Short Communication

HAWAIIAN ENDEMIC HONEYCREEPERS (DREPANIDINAE) ARE NECTAR ROBBERS OF THE INVASIVE BANANA POKA (*PASSIFLORA TARMINIANA*, PASSIFLORACEAE)

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Abstract—The human transport and subsequent naturalization of species outside their natural ranges has led to novel interactions between introduced and native species throughout the world. Understanding how introduced species impact pollination networks is useful for both invasive species management and native species conservation and restoration. Banana poka (*Passiflora tarminiana*), a hummingbird pollinated liana native to South America, has naturalized in higher elevation forests on the islands of Kauaʻi, Maui and Hawaiʻi in the Hawaiian archipelago, habitats in which endemic honeycreepers still occur. To develop an understanding of the interaction between banana poka and honeycreepers, we undertook a floral visitation study at Hakalau Forest National Wildlife Refuge on the island of Hawaiʻi where three nectivorous honeycreepers and banana poka co-occur. Two honeycreeper species, ʻiʻiwi (*Drepanis coccinea*) and Hawaiʻi ʻamakihi (*Chlorodrepanis virens*), nectar robbed all of the banana poka flowers that they visited, ostensibly due to the length of the corolla tubes (60–90 mm long) which physically inhibits both honeycreeper species from accessing nectar via the mouth of the corolla. In addition, the standing crop and sugar composition of banana poka floral nectar were assessed. Flowers produced large standing crops (375 ± 132 µL) of nectar containing 29.1 ± 1% (w/v) of sugar that was sucrose-dominant (mean: 95.6 ± 0.5% sucrose in each sample). Our observations suggest that the floral nectar of banana poka may form a substantial component of the diet of both honeycreeper species at the study site. Further research is needed to understand how infestations of banana poka affect bird pollination networks at this and other sites in Hawaiʻi.

Keywords—food web, invasion ecology, island biology, nectar larceny, pollination network, species interactions.

INTRODUCTION

The human mediated movement of species beyond their natural ranges is resulting in novel interactions between previously geographically isolated species (Mooney & Cleland 2001; Gutiérrez et al. 2014; Mollot et al. 2017). The effects of these novel interactions on pollination networks are often complex (Lopezaraiza–Mikel et al. 2007; David et al. 2017; Vitt et al. 2020). Pollination networks on oceanic islands are potentially at higher risk of being infiltrated by non-native species due to the increased vulnerability of these ecosystems to biological invasion (Vitousek 1988; D'Antonio & Dudley 1995; Dulloo et al. 2002; Tershy et al. 2015; Bellard et al. 2016; Russell et al. 2017; Zenni et al. 2019), an assumption that is being increasingly supported by pollinator observation studies (Waring et al. 1993; Fancy & Ralph 1998; Olesen et al. 2002; Sugishita 2008; Junker et al. 2010;

Pleasants & Wendel 2010; Pratt et al. 2011; Aslan et al. 2013; Traveset et al. 2013; Sahli et al. 2016; Shay et al. 2016; Aslan et al. 2019; Cortina et al. 2019; Millikin et al. 2021; Grave et al. 2021).

The widescale introduction of non-native species to the Hawaiian archipelago has resulted in the establishment of 1,487 plant taxa considered as naturalized (Imada 2019), exceeding the number of native plant taxa (1,367; Wagner et al. 2005-). Many of these naturalized species are invasive, which has catalysed the extinction of native species and modified native habitats through direct competition and changes in ecosystem processes (e.g. nutrient cycling and fire regimes; Vitousek et al. 1987; Stone et al. 1992; Ellsworth et al. 2014). Although the impacts of invasive species in the Hawaiian Islands are overwhelmingly negative (D'Antonio et al. 1998; Pattison et al. 1998; Asner et al. 2008; Ellsworth et al. 2014; Barton et al. 2021), a number of studies have shown that some novel plant-animal pollination interactions involving native and non-native species may, at least partially, compensate for native animal pollinator decline (for native plants) or provide foraging resources (for native animals) (Waring et al. 1993; Fancy & Ralph 1998; Junker et al. 2010; Pleasants & Wendel 2010; Pratt et al. 2011; Aslan et al. 2013; Sahli et al. 2016; Shay et al. 2016; Aslan et al. 2019; Cortina et al. 2019; Millikin et al. 2021; Grave et al. 2021).

Banana poka (*Passiflora tarminiana* Coppens & Barney) is a hummingbird pollinated liana native to montane areas of tropical South America (D'Eeckenbrugge et al. 2001). The species was introduced to Hawai'i Island in the early twentieth century and was first recorded as naturalizing at Pu'uwa'awa'a on the western side of the island in 1926 (BPBM 2020). Banana poka is now widely naturalized in mesic montane forests on the islands of Kaua'i and Hawai'i (Wagner et al. 1999), and has formed naturalized populations on Maui (BPBM 2020). La Rosa (1984) studied the invasion ecology and life history of banana poka on the island of Hawai'i, stating that the "mechanism of pollination is unknown in Hawai'i." Anecdotal observations of endemic honeycreepers interacting with banana poka flowers have been recorded on Kaua'i and Hawai'i Island (Conant et al. 1998; Fancy & Ralph 1998). On Kaua'i, Conant et al. (1998) observed 'i'iwi piercing holes in the base of banana poka corollas to access nectar, and Kaua'i 'amakihi (*Chlorodrepanis stejnegeri*), 'anianiau (*Magumma parva*), and 'apapane (*Himatione sanguinea*) visiting flowers. Fancy & Ralph (1998) recorded 'i'iwi (*Drepanis coccinea*) foraging for nectar from banana poka flowers on Hawai'i Island. However, these observations did not quantify the rate of visitation or determine the proportion of flowers that were nectar robbed.

We undertook a floral visitation study of banana poka at a single site on Hawai'i Island to better understand the interaction between Hawaiian honeycreepers and this invasive liana. We aimed to determine which honeycreeper species present at the site visit banana poka flowers, the comparative duration and frequency of their visits, and whether they are potential pollinators. In addition, we analysed the volume, concentration, and sugar composition of banana poka floral nectar as a first step to understanding the role that banana poka plays as a nectar source for Hawaiian honeycreepers.

MATERIALS AND METHODS

STUDY SITE

The study was conducted at Hakalau Forest National Wildlife Refuge (HFNWR), a mesic to wet forest located on the windward slopes of Mauna Kea, Hawai'i Island. An area of approximately one hectare in the upper reaches of the Maulua Tract that contains populations of mature banana poka was selected for the study (located at 19º 52′ 05.07″ N, 155 º 18′ 28.38″ W; 1632 m elevation). The former forest at the site was cleared for cattle ranching and now comprises a sporadic canopy of old-growth koa (*Acacia koa*) and 'ōhi'a (*Metrosideros polymorpha*) over kikuyu grass (*Cenchrus clandestinus*) grassland. Patches of regenerating trees of koa, 'ōhi'a, 'ōlapa (*Cheirodendron trigynum* subsp. *trigynum*) and kōlea (*Myrsine lessertiana*), and shrubs of pilo (*Coprosma rhynchocarpa*), kāwa'u (*Ilex anomala*), 'ākala (*Rubus hawaiensis*) and 'ōhelo (*Vaccinium calycinum*) are present within the subcanopy. Three nectar feeding Hawaiian endemic honeycreeper species, 'i'iwi, 'apapane, and Hawai'i 'amakihi (*Chlorodrepanis virens*), are common in the forest at HFNWR (Camp et al. 2010), and occur at the site (Pender 2013).

Field observations

Twenty-nine separate mature banana poka vines, potentially representing multiple plants, were haphazardly selected and tagged. Using binoculars, observations were conducted between 15 and 20 m from each plant during fifty-four 20-minute observation periods between 07:30 and 17:00, conducted over three consecutive days (July 26–28, 2010). The periods in which the observations were conducted were constrained by the travel time to and from the study site. However, it is unlikely that extended observation periods would greatly alter the reported visitation results, because the birds were active throughout the day. A single plant was observed during each observation period, and the species of bird(s) visiting banana poka flowers, the number of flowers visited by each bird species per visit, the duration of each visit to the plant, and whether the bird contacted the reproductive organs or nectar robbed the flowers was recorded. In addition, 320 mature (i.e., in anthesis) banana poka flowers were haphazardly selected (ten each from 32 plants) at the end of the observation study to record the percentage of flowers that had visible signs of damage from nectar robbing. The location and type of damage (holes or slits) to the banana poka corollas was assessed, and the size of the perforations measured using measuring tape.

Nectar standing crop and sugar composition

Individual banana poka flowers that had not been damaged by nectar robbing were collected from five separate plants. The nectar chamber was cut open using a razor blade and the nectar extracted from flowers using a Fisherbrand® polyethylene transfer pipet (model: 13-711-5A; Thermo Fisher Scientific, Massachusetts, U.S.A) with a 50 mm long by 2 mm wide polyethylene tube (model: AAC00004; Saint-Gobain Performance Plastics, Paris, France) inserted into the tip. Nectar samples were transferred to 1.5 mL microcentrifuge tubes (model: MH 815EZ; Phenix Research Products, North Carolina, U.S.A) and stored at -20°C until analyses were performed. Nectar standing crop was quantified using a calibrated micropipette (0-200 µl; model: PR 200; Mettler-Toledo, Ohio, U.S.A) that was adjusted to precisely calculate the nectar volume. The concentration of sugar in each nectar sample was determined using a handheld refractometer (model: Eclipse 0-50% w/v; Bellingham & Stanley LTD, Basingstoke, U.K.). Nectar sugars (sucrose, fructose and glucose) were separated and quantified by high performance liquid chromatography (HPLC) following the methods outlined in Pender et al. (2014).

Data analyses

Percentage was calculated to compare the proportion of visitation events made by each pollinator, the total flowers visited, and the different types of damage to the flowers caused by nectar robbing. A Wilcoxon rank sum test was used to compare differences in the mean number of banana poka flowers visited per observation hour, the number of flowers visited per visit, and the duration of time (seconds) spent at an individual banana poka plant per visit between different visiting species. Analyses were completed in R version 4.0.2 (R Core Team 2020) and RStudio (RStudio Team 2021). Significance was accepted at an alpha (α) level of 0.05. All means are presented ± one standard deviation.

Results

Field observations

ʻIʻiwi and Hawaiʻi ʻamakihi (hereafter ʻamakihi) were regular floral visitors to banana poka flowers during the 18 hours of observations. The mean number of flowers recorded per plant was 62 ± 41. The mean number of flowers available on observed plants per observation hour was 185 ± 69. Of the bird visitation events recorded (N = 279), ʻiʻiwi made 64% of the visits and ʻamakihi 36%. Of all of the flowers visited during the study (N = 673), 72% were visited by ʻiʻiwi with the remainder visited by ʻamakihi. ʻIʻiwi visited significantly more flowers per observation hour compared to ʻamakihi (ʻiʻiwi = 30 ± 21; ʻamakihi = 11 ± 8; W = 45; P < 0.001; Fig. 1). ʻIʻiwi also visited significantly more flowers per visit compared to ʻamakihi (ʻiʻiwi = 3 ± 2; ʻamakihi = 2 ± 2 flowers; W = 6766; P < 0.001). However, there was no significant difference in the mean amount of time either bird species spent visiting individual plants (ʻiʻiwi = 43 ± 38.7 seconds; ʻamakihi = 37 ± 34.5 seconds, W = 7992; P = 0.12). All flowers visited by both bird species were nectar robbed. All but one of the flowers that were randomly selected for visual inspection had been damaged by nectar robbing (N = 319; 99.7%). Flowers had holes drilled through

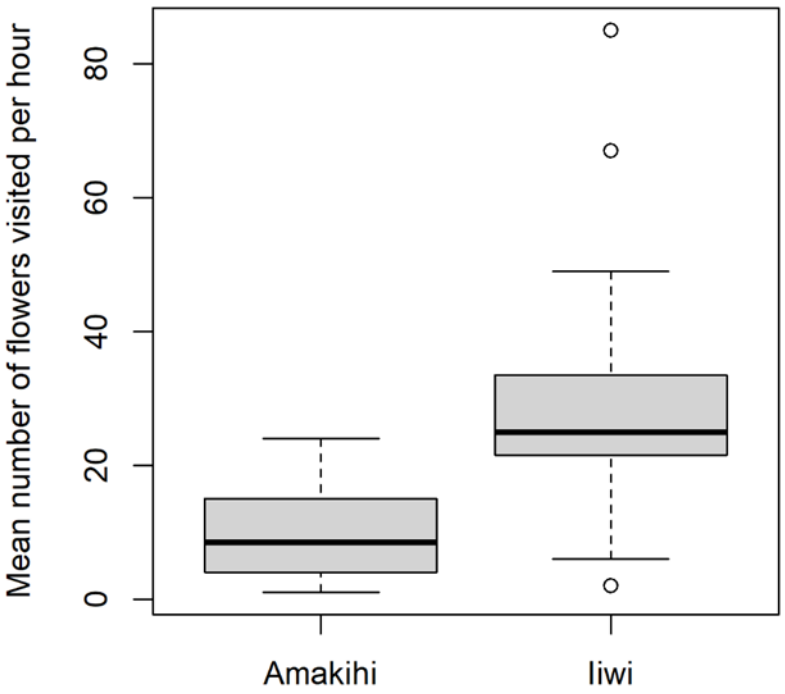

Figure 1. Mean number of banana poka (*Passiflora tarminiana*) flowers visited per observation hour by Hawai'i 'amakihi (*Chlorodrepanis virens*) and 'i'iwi (*Drepanis coccinea*).

the wall of the nectar chamber (98.4% of flowers) and/or slits in the base of the corolla tubes (27.2% of flowers). Flowers with holes contained 2 ± 0.3 holes per flower that were 3 ± 0.3 mm in diameter. Flowers with slits had 1 ± 0.2 slits per flower that were, on average, 36 ± 10.4 mm long.

Nectar standing crop and sugar composition

The mean nectar standing crop of banana poka flowers was 375 ± 132 µL. The mean percentage (w/v) of sugar was 29.1 ± 1%. The nectar samples were sucrose-dominant (mean: 95.6 ± 0.5% sucrose in each sample), containing only trace amounts of fructose and glucose.

Discussion

The results of our study suggest that both ʻiʻiwi and ʻamakihi nectar rob the flowers of banana poka on all occasions and are unlikely to act as pollinators. Furthermore, the nectar from banana poka flowers may form a substantial component of the diet of both honeycreeper species in habitats where this invasive liana is present.

The long, tubular corollas of banana poka (60–90 mm; Wagner et al. 1999) likely physically exclude both ʻiʻiwi and ʻamakihi from simultaneously accessing nectar and contacting the stigma/anthers of the flowers, and therefore these bird species nectar rob the flowers from the base of the corolla to access the nectar chamber. ʻIʻiwi have strongly decurved bills that are 25–28 mm long (Fancy & Ralph 1998), while Hawaiʻi ʻamakihi have bills that are *ca.* 13–16 mm long (Freed et al. 2015). By contrast, the pollinator of banana poka in its native range, the sword-billed hummingbird (*Ensifera ensifera*), has a bill that is up to 110 mm long (Abrahamczyk et al. 2014). Although we observed both ʻiʻiwi and ʻamakihi feeding from both the slits and holes in the flowers, previous observations at HFNWR have observed ʻiʻiwi only making slits and Hawaiʻi ʻamakihi only making holes (J. Jeffrey, pers. comm.).

The higher flower visitation rates per visit and hour recorded for ʻiʻiwi compared to ʻamakihi are potentially the result of differences in the diet, behaviour and the relative size of the two bird species. ʻIʻiwi is a highly active, medium-sized (mean mass = 15.0 g), nectivorous species that is known to be territorial towards birds of the same or different species (Carpenter & MacMillen 1975; MacMillen 1981; Fancy & Ralph 1988). By contrast, ʻamakihi is a smaller (mean mass = 10.7 g) species with a generalist diet and is typically less territorial compared to ʻiʻiwi (MacMillen 1981). MacMillen (1981) found that ʻiʻiwi has a higher metabolic rate and daily energy expenditure than smaller honeycreeper species such as ʻamakihi, and

concluded that these factors influence the foraging and social behaviour of the former species. Although many of the floral visits were likely made by a small number of individuals of either species, and the relative density of these honeycreeper species appeared to be low at the site at the time of the study, ʻiʻiwi were observed actively defending floral resources of banana poka plants from both other ʻiʻiwi and ʻamakihi.

Although ʻiʻiwi and ʻamakihi are unlikely to act as pollinators of banana poka, fully formed fruits were abundant on the plants at our study site, suggesting that other animals are acting as pollinators. La Rosa (1984) found that whilst banana poka are self-compatible when hand pollinated (achieving close to 50% fruit set), natural rates of selfing are low in the absence of pollinators (4% fruit set from bagged flowers) in Hawaiʻi. Although no other floral visitor studies have been conducted on banana poka in Hawaiʻi, Beavon & Kelly (2011) found that introduced honeybees (*Apis mellifera*; present in Hawaiʻi) and bumblebees (*Bombus* spp.; absent in Hawaiʻi) were the most frequent floral visitors of banana poka in New Zealand, where the species is also invasive, and are playing an important role in fruit production. Further pollination studies of banana poka in Hawaiʻi are needed to determine if any of the fifteen introduced bee species (Snelling 2003) and/or other insects are pollinators of banana poka and whether nectar robbing by honeycreepers impacts pollinator visitation and reproductive fitness (i.e., rates of fruit and seed production).

It's unclear whether the presence of banana poka affects the pollination of coexisting native bird pollinated plant species. A pollination study of restoration plantings of two Hawaiian lobeliads (*Clermontia lindseyana* and *C. pyrularia*) in the immediate vicinity and during the same time period of the present study found that ʻiʻiwi and ʻamakihi visitation rates were much lower than those recorded for banana poka (Pender 2013). Although banana poka is proportionately more common and occurs over a wider area than the two lobeliad species, it is possible that honeycreepers preferentially visit banana poka flowers. Alternatively, the presence of banana poka may potentially increase visitation to co-occurring native plant species. Interestingly, both bird species primarily nectar rob both lobeliad species (Pender 2013). Whether this is a learned behaviour from nectar robbing banana poka flowers, or is also the result of a mismatch in size between the flowers of the lobeliad species and the birds is difficult to determine. Conant et al. (1998) observed ʻiʻiwi nectar robbing flowers of native *Clermontia fauriei* and *Scaevola glabra* on Kauaʻi, and speculated that this behaviour may have resulted from nectar robbing flowers of introduced species.

Following the nectar-sugar classification of Baker & Baker (1983), we found that the nectar of banana poka flowers is sucrose-rich (c.f. specialized bird pollination; Johnson & Nicholson 2008). Based on the results of floral nectar studies (Cory 1984; Lammers & Freeman 1986; Elmore 2008; Pender et al. 2014), Hawaiʻi's bird pollinated flora likely produces nectar that is comparable to the generalist bird pollination syndrome (dilute nectar that is rich in hexose sugars; Johnson & Nicholson 2008). The frequency of banana poka flower visitation suggests that ʻiʻiwi and ʻamakihi possess intestinal sucrase, the enzyme that catalyses the hydrolysis of sucrose to fructose and glucose. Although no sugar preference or absorption studies have been conducted on nectivorous Hawaiian honeycreepers, sucrase is present in other members of the Fringillidae (Nicolson & Fleming 2003; Lotz & Schondube 2006).

The nectar robbing of banana poka flowers by honeycreepers represents an interesting novel interaction between endemic nectivorous birds and an invasive plant species in Hawaiʻi. The impacts each interacting party are having on one another and the broader pollination networks at this and other sites in Hawaiʻi warrants further investigation.

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