Treatments defined in first column

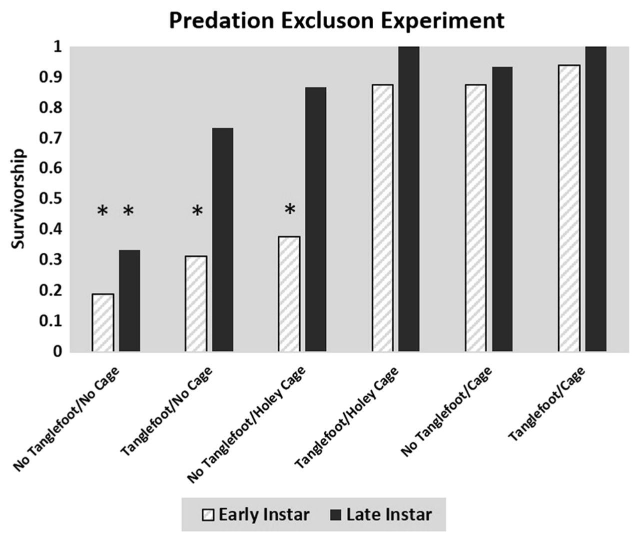

Fig. 5 The predator exclusion experiment involved 6 treatments, with physical barriers (tanglefoot and mesh cages) used in different combinations on *Zanthoxylum fagara* to compare caterpillar (early and late instar) survivorship against crawling and non-crawling predators. Survivorship was defined as persistence on leaf for 5 days. A contingency table analysis was performed. *Asterisks* denote significance in survivorship for the various treatments. Each treatment using early instar caterpillars had 16 trials, each treatment using late instar caterpillars had 15 trials. Refer to Table 4 for more details

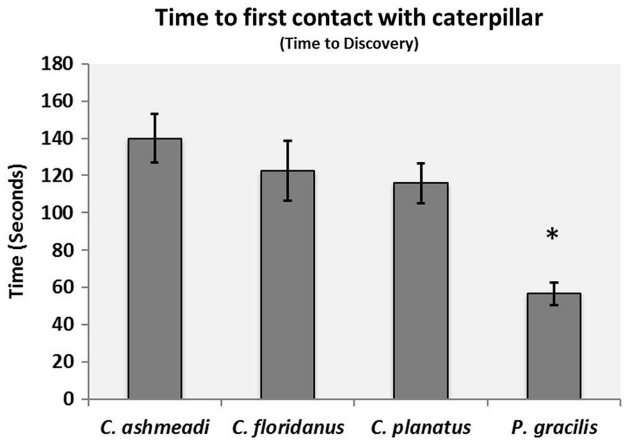

Fig. 6 The average time (±SE) the four most abundant ant species took to discover *Heraclides cresphontes* caterpillars placed on *Amyris elemifera* and *Zanthoxylum fagara* at Elliott Key, Biscayne National Park, Florida. A one-way ANOVA was performed followed by the Fisher's Least Significant Difference post-hoc test. *Asterisk* denotes significance

tropical ecosystems (Jeanne 1979; Montllor and Bernays 1993; Reavey 1993; Floren et al. 2002; Sam et al. 2015). Late instar and large caterpillars are negatively associated with birds especially in temperate ecosystems (Heinrich 1993; Reavey 1993; Remmel et al. 2009). Generalist and specialist parasitoids typically attack eggs, caterpillars and even the pupal stage (Weseloh 1993; Gentry and Dyer 2002; Stireman et al. 2009). We did not investigate either bird or parasitoid impacts during this study, which are other areas of research interest for future studies (Gentry and Dyer 2002; Timms et al. 2016).

Results from the predator exclusion experiment demonstrated that early instar caterpillars were less likely to survive when exposed to crawling and non-crawling predators

(Fig. 5), but this conclusion was based on several assumptions. For example, caterpillar absence assumed caterpillar mortality, though caterpillars can drop off the leaf or migrate to another area if conditions are less than desirable (Castellanos et al. 2015). We accounted for this by scanning the entire tree after each trial to see if the caterpillar relocated to a different section on the tree. Early instar caterpillars experienced reduced survivorship in treatments when crawling insects gained access to them (no tanglefoot and holes in the cage), with the exception of tanglefoot present and no cage to protect the caterpillar. This outcome suggests that crawling predators such as ants, beetles, true bugs, spiders, and even lizards play a significant predator role. Late instar caterpillars had high survivorship for all treatments, except the treatment without barriers. As mentioned above, late instar caterpillar absence assumed caterpillar mortality, despite caveats including migration

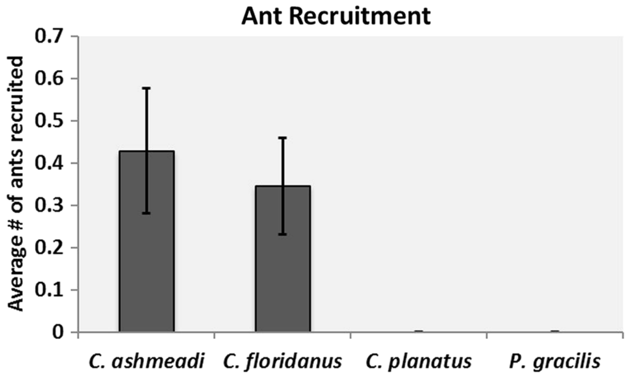

Fig. 7 Ant recruitment to *Heraclides cresphontes* caterpillars placed on *Amyris elemifera* and *Zanthoxylum fagara* by the four most abundant ant species at Elliott Key, Biscayne National Park, Florida. Recruitment is displayed as the average number of ants attracted to caterpillars (±SE). Ant recruitment allows ants to overwhelm larger prey such as late instar caterpillars

Table 5 Results from the ant-caterpillar interaction study. Four common ant species interacted with early and late instar caterpillars placed on *Amyris elemifera* and *Zanthoxylum fagara*

Ant species	Early instars			Late instars		
	Removed by ant(s)	Aborted leaf	Mortality (removed + aborted) # of trials	Removed by ant(s)	Aborted leaf	Mortality (removed + aborted) # of trials
Camponotus planatus	0	0	0/16 = 0%	0	0	0/15 = 0%
Crematogaster ashmeadi	1	1	2/10 = 20%	0	0	0/11 = 0%
Camponotus floridanus	7	2	9/16 = 56.3%	0	6	6/15 = 40%
Pseudomyrmex gracilis	11	2	13/15 = 86.7%	0	0	0/15 = 0%

Total mortality based on interactions with ants included larvae (caterpillar) removal or leaf abortion. Major damage was caused by *Pseudomyrmex gracilis* (early instar mortality was 86.7%) and *Camponotus floridanus* (early instar mortality was 56.3%, late instar mortality was 40%)

Table 6 Ant Danger Index (ADI) based on cumulative scores from: (1) ant species relative abundance, (2) time to discover caterpillar, (3) ability to recruit more ants, (4) early instar (small) mortality, and (5) late instar (large) mortality

Ant species	Origin	(1) Abundance	(2) Discovery	(3) Recruit	(4) Mortality (small)	(5) Mortality (large)	ADI total score (max: 100)
Scale used for each category (how the values 0–5 were assigned)		(0) 0% (1) 1–10% (2) 11–20% (3) 21–30% (4) 31–40% (5) > 40%	(0) > 300s (1) 181–300s (2) 121–180s (3) 61–120s (4) 11–60s (5) 0–10s	(0) 0 ants (1) 1 ant (2) 2–3 ants (3) 4–6 ants (4) 7–10 ants (5) > 10 ants	(0) 0% (1) 1–20% (2) 21–40% (3) 41–60% (4) 61–80% (5) 81–100%	(0) 0% (1) 1–20% (2) 21–40% (3) 41–60% (4) 61–80% (5) 81–100%	
(A) *Crematogaster ashmeadi*	Native	2	2	1	1	0	24
(B) *Camponotus planatus*	Exotic	3	3	0	0	0	24
(C) *Camponotus floridanus*	Native	2	2	1	3	2	40
(D) *Pseudomyrmex gracilis*	Exotic	4	4	0	5	0	52

The total score for each ant species was divided by 25 (max score each ant species could acquire) and then multiplied by 100 for a final max score. The final max score with a range 0–100 ranked each ant species against the other three ant species. All interactions between native and exotic ants and caterpillars occurred on *Amyris elemifera* and *Zanthoxylum fagara* in the forests at Elliott and Adams Keys to pupate, foraging for more food resources, or leaf abandonment. Overall, results were consistent with past studies that concluded early instar (small) caterpillars suffered higher mortality than late instar (bigger) caterpillars (Tilman 1978; Watanabe 1981; Sam et al. 2015). The predator exclusion experiment elucidated coarse predator impacts (caterpillars present or absent) without defining specific causes (what agents were the cause of caterpillar mortality or disappearance). Since ants are ubiquitous in the forest in BNP, we assumed they would interact with caterpillars more frequently than other predators, though certainly other invertebrates (wasps, parasitoids, spiders), birds, and other vertebrates (lizards, treefrogs) may also play a role (Jeanne 1979; Sam et al. 2015; Seifert et al. 2016).

Ants, particularly *P. gracilis*, may pose a significant threat to butterfly eggs and larvae, but butterflies have developed ways to cope with such predators (Morais et al. 1999). *Heraclides aristodemus ponceanus* and other closely related swallowtails physically resemble lizard and bird droppings, an adaptation that may thwart vertebrate predation for predators that rely upon visual detection (Minno and Emmel 1992). Accordingly, invertebrate predators are more likely deterred by defensive tactics such as offensive chemicals stored in the caterpillars' osmeteria (defensive organs that discharge a noxious odor), as well as physical head butts by the caterpillar to its attacker(s) (Fig. 8), and the most extreme response, leaf abandonment, where some caterpillars silk off (with a strand of silk that enables them to climb back up once the threat is gone) or directly drop off the leaf to escape predators (Honda 1983; Nafus 1993; Salazar and Whitman 2001; Gentry and Dyer 2002; Frankfater et al. 2009). All these defensive strategies may be less effective against aggressive, exotic ants (Forys et al. 2001; Lach et al. 2016). Introduced predators can overwhelm and eat their prey to extinction when the prey population reaches dangerously low numbers; predation effects are exacerbated when prey populations are constrained by other environmental factors such as habitat loss, inclement weather, climate change, and local anthropogenic impacts (Schoener et al. 2001; Lach et al. 2016). The most common ant on *A. elemifera* and *Z. fagara* in BNP was *P. gracilis*, which aggressively attacked and removed early instar caterpillars (86.7%; Table 5). Field observations revealed that sheer caterpillar size was a fair defense against these ants; in fact, head butting and everting osmeteria were also effective against more aggressive individual ants. As these experiments employed a surrogate species of caterpillars, *H. cresphontes*, we do not know how often ants of this species encounter *H. a. ponceanus* caterpillars in the field. Continued research should take steps to quantify those encounters.

Camponotus floridanus ants did attack some late instar caterpillars (40%), but the attacks did not result in direct mortality. Harassed late instar caterpillars initially defended themselves, until more ants were recruited to attack. Eventually, the late instar caterpillar abandoned its leaf, falling to lower leaves or to the ground. Conversely, *C. floridanus* ants attacked and killed early instar caterpillars by simply carrying them away. Overall, late instar caterpillars are more equipped to defend themselves and avoid direct predation from these ants, the most common native ant species foraging on *A. elemifera* and *Z. fagara*.

Fig. 8 Early instar *Heraclides aristodemus ponceanus* caterpillar fends off an approach by *Camponotus planatus*. This approach is not aggressive; however, the *H. a. ponceanus* caterpillar does not tolerate contact by other organisms

Amyris elemifera should be inspected for the presence of extrafloral nectaries (EFNs) since *P. gracilis* was significantly more frequent on them compared to *Z. fagara* and non-host trees (Fig. 4). In the same plant family, *Z. fagara* does have minute EFNs (Koptur 1992), which might explain the higher frequency of *P. gracilis* on both *A. elemifera* and *Z. fagara*. Many non-host trees sampled at Elliott and Adams Keys also have EFNs, including blackbead (*Pithecellobium keyense*), catclaw blackbead (*P. unguis-cati*), and soldierwood (*Colubrina elliptica*), but presence of EFNs on trees does not solely determine whether ants will actively forage on them. The presence of exudate-producing insects can also encourage ants to occupy and forage on plants (Sendoya et al. 2016). This project did not record and quantify the presence and abundance of exudate producing insects, but future investigations should incorporate plant attractiveness to ants and other invertebrate predators due to intrinsic and extrinsic plant characteristics. Numerous studies conducted on ant attracting plants have demonstrated some caterpillar species are well-equipped to thwart ant attacks using behavioral, chemical, and physical means (Oliveira and Freitas 2004; Bächtold et al. 2012; Sendoya and Oliveira 2015).

Biscayne National Park and North Key Largo are the last remaining sanctuaries for the federally endangered

H. a. ponceanus (Daniels 2014; Minno 2015); Biscayne National Park supports the largest population of *H. a. ponceanus* (Minno 2015). The Schaus swallowtail habitat enhancement project was initiated to bolster *H. a. ponceanus* populations on Elliott and Adams Key through planting thousands of native trees interspersed with nectar plants in the restored sites. Additional host plants, supplemented with captive-bred *H. a. ponceanus* reintroductions being conducted by scientists and staff at the University of Florida, present options for a better future for *H. a. ponceanus* in BNP (Daniels 2014).

Resource managers and scientists should continue to monitor *H. a. ponceanus* populations over time (Minno 2015). Long-term quantitative research (including video surveillance) may be necessary to assess potential risks imposed by exotic ants. High definition video surveillance cameras can capture predation events in natural settings day and night over an extended period of time to more accurately assess the effects of predator (particularly ants) interactions with all immature stages of *H. a. ponceanus* (Grieshop et al. 2012). In BNP, *P. gracilis* is the most potentially destructive force against *Heraclides* species on *A. elemifera* and *Z. fagara*. These negative impacts probably extend to other caterpillar species, since this exotic ant is omnipresent and an opportunistic forager (Wetterer 2010).

Different predators may be more or less deleterious at different life-history stages of butterflies (Nafus 1993; Seifert et al. 2015; Sam et al. 2015). Results obtained from these studies can guide future efforts to re-establish rare butterflies in areas they were once known to exist, by utilizing different techniques for protecting eggs and larvae of endangered butterflies at different life stages in reintroduction programs. A better understanding of which predators interact with butterfly eggs and larvae in natural habitats can help scientists determine suitable habitats for captive-reared butterflies before release. If exotic ants are found to be significantly deleterious to butterflies (Lach et al. 2016), then potential sites should be surveyed for exotic ants before release. Ant control measures could be taken, but in the past, chemical control of ants did more damage to the environment than to the targeted ant species (Summerlin et al. 1977; Williams et al. 2001; Oi et al. 2004; Tschinkel 2006; Plentovich et al. 2010). Future investigations will continue to document winners and losers as exotic and native species co-mingle in positive, neutral, and negative ways (Schoener et al. 2001; Allen et al. 2004; King and Tschinkel 2006; Didham et al. 2007; Moreau et al. 2014; Lach et al. 2016). Protecting pristine habitats and minimizing loss and degradation should be top priority to maintain rare, specialist organisms sensitive to anthropogenic-mediated actions.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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