Quantifying the effects of an invasive thief ant on the reproductive success of rare Hawaiian picture-winged flies

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ABSTRACT

Threats to endangered insect species that act independently of those associated with habitat loss are often suspected, but are rarely confirmed or quantified. This may hinder the development of the most effective recovery strategies, which are increasingly needed for listed insects. Since 2006, 14 species of flies within the large, showy Hawaiian picture-winged Drosophila group have been added to the US threatened and endangered species list. Many of these species are thought to be limited by host plant rarity, but also by predation on immature stages by invasive ants. We tested the latter hypothesis with a field experiment involving Drosophila crucigera, a more common surrogate for sympatric endangered species, and the invasive ant Solenopsis papuana, on the island of O‘ahu. We established ant suppression and control plots across three forest sites. Within each plot we placed a host plant branch piece, into which lab-reared flies had oviposited, and subsequently tracked weekly emergence of adults. Numbers of flies that emerged were 2.4 times higher in ant-suppressed plots than in control plots; this 58% reduction in survival from egg to adult in the presence of ants was similar across all three sites. Among plots, numbers of emerged flies exhibited a pattern suggesting that the detrimental effect of ants is density dependent. These results confirm that S. papuana, and possibly other invasive ant species, can strongly impact the reproductive success of Hawaiian picture-winged Drosophila. They also point to several management actions, beyond habitat restoration, that may improve the recovery of these imperiled flies.

1. Introduction

Conservation of endangered and other rare species is often hindered by an incomplete understanding of their ecological requirements and threats, including the importance of potentially numerous interspecific interactions (Lawler et al., 2002). This is especially true for small and understudied taxa like insects (New, 2007b), whose daunting diversity amplifies this knowledge deficit. As a consequence, conservation of insects has generally focused first on the basic need to protect or restore habitat (New, 2007b; Samways, 2007), and the potential roles of additional threats, such as negative interactions with invasive species, are usually recognized but often remain uncharacterized. Confirming and quantifying such threats can therefore provide a more complete set of biological parameters for assessing the viability of endangered insect populations, and thereby lead to improved recovery strategies (Schultz and Hammond, 2003; New, 2007a).

Within the United States, Hawai‘i has many more federally listed threatened and endangered species than any other state (USFWS, 2017). The majority of these are plants and vertebrates, but endemic Hawaiian insects and other invertebrates are increasingly being considered for listing, with 76 species now formally designated (USFWS, 2017). Among these, 14 species of Hawaiian picture-winged Drosophila flies have been added to the federal threatened and endangered species list since 2006 (USFWS, 2006, 2010, 2013). As with other taxa, this has triggered a need among land managers for practical information on the importance of, and potential ways to mitigate against, the various factors hypothesized to impact picture-winged fly populations, including factors that may be viewed as secondary to habitat loss.

Picture-winged Drosophila form a subset within the larger radiation of Drosophila in Hawai‘i, and the > 100 recognized species are so named because of the striking and highly diverse patterns of pigmentation on their wings (Edwards et al., 2007). Most or all picture-winged species are saprophytic, with their larvae feeding on bacteria and other microbes within rotting tissues of their host plant species, typically in

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the cambium layer beneath the bark of decomposing branches or stems (Montgomery, 1975; Magnacca et al., 2008). Although a wide range of host plants are used by the picture-winged group, most species are moderately to highly specific in their host plant preferences, while a few species are known to be generalists (Montgomery, 1975; Magnacca et al., 2008). Rarity of host plants is therefore one of the primary causes of endangerment of some of the picture-winged species (Foote and Carson, 1995; USFWS, 2006, 2010, 2013).

While restoration of host plants is important for the recovery of many of the listed picture-winged species, it may not always represent a sufficient strategy. This is because non-native insect predators and competitors are believed to be important additional threats that may act independently of or synergistically with host plant declines (Foote and Carson, 1995, USFWS, 2006, 2010, 2013). The most important invasive predators are thought to be yellowjacket wasps (Vespula pen-sylvanica), which may prey on both adult and exposed larval flies in areas where they occur, and a variety of ant species, which are most likely to impact the more sedentary immature stages but are also known to attack adults (K. Magnacca pers. obs.). Invasive ants, especially a handful of ecologically dominant species such as Linepithema humile, Pheidole megacephala, Anoplolepis gracilipes and Wasmannia auropunctata, are well-known to impact invertebrate species and communities both on oceanic islands and in continental ecosystems (e.g., Perkins, 1913; Cole et al., 1992; Human and Gordon, 1997; Hoffmann et al., 1999; Le Breton et al., 2003; Carpintero et al., 2005; Abbott, 2006; Walker, 2006). Attempts to eradicate populations of these ants for the conservation benefit of native species are increasingly common, though with varying degrees of success (Hoffmann et al., 2016). While all of these ant species and others are established in Hawai‘i, they tend to be absent or occur at low densities in the mesic to wet montane forests where many of the listed picture-winged flies occur (Reimer, 1994; Krushelnycky et al., 2005; Krushelnycky, 2015), especially in the more shaded closed-canopy gulches typically favored by the flies and their host plants.

One relatively inconspicuous and globally obscure species that violates this generality is Solenopsis papuana. This small (ca. 1.5 mm long) thief ant, which belongs to a taxonomically confused group and whose name may change in the future (see Ogura-Yamada and Carson, 2006). Solenopsis papuana is generally rare on vegetation distant from the ground (Krushelnycky, 2015), but has occasionally been observed foraging up to a height of at least two meters on tree trunks. More commonly, it attains high densities and is most active in the soil and leaf litter (Ogura-Yamada and Krushelnycky, 2016, unpub. data). Although information on the biology and ecology of this ant is limited, other species of thief ants (small Solenopsis species formerly placed in the subgenus Diplorhoptrum) are reported to be generalist predators, scavengers, and tenders of honeydew-producing Hemiptera in subterranean environments (Thompson, 1980, 1989; Tschinkel, 2006). Solenopsis papuana may therefore encounter and prey upon eggs and larvae developing within decomposing host plant branches, especially if the branches have been downed by tree fall or wind breakage and then decompose on the ground. Fully grown larvae subsequently exit the branches to pupate in the soil, exposing them directly to foraging ants. Even eclosing, teneral adults may be vulnerable as they dig to the surface and rest there to harden and melanize their cuticles before they become fully flighted. Another invasive ant species, L. humile, has been observed or inferred to attack larvae or eclosing adults of fruit flies (Tephritidae) in orchards (Wong et al., 1984; Buczkowski et al., 2014). Alternatively, picture-winged Drosophila eggs and larvae may be protected from ants within their internal feeding environments, and late instar larvae, pupae and adults in the soil may not be preferred prey for tiny ants like S. papuana.

Our objective was to test whether S. papuana reduces the reproductive success of picture-winged Drosophila flies with an experiment that employed realistic field conditions for the ants and developing flies. We used a more common picture-winged species, Drosophila crucigera, that is a generalist in its host plant usage, but is sympatric with six endangered Drosophila species on the island of O‘ahu, and has the same life history strategy and potential exposure to ants as the rarer picture-winged species (Magnacca et al., 2008; Magnacca, 2014). This surrogate Drosophila species should therefore provide a good representation of the vulnerability of this group of flies to S. papuana and possibly other invasive ants in Hawai‘i, and clarify the magnitude of the threat posed by ants to picture-winged fly recovery.

2. Materials and methods

2.1. Field plots

Twenty-eight 5 × 5 m plots were established in November of 2016 across three mesic forest sites in the central to northern Wai‘anae Mountain range of O‘ahu: eight plots at Pu‘u Hāpapa (810 m elevation, 1185 mm annual rainfall), eight plots at ‘Ekahau (635 m elevation, 1210 mm annual rainfall), and 12 plots at Pahole Natural Area Reserve (NAR) (480 m elevation, 1375 mm annual rainfall). Annual rainfall estimates are obtained from Giambelluca et al. (2013). Each of the three sites is characterized by a mix of native and alien vegetation, and each is known to support both natural populations of picture-winged Dro- sophila flies (Magnacca, 2014) and high densities of S. papuana ants (as determined by prior mapping, Ogura-Yamada and Krushelnycky, unpub. data). Other ant species were uncommon or absent in the plots.

At each site, half of the plots were randomly assigned to an ant suppression treatment (suppressed), and the other half to an untreated control (control). A shortage of flies in the lab colony (see below) prevented the use of one of the plots at Pahole NAR, resulting in a total of 27 plots used (13 suppressed, 14 control). Numbers of S. papuana ants (hereafter ‘ants’) were monitored in each plot using nine cards (half of a 7.6 × 12.7 cm index card) baited with a smear of peanut butter: five cards were spaced around the perimeter of the fly emergence cage in the middle of the plot (used to trap emerging adult Drosophila, see below), and four cards were placed on the plot perimeters midway between each of the four corners. The cards were placed on the ground, collected after 90 min, and numbers of ants were summed over the upper and lower surfaces of each card. Although monitoring of ant activity with baits does not necessarily indicate ant colony density and may be influenced by weather and other factors, it is a commonly used method for assessing relative abundances of foraging ants in a given area, and is considered to be reasonably accurate provided that baiting is conducted with consistent methods and under similar conditions (Bestelmeyer et al., 2000).

Following the initial ant monitoring event, 17 stations filled with toxic ant bait were placed in each ant suppression treatment plot to suppress ants over the course of the experiment. Sixteen stations were spaced every 1.25 m in a grid pattern, with an extra station placed in similar conditions (Bestelmeyer et al., 2000). Twenty-eight 5 × 5 m plots were established in November of 2016 across three mesic forest sites in the central to northern Wai‘anae Mountain range of O‘ahu: eight plots at Pu‘u Hāpapa (810 m elevation, 1185 mm annual rainfall), eight plots at ‘Ekahau (635 m elevation, 1210 mm annual rainfall), and 12 plots at Pahole Natural Area Reserve (NAR) (480 m elevation, 1375 mm annual rainfall). Annual rainfall estimates are obtained from Giambelluca et al. (2013). Each of the three sites is characterized by a mix of native and alien vegetation, and each is known to support both natural populations of picture-winged Dro- sophila flies (Magnacca, 2014) and high densities of S. papuana ants (as determined by prior mapping, Ogura-Yamada and Krushelnycky, unpub. data). Other ant species were uncommon or absent in the plots.

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2.2. Lab fly colonies

Wild *D. crucigera* flies were caught between March and May of 2016 from the Kalua‘i, Pual'i, and Palikea areas of the central to southern Wai‘anae Mountains, O‘ahu. Isolines were established from laying females in the Drosophila Lab of the Pacific Biosciences Research Center at the University of Hawai‘i at Mānoa, and resulting colonies were maintained at 18–19 °C on a 12 h light/dark cycle, and kept in vials with Wheeler-Clayton medium (*Wheeler and Clayton, 1965*). In November of 2016, mature females from the most productive colony were segregated into groups of three, and each triplet was subsequently observed for several weeks to confirm ample egg laying. Reproductively active triplets were then used for oviposition on host plant material (see below).

2.3. Host plant preparation

Live branches of *Pisonia umbellifera* trees (Nyctaginaceae), the most common host plant of *D. crucigera*, were harvested from Kahanahāki Valley, in the northern Wai‘anae Mountains on 25 September 2016. The branches were cut into 28 pieces approximately 20 cm in length and 2.0–2.5 cm in diameter, and were put into a standard freezer for four days to break cell walls and hasten decomposition upon thawing, and to kill any insects that might already be in them. Soil and leaf litter was also collected from Kahanahāki Valley to inoculate the branch pieces with the wild strains of bacteria and other microorganisms upon which the fly larvae feed. This soil and leaf material was placed into plastic tubs (30 × 18 × 11 cm), moistened with approximately 150 ml of water per tub, and was covered with a snug but non-airtight plastic lid to create a humid rotting environment. On 29 September, the host plant branch pieces were thawed and paired to match diameters as closely as possible, placed into screen bags (Phifer BetterVue Screen, charcoal fiberglass window screen), and each pair was then placed into one of the aforementioned tubs under a cover of damp leaf litter to initiate the rotting process. The screen bags were used to exclude larger detritivorous insects within the soil and leaf litter that might compete with *D. crucigera* larvae, while allowing entry of smaller invertebrates like Acari and Collembola that might help transfer microorganisms to the rotting branches. After 27 days, the branch pieces were judged to have achieved a desirable stage of decomposition; to avoid further breakdown, they were placed back into the freezer until needed.

2.4. Oviposition and field trial

Frozen prepared host branch pieces were thawed for three days prior to oviposition, and each branch piece from a matched pair was randomly assigned to either the ant suppression or control treatment. Branch pieces were then individually placed in clean tubs (same dimensions as above) lined on the bottom with 2–3 cm of damp sand, and a randomly selected triplet of female flies (subject to constraints described below) was added to each tub for an oviposition period of approximately 72 h, then returned to a vial containing Wheeler-Clayton medium. The next day, we carried the egg-laden branch pieces to the field and placed them in the plots that matched their predetermined random treatment assignments. Each branch piece was placed on the ground in the center of its plot, loosely covered with leaf litter taken from nearby, and a conical emergence cage was affixed over it. Emergence cages were constructed of standard fiberglass window screen material (Phifer BetterVue Screen, charcoal), and were 1 m in diameter and supported by a central PVC post approximately 1 m tall, with the perimeter staked to the ground with wire. This allowed *Drosophila* larvae leaving the host branch to pupate in the soil, and trapped adults subsequently emerging after pupation, while excluding naturally-occurring *Drosophila* in the forest but presenting little if any barrier to the movement of ants. Inside each cage, we placed a yellow sticky trap (7.6 × 12.7 cm, Bioquip Products) held approximately 20 cm above the ground, and hung a Multilure (McPhail) trap (Better Trap, Inc.) containing a 50:50 propylene glycol:water preservative mixture and smeared on the interior surfaces with an attractant bait consisting of fermenting mashed bananas inoculated with baker’s yeast. Emergence was monitored by checking for adult flies caught by either trap, or resting on the cage walls, on a weekly basis from approximately three to ten weeks post oviposition. Any flies detected were removed through a zippered opening, without removing the cage; monitoring was terminated after two consecutive weeks passed with no new adult emergence at a site.

Due to a shortage of reproductively active triplets of female flies in the lab colony, oviposition on the branch pieces destined for each of the three field sites was conducted in turn, re-using some of the triplets for more than one site. We used eight fly triplets for the eight Pu‘u Hāpapa branch pieces (randomly assigned) from 9 to 12 December 2016; the same triplets were then used again for the eight ‘Ekahau branch pieces from 15 to 18 December 2016, with the constraint that each triplet was randomly assigned to a branch piece with the opposite treatment designation (ant suppression vs. control) as in the first.
oviposition period. Mortality of flies in the lab after the second oviposition period necessitated replacement of many of the original females with new females that became available, and three new triplets were added for the 11 branch pieces used during the third oviposition period, from 26 to 29 December 2016, for the Pahole site.

2.5. Analysis

To compare numbers of ants between ant-suppressed and control plots prior to treatment application, we used a Wilcoxon test comparing the averages of the ant counts for each plot \( (n = 13 \text{ suppressed, } n = 14 \text{ control}) \) on the initial monitoring dates. To compare numbers of ants between treatments during the fly development period, we used a median test to compare average ant counts for each plot because of highly divergent variances between suppressed and control plot data after ant-suppression was imposed. For this comparison, we used the average of all ant counts over the final three monitoring events for each plot \( (n = 13 \text{ suppressed, } n = 14 \text{ control}), \) which roughly spanned the period from when egg-laden branch pieces were placed in the plots to when the final adults emerged (Fig. 1). To compare numbers of adult flies emerged between ant-suppressed and control plots, we used a generalized linear model with a negative binomial distribution and a log link function to address the overdispersed nature of the count data. Explanatory variables included in the model were treatment (suppressed, control) and site (Puʻu Hāpapa, ʻĒkahanui, Pahole). Statistical analyses were performed using JMP Pro Version 13.

3. Results

Ant numbers in the field plots on the initial monitoring date averaged approximately 50–120 ants/card (Fig. 1), and were not significantly different between plots assigned to ant suppression and control treatments (Wilcoxon test, \( S = 173, p = 0.680 \)). Ant numbers subsequently dropped sharply in the suppressed plots after bait stations were deployed, but remained relatively stable in the control plots (Fig. 1). Over the final three monitoring events that spanned the period during which flies were present in the plots, ant numbers in suppressed plots were reduced relative to pre-treatment values by 96.5% ± 1.1% (mean ± SE), compared to a 3.0% ± 10.9% increase in the control plots. Ant numbers during this period were highly significantly different between suppressed and control treatments (median test, \( S = 0, p < 0.001 \)).

*Drosophila crucigera* adults emerged in the field cages from approximately four weeks after oviposition to about nine weeks after oviposition, with a peak emergence at around six weeks after oviposition (Fig. 2). The timing of emergence was very similar between all three sites, but numbers of flies emerged per plot were much lower at Pahole compared to the other two sites (Fig. 2). We believe this likely resulted from lower rates of oviposition on the branch pieces used at Pahole, rather than from lower survival rates at Pahole. We infer this because 51.5% (17 of 33) of the lab flies died during the 3-day oviposition period for the Pahole site. This compared to 0% (0 of 24) mortality during the Puʻu Hāpapa oviposition period and 4.2% (1 of 24) during the ʻĒkahanui oviposition period.

Higher numbers of flies emerged in the ant-suppressed plots compared to the control plots at all three sites, even at Pahole where fewer flies emerged overall (Fig. 3, left panel). Across all plots, the treatment factor contributed significantly to variation in emerged fly numbers (GLM, Wald \( \chi^2 = 6.38, p = 0.012 \)), indicating that emergence rates were different between suppressed and control plots (Fig. 3, right panel). The site factor also contributed significantly to variation in fly numbers (GLM, Wald \( \chi^2 = 13.99, p = 0.001 \)), owing to the large difference in emergence rates between Pahole and the other two sites. Back-transformation of fitted coefficient estimates from the model yielded estimates of 6.8 flies per ant-suppressed plot (4.2–10.8, 95% CI) and 2.9 flies per control plot (1.7–4.8, 95% CI), indicating that an estimated 2.4 times as many flies emerged, on average, in plots where ants were suppressed. One fly was observed on the central post of the emergence cage in one of the control plots at ʻĒkahanui immediately after the cage was removed at the end of the experiment, two weeks after the last fly was seen inside the cage. We believe that this was likely a naturally-occurring fly that landed on the post from outside the cage after it was lifted, attracted to the baited trap inside. However, we ran the GLM analysis with this fly included: the results were very similar (Wald \( \chi^2 = 6.05, p = 0.014 \) for the treatment factor), so we felt comfortable excluding this fly from the dataset.

Excluding the 11 Pahole plots in which low fly emergence was likely due to low oviposition rates in the lab, numbers of flies emerged per plot exhibited a general negative relationship with the mean number of ants recorded in the central portion of the plot (central five bait cards, averaged over the final three monitoring events) (Fig. 4). However, variation in fly emergence rates was high at lower ant densities, and the strongly uneven variation in fly emergence across the range in ant density (strong heteroscedasticity), as well as an under-representation of values at higher ant densities, precludes a robust statistical test of this relationship.

4. Discussion

Our results provide confirmation of the presumed detrimental effects of invasive ants on Hawaiian picture-winged *Drosophila* flies. For our study species, *D. crucigera*, suppression of *S. papuana* ants in field plots resulted in a 2.4-fold increase, on average, in the rate of successful development from egg to adult. Equivalently, ambient densities of these ants reduced the fly’s survival rate to adulthood by 58%. This mortality figure provides an important metric that can be used to parameterize population models, and may help prioritize different management actions aimed at recovery of similar listed species.

We observed no evidence for direct impacts of our ant-suppression treatment on non-target predatory arthropods, as no other species were seen inside our bait stations with the exception of several individual detritivorous springtails (Collembola). It is possible that some secondary effects on non-ant predators, arising from their consumption of poisoned ants, could have occurred and thereby contributed to the observed increase in *Drosophila* survival. However, we believe such an effect is likely to be very minimal. In a concurrent study that examined the effects of *S. papuana* suppression on the wider soil arthropod community, there was no evidence for declines in the abundances of predatory (or other) taxa post-treatment (Ogura-Yamada unpub. data). Similarly, no non-target impacts on soil-surface arthropods were detected when the same bait was applied in bait stations on Cousine
Revitalization or control treatment is indicated for each plot. Ephemeral breeding sites, namely the decay of tissues of a limited range of host plant species, likely predisposes them to possessing relatively small, fluctuating populations, even in the absence of novel limiting factors.

Although we did not perform our experiment on any federally listed threatened or endangered Drosophila species, we see no reasons why the resulting inferences should not apply to listed species occurring in the same mesic forest ecosystems. Six species of endangered picture-winged Drosophila species occur or were historically collected in the Wai‘anae Mountains of O‘ahu in the same or similar habitats represented by our field sites (USFWS, 2006), and are therefore potentially threatened by S. papuana ants. Solenopsis papuana is also widespread in wetter mid-elevation forests of the Ko‘olau Mountains of O‘ahu, where four of the same endangered species occur or were historically collected (USFWS, 2006). Moreover, many other Hawaiian Drosophila species in these ecosystems also appear to be quite rare, even though they have not received federal protection (Magnacca, 2014). Similarly, rare Drosophila species on other islands, including federally listed taxa, also likely co-occur with S. papuana or other invasive ant species (USFWS, 2006, 2010; 2013). The populations of most or all of these rare species may in fact be more strongly impacted than D. crucigera by ant predation, as a result of synergism with other factors contributing to their rarity. Conversely, Drosophila species occurring in higher elevation wet forests should be largely unaffected by ants, owing to the absence or low density of ants in these habitats (Reimer, 1994; Krushelnicky et al., 2005).

Not surprisingly, our results exhibited a pattern suggesting that ant-induced fly mortality may be related to the local density of ants, with few adults emerging in plots supporting high relative ant abundances. Fly emergence rates were more variable in plots with low ant densities, including the ant-suppressed plots. This likely resulted from variation in oviposition rates, or perhaps from variable pressure from non-ant predators or competitors among plots, or possibly because low ant densities result in variable detection of fly prey. More complete distribution and density mapping of S. papuana and other invasive ants across habitats supporting picture-winged Drosophila flies, particularly in the vicinity of host plants of rare species, would therefore be valuable. This would identify breeding locations where ant pressures are highest, as well as potential refuge sites where ants are absent or occur at low densities, and where flies might be translocated. Furthermore, while S. papuana is now too widespread to make eradication realistic, our method for suppressing it using bait stations was quite effective, if laborious, and could be used to create relatively small ant-free refuges at
important existing or restored breeding locations. Gaigher et al. (2012) report on an analogous effort to conserve native species on a tropical island through the targeted control of invasive ants using bait stations. Broadcasting the granular ant bait to control S. papuana at high-value sites would be considerably less labor intensive, and may also result in more effective suppression of ants, but for longer-term management scenarios we would advise careful examination of non-target risks to native insects before considering this approach.

In summary, our results clarify the nature of an important limiting factor for potentially many rare species of Hawaiian picture-winged Drosophila flies, and point to several practical actions that could be taken to assist the recovery of this imperiled group of insects. Quantifying the threats posed by invasive species on endangered species is likely to be especially important on highly invaded oceanic islands, but many other regions worldwide also now support moderate numbers of invasive species, including ants (Dawson et al., 2017). Furthermore, although invasive ants have been found to impact a wide variety of native arthropods both in Hawai‘i and in many other locations (Lach and Hooper-Bui, 2010), not all species appear to be affected, and it has been a challenge to identify comprehensive taxonomic or trait-based criteria that reliably separate vulnerable from more resistant species (Howay et al., 2002; Krushelnicky and Gillespie, 2010). This is likely to be true with respect to other invasive predators as well. For rare species that are difficult to sample quantitatively with standard monitoring methods, specialized and targeted experimental studies such as the present one may therefore be needed to understand the level of risk from non-native predators or competitors. Consideration of these types of pressures in conjunction with efforts to restore habitat may in turn greatly strengthen recovery strategies for threatened and endangered insects and other invertebrates.

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