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HOST PLANT ASSOCIATIONS OF LEPIDOPTERA AND IMPLICATIONS FOR FOREST BIRD MANAGEMENT AT HAKALAU FOREST NATIONAL WILDLIFE REFUGE

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ABSTRACT

Forests dominated or co-dominated by ʽōhiʽa (*Metrosideros polymorpha*) are critical to most Hawaiian forest birds, but fungal diseases causing Rapid ʽŌhiʽa Death (ROD) threaten ʽōhiʽa-based food webs that support native bird communities on Hawaiʽi Island. Caterpillars are the most frequently consumed arthropod prey of native birds and their young and are especially frequent in the diets of one threatened (T) and three endangered (E) species ("listed" species) at Hakalau Forest National Wildlife Refuge (Hakalau): ʽakiapōlāʽau (*Hemignathus wilsoni*, E), ʽalawī (Hawaiʽi creeper; *Loxops mana*, E), Hawaiʽi ʽākepa (*L. coccineus*, E), and ʽiʽiwi (*Drepanis coccinea*, T). Hakalau harbors the largest and most stable populations of listed forest birds in Hawaiʽi, presumably due to the availability of food resources and the extent of suitable, managed habitat above the range of mosquito-borne avian malaria. Because a previous study indicated that only a few caterpillar species were important in the diets of listed birds at Hakalau, we investigated the distribution of caterpillars on common host plants available to foraging birds. Eleven native plant species hosted two or more taxa identified to genus or species, with at least seven from ʽōhiʽa, six from koa (*Acacia koa*), and five from ʽākala (*Rubus hawaiensis*). We identified 16 taxa to genus or species from 9 families, assigning 11 to species. Leaves, which were the focus of our sampling effort, were the substrate used by 20 caterpillar taxa, and dead wood or bark was used by 7 taxa. In a previous study, we classified 19 morphotypes of caterpillar mandibles in the diets of native and alien birds at Hakalau, and in the present study we dissected mandibles from caterpillars that likely matched 10 of those morphotypes. These 10 morphotypes potentially represented >95% of caterpillar prey found in the earlier diet study and were collected from 11 host plant species, with ʽōhiʽa hosting 8 morphotypes, 4 of which were exclusive to ʽōhiʽa. The most widely hosted morphotype was found on all 11 plant species that we sampled, including ʽōhiʽa, but the other 9 morphotypes were found on 1–7 hosts. As shown by the previous diet study, each of the listed bird species consumed caterpillar prey consisting mostly of combinations of two morphotypes drawn from a pool of only five, indicating a high degree of specialization. In the present study, we collected three of the five key morphotypes only on ʽōhiʽa, highlighting the importance of this tree to listed bird species. Because ʽōhiʽa forests in Hakalau remain vulnerable to ROD, measures to mitigate the impacts of reduced ʽōhiʽa cover are important to consider from the perspective of forest bird food webs and diet. Ongoing reforestation of former pasturelands with koa and common understory species should provide alternative caterpillar prey for forest birds. Our results and information from the literature indicate that koa supports, to varying degrees, nearly all forest birds at Hakalau, while ʽākala, ʽōhelo (*Vaccinium calycinum*), kōlea (*Myrsine lessertiana*), ʽōlapa (*Cheirodendron trigynum*), pūkiawe (*Leptecophylla tameiameiae*), and māmaki (*Pipturus albidus*) could benefit bird populations by increasing prey availability and structural complexity in koa-dominated stands. Foraging studies and additional research to identify species and host plant associations of important forest bird prey, including caterpillars and other arthropods, can help managers evaluate the complex interactions between native forest birds and their food webs and habitats.

INTRODUCTION

A critical management goal at Hakalau Forest National Wildlife Refuge (Hakalau), Hawaiʽi, is protecting the native forest habitats of bird species listed as threatened (T) and endangered (E), as well as all other native species, regardless of their listing status (USFWS 2010). Hakalau provides essential wet montane habitat for eight endemic passerine species and supports the largest and most viable populations of three endangered specialist insectivores, ʽakiapōlāʽau (*Hemignathus wilsoni*), ʽalawī (Hawaiʽi creeper; *Loxops mana*), and Hawaiʽi ʽākepa (*L. coccineus*), and a threatened specialist nectarivore, ʽiʽiwi (*Drepanis coccinea*; Gorresen *et al.* 2009, Camp *et al.* 2010, Paxton *et al.* 2013, Camp *et al.* 2015). Due to the expanse of upper montane forest available and long-term efforts to restore degraded habitats, Hakalau provides a critical refuge for endemic forest birds against the upslope movement of mosquito-borne avian malaria, driven by climate change, and the invasion of many weeds and pests that infest lowland habitats.

Entire watersheds have recently come under severe threat from Rapid ʽŌhiʽa Death (ROD), a fast-spreading fungal disease (Keith *et al.* 2015; CTAHR 2016a,b; Barnes *et al.* 2018) that could decimate stands of ʽōhiʽa (*Metrosideros polymorpha*), the dominant tree species at Hakalau and across Hawaiʽi. ʽŌhiʽa composes 90% of the forest canopy at Hakalau (Hart 2010) and preventing or mitigating heavy losses of ʽōhiʽa will affect the survival of birds and the structure and function of the forest ecosystem. Although ROD has not yet been confirmed at Hakalau, it has been reported from forests adjacent to the southern boundary of the refuge (D. L. Ball, U.S. Fish and Wildlife Service, personal communication, 29 Nov 2021). It is likely that the disease is already at Hakalau or will be there soon. An estimated 130,000 ha on Hawaiʽi Island were affected by ROD through 2020 (Perroy *et al.* 2021). The potential loss of ʽōhiʽa at Hakalau, therefore, could be widespread and severe with devastating impacts on the forest ecosystem.

ʽŌhiʽa is an important foraging substrate used by two of the three endangered insectivorous bird species found at Hakalau, the ʽākepa and ʽalawī (Lepson and Freed 2020, Lepson and Woodworth 2020), whereas koa (*Acacia koa*) is the primary substrate of the ʽakiapōlāʽau (Pratt *et al.* 2020). The nectarivorous ʽiʽiwi is strongly associated with ʽōhiʽa for nectar but forages for arthropods on ʽōhiʽa, koa, and other species (Fancy and Ralph 2020).

Diet studies indicate that caterpillars are the primary arthropod prey of Hawaiian forest birds (Perkins 1903, 1913; Baldwin 1953; Ralph *et al.* 1985; Peck *et al.* 2015), but only 3 of 19 morphotypes (species unknown but distinguished by mandible morphology) composed 72% of the caterpillars eaten by birds generally at Hakalau and 63–100% of the caterpillars eaten by the endangered and threatened species (Banko *et al.* 2015). Of the 720 caterpillars identified in diet samples, 42% were of one morphotype, which was consumed by all bird species.

The prevalence of a small number of caterpillar morphotypes in bird diets underscores the extreme vulnerability of endangered specialist species to food web disruption due to ROD, invasive species, and climate change, but impacts to the entire bird community should also be expected with the loss of ʽōhiʽa cover. Critically important to helping endangered and other native bird species survive major environmental change is identifying the host plants, threats, and life histories of the caterpillar morphotypes most frequently consumed by birds. Knowing associations between key caterpillar species and hosts other than ʽōhiʽa could guide efforts to increase the abundance of these species in the event of substantial ʽōhiʽa loss or other perturbations. The problem for managers is that the full range of associations between caterpillar species and host plants is unknown. There also is scant information about the level of threat to caterpillars from invasive parasitoid wasps and other important aspects of the ecology of key caterpillar species. Detailed information about host plant associations and other aspects of caterpillar ecology can help managers select alternative host species and planting schemes that would most benefit birds in the event of heavy ʽōhiʽa loss.

The first objective of this study was to determine associations between caterpillar species and host plants. We did this by collecting caterpillars from ʻōhiʻa and other common native trees and shrubs in the field, rearing them to moths in the lab, and identifying moths to species when rearing was successful. We also reviewed the literature to compile data on host plant relationships. Our second objective was to compare the mandibles of caterpillars collected in the field to the 19 morphotypes identified in the diets of birds by Banko *et al.* (2015) and to identify the host plants of important caterpillar prey.

METHODS

Study Area

This study took place within upper elevations of the Pua Akala section of the Hakalau Unit of Hakalau Forest National Wildlife Refuge, Hawaiʻi Island, Hawaiʻi (Figure 1). The canopy of this wet montane forest is dominated by old-growth ʻōhiʻa and koa but contains other tree species, including ʻōlapa (*Cheirodendron trigynum*), kōlea (*Myrsine lessertiana*), and kāwaʻu (*Ilex anomala*). Common understory shrubs are ʻākala (*Rubus hawaiensis*), ʻōhelo (*Vaccinium calycinum*), pūkiawe (*Leptecophylla tameiameiae*), and pilo (both *Coprosma ochracea* and *C. rhynchocarpa*, which here we do not distinguish one from the other). Mean annual rainfall at the study sites is about 2,400 mm (Giambelluca *et al.* 2013), although amounts can vary greatly within and among years. Historically, the study area has been impacted by cattle and feral pigs that reduced the diversity and biomass of native understory plants, but habitats are now largely free of these ungulates and are in the process of recovery. A significant restoration effort carried out over the past 30 years has resulted in re-establishment of koa and other native plants across large swaths of former pastureland.

Caterpillar Sampling

Caterpillars were collected from most of the common tree and shrub species in areas with relatively high densities of native and introduced bird species (Camp *et al.* 2010) and were centered around the rain shelter at Pua Akala (~1,890 m elevation), the bottom of Pedro Road (~1,625 m elevation), and near the gate leading into the administration area of the refuge, at the interface between montane and subalpine habitat and where species typically found in the subalpine zone had been planted (~1,970 m elevation; Figure 1). This range of elevation was too narrow to allow for an assessment of the effect of elevation on caterpillar distribution and abundance. We sampled host plants when birds were unlikely to be nesting (October and November) and likely to be nesting or feeding fledglings (June) to assess seasonal trends in caterpillar availability. Sampling took place on 6 October 2017 (Pua Akala), 11 October 2017 (Pedro low), 2 November 2017 (Pua Akala), 20 November 2017 (Pedro low and administration area), and 21 June 2018 (Pua Akala). We had planned for at least one additional collecting trip in each season, but access to the refuge was curtailed due to prolonged closure of Mauna Kea Access Road and later by the Covid-19 pandemic; therefore, we were unable to evaluate seasonal trends.

Caterpillars were obtained by gently shaking vegetation to dislodge them onto a white sheet held beneath the foliage. Immediately following collection, caterpillars were placed into plastic vials containing fresh foliage from the plant on which they were removed and stored in a cooler for transport to the laboratory. This sampling technique missed caterpillars within unopened leaf and flower buds as well as within fruits and wood. It also underrepresented caterpillars found under bark.

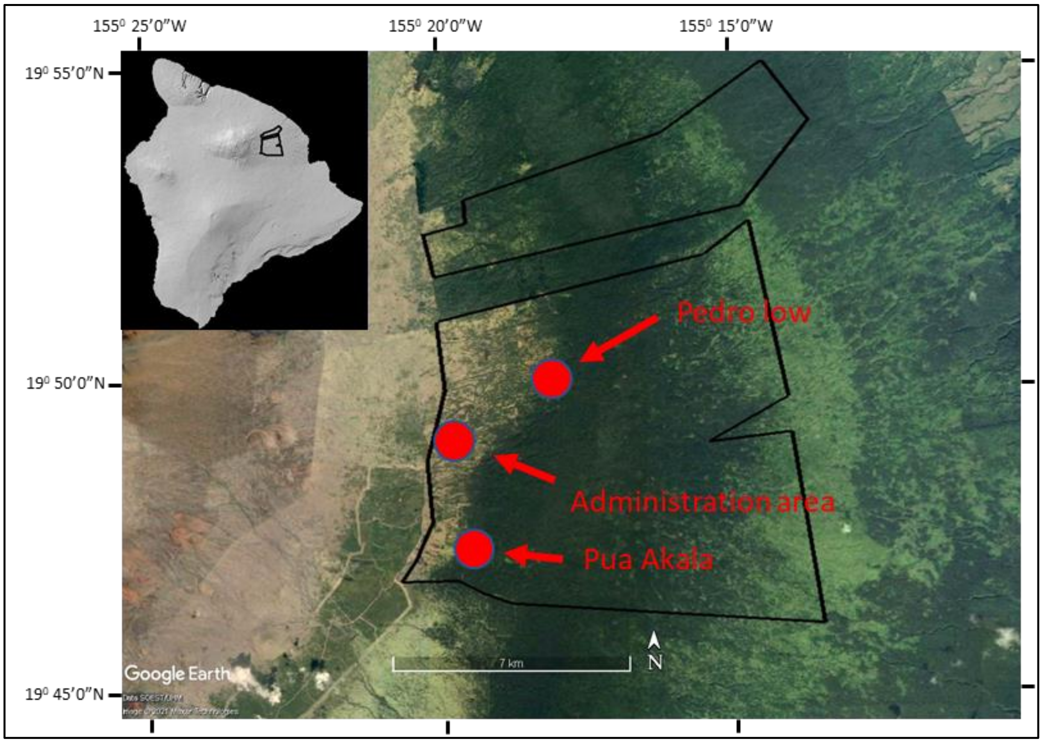

Figure 1. General locations where plants were sampled for caterpillars at Hakalau. Pua Akala and Pedro low sites were in forest dominated by mature ʻōhiʻa and koa, while the administration site was in an area dominated by young plantation-age koa. The inset map shows the location of the Hakalau Unit of Hakalau Forest National Wildlife Refuge on Hawaiʻi Island. Background map source: Google Earth.

To standardize sampling effort across plant species, we recorded the number of individual branches or fronds shaken for caterpillars from each plant. The biomass of foliage on branches is likely to have varied somewhat within species and greatly among species, but we did not measure this variation. We attempted to sample most branches or fronds that could be reached from the ground for each plant encountered. Once a plant was thoroughly sampled, we moved on to sample a nearby plant. The selection of plants was haphazard, and our effort was designed to distribute sampling across plant species within the sampling area. The number of branches or fronds sampled was recorded on all sampling dates except the first.

In the lab, live caterpillars were placed individually into plastic cups with foliage from the plant species on which they were found and monitored two to three times per week for developmental stage (instar progression) and food consumption. Foliage was replaced once or twice per week until caterpillars pupated. Individuals that emerged as moths were euthanized by freezing or exposure to ethyl acetate, labeled, and pin-mounted for identification. A subset of caterpillars was placed directly into 70% ethanol for preservation and subsequent dissection of mandibles. A shortage of host plant material limited our ability to rear caterpillars from some plant species (e.g., ʻāweoweo [*Chenopodium oahuense*]). Mortality from parasitism as well as unknown causes resulted in the death of numerous caterpillars.

Mandibles were dissected from caterpillars using fine-tipped forceps under a dissecting microscope. Mandibles were measured, photographed, and archived in isopropyl alcohol (70%). In addition to preserved caterpillars as a source, mandibles were dissected from head capsules that were shed by caterpillars during molt between growth stages. Molted head capsules sometimes provided a series of mandibles representing changes in morphology across an age series (Appendix II). We compared these mandibles to those identified in the diets of Hakalau birds in an earlier study (Banko *et al.* 2015).

Species Identification

We reared caterpillars collected from the field at Kīlauea Field Station in Hawaiʽi Volcanoes National Park and identified moths that emerged using keys (Zimmerman 1958a,b; 1978) and reference specimens. In many cases, moths did not emerge, which limited the level of identification, especially for *Hyposmocoma*. Some caterpillars were identified to the family level based on a key to the caterpillars (Zimmerman 1978). We could not identify some specimens to family, genus, or species without comparing them with known material at the Bishop Museum, Honolulu. We were unable to schedule a session at the museum due to Covid-19 travel restrictions, which was a problem especially for *Scotorythra* and *Thyrocopa*. Additionally, *Hyposmocoma* specimens require DNA barcoding for species identification.

Data Availability

Data and metadata associated with this report are available at https://doi.org/10.5066/P9O77HNV (Peck *et al.* 2022).

RESULTS

Caterpillar Abundance on Host Plants

We collected 777 caterpillars from 19 native and 3 alien host plant species at Hakalau during October and November 2017 and June 2018 (Table 1). Of the native species, 16 were endemic and 3 were indigenous. Populations of all three alien species, English holly (*Ilex aquifolium*), gorse (*Ulex europaeus*), and blackberry (*Rubus argutus*), are controlled at Hakalau, and only blackberry was widespread where we sampled. Most of our caterpillars were obtained from the most common shrubs and trees growing naturally in native-dominated forest. We did not sample koa and ʽōhiʽa trees planted in groves to restore former pasturelands. The few pāwale (*Rumex giganteus*) we sampled were highly localized in an open, disturbed area surrounded by native koa-ʽōhiʽa forest recovering from grazing, but the endangered *Clermontia lindseyana* and possibly a few small patches of the endangered mint, *Phyllostegia brevidens*, were planted in the forest matrix. Although we may have sampled one or two *P. brevidens*, we primarily sampled a few scattered patches of *Stenogyne calaminthoides*, an endemic mint occurring naturally in the forest. ʽĀweoweo, māmane (*Sophora chrysophylla*), and naio (*Myoporum sandwicense*) were planted in former pastureland along the upper margin of the refuge.

Of the 22 plant species we sampled, our effort focused on the 11 species that were widespread, common, naturally growing in native-dominated forest, and known or suspected to be visited by birds. From these 11 species, we sampled 1,435 branches and collected 463 caterpillars (3.2 caterpillars/10 branch samples). Caterpillar abundance was highest for koa (7.4 caterpillars/10 samples), with māmane second (6.4 caterpillars/10 samples; Table 1). Following in rank order, ʽōhelo, pūkiawe, and both species of pilo all yielded >3 caterpillars/10 samples, but ʽōhiʽa yielded only 2.1 caterpillars/10 samples and was ranked last among the 11 focal species.

Table 1. Numbers of caterpillars collected from 22 native and alien plant species at Hakalau. Eleven common host plants are indicated with an asterisk.

Family	Scientific name	Common name	Status[1]	Life form[2]	Branch samples[3]	Larvae[4]	Larvae/10 samples	Larvae[5]	Total larvae
Amaranthaceae	*Chenopodium oahuense*	ʽāweoweo	E	s	39	14	3.6	8	22
Aquifoliaceae	*Ilex anomala*	kāwaʽu	I	t	11	1	0.9	0	1
Aquifoliaceae	*Ilex aquifolium*	Eng. holly	A	s,t	1	0	0	0	0
Araliaceae	**Cheirodendron trigynum*	ʽōlapa	E	t	168	36	2.1	4	40
Campanulaceae	*Clermontia lindseyana*	ʽōhā wai	E	s	52	2	0.4	1	3
Cibotiaceae	*Cibotium glaucum*	hāpuʽu pulu	E	f	42	4	1.0	0	4
Dryopteridaceae	*Dryopteris wallichiana*	lau-kahi	I	f	132	13	1.0	27	40
Epacridaceae	**Leptecophylla tameiameiae*	pūkiawe	E	s	157	56	3.6	13	69
Ericaceae	**Vaccinium calycinum*	ʽōhelo	E	s,t	204	91	4.5	25	116
Fabaceae	**Acacia koa*	koa	E	t	110	81	7.4	34	115
Fabaceae	**Sophora chrysophylla*	māmane	E	t	28	18	6.4	7	25
Fabaceae	*Ulex europaeus*	gorse	A	s	1	1	10.0	0	1
Gleicheniaceae	*Dicranopteris linearis*	uluhe	I	f	12	1	0.8	0	1
Lamiaceae	*Stenogyne calaminthoides*[6]	N/A	E	l	9	3	3.3	4	7
Myoporaceae	**Myoporum sandwicense*	naio	E	t	28	7	2.5	13	20
Myrsinaceae	**Myrsine lessertiana*	kōlea	E	t	89	22	2.5	22	44
Myrtaceae	**Metrosideros polymorpha*	ʽōhiʽa	E	t	399	82	2.1	34	116
Polygonaceae	*Rumex giganteus*	pāwale	E	h	3	2	6.7	0	2
Rosaceae	**Rubus hawaiensis*	ʽākala	E	s	199	52	2.6	24	76
Rosaceae	*Rubus argutus*	blackberry	A	s	30	10	3.3	33	43
Rubiaceae	**Coprosma* spp.[7]	pilo	E	s,t	53	18	3.4	13	31
TOTAL					1,767	514	2.9	317	777

[1] A = alien, E = endemic, I = indigenous
[2] f = fern, h = herb, l = liana, s = shrub, t = tree
[3] Number of branches shaken over a 1x1-m collecting sheet
[4] Caterpillars collected per number of branches sampled (note that foliage biomass per branch of different species varies widely)
[5] Caterpillars collected but branch samples were not counted
[6] *Phyllostegia brevidens*, an endangered endemic mint planted in our study areas, may also have been sampled.
[7] *Coprosma ochracea* and *C. rhynchocarpa* were both sampled but were not distinguished from one another.

Among the 11 less common species with at least 30 branches sampled, only ʻāweoweo and blackberry yielded >3 caterpillars/10 samples.

We identified at least to family the caterpillars collected from 11 of the 13 most common shrub and tree species, excluding only ʻāweoweo and kāwaʻu, which we sampled only sparingly. From several plant species we also collected some caterpillars that we were not able to confidently identify to the family level, including one found on *Coprosma ochracea* or *C. rhynchocarpa* that looked similar to tortricid caterpillars found on other host plants. We are cautious to call it a tortricid because, to our knowledge, tortricids have not been reported from *Coprosma* on Hawaiʻi Island.

All plant species hosted two or more taxa that were identified to genus or species, with at least seven from ʻōhiʻa, six from koa, and five from ʻākala (Table 2). Based on published host associations, more species may have been collected from most plants, but uncertainty with identifications precluded assigning additional names. For example, *Hyposmocoma* caterpillars were collected from seven of the common shrub and tree species, but we were not able to assign species names to any of these small moths. It is possible that they represented one or more of the four species or subspecies previously identified from these plants by others. Similarly, we could not make species determinations for some of the morphologically variable *Scotorythra*, which were designated as *Scotorythra* sp. 1 or *Scotorythra* sp. 2. More detailed examination of these *Scotorythra* would likely place them among those identified to species during this study. Overall, we identified 16 taxa to genus or species from 9 families, assigning 11 to species (Table 2). Geometridae was represented by at least six species, the most of any family (Table 2). A geometrid that we could not identify to species, *Scotorythra* sp. 1, was found on all 11 host plants. More detailed examination of *Scotorythra* sp. 1 as well as *Scotorythra* sp. 2, which we found only on ʻōhiʻa, would likely place them among those identified to species during this study. The next most widely hosted family was Cosmopterigidae, with one or more species of *Hyposmocoma* found on seven host species, including ʻōhiʻa and koa. In the Xyloryctidae, an unidentified species of *Thyrocopa* was found on ʻōhiʻa, koa, and four other hosts. Other families were distributed across one to three plant species, but additional hosts may be confirmed when more caterpillar taxa are identified to species.

Leaves (or phyllodes in the case of koa) and dead wood or bark were typically the host plant substrates from which caterpillars were collected and reared. Leaves, which were the focus of our sampling effort, were the substrate used by 20 caterpillar taxa, and dead wood or bark was used by 7 taxa (Table 2). ʻŌhiʻa leaves were the substrate used by six caterpillar taxa, two were found on dead wood or bark, one was boring into a stem, and the substrate of one was undetermined. Koa hosted four caterpillar taxa each on leaves and dead wood or bark, whereas ʻākala hosted four taxa on leaves and at least five on dead wood or bark.

Associations of Caterpillar Mandible Morphotypes with Bird Diets

In a previous study, we classified 19 morphotypes of caterpillar mandibles in the diets of native and alien birds at Hakalau (Banko *et al.* 2015), and in the present study we dissected mandibles from caterpillars that likely matched 10 of those morphotypes (Table 3). We were able to classify seven of those morphotypes to family or genus while three morphotypes could be identified only as non-geometrid Lepidoptera, as they were not reared to adults. Six mandible types (morphotypes B, C, F, J, K, and N) were strong matches to morphotypes identified during the diet study by Banko *et al.* (2015), and four types were likely matches (E, G, L, P). Two types of mandibles earlier estimated to be distinct morphotypes (L and P) may be represented

Table 2. Caterpillar species collected and reared to moths from 11 common endemic host trees and shrubs. *Coprosma ochracea/C. rhynchocarpa* were counted as two host species. Taxa that were positively identified are indicated by †. Based on published host plant associations, we identified additional possible species, indicated by ††. Caterpillar-host plant associations noted by other authors are indicated by the single initial of their last name: H = Heddle (2003), M = Montgomery (1983), R = Robinson *et al.* (2010), S = Swezey (1954), Z = Zimmerman (1958a,b; 1978). Substrates from which caterpillars were collected are indicated in brackets: leaf = [lf], flower = [fl], dead wood/bark = [dw/bk], stem borer [sb], undetermined substrate = [?].

Family	Taxa	*Acacia koa*	*Cheirodendron trigynum*	*Coprosma ochracea/ rhynchocarpa*	*Leptecophylla tameiameiae*	*Metrosideros polymorpha*	*Myoporum sandwicense*	*Myrsine lessertiana*	*Rubus hawaiensis*	*Sophora chrysophylla*	*Vaccinium calycinum*
Carposinidae	*Carposina* sp.	-	-	-	-	† [lf]	-	-	-	-	-
Cosmopterigidae	*Hyposmocoma chilonella*	-	-	-	-	-	-	-	††,S [dw/bk]	-	-
Cosmopterigidae	*H. c. chilonella*	-	††,R,Z [dw/bk]	-	-	††,Z [dw/bk]	-	-	††,Z [dw/bk]	-	-
Cosmopterigidae	*H. c. triocellata*	-	††,Z [dw/bk]	-	-	-	-	-	††,S,Z [dw/bk]	-	-
Cosmopterigidae	*Hyposmocoma crytogamiella*	-	-	-	-	††,Z [sb]	-	-	-	-	-
Cosmopterigidae	*Hyposmocoma* sp.	† [dw/bk]	† [dw/bk?]	-	† [dw/bk?]	† [?]	-	† [?]	† [dw/bk?]	-	† [dw/bk?]
Crambidae	*Udea endopyra*	-	-	-	-	-	-	-	†,R,Z [lf]	-	-
Crambidae	*Udea pyranthes*	-	-	-	-	-	-	-	-	-	††,R,Z [lf]
Geometridae	*Eupithecia monticolans*	-	-	-	††,S,Z [lf]	†,M,Z [lf/fl]	-	-	-	-	-
Geometridae	*Scotorythra artemidora*	-	-	-	-	-	-	-	-	†† [lf]	-
Geometridae	*Scotorythra corticea*	†,H,S,Z [lf]	-	-	-	-	-	-	-	-	-
Geometridae	*Scotorythra euryphaea*	-	††,H [lf]	-	-	†,H [lf]	-	-	-	-	-

Family	Taxa	*Acacia koa*	*Cheirodendron trigynum*	*Coprosma ochracea/ rhynchocarpa*	*Leptecophylla tameiameiae*	*Metrosideros polymorpha*	*Myoporum sandwicense*	*Myrsine lessertiana*	*Rubus hawaiensis*	*Sophora chrysophylla*	*Vaccinium calycinum*
Geometridae	*Scotorythra goniastis*	-	-	-	††,H [lf]	-	-	-	-	-	-
Geometridae	*Scotorythra paludicola*	†,H,S,Z [lf]	-	-	-	-	-	-	-	-	-
Geometridae	*Scotorythra rara*	††,H,S,Z [lf]	†,H,R [lf]	-	-	††,H,S,Z [lf]	-	-	††,S,Z [lf]	-	-
Geometridae	*Scotorythra willisi*	-	-	-	-	-	-	-	†,H [lf]	-	-
Geometridae	*Scotorythra* sp. 1	† [lf]	† [lf]	† [lf]	† [lf]	† [lf]	† [lf]	† [lf]	† [lf]	† [lf]	† [lf]
Geometridae	*Scotorythra* sp. 2	-	-	-	-	† [lf]	-	-	-	-	-
Lycaenidae	*Udara blackburni*	†,S [lf]	-	-	-	-	-	-	-	-	-
Noctuidae	*Peridroma albiorbis*	-	-	-	-	-	-	-	-	† [lf]	-
Sphingidae	*Hyles wilsoni*	-	-	† [lf]	-	-	-	-	-	-	-
Tortricidae	*Epiphyas postvittana*	-	-	-	-	-	† [lf]	-	-	-	-
Tortricidae	*Pararrhaptica longiplicata*	-	-	-	-	-	-	††,R [lf]	-	-	-
Tortricidae	*Spheterista pleonectes*	-	††,S [lf]	-	-	-	-	-	-	-	-
Tortricidae	Tortricidae sp.	-	† [?]	-	-	-	-	† [lf]	-	-	-
Xyloryctidae	*Thyrocopa argentea*	††,S,Z [dw/bk]	-	-	-	-	-	-	††,S [dw/bk]	-	-
Xyloryctidae	*Thyrocopa indecora*	††,S,Z [dw/bk]	-	-	-	-	-	-	-	-	-
Xyloryctidae	*Thyrocopa* sp.	† [dw/bk]	-	-	† [dw/bk]	† [dw/bk]	-	† [dw/bk]	† [dw/bk]	-	† [dw/bk]

Table 3. Caterpillar mandibles identified to morphotype in this study that correspond to bird diet samples described in Banko *et al.* (2015). Plant host codes are: AcaKoa (*Acacia koa*), CheTri (*Cheirodendron trigynum*), CopOch/CopRhy (*Coprosma ochracea/C. rhynchocarpa*), LepTam (*Leptecophylla tameiameiae*), MetPol (*Metrosideros polymorpha*), MyoSan (*Myoporum sandwicense*), MyrLes (*Myrsine lessertiana*), RubHaw (*Rubus hawaiensis*), SopChr (*Sophora chrysophylla*), VacCal (*Vaccinium calycinum*). Taxa and host plants are unknown for nine mandible morphotypes. Family and taxon are unknown for an additional three mandible morphotypes that were found on *Metrosideros polymorpha*.

Mandible morphotype	Family	Taxon collected from host plants	Preliminary host plant range
A	unknown	unknown	unknown
B	Crambidae	*Udea* sp.	RubHaw, VacCal
C	Crambidae	*Udea* sp.	RubHaw, VacCal
D	unknown	unknown	unknown
E	Cosmopterigidae	*Hyposmocoma* sp.?	AcaKoa, CheTri, LepTam, MetPol, MyrLes, RubHaw, VacCal
F	Cosmopterigidae	*Hyposmocoma* sp.	AcaKoa, CheTri, LepTam, MetPol, MyrLes, RubHaw, VacCal
G	unknown	unknown	MetPol
H	unknown	unknown	unknown
I	unknown	unknown	unknown
J	Geometridae	*Scotorythra* sp.?	AcaKoa, CheTri, CopOch/CopRhy, LepTam, MetPol, MyoSan, MyrLes, RubHaw, SopChr, VacCal
K	Carposinidae	*Carposina* sp.	MetPol
L	unknown	unknown	MetPol
M	unknown	unknown	unknown
N	Xyloryctidae	*Thyrocopa* sp.	AcaKoa, LepTam, MetPol, MyrLes, RubHaw, VacCal
O	unknown	unknown	unknown
P	unknown	unknown	MetPol
Q	unknown	unknown	unknown
R	unknown	unknown	unknown
S	unknown	unknown	unknown

by a single species found on ʽōhiʽa. Further study is required to confirm the identity of these species.

Host plant associations cannot be definitively determined until caterpillar morphotypes have been identified at the species level. Therefore, we cannot be certain of the importance or full range of host plants of caterpillars identified only to family or genus level. Our preliminary determinations suggest that one or more caterpillar morphotypes occurs on each of the 11 host species sampled (Table 3, Figure 2). ʽŌhiʽa may be the exclusive host of morphotypes G, K, L, and P and likely also hosts E, F, J, and N. ʽĀkala and ʽōhelo may each host six morphotypes, while koa, kōlea, and pūkiawe may each host four. It is likely that host plants share a caterpillar species. For example, *Scotorythra rara* has been found to feed on four of the host plants sampled.

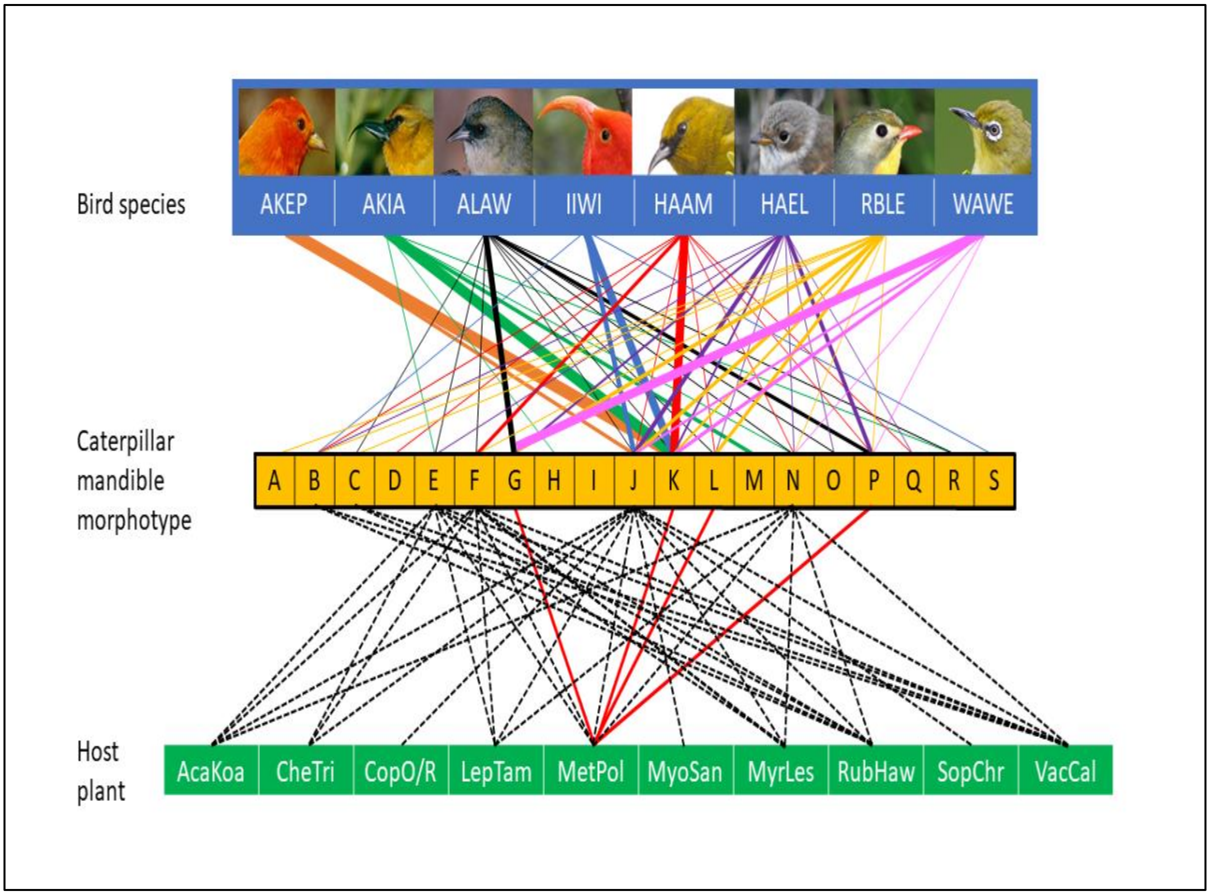

Figure 2. Web of bird-caterpillar-host plant interactions. Each plant species hosted at least one caterpillar morphotype consumed by birds. Morphotype I was eaten only by ʻōmaʻo (*Myadestes obscurus*; not shown on chart). Lines connecting birds and caterpillar morphotypes vary in thickness according to the proportion of a morphotype in the diet (see Banko *et al.* 2015; Appendix II). ʻŌhiʻa may be the exclusive host of four caterpillar morphotypes (red lines), all of which are major prey of listed bird species. Dashed black lines represent potential caterpillar-host plant associations. Alpha codes for plant names are as in Table 3. Bird species are: AKEP (Hawaiʻi ʻākepa, *Loxops coccineus*), AKIA (ʻakiapōlāʻau, *Hemignathus wilsoni*), *AKIA (ʻakiapōlāʻau nestling), ALAW (ʻalawī, *L. mana*), HAAM (Hawaiʻi ʻamakihi, *Chlorodrepanis virens*), HAEL (Hawaiʻi ʻelepaio, *Chasiempis sandwichensis*), IIWI (ʻiʻiwi, *Drepanis coccinea*), RBLE (red-billed leiothrix, *Leiothrix lutea*), WAWE (warbling white-eye, *Zosterops japonicus*). Insectivores include AKEP, AKIA, ALAW, which are Hawaiian honeycreepers (Fringillidae: Drepanidinae) and HAEL, a monarch flycatcher (Monarchidae); IIWI is a nectarivorous Hawaiian honeycreeper; HAAM is an insectivorous-nectarivorous Hawaiian honeycreeper; and RBLE, a laughingthrush (Leiothrichidae), and WAWE, a white-eye (Zosteropidae), are introduced omnivores.

Overall, mandibles of the 10 caterpillar morphotypes identified in this study represented 95.3% of the mandibles (n = 720) assigned to the 19 morphotypes identified in the earlier study by Banko *et al.* (2015). A species of *Carposina* (Carposinidae) was associated with mandible morphotype K, the most widely distributed morphotype among Hakalau forest bird diet samples and representing 41.9% of all caterpillar prey (Appendix II, Figure 3). It was not possible to

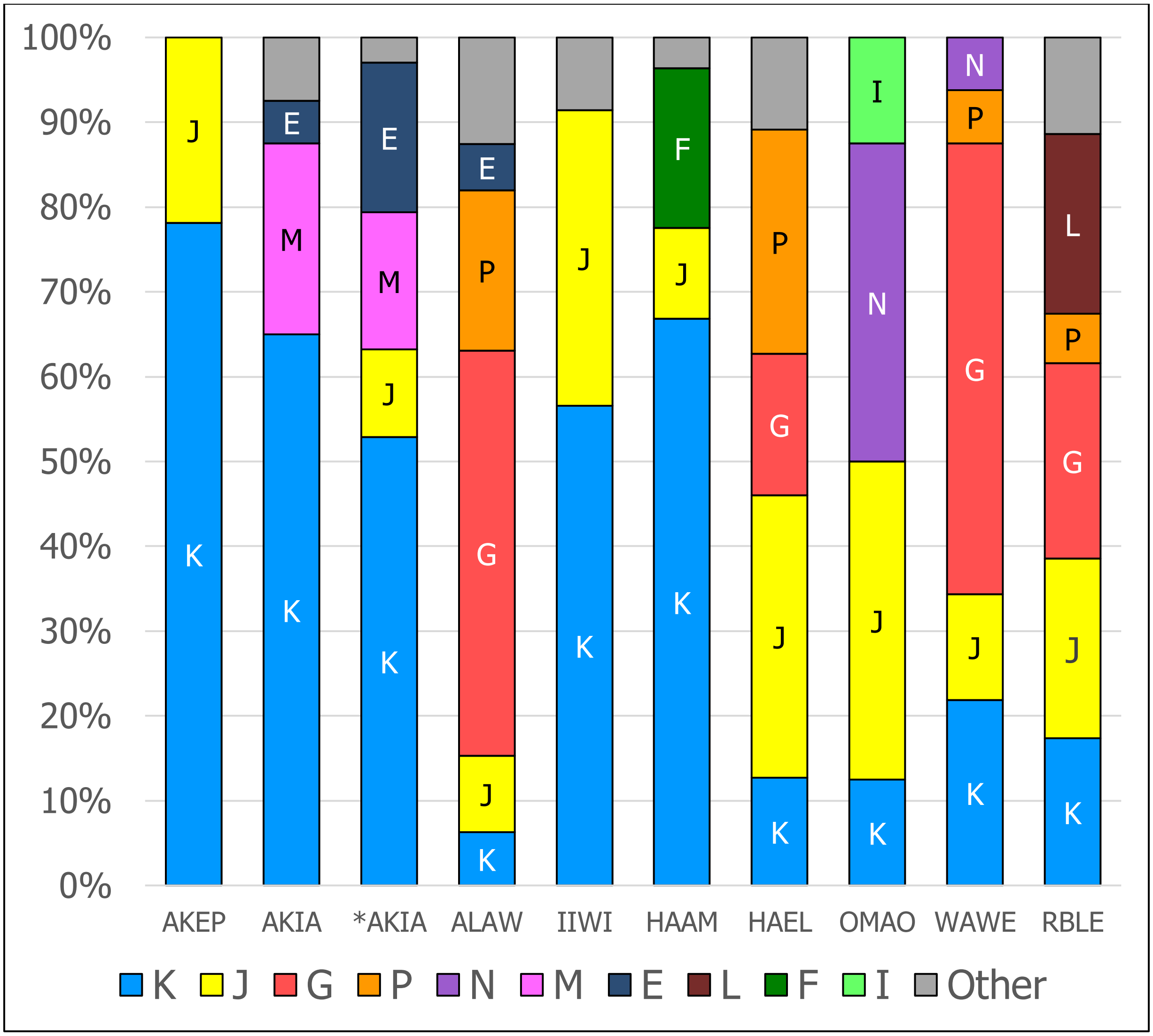

Figure 3. Ten major caterpillar mandible morphotypes in diet samples of Hakalau forest birds (from Banko *et al.* 2015). Morphotypes were included only if they composed at least 5% of the morphotypes eaten by each bird species. Morphotypes represented by less than 5% were included as "other." See Figure 2 for bird alpha codes.

differentiate mandibles among the several *Carposina* species that occur at Hakalau, but the majority of those that we identified in bird diets are likely from a species found feeding on ʻōhiʻa leaves, as other *Carposina* at Hakalau live concealed within fruit such as ʻōhelo and kōlea, which we did not sample in this study.

Banko *et al.* (2015) found that mandible morphotype K accounted for all of the caterpillar prey in ʻapapane diet samples (*n* = 4) and most of the caterpillar prey for Hawaiʻi ʻākepa (78%), Hawaiʻi ʻamakihi (*Chlorodrepanis virens*, 67%), ʻakiapōlāʻau (65% in adult samples, 53% in nestling samples), and ʻiʻiwi (56%; Appendix II, Figure 3). K composed 6% of the caterpillar prey eaten by ʻalawī and ranged from 12% to 22% of caterpillar prey in the diets of other birds except the northern cardinal (*Cardinalis cardinalis*, *n* = 3).

Caterpillars of the Geometridae, especially in the endemic genus *Scotorythra*, were the second-most abundant caterpillars consumed by birds at Hakalau and were represented by morphotype J (Banko *et al.* 2015; Appendix II, Figure 3). We collected at least six species of *Scotorythra* from 10 different host plants (Table 2). In addition, we collected *Eupithecia monticolens* from ʽōhiʽa and pūkiawe. We were not able to differentiate among the geometrids based on mandible morphology, but they collectively composed 15.3% of all caterpillars consumed by Hakalau bird species. Morphotype J constituted major proportions of the caterpillars eaten by ʽōmaʽo (*Myadestes obscurus*, 37%), ʽiʽiwi (35%), Hawaiʽi ʽelepaio (*Chasiempis sandwichensis*, 33%), and ʽākepa (22%; Banko *et al.* 2015). Morphotype J also made up 10% of the caterpillar diet of ʽakiapōlāʽau nestlings. J appeared in the diets of all other species except adult ʽakiapōlāʽau, ʽapapane (*Himatione sanguinea*), and northern cardinal, although their sample sizes were small.

Three unidentified caterpillar types collected from ʽōhiʽa were likely matches for mandible morphotypes G, P, and L that were previously found in bird diets by Banko *et al.* (2015). Collectively, these morphotypes composed 25% of all caterpillars consumed by birds at Hakalau, with G at 15%, P at 8%, and L at 2% (Banko *et al.* 2015; Appendix II, Figure 3). All three morphotypes were associated with unidentified caterpillars (family unknown) collected only from ʽōhiʽa. Mandible morphotype G was the principal caterpillar prey of the warbling white-eye (*Zosterops japonicus*, 53%) and the ʽalawī (48%). G was frequent in the caterpillar diet of the red-billed leiothrix (*Leiothrix lutea*, 23%) and Hawaiʽi ʽelepaio (17%), and it was a minor component in the diet of nestling ʽakiapōlāʽau. The unidentified caterpillar with mandible morphotype P was important in the caterpillar diet primarily of the Hawaiʽi ʽelepaio (26%) and ʽalawī (19%), both of which consumed a relatively wide variety of caterpillar prey. Mandible morphotype L, the third unidentified caterpillar found only on ʽōhiʽa, was most frequently seen in the diet of the red-billed leiothrix (21%) but also showed up as minor or trace components of the caterpillar diet of Hawaiʽi ʽelepaio (3%), ʽalawī (0.9%), and Hawaiʽi ʽamakihi (trace).

Species of *Hyposmocoma*, mandible morphotypes E and F, represented 10% of all caterpillars consumed by birds (Banko *et al.* 2015; Appendix II). *Hyposmocoma* caterpillars, all likely inhabiting dead wood or bark, were collected during this study from ʽōhiʽa and six other abundant host plants (Table 3). E made up 5% of the caterpillar diet of adult ʽakiapōlāʽau and 18% of the nestling diet (Banko *et al.* 2015). E also composed 5% of the caterpillars in ʽalawī diet samples. Morphotype F was prominent (19%) among caterpillars eaten by Hawaiʽi ʽamakihi but was a minor (3%) component of the ʽalawī diet.

Unidentified *Thyrocopa* (Xyloryctidae) caterpillars were also found on dead wood or bark and were associated with mandible morphotype N. *Thyrocopa* were collected from ʽōhiʽa and five other common host plant species. Morphotype N represented >2% of caterpillars in bird diets overall and 38% of the caterpillars eaten by ʽōmaʽo (Banko *et al.* 2015; Appendix II).

Caterpillar morphotypes B and C were represented by unidentified species of *Udea* (Crambidae). We reared *U. endopyra* from ʽākala and *U. pyranthes* from ʽōhelo, so one or both species likely account for these two mandible morphotypes. They each compose <1% of the caterpillars eaten by Hawaiʽi ʽelepaio, Hawaiʽi ʽamakihi, ʽalawī, ʽiʽiwi, and red-billed leiothrix (Banko *et al.* 2015; Appendix II).

We were unable to match nine mandible morphotypes (A, D, H, I, M, O, Q, R, and S) identified in the earlier diet study (Banko *et al.* 2015) to any of the caterpillars we collected during the present study, but of this subset only M was found frequently in bird diets (Banko *et al.* 2015; Appendix II, Figure 3). M was the second-most frequent caterpillar in the diet of adult ʽakiapōlāʽau (22%) and represented 16% of the caterpillars in ʽakiapōlāʽau nestling samples. It likely represents a species that bores into wood and is not easily collected by shaking vegetation. ʽAkiapōlāʽau may forage on wood-boring beetle larvae at Hakalau (particularly Cerambycidae), but mandibles from that family of insects are distinctively different from caterpillars and were not found in the diet of the birds examined (Banko *et al.* 2015).

DISCUSSION

Caterpillar Abundance on Host Plants

Our sampling focused on shrub and tree species already common at Hakalau with the expectation that they would be the most immediate sources of caterpillar prey if ROD or other threats to ʽōhiʽa increase. We also sampled some species that are under direct management, either through removal as invasive species or the out-planting of rare native species. Some invasive plants may support alien or native birds through their fruit or arthropods on their foliage or bark. Blackberry was the only invasive species that we sampled sufficiently to evaluate in terms of arthropod availability, and although we did not rear any of the 43 caterpillars collected from blackberry leaves, Robinson *et al.* (2010) report two species from *Rubus* species: *Acleris zimmermani* (Tortricidae) and *Schreckensteinia festaliella* (Schreckensteiniidae). The warbling white-eye is likely attracted to blackberry fruit and may also glean caterpillars from the leaves, but native birds are not reported to find food frequently on this species.

We collected four caterpillars, including two from 52 branch samples, from endangered *Clermontia lindseyana* shrubs that had been planted in the forest. This low level of caterpillar abundance suggests that nectar and fruit would be the main attractants for birds. Nevertheless, the extreme rarity of the species before its rediscovery and management may have led to the loss of specialist caterpillars, if there were any.

Because we did not distinguish between the two species of endemic mints in our study areas, we may have sampled planted patches of the endangered, endemic mint, *Phyllostegia brevidens*, along with the naturally occurring endemic mint, *Stenogyne calaminthoides.* We collected but were unable to rear seven caterpillars from *S. calaminthoides*, which yielded three specimens from nine branch samples. Although some birds may probe *Stenogyne* flowers for nectar, native birds are seldom seen foraging near ground level with the exception of Hawaiʽi ʽamakihi. Nevertheless, *Stenogyne*, a liana, can climb several meters into shrubs and trees, where birds may visit it for nectar and insects (Engilis 1990).

We also sampled some of the larger, abundant ferns in the natural forest, including *Cibotium glaucum* (hāpuʽu pulu), *Dryopteris* sp., and *Dicranopteris linearis* (uluhe). *Cibotium glaucum* is a large tree fern that can form relatively dense cover in the subcanopy of lower, wetter forests at Hakalau. Sometimes birds are seen foraging along the fronds, but it does not seem heavily visited. *Dryopteris* is a shuttlecock fern that grows up to about 1 m in height, and it can be abundant under relatively open or closed forest canopy. We observed Hawaiʽi ʽamakihi that were presumably foraging in *Dryopteris*, but most other native species may not forage so close to the ground. Uluhe forms dense mats and climbs over shrubs and into the lower branches of trees in many areas of the forest, but its complex structure may inhibit birds from foraging on it. Additionally, the relatively low yield of caterpillars on uluhe and the other ferns (Table 1) likely discourages bird activity.

Although it occurs at Hakalau (USFWS 2010), we did not encounter māmaki (*Pipturus albidus*, Urticaceae), which grows as a shrub or small tree and hosts at least 19 caterpillar species or subspecies in 9 families (Swezey 1954; Zimmerman 1958a,b; 1978). Sixteen of these species are found on leaves, dead wood, or bark, and three species are leaf miners. Additional information about the distribution of māmaki at Hakalau and the caterpillars associated with it could help determine whether it would be a good restoration candidate for increasing food availability for native birds.

Although ʻōhiʻa ranked last in caterpillar abundance per unit of foliage among the 11 focal host plants, it is the dominant tree species in naturally recovering native forest at Hakalau (USFWS 2010, Banko *et al.* 2021) and is heavily exploited for arthropods or nectar by all forest bird species. We did not estimate caterpillar abundance as a function of tree density or cover, but ʻōhiʻa likely provides the most caterpillars across the landscape wherever koa is not also abundant. Below the distribution of koa, ʻōhiʻa is the dominant canopy species (Jacobi 1989), therefore any reduction in ʻōhiʻa canopy cover could have severely negative consequences for forest birds.

Associations of Caterpillar Mandible Morphotypes with Bird Diets

Morphometric analysis of caterpillar mandibles proved to be a useful tool for reconstructing diets of forest birds at Hakalau (Banko *et al.* 2015). However, in that study, the ability to identify mandibles in the diets of birds at the species level was limited by the inability to differentiate among closely related caterpillar taxa, such as the six or seven species of *Scotorythra* found at Hakalau. Species level determinations were also confounded by mandible structure that often varied as much, or more, among instars within a species than among species examined during the same instar. DNA barcoding of each caterpillar morphotype would likely allow greater taxonomic resolution of prey within bird diets. Barcoding uses information from one or a few gene regions to identify species and can have high specificity, but it is generally unable to provide robust estimates of the number of caterpillars found within diet samples. In contrast, mandibles can be visually counted to determine the abundance of this important prey. Ideally, research to reconstruct bird diets would utilize both morphometric and barcoding techniques (Hoenig *et al.* 2022).

Although we were unable in this study to identify the species or in some cases even the families of caterpillar mandible morphotypes known from Hakalau bird diets (Banko *et al.* 2015), we identified likely candidates representing >95% of caterpillar prey found in the diet study. Identifying taxa to the species level may be possible with additional diet analysis, collecting and rearing caterpillars from host plants, and genetic barcoding. Nevertheless, our results indicate that ʻōhiʻa is the major source of caterpillars important to birds, both in terms of richness and frequency in the diet. ʻŌhiʻa is apparently the exclusive host of caterpillar mandible morphotype K, which Banko *et al.* (2015) found to be the most frequent caterpillar in the diets of endangered adult and nestling ʻakiapōlāʻau, endangered Hawaiʻi ʻākepa, threatened ʻiʻiwi, and non-listed Hawaiʻi ʻamakihi. ʻŌhiʻa also is the host for morphotype G, which is the most frequent caterpillar eaten by the endangered ʻalawī (Banko *et al.* 2015). Only one of three additional caterpillar morphotypes (J, M, or P) occurred frequently in the diets of these three listed bird species (Banko *et al.* 2015), and in the present study we found that P was associated solely with ʻōhiʻa, the host of M was unknown, and J was associated with multiple host plants, including ʻōhiʻa. Although sample sizes were small, J was found in the diet of ʻakiapōlāʻau nestlings but not in adult samples (Banko *et al.* 2015), suggesting that nestlings receive some prey not taken frequently or at all by adults. Additional diet studies would reveal the full range of host plants utilized by bird species throughout their life cycle.

Perkins (1903, 1913) observed that *Scotorythra* caterpillars were important prey of Hawaiian forest birds and that they were fed to nestlings of many, if not all, species. *Scotorythra* species were also frequent caterpillar prey of forest birds at Hakalau (Banko *et al*. 2015). In the present study, we collected at least 6 species on 10 plant species, including ʻōhiʻa (Table 2), although 11 *Scotorythra* species are known from 13 plant species that occur at Hakalau (Appendix I). Mandible morphotype J was associated with *Scotorythra*, and its importance to several listed and other native bird species warrants additional studies to identify the taxa more definitively and to understand its life history and threats. For example, we cannot adequately quantify the abundance of J on ʻōhiʻa relative to other hosts. Additionally, the later instars of *Scotorythra* are relatively large, and their importance to birds may not be entirely captured by their abundance on host plants or their frequency in diets.

Management Implications

A priority of managers at Hakalau is to maintain or increase the cover of native vegetation (USFWS 2010), but this goal would be undermined by a reduction of ʻōhiʻa cover due to ROD or other threats. Our results indicate that ʻōhiʻa is fundamentally important as a source of caterpillar prey for native birds, and endangered species are especially at risk if ʻōhiʻa cover should decline. Compared to diet generalists, endangered birds at Hakalau specialize in their exploitation of caterpillars (Banko *et al.* 2015), and because diet specialization is associated with relatively slow reproduction, specialists have less capacity to recover from habitat degradation, food web disruption, and other threats (Banko and Banko 2009).

Although protecting ʻōhiʻa against ROD or other harm is fundamentally important to the health of the forest bird community, ʻōhiʻa forests can also undergo transformation due to natural processes, such as ʻōhiʻa die back (Mertelmeyer *et al.* 2019), hurricanes (Herbert *et al.* 1999), and fire (Tunison *et al.* 2001). Therefore, measures to mitigate the impacts of reduced ʻōhiʻa cover are important to consider from the perspective of forest bird food webs and diet.

Managers have implemented reforestation projects over much of the upper portion of the refuge during the past 30 years, focusing most of their attention on converting former pastureland to koa-dominated stands but also bolstering or repatriating endangered plant species (USFWS 2010). Native and alien bird species increasingly forage and nest in these maturing koa stands, but Hawaiʻi ʻākepa are the slowest to do so (Paxton *et al.* 2018). The majority of the caterpillar diet of Hawaiʻi ʻākepa consists of morphotype K, likely a species of *Scotorythra* that in this study we found only on ʻōhiʻa, which is distributed sparsely in the koa stands. Nevertheless, the secondary prey of Hawaiʻi ʻākepa is morphotype J, which is available on koa.

The slow recolonization of Hawaiʻi ʻākepa in koa stands highlights the importance of reforestation strategies for forest bird communities. Although the significance of koa to many forest bird species has long been recognized (Perkins 1903), some species may not benefit fully from koa stands until tree and shrub diversity has increased. Increasing plant diversity, and with it structure complexity, would increase the availability of caterpillar and other arthropod prey as well as provide more sheltering and nesting microhabitats. Our results and information from the literature (Table 2, Appendix I) indicate that ʻākala, ʻōhelo, kōlea, ʻōlapa, pūkiawe, and māmaki would provide both prey and structural complexity to planted stands.

Another consideration is that the natural distribution of koa is truncated in the mid-elevation zone of Hakalau (Jacobi 1989, USFWS 2010), so the benefits of koa to birds may be limited to higher elevations. Even so, habitat restoration is focused on upper montane forests in large part because avian malaria transmission is infrequent or absent there (Atkinson and LaPointe 2009), and additional ways to increase host plant diversity can promote forest bird restoration in these areas. Māmane seems to be a prime candidate for integrating into upper elevation reforestation schemes. We found the J caterpillar mandible morphotype on māmane foliage, and there are likely to be other caterpillar prey discovered in bird diets once diet samples are analyzed from areas where māmane is present. Māmane forests on Mauna Kea support or once supported all the endangered species found at Hakalau (Banko *et al.* 2013), and a mixed koa-māmane forest could expand foraging opportunities for birds.

Our study takes another step toward understanding associations between bird diets and the distribution of caterpillar prey on host plants, but additional research will help evaluate the complex interactions between native forest birds and their food webs and habitats. A future direction may include foraging studies to show how birds integrate host plant selection, forest structure, and prey availability. Additional diet studies to increase sample sizes of underrepresented bird species and to refine prey identification through DNA barcoding would provide greater resolution to questions of the frequency of prey species in diets, diet overlap among species, and the relative importance of prey in terms of their seasonal abundance and distribution, size, and nutrient composition. A program to evaluate variability in caterpillar communities occupying different habitat types and over a greater extent of elevation and area would help managers assess areas where vegetation management might yield more prey for birds. Also important are studies of threats to key caterpillar prey by parasitoids, predators, and diseases. Research into parasitoid impacts on koa-hosted caterpillars is ongoing, but there is no work related to caterpillar species hosted by ʻōhiʻa or other common native plants.

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Appendix I. Caterpillar Species and Host Plants

Appendix I, Table. Caterpillar species reported from native and alien host trees and shrubs occurring at Hakalau or elsewhere on Hawaiʽi Island. Taxa that we positively identified in this study are indicated by †. Based on published host plant associations, we identified additional possible species, indicated by ††. Caterpillar-host plant associations noted by other authors are indicated by the single initial of their last name: H = Heddle (2003), M = Montgomery (1983), R = Robinson *et al.* (2010), S = Swezey (1954), Z = Zimmerman (1958a,b; 1978). Some additional host plant species present at Hakalau or closely related host species are included that were not sampled during this study. Substrates from which caterpillars were collected during this study or that were reported by other authors are indicated in brackets: [?] = undetermined or likely substrate, [dv] = decaying vegetation, [dw/bk] = dead wood/bark, [fr] = fruit, [lc] = lichen, [lf] = leaf, [lf/fl] = leaf/flower, [lm] = leaf miner, [sd] = seed, [sb] = stem borer, [tw/rg] = twig/rust gall.

Plant family	Plant species	Lepidoptera family	Lepidoptera genus and species	Source and feeding substrate
Aquifoliaceae	*Ilex anomala*	Geometridae	*Scotorythra apicalis*	H [lf]
Aquifoliaceae	*Ilex anomala*	Geometridae	*Scotorythra euryphaea*	H [lf]
Aquifoliaceae	*Ilex anomala*	Geometridae	*Scotorythra rara*	H [lf]
Araliaceae	*Cheirodendron trigynum*	Cosmopterigidae	*Hyposmocoma chilonella chilonella*	††,R,Z [dw/bk]
Araliaceae	*Cheirodendron trigynum*	Cosmopterigidae	*Hyposmocoma chilonella triocellata*	††,Z [dw/bk]
Araliaceae	*Cheirodendron trigynum*	Cosmopterigidae	*Hyposmocoma* sp.	† [dw/bk?]
Araliaceae	*Cheirodendron trigynum*	Geometridae	*Scotorythra euryphaea*	††,H [lf]
Araliaceae	*Cheirodendron trigynum*	Geometridae	*Scotorythra rara*	†,H,R [lf]
Araliaceae	*Cheirodendron trigynum*	Geometridae	*Scotorythra* sp. 1	† [lf]
Araliaceae	*Cheirodendron trigynum*	Tortricidae	*Spheterista pleonectes*	††,S [lf]
Araliaceae	*Cheirodendron* sp.	Noctuidae	*Peridroma cinctipennis*	R [lf]
Epacridaceae	*Leptecophylla tameiameiae*	Carposinidae	*Carposina gracillima*	S [fr]
Epacridaceae	*Leptecophylla tameiameiae*	Cosmopterigidae	*Hyposmocoma sp.*	† [dw/bk?]
Epacridaceae	*Leptecophylla tameiameiae*	Geometridae	*Eupithecia monticolens*	††,S,Z [lf]
Epacridaceae	*Leptecophylla tameiameiae*	Geometridae	*Eupithecia stypheliae*	M,S [lf]

Plant family	Plant species	Lepidoptera family	Lepidoptera genus and species	Source and feeding substrate
Epacridaceae	*Leptecophylla tameiameiae*	Geometridae	*Scotorythra goniastis*	H [lf]
Epacridaceae	*Leptecophylla tameiameiae*	Xyloryctidae	*Thyrocopa* sp.	† [dw/bk]
Ericaceae	*Vaccinium calycinum*	Cosmopterigidae	*Hyposmocoma* sp.	† [dw/bk?]
Ericaceae	*Vaccinium calycinum*	Crambidae	*Udea pyranthes*	††,R,Z [lf]
Ericaceae	*Vaccinium calycinum*	Geometridae	*Scotorythra* sp. 1	† [lf]
Ericaceae	*Vaccinium calycinum*	Xyloryctidae	*Thyrocopa* sp.	† [dw/bk]
Ericaceae	*Vaccinium dentatum*	Carposinidae	*Carposina inscripta*	S [fr]
Ericaceae	*Vaccinium dentatum*	Crambidae	*Udea pyranthes*	S [lf]
Ericaceae	*Vaccinium dentatum*	Geometridae	*Scotorythra rara*	H,S [lf]
Ericaceae	*Vaccinium dentatum*	Pterophoridae	*Stenoptilodes littoralis rhynchophora*	S,Z [lf]
Ericaceae	*Vaccinium dentatum*	Tortricidae	*Epiphyas postvittana*	S [lf]
Ericaceae	*Vaccinium reticulatum*	Carposinidae	*Carposina inscripta*	S [fr]
Ericaceae	*Vaccinium reticulatum*	Pterophoridae	*Stenoptilodes littoralis*	R [lf]
Ericaceae	*Vaccinium* sp.	Geometridae	*Scotorythra rara*	H,R,Z [lf]
Ericaceae	*Vaccinium* sp.	Tortricidae	*Epiphyas postvittana*	R [lf]
Fabaceae	*Acacia koa*	Cosmopterigidae	*Hyposmocoma alliterata*	S,Z [lc]
Fabaceae	*Acacia koa*	Cosmopterigidae	*Hyposmocoma candidella*	S,Z [dw/bk]
Fabaceae	*Acacia koa*	Cosmopterigidae	*Hyposmocoma chilonella*	S,Z [dw/bk]
Fabaceae	*Acacia koa*	Cosmopterigidae	*Hyposmocoma cryptogamiella*	S,Z [dw/bk]
Fabaceae	*Acacia koa*	Cosmopterigidae	*Hyposmocoma palmifera*	R [?]
Fabaceae	*Acacia koa*	Cosmopterigidae	*Hyposmocoma* sp.	† [dw/bk?]

Plant family	Plant species	Lepidoptera family	Lepidoptera genus and species	Source and feeding substrate
Fabaceae	*Acacia koa*	Crambidae	*Uresiphita polygonalis virescens*	Z [lf]
Fabaceae	*Acacia koa*	Geometridae	*Macaria abydata*	R [lf]
Fabaceae	*Acacia koa*	Geometridae	*Scotorythra corticea*	†,H,S,Z [lf]
Fabaceae	*Acacia koa*	Geometridae	*Scotorythra paludicola*	†,H,S,Z [lf]
Fabaceae	*Acacia koa*	Geometridae	*Scotorythra rara*	††,H,S,Z [lf]
Fabaceae	*Acacia koa*	Geometridae	*Scotorythra* sp. 1	† [lf]
Fabaceae	*Acacia koa*	Lycaenidae	*Udara blackburni*	S [lf]
Fabaceae	*Acacia koa*	Sphingidae	*Hyles wilsoni*	R [lf]
Fabaceae	*Acacia koa*	Tineidae	*Erechthias minuscula*	R [lf/fl]
Fabaceae	*Acacia koa*	Tineidae	*Opogona omoscopa*	R,S,Z [dv]
Fabaceae	*Acacia koa*	Tortricidae	*Amorbia emigratella*	S [lf]
Fabaceae	*Acacia koa*	Tortricidae	*Cryptophlebia illepida*	S,Z [sd]
Fabaceae	*Acacia koa*	Tortricidae	*Cydia walsinghamii*	S,Z [tw/rg]
Fabaceae	*Acacia koa*	Tortricidae	*Epiphyas postvittana*	S,Z [lf]
Fabaceae	*Acacia koa*	Xyloryctidae	*Thyrocopa argentea*	††,S,Z [dw/bk]
Fabaceae	*Acacia koa*	Xyloryctidae	*Thyrocopa indecora*	†† S,Z [dw/bk]
Fabaceae	*Acacia koa*	Xyloryctidae	*Thyrocopa* sp.	† [dw/bk]
Fabaceae	*Sophora chrysophylla*	Cosmopterigidae	*Hyposmocoma cryptogamiella*	S,Z [dw/bk]
Fabaceae	*Sophora chrysophylla*	Crambidae	*Uresiphita polygonalis virescens*	S,Z [lf]
Fabaceae	*Sophora chrysophylla*	Geometridae	*Scotorythra artemidora*	†† [lf]
Fabaceae	*Sophora chrysophylla*	Geometridae	*Scotorythra* sp. 1	† [lf]
Fabaceae	*Sophora chrysophylla*	Lycaenidae	*Lampides boeticus*	R [lf]
Fabaceae	*Sophora chrysophylla*	Noctuidae	*Peridroma albiorbis*	† [lf]
Fabaceae	*Sophora chrysophylla*	Tortricidae	*Amorbia emigratella*	S [lf]
Fabaceae	*Sophora chrysophylla*	Tortricidae	*Cydia latifemoris*	S [sd]

Plant family	Plant species	Lepidoptera family	Lepidoptera genus and species	Source and feeding substrate
Fabaceae	*Sophora chrysophylla*	Tortricidae	*Cydia montana*	S [sd]
Fabaceae	*Sophora chrysophylla*	Tortricidae	*Cydia plicata*	S,Z [sd]
Fabaceae	*Sophora chrysophylla*	Xyloryctidae	*Thyrocopa indecora*	S [dw/bk]
Myoporaceae	*Myoporum sandwicense*	Geometridae	*Scotorythra* sp. 1	† [lf]
Myoporaceae	*Myoporum sandwicense*	Noctuidae	*Heliothis* sp.	Z [f]
Myoporaceae	*Myoporum sandwicense*	Tortricidae	*Epiphyas postvittana*	† [lf]
Myrsinaceae	*Myrsine lessertiana*	Carposinidae	*Carposina nigronotata*	S [fr]
Myrsinaceae	*Myrsine lessertiana*	Cosmopterigidae	*Hyposmocoma* sp.	† [?]
Myrsinaceae	*Myrsine lessertiana*	Geometridae	*Scotorythra* sp. 1	† [lf]
Myrsinaceae	*Myrsine lessertiana*	Tortricidae	Tortricidae sp.	† [lf]
Myrsinaceae	*Myrsine lessertiana*	Xyloryctidae	*Thyrocopa* sp.	† [dw/bk]
Myrsinaceae	*Myrsine lessertiana*	Tortricidae	*Pararrhaptica longiplicata*	†,R [lf]
Myrsinaceae	*Myrsine* sp.	Gracillariidae	*Philodoria auromagnifica*	S,Z [lm]
Myrsinaceae	*Myrsine* sp.	Gracillariidae	*Philodoria succedanea*	S,Z [lm]
Myrtaceae	*Metrosideros polymorpha*	Carposinidae	*Carposina* sp.	† [lf]
Myrtaceae	*Metrosideros polymorpha*	Cosmopterigidae	*Hyposmocoma chilonella chilonella*	††,Z [dw/bk]
Myrtaceae	*Metrosideros polymorpha*	Cosmopterigidae	*Hyposmocoma cryptogamiella*	††,Z [sb]
Myrtaceae	*Metrosideros polymorpha*	Cosmopterigidae	*Hyposmocoma* sp.	† [?]
Myrtaceae	*Metrosideros polymorpha*	Geometridae	*Eupithecia monticolens*	†,M,Z [lf/fl]
Myrtaceae	*Metrosideros polymorpha*	Geometridae	*Scotorythra euryphaea*	H [lf]

Plant family	Plant species	Lepidoptera family	Lepidoptera genus and species	Source and feeding substrate
Myrtaceae	*Metrosideros polymorpha*	Geometridae	*Scotorythra hyparcha*	S,Z [lf]
Myrtaceae	*Metrosideros polymorpha*	Geometridae	*Scotorythra pachyspila*	S,Z [lf]
Myrtaceae	*Metrosideros polymorpha*	Geometridae	*Scotorythra rara*	††,H,S,Z [lf]
Myrtaceae	*Metrosideros polymorpha*	Geometridae	*Scotorythra* sp. 1	† [lf]
Myrtaceae	*Metrosideros polymorpha*	Geometridae	*Scotorythra* sp. 2	† [lf]
Myrtaceae	*Metrosideros polymorpha*	Gracillariidae	*Philodoria basalis*	S,Z [lm]
Myrtaceae	*Metrosideros polymorpha*	Gracillariidae	*Philodoria splendida*	S,Z [lm]
Myrtaceae	*Metrosideros polymorpha*	Noctuidae	*Peridroma cinctipennis*	††,Z [lf]
Myrtaceae	*Metrosideros polymorpha*	Xyloryctidae	*Thyrocopa* sp.	† [dw/bk]
Rosaceae	*Rubus hawaiensis*	Cosmopterigidae	*Hyposmocoma chilonella*	††,S [dw/bk]
Rosaceae	*Rubus hawaiensis*	Cosmopterigidae	*Hyposmocoma chilonella chilonella*	††,Z [dw/bk]
Rosaceae	*Rubus hawaiensis*	Cosmopterigidae	*Hyposmocoma chilonella triocellata*	††,S,Z [dw/bk]
Rosaceae	*Rubus hawaiensis*	Cosmopterigidae	*Hyposmocoma* sp.	† [dw/bk?]
Rosaceae	*Rubus hawaiensis*	Crambidae	*Udea endopyra*	†,R,Z [lf]
Rosaceae	*Rubus hawaiensis*	Geometridae	*Scotorythra rara*	††,S,Z [lf]
Rosaceae	*Rubus hawaiensis*	Geometridae	*Scotorythra* sp. 1	† [lf]
Rosaceae	*Rubus hawaiensis*	Geometridae	*Scotorythra willisi*	†,H [lf]
Rosaceae	*Rubus hawaiensis*	Tineidae	*Opogona omoscopa*	S [dv]
Rosaceae	*Rubus hawaiensis*	Tortricidae	*Amorbia emigratella*	S [lf]
Rosaceae	*Rubus hawaiensis*	Tortricidae	*Epiphyas postvittana*	S [lf]
Rosaceae	*Rubus hawaiensis*	Xyloryctidae	*Thyrocopa argentea*	††,S [dw/bk]
Rosaceae	*Rubus hawaiensis*	Xyloryctidae	*Thyrocopa* sp.	† [dw/bk]
Rosaceae	*Rubus* sp.	Schreckensteiniidae	*Schreckensteinia festaliella*	R,Z [lf]
Rosaceae	*Rubus* sp.	Tortricidae	*Acleris zimmermani*	R [lf]

Plant family	Plant species	Lepidoptera family	Lepidoptera genus and species	Source and feeding substrate
Rubiaceae	*Coprosma foliosa*	Cosmopterigidae	*Hyposmocoma chilonella*	S,Z [dw/bk]
Rubiaceae	*Coprosma ochracea*	Geometridae	*Scotorythra* sp. 1	† [lf]
Sapindaceae	*Dodonaea viscosa*	Geometridae	*Scotorythra rara*	H,Z [lf]
Sapindaceae	*Dodonaea viscosa*	Geometridae	*Scotorythra trapezias*	S,Z [lf]
Sapindaceae	*Dodonaea viscosa*	Lycaenidae	*Udara blackburni*	R,Z [lf]
Sapindaceae	*Dodonaea viscosa*	Tortricidae	*Amorbia emigratella*	S [lf]
Sapindaceae	*Dodonaea viscosa*	Tortricidae	*Cryptophlebia illepida*	S [sd]
Sapindaceae	*Dodonaea viscosa*	Tortricidae	*Epiphyas postvittana*	S [lf]
Urticaceae	*Pipturus albidus*	Cosmopterigidae	*Hyposmocoma chilonella*	S [dw/bk]
Urticaceae	*Pipturus albidus*	Cosmopterigidae	*Hyposmocoma chilonella triocellata*	Z [dw/bk]
Urticaceae	*Pipturus albidus*	Cosmopterigidae	*Hyposmocoma chilonella triocellata*	S,Z [dw/bk]
Urticaceae	*Pipturus albidus*	Cosmopterigidae	*Hyposmocoma liturata*	S,Z [dw/bk]
Urticaceae	*Pipturus albidus*	Crambidae	*Udea stellate*	S,Z [lf]
Urticaceae	*Pipturus albidus*	Geometridae	*Eupithecia monticolans*	S,Z [lf]
Urticaceae	*Pipturus albidus*	Geometridae	*Scotorythra rara*	H,S,Z [lf]
Urticaceae	*Pipturus albidus*	Gracillariidae	*Philodoria floscula*	S,Z [lm]
Urticaceae	*Pipturus albidus*	Gracillariidae	*Philodoria neraudicola*	S,Z [lm]
Urticaceae	*Pipturus albidus*	Gracillariidae	*Philodoria pipturiana*	S,Z [lm]
Urticaceae	*Pipturus albidus*	Lycaenidae	*Udara blackburni*	S,Z [lf]
Urticaceae	*Pipturus albidus*	Noctuidae	*Plusia chalcites*	Z [lf]
Urticaceae	*Pipturus albidus*	Nymphalidae	*Vanessa atalanta*	S,Z [lf]
Urticaceae	*Pipturus albidus*	Nymphalidae	*Vanessa tameamea*	S,Z [lf]
Urticaceae	*Pipturus albidus*	Tineidae	*Erechthias minuscula*	S [dw/bk]
Urticaceae	*Pipturus albidus*	Tineidae	*Opogona aurisquamosa*	S [dw/bk]
Urticaceae	*Pipturus albidus*	Tortricidae	*Amorbia emigratella*	S [lf]
Urticaceae	*Pipturus albidus*	Tortricidae	*Epiphyas postvittana*	S [lf]
Urticaceae	*Pipturus albidus*	Tortricidae	*Spheterista infaustana*	S [lf]

APPENDIX II. CATERPILLAR MANDIBLE MORPHOTYPES IN BIRD DIETS

Appendix II, Table. Caterpillar mandible morphotypes (A–S) identified in diet samples of Hakalau forest birds. All data from Banko *et al.* (2015). The number of diet samples analyzed is shown in parentheses below each bird code. The number of individual caterpillar prey of each morphotype is shown for each bird species, and the percentage of all caterpillars of each morphotype in the diet is shown below in brackets. Bird species are: AKEP (Hawai'i 'ākepa, *Loxops coccineus*), AKIA ('akiapōlā'au, *Hemignathus wilsoni*), *AKIA ('akiapōlā'au nestling), ALAW ('alawī, *L. mana*), APAP ('apapane, *Himatione sanguinea*), HAAM (Hawai'i 'amakihi, *Chlorodrepanis virens*), HAEL (Hawai'i 'elepaio, *Chasiempis sandwichensis*), IIWI ('i'iwi, *Drepanis coccinea*), OMAO ('ōma'o, *Myadestes obscurus*), NOCA (northern cardinal, *Cardinalis cardinalis*), RBLE (red-billed leiothrix, *Leiothrix lutea*), WAWE (warbling white-eye, *Zosterops japonicus*).

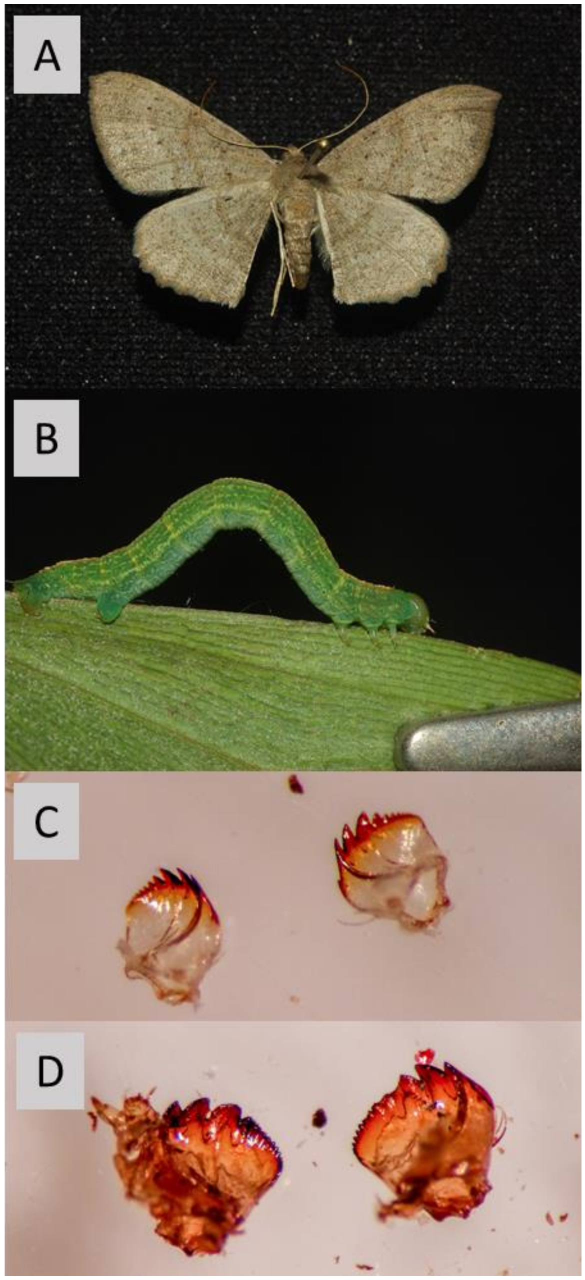
Mandible morphotype	AKEP (10)	AKIA (7)	*AKIA (4)	ALAW (32)	APAP (4)	HAAM (71)	HAEL (92)	IIWI (25)	OMAO (10)	NOCA (3)	RBLE (58)	WAWE (29)	Total (345)
A	-	-	-	-	-	-	-	-	-	-	1 [1.9]	-	1 [0.1]
B	-	-	-	-	-	1 [0.4]	2 [2.0]	1 [4.3]	-	-	1 [1.9]	-	5 [0.7]
C	-	-	-	1 [0.9]	-	-	-	-	-	-	1 [1.9]	-	2 [0.3]
D	-	-	-	-	-	1 [0.4]	-	-	-	-	-	-	1 [0.1]
E	-	2 [5.0]	12 [17.6]	6 [5.4]	-		2 [2.0]	-	-	-	-	-	22 [3.1]
F	-	-	-	3 [2.7]	-	46 [18.9]	-	-	-	-	1 [1.9]	-	50 [6.9]
G	-	-	1 [1.5]	53 [47.7]	-	-	17 [16.7]	-	-	5 [83.3]	12 [23.1]	17 [53.1]	105 [14.6]
H	-	1 [2.5]	-	-	-	-	-	-	-	-	-	-	1 [0.1]

Mandible morphotype	AKEP (10)	AKIA (7)	*AKIA (4)	ALAW (32)	APAP (4)	HAAM (71)	HAEL (92)	IIWI (25)	OMAO (10)	NOCA (3)	RBLE (58)	WAWE (29)	Total (345)
I	-	-	-	-	-	-	-	-	1 [12.5]	-	-	-	1 [0.1]
J	7 [21.9]	-	7 [10.3]	10 [9.0]	-	26 [10.7]	34 [33.3]	8 [34.8]	3 [37.5]	-	11 [21.2]	4 [12.5]	110 [15.3]
K	25 [78.1]	26 [65.0]	36 [52.9]	7 [6.3]	2 [100]	163 [66.8]	13 [12.7]	13 [56.5]	1 [12.5]	-	9 [17.3]	7 [21.9]	302 [41.9]
L	-	-	-	1 [0.9]	-	1 [0.4]	3 [2.9]	-	-	-	11 [21.2]	-	16 [2.2]
M	-	9 [22.5]	11 [16.2]	-	-	-	-	-	-	-	-	-	20 [2.8]
N	-	1 [2.5]	1 [1.5]	4 [3.6]	-	2 [0.8]	2 [2.0]	-	3 [37.5]	1 [16.7]	2 [3.8]	2 [6.3]	18 [2.5]
O	-	-	-	4 [3.6]	-	-	1 [1.0]	-	-	-	-	-	5 [0.7]
P	-	-	-	21 [18.9]	-	3 [1.2]	27 [26.5]	-	-	-	3 [5.8]	2 [6.3]	56 [7.8]
Q	-	-	-	-	-	1 [0.4]	1 [1.0]	-	-	-	-	-	2 [0.3]
R	-	1 [2.5]	-	1 [0.9]	-	-	-	-	-	-	-	-	2 [0.3]
S	-	-	-	-	-	-	-	1 [4.3]	-	-	-	-	1 [0.1]
Total prey	32	40	68	111	2	244	102	23	8	6	52	32	720
Total morphotypes	2	6	6	11	1	9	10	4	4	2	10	5	19

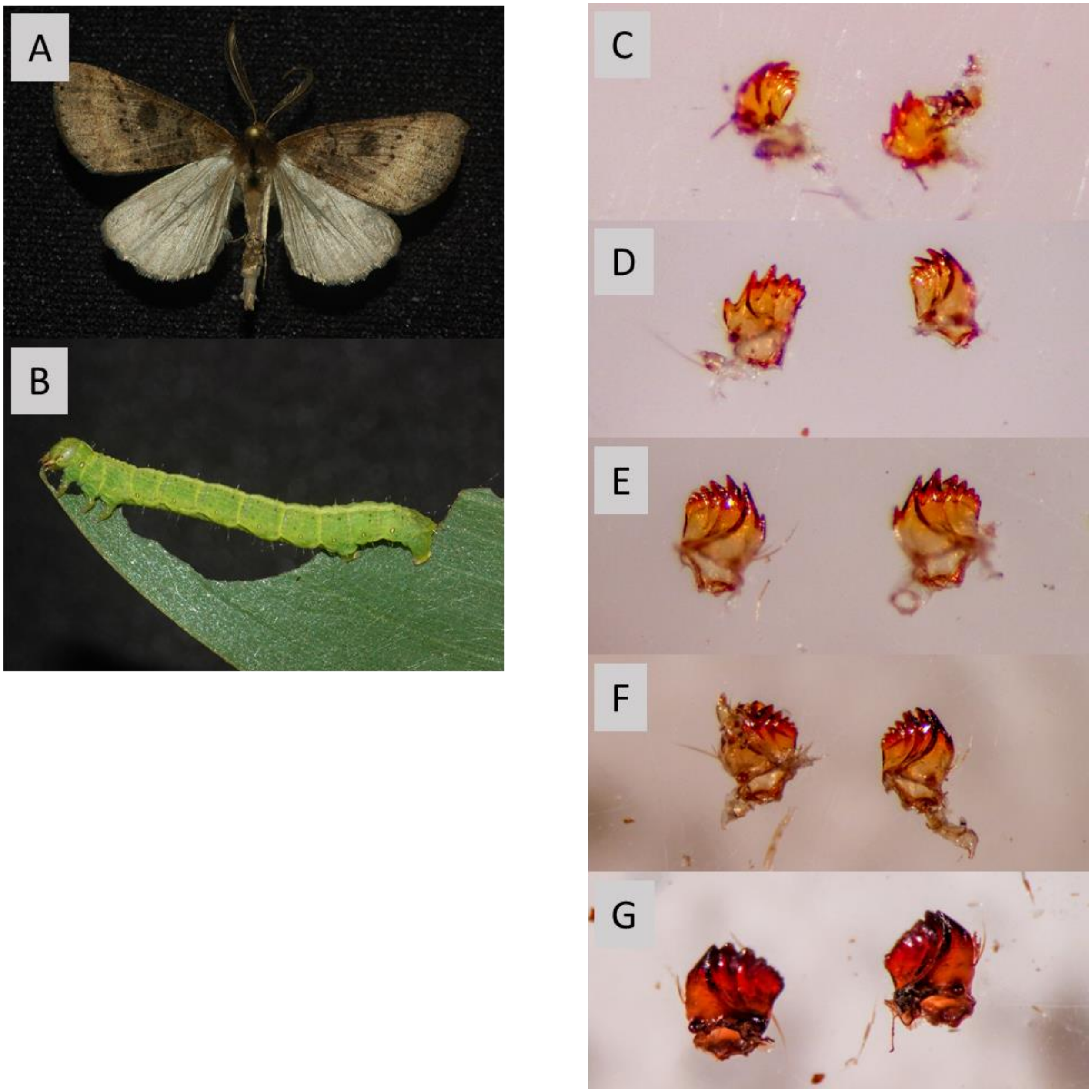
APPENDIX III. PHOTO GUIDE OF SPECIMENS

Appendix III, Figures 1–10. The following is a photo guide of specimens of moths, caterpillars, and mandibles associated with host plants at Hakalau Forest National Wildlife Refuge. The guide is intended to aid in the identification of caterpillar species found both on host plant species and in the diets of birds.

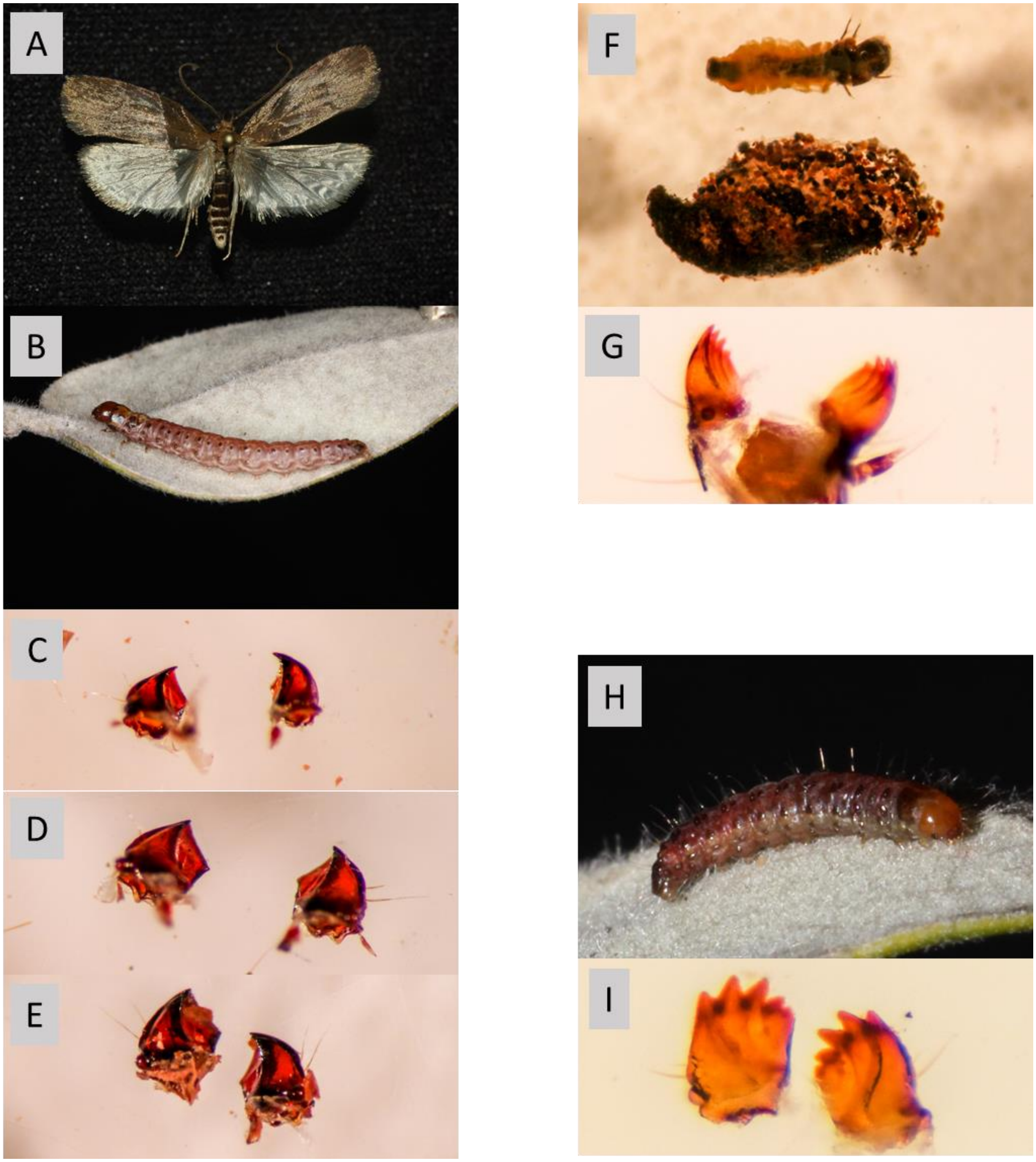
Morphometric analysis of caterpillar mandibles proved to be a useful tool for reconstructing diets of forest birds at Hakalau (Banko *et al.* 2015). However, the ability to identify mandibles in the diets of birds at the species level was limited by the inability to differentiate among closely related caterpillar taxa, such as the six or seven species of *Scotorythra* found at Hakalau. Species level determinations were also confounded by mandible structure that often varied as much, or more, among instars within a species than among species examined during the same instar. It is likely that DNA barcoding of each caterpillar morphotype would allow greater taxonomic resolution of prey within bird diets. While barcoding can have high specificity, it is generally unable to provide robust estimates of the number of caterpillars found within diet samples. In contrast, mandibles can be visually counted to determine the abundance of this important prey. Ideally, research aimed to reconstruct bird diets would utilize both morphometric and barcoding techniques.



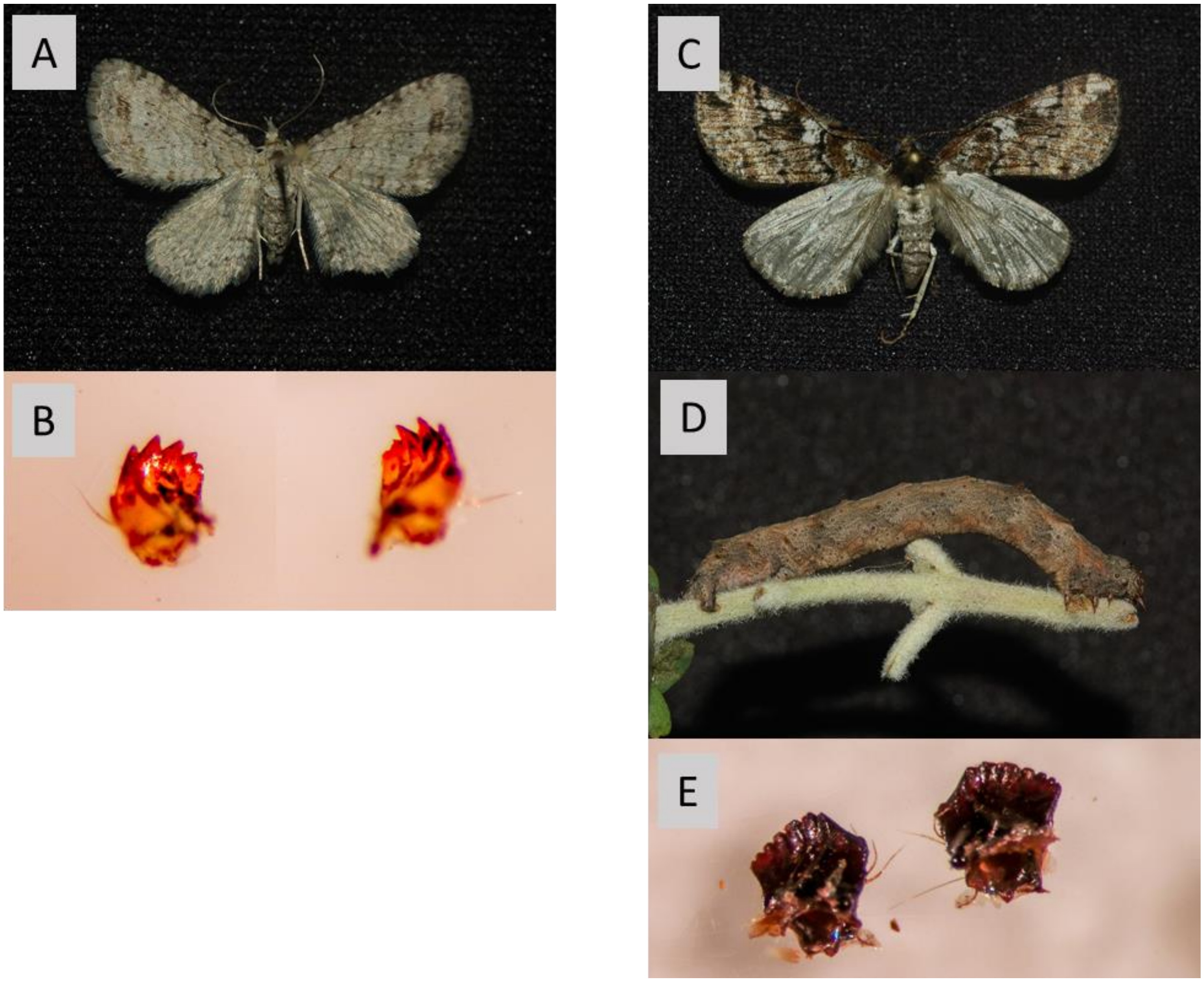
Appendix III, Figure 1. Caterpillars collected from koa (*Acacia koa*) at Hakalau Forest National Wildlife Refuge. Species shown is *Scotorythra corticea* (Geometridae; A–D). Each pair of mandibles is from a different instar collected from the same individual. Mandibles are shown from youngest (C) to oldest (D) instar.



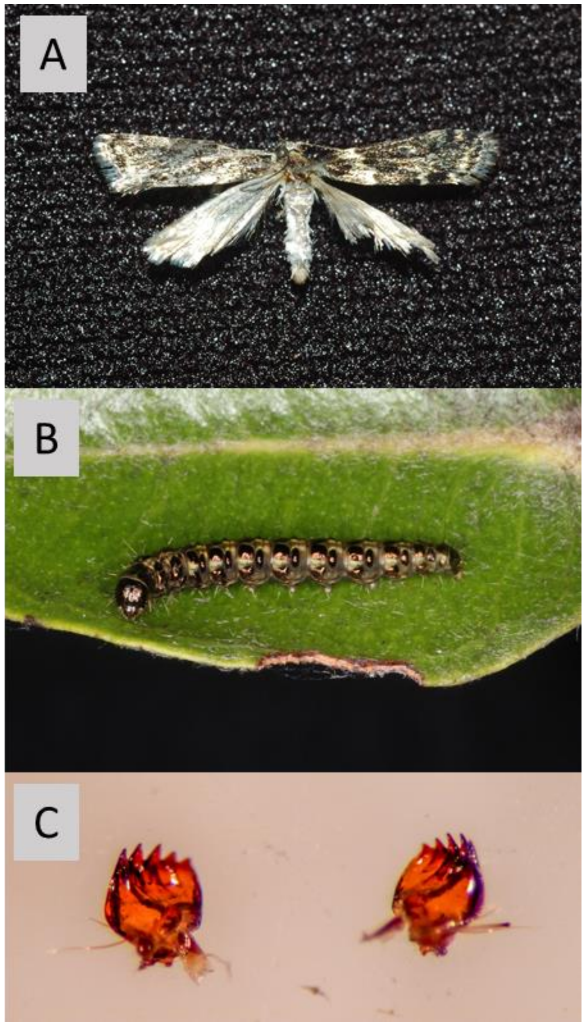
Appendix III, Figure 2. Caterpillars collected from koa (*Acacia koa*) at Hakalau Forest National Wildlife Refuge. Species shown is *Scotorythra paludicola* (Geometridae; A–G). Each pair of mandibles is from a different instar collected from the same individual. Mandibles are shown from youngest (C) to oldest (G) instar.



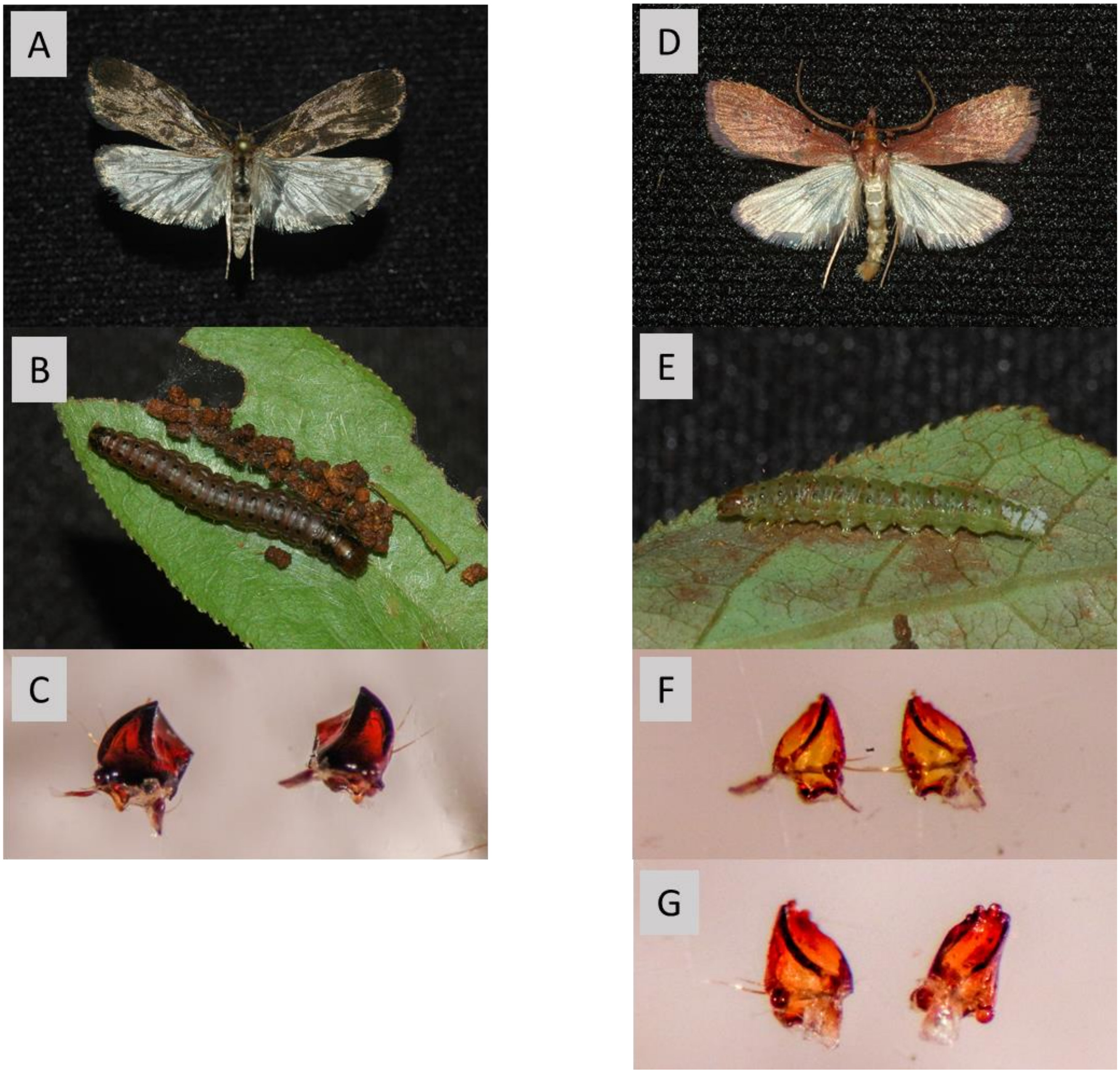
Appendix III, Figure 3. Caterpillars collected from ʻōhiʻa (*Metrosideros polymorpha*) at Hakalau Forest National Wildlife Refuge. Species shown are *Thyrocopa* sp. (Xyloryctidae; A–E), *Hyposmocoma* sp. (Cosmopterigidae; F–G), and *Carposina* sp. (Carposinidae; H–I). For *Thyrocopa* sp., each pair of mandibles is from a different instar collected from the same individual. Mandibles are shown from youngest (C) to oldest (E) instar.



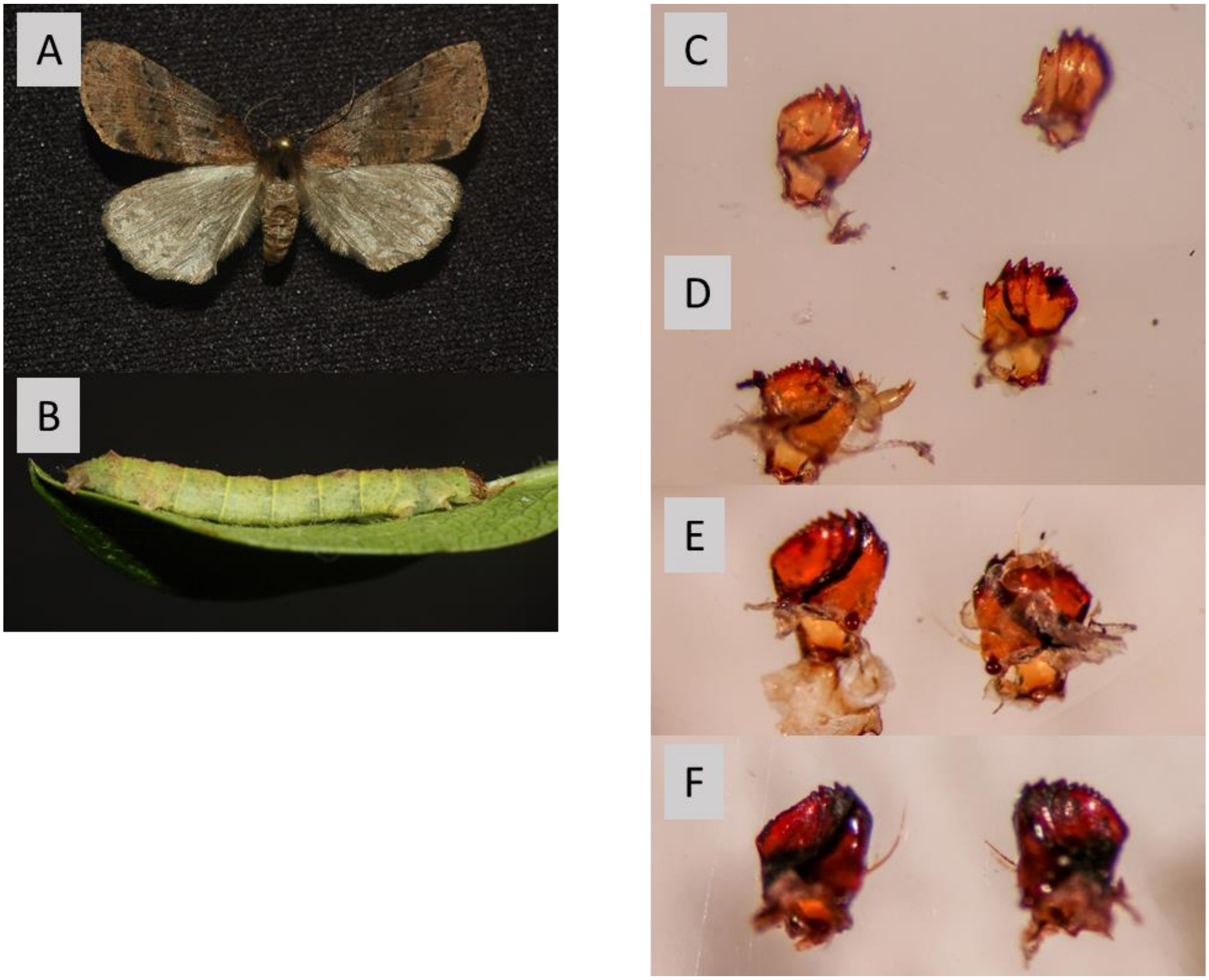
Appendix III, Figure 4. Caterpillars collected from ʻōhiʻa (*Metrosideros polymorpha*) at Hakalau Forest National Wildlife Refuge. Species shown are *Eupithecia monticolens* (Geometridae; A–B) and *Scotorythra* sp. (Geometridae; C–E). Note the worn tips of the teeth on the *Scotorythra* mandibles, likely a sign of age.



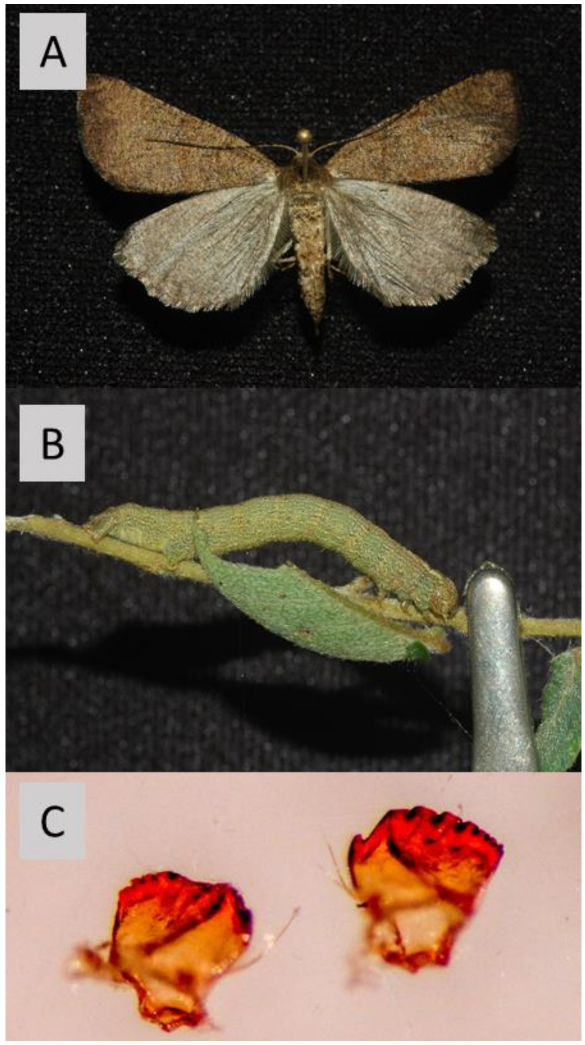
Appendix III, Figure 5. Caterpillars collected from ʻōhiʻa (*Metrosideros polymorpha*) at Hakalau Forest National Wildlife Refuge. Species shown is an undetermined Lepidoptera (A–C).



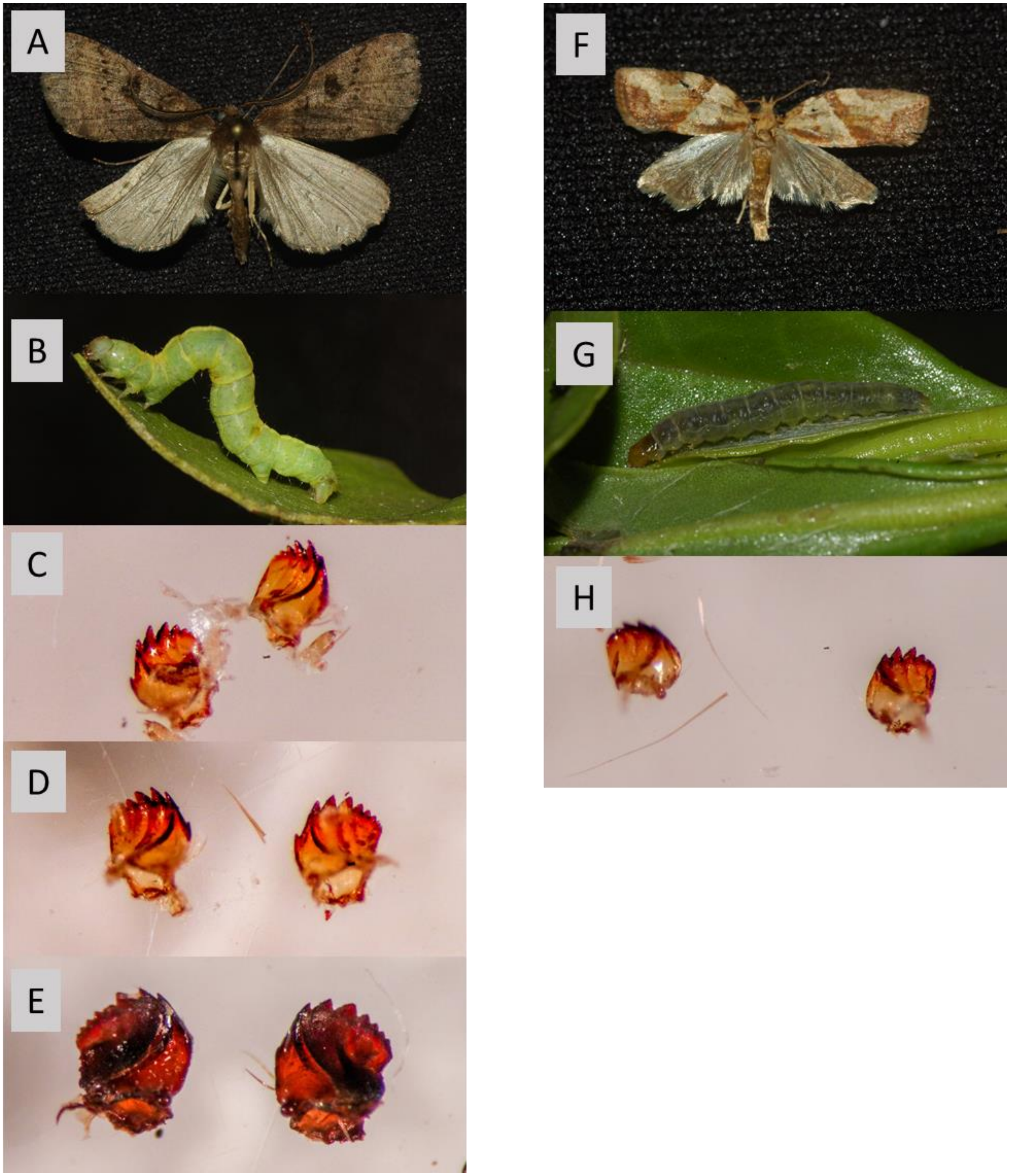
Appendix III, Figure 6. Caterpillars collected from ʻōhelo (*Vaccinium calycinum*) at Hakalau Forest National Wildlife Refuge. Species shown are *Thyrocopa* sp. (Xyloryctidae; A–C) and *Udea pyranthes* (Crambidae; D–G).



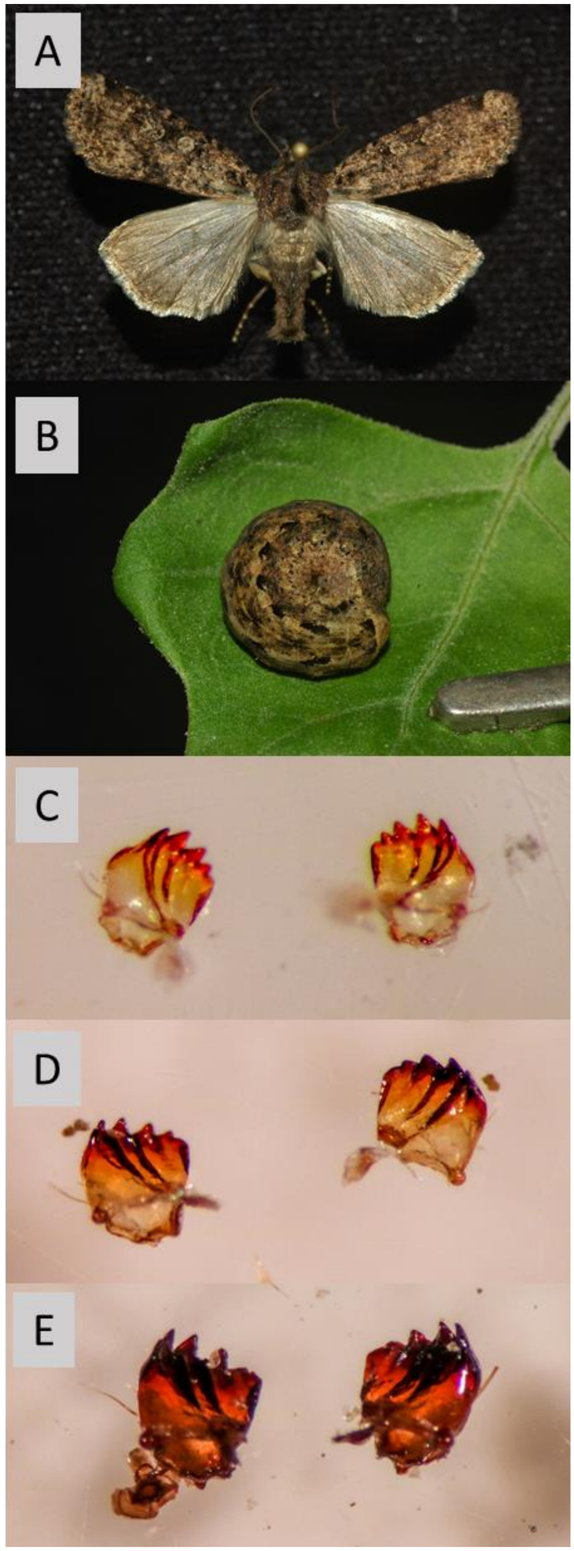
Appendix III, Figure 7. Caterpillars collected from pilo (*Coprosma ochracea*) at Hakalau Forest National Wildlife Refuge. Shown is an undetermined species of *Scotorythra* (Geometridae; A–G) that may or may not be the same species found on other host plants. Each pair of mandibles is from a different instar collected from the same individual. Mandibles are shown from youngest (C) to oldest (F) instar.



Appendix III, Figure 8. Caterpillars collected from māmane (*Sophora chrysophylla*) at Hakalau Forest National Wildlife Refuge. Shown is an undetermined species of *Scotorythra* (Geometridae; A–G) that may or may not be the same species found on other host plants.



Appendix III, Figure 9. Caterpillars collected from kōlea (*Myrsine lessertiana*) at Hakalau Forest National Wildlife Refuge. Shown is an undetermined species of *Scotorythra* (Geometridae; A–E) that may or may not be the same species found on other host plants. Also shown is *Epiphyas postvittana* (Tortricidae; F–H). Each pair of mandibles in a series is from a different instar collected from the same individual. Mandibles are shown from youngest (C) to oldest (E) instar.



Appendix III, Figure 10. Caterpillars collected from ʻāweoweo (*Chenopodium oahuense*) at Hakalau Forest National Wildlife Refuge. Species shown is *Peridroma albiorbis* (Noctuidae; A–E). Each pair of mandibles is from a different instar collected from the same individual. Mandibles are shown from youngest (C) to oldest (E) instar.