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AN ASSESSMENT OF ARTHROPOD PREY RESOURCES AT NAKULA NATURAL AREA RESERVE, A POTENTIAL SITE OF REINTRODUCTION FOR KIWIKIU (*PSEUDONESTOR XANTHOPHRYS*) AND MAUI `ALAUAHIO (*PAROREOMYZA MONTANA*)

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Hawaiian forest birds have declined dramatically since humans arrived in the archipelago. Birds from all foraging guilds have been affected but insectivorous species are currently at greatest risk of extinction. On the island of Maui, populations and ranges of the insectivorous kiwikiu (Maui parrotbill; *Pseudonestor xanthophrys*) and Maui ʻalauahio (Maui creeper; *Paroreomyza montana*) have declined significantly from historic levels primarily due to habitat loss, predation, disease, and food web disruption, leading to federal listings of endangered species and species of concern, respectively. Recovery plans for these birds include reestablishment of populations in parts of their former range. Nakula Natural Area Reserve on the leeward side of Haleakalā Volcano has been targeted for release of wild-caught or captive-bred individuals. The mesic, montane koa-ʻōhiʻa (*Acacia koa-Metrosideros polymorpha*) forest at Nakula has been heavily impacted through grazing by feral ungulates, but recent management actions to exclude these animals are promoting forest recovery. The objective of this study was to assess the arthropod prey base at Nakula in preparation for reintroductions of kiwikiu and Maui ʻalauahio. To accomplish that goal, we compared arthropod abundances at Nakula to those at Hanawi Natural Area Reserve and Waikamoi Preserve, areas where kiwikiu and Maui ʻalauahio are currently found. We also identified diets of kiwikiu and Maui ʻalauahio from fecal samples to better understand and evaluate the prey base at Nakula. Assessment methods included clipping branch tips to sample arthropods within the foliage of koa and ʻōhiʻa, using traps to quantify arthropods on koa and ʻōhiʻa bark surfaces, counting exit holes to quantify abundances of beetles (Coleoptera) within dead branches of koa, and measuring the density of arthropods within the stems of ʻākala (*Rubus hawaiiensis*). The diet of kiwikiu was dominated by caterpillars (Lepidoptera larvae), which comprised 90% of all prey items for 50 adult birds and 98% of all prey for two nestlings. Caterpillars were also the most important prey for Maui ʻalauahio (43% for 104 adult birds) although spiders (Araneae, 16%), beetles (12%) and true bugs, planthoppers and psyllids (Hemiptera; 12%) were also important. Caterpillars were generally the most abundant type of arthropod in the foliage of koa and ʻōhiʻa, although spiders, beetles and hemipterans were also common. Total arthropod biomass and caterpillar biomass at Nakula was as great, or greater, than that observed at Hanawi and Waikamoi per unit of foliage of both koa and ʻōhiʻa. Spiders generally dominated the bark fauna on both koa and ʻōhiʻa at all sites although isopods (Isopoda), millipedes (Myriapoda: Millipeda) and lacewings (Neuroptera) were also abundant at Waikamoi and Hanawi. Total arthropod biomass on bark, as well as the biomass of several individual taxa, was significantly lower at Nakula than the other sites. Our measurement of the density of beetle exit holes in dead koa branches found no difference between Nakula and Waikamoi. Finally, no difference existed in the abundance of arthropods (primarily caterpillars and moth pupae) within ʻākala stems among sites. With the exception of bark surfaces, our results suggest that the arthropod prey base for birds on primary foraging substrates at Nakula is similar to that found at two sites within the current range of kiwikiu and Maui ʻalauahio. However, our results should be viewed with caution because they are limited to the scale of individual branch, tree, or ʻākala stem. To complete the assessment, our results should be scaled up to the landscape level by determining the density of each substrate within each site. Key arthropod prey of kiwikiu and Maui ʻalauahio are available at Nakula and, as habitat restoration continues, food abundance should increase to the point at which populations of these birds can be supported.

Human colonization of the Hawaiian Archipelago has resulted in a continual decline in the diversity and abundance of native forest birds (Scott *et al.* 1986, W. Banko and P. Banko 2009). The Hawaiian honeycreepers (Fringillidae: Drepanidinae) have been hit particularly hard, with 38 of 55 known species and subspecies now extinct, and several additional species uncommon or rare (summarized in Pratt 2009). Numerous factors have contributed to the decline of the Hawaiian honeycreepers and other native forest birds including disease (Warner 1968, van Riper *et al.* 1986, Atkinson and LaPointe 2009), habitat degradation and loss (Pratt and Jacobi 2009), and predation (Atkinson 1977, Lindsey *et al.* 2009). While these factors are clearly limiting, a more insidious factor may be a reduction in the availability of food resources, particularly the arthropods required for the maintenance of adult birds and development of their young (P. Banko and W. Banko 2009, W. Banko and P. Banko 2009). A wide range of factors may suppress arthropod populations but pressure applied by social and parasitic wasps (Hymenoptera) may have the greatest impacts (Howarth 1985, Gambinio *et al.* 1987, Henneman and Memmott 2001, Peck *et al.* 2008). Regardless of the cause, several insectivorous Hawaiian forest birds are currently found at critically low population densities and are at significant risk of extinction.

The island of Maui currently supports three species of insectivorous Hawaiian honeycreepers, the Hawai'i 'amakihi (*Hemignathus virens wilsoni*), kiwikiu (or Maui parrotbill; *Pseudonestor xanthophrys*) and the Maui 'alauahio (or Maui creeper; *Paroreomyza montana*). While Hawai'i 'amakihi remain relatively common within native habitat, kiwikiu and Maui 'alauahio are now absent, rare, or uncommon over much of their former range. Kiwikiu are currently restricted to about 50 km^2 of montane rainforest between 1,700 and 2,100 m elevation on the northeast slopes of Haleakalā Volcano, East Maui, an area encompassing about 5% of their original range (Scott *et al.* 1986, Simon *et al.* 1997). Their largely contiguous population is estimated to be about 500 individuals (Scott *et al.* 1986), with the majority (421, 95% CI = 209–674) found densely packed (MFBRP unpublished data) within habitat centered in the Hanawi Natural Area Reserve (James and Olson 1991, Camp *et al.* 2009, Gorresen *et al.* 2009, Brinck *et al.* 2012). Kiwikiu were listed as endangered under the Endangered Species Preservation Act on March 11, 1967 (35 FR 4001). The range of Maui 'alauahio largely overlaps that of kiwikiu, but a second, possibly isolated population exists in and around Polipoli State Park on the southwest flank of Haleakalā (Baker and Baker 2000). A small, third population was recently reported from Kahikinui Forest Reserve on leeward Haleakalā (pers. comm. by F. Duval cited in Baker and Baker 2000) but appears to no longer exist. With a population likely exceeding 55,000 individuals (Brinck *et al.* 2012), Maui 'alauahio is considered a species of conservation concern (U.S. Fish and Wildlife Service 2008).

Kiwikiu is a specialized forager (W. Banko and P. Banko 2009) that feeds heavily on wood-boring beetles (Coleoptera), and to a lesser extent, caterpillars (Lepidoptera; Perkins 1903). Kiwikiu most commonly use their powerful bill to excavate arthropods from the wood of branches, but they are also adept at obtaining prey by splitting twigs, gleaning leaf and bark surfaces, probing flowers and leaves, and plucking arthropods from within small fruit (Mountainspring 1987). Seasonal differences in foraging behaviors and prey capture exist as a response to the availability of ephemeral prey such as caterpillars within fruit and herbaceous stems (Mountainspring 1987). In contrast, Maui 'alauahio possess an intermediate degree of foraging specialization (W. Banko and P. Banko 2009), obtaining arthropods from a wide range of substrates (Baker and Baker 2000). From the stomachs of wild birds, Perkins (1903)

identified caterpillars and spiders (Araneae) as important prey but also found myriapods (Myriapoda: centipedes, millipedes), slugs (Gastropoda), beetles and moths. In particular, Perkins (1903) noted that Maui ʻalauahio routinely searched the surface of standing dead wood for looper caterpillars (Geometridae) that often took refuge during the day. While primarily insectivorous, Maui ʻalauahio also occasionally consumes nectar, although inefficiently compared to other nectar-feeding honeycreepers (Carothers 1982).

Recovery plans for both kiwikiu and Maui ʻalauahio include the reintroduction and reestablishment of self-sustaining populations into suitable habitat within their former ranges. Several sites have been considered for release of captive-bred or wild-caught birds, but mesic forest within Nakula Natural Area Reserve on the leeward slope of Haleakalā is the area currently targeted (U.S. Fish and Wildlife Service 2006). Overall, Nakula encompasses about 614 ha, but remnant forest that is potentially suitable habitat for these birds exists within about 120 ha between approximately 1,070 and 1,700 m elevation. While Nakula has been degraded by many years of grazing and browsing by cattle (*Bos taurus*), goats (*Capra hircus*), and pigs (*Sus scrofa*), it still supports significant numbers of mature canopy-forming koa (*Acacia koa*) and ʻōhiʻa (*Metrosideros polymorpha*). Following recent fencing and the removal of feral ungulates, Nakula is on a trajectory for habitat recovery (Figure 1). Significantly, Nakula is considered to be at low risk of harboring avian diseases due to the absence of standing water that can support mosquitoes that vector avian malaria and avian pox (Warner 1968, van Riper *et al.* 1986).

Figure 1. Forest habitat at Nakula Natural Area Reserve. The photo on the left shows remnant mature koa and ʻōhiʻa trees that survived many years of grazing by cattle and goats. The photo on the right illustrates how many native plants have clung to the steep walls of gulches that were inaccessible to ungulates.

The primary objective of this project was to assess the arthropod prey base at Nakula as part of an evaluation of the suitability of the site for reintroducing kiwikiu and Maui ʻalauahio. To do that, we compared arthropod abundances on several foraging substrates at Nakula to those

found at two sites that currently represent core habitat for these birds: upper montane forest within Hanawi Natural Area Reserve and Waikamoi Preserve. Arthropod abundances at Hanawi and Waikamoi were considered baseline abundances for comparison with Nakula. Foraging substrates assessed included the foliage and bark of koa and 'ōhi'a, dead koa branches, and dead 'ākala stems. Each of these substrates supports a diverse assemblage of arthropods (Swezey 1954) and is commonly utilized by kiwikiu (Mountainspring 1987). Because seasonal changes in arthropod abundance on koa and 'ōhi'a are unknown in these habitats, we quantified their abundance during two opposing seasons. In contrast, 'ākala stems generally senesce and die during September and October (Berlin et al. 2000), so they were sampled in the spring to allow the arthropod fauna to develop for several months. Our assessment of dead koa branches was based on previous beetle activity and was not seasonally dependent. Additionally, to aid in our assessment of the arthropod prey base of these two species, we determined the diets of kiwikiu and Maui 'alauahio by identifying arthropods in fecal samples. Reintroducing kiwikiu into Nakula is a higher priority than reintroducing Maui 'alauahio, but reestablishing both will increase bird diversity. Moreover, if Maui 'alauahio are reintroduced first, potentially as a surrogate to develop translocation techniques for kiwikiu, it will be equally important to assess the resource base relevant to their diet.

METHODS

Study Areas

This study was conducted at Hanawi Natural Area Reserve, Waikamoi Preserve and Nakula Natural Area Reserve (Figure 2). Hanawi represents core habitat for kiwikiu and supports the highest density of birds (Camp *et al.* 2009). At the western edge of the kiwikiu's range, Waikamoi supports considerably fewer birds than does Hawani. Hanawi and Nakula are part of Hawai'i Department of Forestry and Wildlife's Natural Area Reserve system and receive the highest level of habitat protection on state land. Waikamoi Preserve is managed by The Nature Conservancy of Hawai'i and is managed similarly to Hanawi and Nakula.

Hanawi protects approximately 3,035 ha of native forest between 610 and 2,285 m elevation on the windward slope of Haleakalā Volcano. Our work was conducted between approximately 1,830 and 2,040 m elevation along existing transects that lie between the east and west forks of Hanawi Stream in the area below Frisbee Meadow camp (Figure 3). This is a site of long-term demographic and behavioral studies of kiwikiu and other forest birds (e.g. Mountainspring 1987, Berlin *et al.* 2000, Simon *et al.* 2000, Pratt *et al.* 2001, Becker *et al.* 2010; Mounce *et al.* 2013, Mounce *et al.* 2014). 'Ōhi'a dominates the canopy of this area, while the understory is primarily comprised of 'ākala, kāwa'u (*Ilex anomala*), pilo (*Coprosma* spp.), kanawao (*Broussaisia arguta*), alani (*Melicope* spp.), 'ōhelo (*Vaccinium calycinum*), and 'ōlapa (*Cheirodendron trigynum*). The phenology of the Hanawi plant community was described by Berlin *et al.* (2000).

Waikamoi Preserve encompasses about 2,117 ha of forest habitat directly west of Hanawi (Figure 2). Our study site was located below the Hosmer Grove area of Haleakalā National Park, between about 1,830 and 1,935 m elevation, bordered by Hawai'i Forest Bird survey transect 3 on the west and Pepperomia Trail on the east (Figure 3). The composition of the forest in this area is similar to that found at Hanawi, but contains significant numbers of canopy-forming koa.

In contrast to Hanawi and Waikamoi, Nakula is located on the leeward slope of Haleakalā (Figure 2). Currently, the overstory within the study area is dominated by scattered mature

ʻōhiʻa and koa while the understory is primarily comprised of alien grasses. Other native plants are primarily restricted to the steep walls of the gulches that dissect the area. In these locations, scattered ʻōlapa, kōlea (*Myrsine* sp.), kāwaʻū, and ʻākala persist in small numbers. Primarily above about 1,700 m elevation, remnant patches of mature māmane (*Sophora chrysophylla*), ʻiliahi (*Santalum freycinetianum*) and naio (*Myoporum sandwicense*) are also found. Little regeneration of native plants exists outside of the gulches. Nakula, formerly a part of Kahikinui Forest Reserve, was designated a Natural Area Reserve (NAR) in 2011. Our work took place between about 1,460 and 1,720 m elevation in the areas bounded by the western edge of the NAR and Wailaulau gulch (Figure 3).
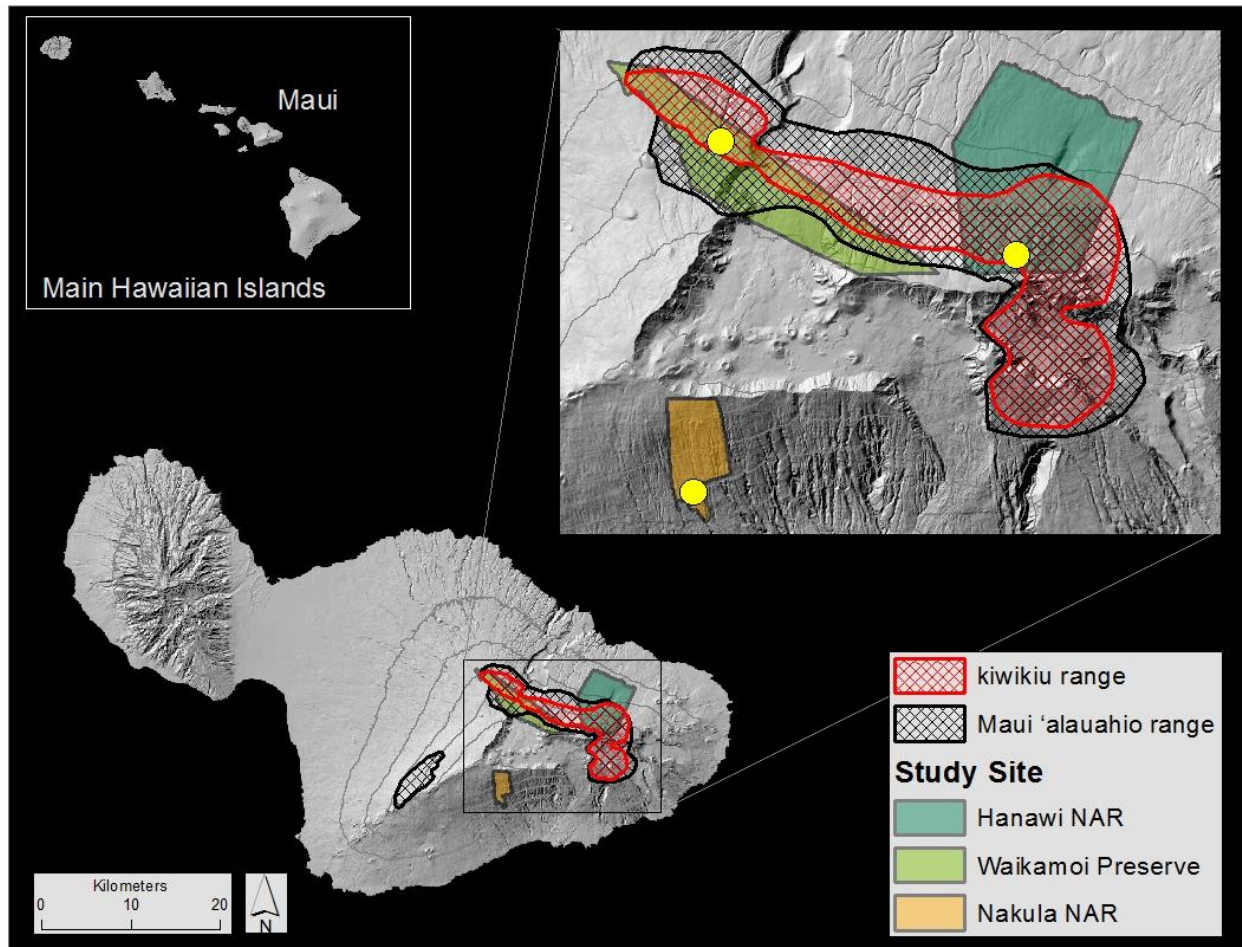
Figure 2. Location of study sites (yellow dots) within Hanawi and Nakula Natural Area Reserves and Waikamoi Preserve on the island of Maui. The red cross-hatched area is the approximate distribution of kiwikiu and the black cross-hatched area that of Maui ʻalauahio.

Due to the orographic influence of Haleakalā Volcano, mean annual rainfall varied considerably among sites, averaging approximately 5,300 mm/year at Hanawi, 2,250 mm/year at Waikamoi, and 1,000 mm/year at Nakula (Giambelluca *et al.* 2013). Despite the significant difference in

total rainfall accumulation among sites, the dominant plant species differed relatively little; however, one key difference is the absence of koa at Hanawi.
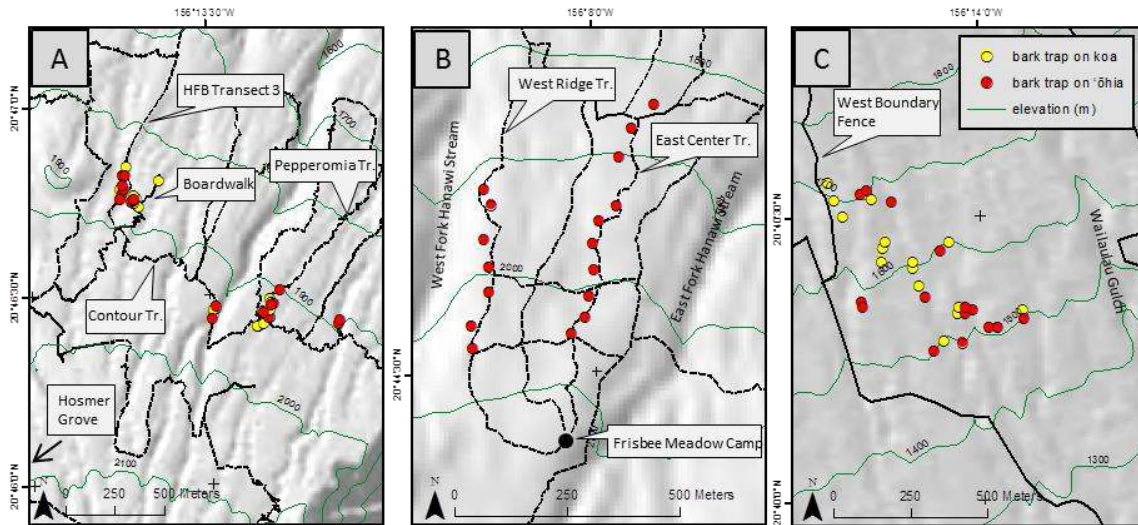
Figure 3. Location of study sites within Waikamoi Preserve (A), Hanawi NAR (B), and Nakula NAR (C). The yellow and red circles indicate locations of koa and ʻōhiʻa trees on which bark traps were placed. All other arthropod sampling took place within the general area of these trees.

Diet analyses

Diet composition

Diets of kiwikiu and Maui ʻalauahio were reconstructed through dissection and microscopic examination of fecal material collected during mist net-based demographic studies conducted at Hanawi and Waikamoi by the U.S. Geological Survey (USGS) during 1994–1996 (1 adult and 2 nestling kiwikiu and 7 Maui ʻalauahio) and the Maui Forest Bird Recovery Program (MFBRP) during 1998 (1 kiwikiu), 2002 (2 kiwikiu) and 2006–2010 (51 kiwikiu and 72 Maui ʻalauahio). Fecal samples were collected from cotton bags that were used to temporarily house birds captured in nets and preserved in 70% EtOH. In the lab, fecal samples were teased apart using forceps, and arthropod body fragments were photographed for later identification. Arthropod fragments were identified using reference specimens collected at the study sites, or in similar habitats elsewhere. Our estimates of the number of individuals per sample was conservative, so, for example, if three spider fangs similar in size and structure were found in a sample, it was assumed that there were two individuals in the sample, rather than three, since each spider has two fangs.

From one kiwikiu nest, 11 fecal samples were collected. But because several of these samples appeared to consist of more than one fecal deposit, it was not possible to make per-sample determinations and samples were pooled for analysis. Similarly, on several occasions ($n = 11$)

fecal material from more than one Maui 'alauahio was pooled into a single vial in the field (range = 2–6 samples) resulting in a total of 101 samples; those pooled samples were excluded when calculating mean and standard error values for all samples.

Diet richness and diversity

We evaluated the richness and diversity of prey within the diets of kiwikiu and Maui 'alauahio in terms of the range of arthropod fragments found in fecal samples. We pooled samples for each species; therefore, we do not attempt to distinguish possible differences between sexes, ages, seasons, or localities. The analyses include all arthropod taxa at the level of order (insects, spiders) or subclass (mites), regardless of their frequency of use or abundance in bird diets.

We calculated diet richness and diversity indices from our prey abundance and incidence data using EstimateS (ver. 9.1.0 for Windows; Colwell 2013), which provided: 1) sample-based rarefaction and extrapolation methods for comparing richness based on equivalent numbers of samples or individuals, 2) non-parametric estimators of richness that use information on the rare taxa to adjust for the number of taxa present but not detected to determine the minimum number of taxa (Gotelli and Colwell 2011), and 3) widely-used indices of diversity.

Rarefaction curves estimate taxon richness for a subsample of the pooled total taxa richness, based on an empirical reference sample, whereas asymptotic richness estimators determine total (true) taxon richness, including taxa that may not occur in any sample (Colwell 2013). By using statistical sampling models (rather than fitting mathematical functions), EstimateS extrapolates from a reference sample to the expected richness (and its unconditional standard deviation) for an augmented number of individuals or sampling units, which in our case was set at 100 total samples. As a target for estimating asymptotic richness for the extrapolation, EstimateS uses the biased-corrected form of Chao1 for abundance data and Chao2 for incidence data. We used the classic versions of Chao1 and Chao2 when EstimateS warned that the coefficient of variation of the abundance or incidence distribution exceeded 0.5 (the size of a sample was sufficient when the proportion of "singletons" [Chao1] or "uniques" [Chao2] was less than 50%).

EstimateS computes four, widely-used indices of diversity that combine information on taxon richness and relative abundance (or evenness) in different ways (Colwell 2013 and references therein): Fisher's alpha (the alpha parameter of a fitted logarithmic series distribution), Shannon diversity (using natural logarithms), exponential Shannon diversity, and Simpson diversity ("inverse" form). The indices were calculated using rarefied subsamples of the reference sample. The Shannon exponential and inverse Simpson indices indicate units of equivalent, equally abundant taxa, as do the richness indices. Sensitivity to rare species is greater for the richness indices, least for the Simpson diversity index, and intermediate for the Shannon diversity index. For richness, EstimateS uses exact analytical methods to compute the expected number of taxa (and its unconditional standard deviation) for each level of sample accumulation. For measures of diversity, EstimateS resamples sampling units stochastically over many iterations using a random-number-driven algorithm, and it reports the means and conditional standard deviations among resamples for each level of accumulation, which reduces the effects of differences in sample sizes when diversity statistics for multiple samples are compared at similar levels of taxa accumulation.

As in the case of richness estimators, EstimateS computed the four diversity indices for each level of sample pooling, from one sample to the total number of samples collected, which

allowed us to determine whether and when each index stabilized with increasing numbers of samples (Colwell 2013). EstimateS added samples to the pool at random, and we specified 100 random iterations (with replacement) to compute the mean and bootstrapped standard deviation (conditional on the reference sample except for Fisher's alpha, for which an unconditional SD was computed) for the indices at each level of pooling. We chose to randomize with replacement to facilitate comparisons between diets, but this option would likely have produced a final value of richness for the averaged, random-order taxon accumulation curve that was less than the total number of observed taxa due to the chance of missing or duplicating some samples for any given run (Colwell 2013).

Arthropod prey assessment

Arthropods on koa and ʻōhiʻa foliage

Tips of koa and ʻōhiʻa branches were collected to measure the abundance of arthropods living within their foliage. To sample this community, branch tips were obtained using two extendable poles manipulated in concert: one pole was used to clip the branch while a second pole, supporting a metal hoop from which a nylon bag (approximately 75 cm diameter by 90 cm deep) was suspended, was held directly beneath the foliage to catch the sample as it dropped. For all trees sampled, a single terminal foliage cluster approximately 50 cm long was obtained. In the field, arthropods were extricated from foliage by vigorously shaking the branch tips while still in the bag. Dislodged arthropods were collected using an aspirator and immediately preserved in propylene glycol (50% solution). Foliage was removed from branches and placed in zip lock plastic bags for transport to the lab. Foliage was oven-dried at 20 °C to constant mass and recorded. Variation among the sizes of foliage samples was standardized by dividing arthropod abundance by the dry biomass of leaves from which the arthropods were collected.

During 1 Mar–24 May 2011 and 28 Sep–21 Nov 2011, 15 samples were obtained from koa and ʻōhiʻa at each site, except for Hanawi where only ʻōhiʻa was sampled. Sample trees were randomly selected from a subset of all trees supporting foliage that could be reached from ground.

Arthropods on koa and ʻōhiʻa bark

Bark traps were used to sample the arthropod community associated with the trunks of koa and ʻōhiʻa. Bark traps utilize a mesh fence radiating from the bottom of an inverted metal funnel sealed tightly against the bark of the tree to guide arthropods moving up the trunk into a collection head containing liquid preservative (50% solution of propylene glycol). The distance between bottom edges of the fence was approximately 1 m except where the circumference of the tree was < 1 m; in those cases the fence encompassed the entire trunk of the tree. The bark trap is described in detail in Peck *et al.* (2014). Bark traps have been used elsewhere to assess arthropod food resources for birds and are particularly effective at capturing spiders, caterpillars and some beetles (Hanula and New 1996, Hanula and Franzreb 1998, Halaj *et al.* 2009, Peck *et al.* 2014).

At each site, a single bark trap was placed on the main stem of 15–17 koa and ʻōhiʻa, except at Hanawi where traps were placed only on ʻōhiʻa. Trees were randomly selected from a subset of trees that could be safely climbed. Traps were generally placed in the tree canopy but in a few cases were placed 2–3 m above the ground. The canopy was accessed using single rope techniques (Perry 1978, Moffett and Lowman 1995).

Once installed, bark traps were operated continuously at each site during the following dates: Waikamoi during 26 February–24 May 2011 and 26 September–20 November 2011; Nakula during 11 March–24 May 2011 and 27 September–16 November 2011; and Hanawi during 14 April–26 May 2011 and 30 September–12 November 2011. Samples collected during February–May are referred to as "spring" samples and those collected during September–November are referred to as "fall" samples. Samples were collected once or twice each season at intervals ranging from 20–50 days. To standardize the sampling effort among traps that were active for varying amounts of time, arthropod abundance in each trap was divided by the number of days that the trap was open (trap-day).

Beetle activity in dead koa branches

The abundance of beetles in branches of dead koa was quantified at Waikamoi and Nakula by counting exit holes on the bark surface. Exit holes are the remnant sign of adult beetles that emerged from larvae that mature and pupate in the wood. Because the window of time during which immature beetles live in branches of dying and dead wood is often narrow and difficult to predict, we quantified exit holes on older dead branches from which most beetles would have been expected to have already emerged. To standardized branch age (the length of time the branch had been dead), we selected dead branches that had lost their leaves and fine twigs but retained their bark.

During 16–20 May 2012, one dead branch (< 100 cm diameter) was cut from 15 randomly selected koa trees at Waikamoi and Nakula. Low branches were collected using a hand-held pruning saw while branches in the canopy were cut using a rope-operated high-limb chain saw (Green Mountain Products, Inc.).

Once on the ground, branches were cut into individual straight-limb sections (i.e. side branches were separated from main branches) and their length and basal and distal diameters were measured. Exit holes were then quantified. The diameter of each exit hole and the diameter of the branch section at the point of the hole, were measured to the nearest 0.1 mm using a digital caliper. Exit hole density (number/m^2 bark surface) was estimated by dividing the number of exit holes on each branch section by the area of the branch section searched. The area of each branch section was calculated using a pipe model (2 * π * branch radius [average of the two ends] * branch length). Exit hole densities per branch sections were summed to yield overall branch density.

Arthropods in ʻākala stems

Between 16 Mar and 20 May 2012, standing dead ʻākala stems were collected at each site and dissected in the lab to determine the density of arthropods living in, or that had recently emerged from, stem tissue. Due to the relatively rapid rate which ʻākala stems decompose following death, stems collected for this study are thought to have died the previous late summer or early fall (woody die-back primarily occurs during August–October at Hanawi; Berlin *et al.* 2000). From multiple ʻākala patches at each site, one or two stems were randomly selected from multiple stems identified as being dead (a dead stem was indicated by tissue beneath the surface being brown rather than green), cut into sections approximately 30 cm long, labeled, and placed into large zip lock bags for immediate transport from the field. Once in the lab, the stems were frozen to kill and preserve arthropods. Two stems were collected from each patch at Hanawi and Waikamoi, but only one dead stem could be found within several patches at Nakula because of stem density at that site.

In the lab, the length and diameter of each stem segment were measured and the external surface was examined for exit holes that represented the emergence of adult arthropods. When found, the diameter of each exit hole was measured to the nearest 0.1 mm using a digital caliper. Stems were then split longitudinally using a hand pruner and the internal tissue was searched for arthropods. For each stem segment, all arthropods and arthropod remains (e.g. empty caterpillar pupal cases and caterpillar head capsules) were collected. We combined into a single taxonomic category caterpillar pupae that were alive at the time of collection with empty pupal cases from which moths had already emerged because the phenology of ʻākala and the development of caterpillars in stems may have differed among sites, potentially resulting in biased results. For example, the phenology of ʻākala at Nakula may have preceded that at Hanawi due to it being at lower elevation.

Arthropod densities (number of arthropods/cm^3 stem tissue) were determined for each stem by dividing the number of arthropods found by the volume of each stem searched. Stem volume was calculated using the following formula: π * stem radius^2 * stem length. The density of exit holes on ʻākala stems (number/cm^2 of surface area) was determined using the same protocols as for dead koa branches.

For patches from which two stems were collected instead of one, all measurements were averaged between stems to obtain a single value for each patch. Thus, site-level values represent the mean of all patches sampled.

Data analysis

For all collections on foraging substrates, arthropods were identified to the genus, family or order level and the body length of each individual was measured using a micrometer mounted within the ocular lens of Leica MZ-6 and MZ-12 microscopes. Estimates of arthropod biomass were obtained using length-to-mass regression equations specific to Hawaiian arthropods (Gruner 2003). In most cases, we used arthropod biomass rather than the number of individuals because we considered biomass to be a more relevant metric for assessing potential food resources for birds; however, abundance was used for arthropods in ʻākala stems because many individuals were damaged during dissection of the stems.

Due to a high level of variability among samples within most datasets, assumptions required for parametric analyses were rarely met, so non-parametric tests were used (SYSYAT 13.1). Mann-Whitney tests were used when comparing two factors (e.g. study sites for koa) and Kruskal-Wallis tests were used when comparing three (e.g. study sites for ʻōhiʻa). All *P*-values presented are the results of these tests unless otherwise specified. For analyses that included multiple arthropod taxa from the same dataset, critical values used for detecting significant levels of difference were adjusted using the Bonferroni correction. For arthropods in foliage and on the bark of koa and ʻōhiʻa, this resulted in significant differences recognized at $P < 0.0055$. Pairwise comparisons among sites following Kruskal-Wallis tests that indicated a significant overall difference were made using the Conover-Inman test (SYSTAT 13.1). Throughout the report, values are presented as mean ± SEM.

RESULTS

Diet analysis

Diet composition

Kiwikiu

Overall, 714 prey items were identified from 50 adult kiwikiu (Table 1). The mean number of arthropods per sample was 14.06 ± 1.74, with no difference between females (18.05 ± 3.15) and males (12.56 ± 2.59; P = 0.184). Overall, more arthropods per sample were documented from fecal samples collected at Hanawi (14.78 ± 1.93; n = 45) compared to Waikamoi (9.80 ± 2.78; n = 5), but the small number of samples at Waikamoi precluded statistical comparison. Caterpillars were consistently the prey taxon most frequently consumed, comprising between 72% of the diet for three males at Waikamoi to 95% of the diet for 19 females at Hanawi (Figure 4). Cerambycid beetle larvae made up 16% of the diet of 3 males at Waikamoi.

We identified 415 prey items from fecal samples from the two kiwikiu nestlings from Hanawi (Table 1). The single fecal sample from nestling 1 contained 40 arthropods while the 11 fecal samples from nestling 2 yielded 375 arthropods. Caterpillars dominated the samples, comprising 95% of the diet of nestling 1 and 98% of the diet of nestling 2. Mites (Acari), the larvae of carabid beetles, and spiders were of more minor importance to the nestlings.

Caterpillars were the dominant prey in kiwikiu fecal samples during most months that samples were available, ranging from 50% of the total during July (n = 4 arthropods) to 96.9% during November (n = 127 arthropods). The exception was during August when unidentified arthropods comprised 60% of all arthropods and "other" arthropods (flies [Diptera] and wasps) made up the remaining 40% (Figure 5). However, only five arthropods were identified from a single sample during August.

Maui ʻalauahio

In total, 877 arthropod prey items were identified from 101 adult Maui ʻalauahio fecal samples collected at Hanawi (Table 2). Overall, caterpillars were consumed most frequently (43%), followed by spiders (16%) and a collection of unidentified taxa (7.6%). Five additional taxa comprised 3.0–4.8% of the total. Although relatively few birds were sexed, the arthropods identified from fecal samples was generally similar between females (n = 3), males (n = 6) and birds for which the sex was not determined (n = 95). The mean number of arthropods in each fecal sample was 10.4 ± 0.7 (n = 68).

Table 1. Percent abundance of arthropods from adult and nestling kiwikiu fecal samples collected at the Hanawi and Waikamoi study areas. Total numbers of fecal samples and prey items are indicated in parentheses, respectively. Prey identified for females, males, unsexed individuals and adults, and nestlings were combined at each site.

Prey taxon[1]	Hanawi (adult)			Hanawi (nestling)		Waikamoi (adult)		total adult	total nestling	grand total
	female (19,348)	male (15,208)	unknown (11,109)	nestling 1 (1,40)	nestling 2 (11,375)	female (2,31)	male (3,18)	(50,714)	(12,415)	(62,1129)
Acari	0.3	0.5	0.9	2.5	0.3	3.2	0.0	0.6	0.5	0.5
Araneae	1.7	1.4	1.8	0.0	0.8	6.5	0.0	1.8	0.7	1.4
Coleoptera										
Carabidae larva	0.0	0.0	0.0	2.5	0.0	0.0	0.0	0.0	0.2	0.1
Curculionoidea[2]	0.3	0.5	0.0	0.0	0.3	0.0	0.0	0.3	0.2	0.3
Nitidulidae	0.3	0.5	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.2
Cerambycidae larva	0.0	2.4	0.9	0.0	0.0	0.0	16.7	1.3	0.0	0.8
Diptera	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.1	0.0	0.1
Hemiptera										
Sternorrhyncha										
Psyllidae	0.6	0.5	0.9	0.0	0.3	0.0	0.0	0.6	0.2	0.4
Hymenoptera	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.1	0.0	0.1
Lepidoptera larva	94.8	89.9	84.4	95.0	98.4	87.1	72.2	90.9	98.1	93.5
Psocoptera	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1
Thysanoptera	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1
Undetermined	1.7	3.8	9.2	0.0	0.0	3.2	11.1	3.8	0.0	2.4

[1]Common names for prey taxa are: Acari = mites; Araneae = spiders; Coleoptera = beetles; Carabidae = ground beetles; Curculionidae = weevils; Nitidulidae = sap beetles; Cerambycidae = long-horned beetles; Diptera = flies; Hemiptera = true bugs; Sternorrhyncha = suborder with no common name; Psyllidae = psyllids; Hymenoptera = wasps and bees; Lepidoptera = moths and butterflies; Psocoptera = bark lice; Thysanoptera = thrips.

[2]Includes the weevil families Aglycyderidae (primitive weevils) and Curculionidae (true weevils).
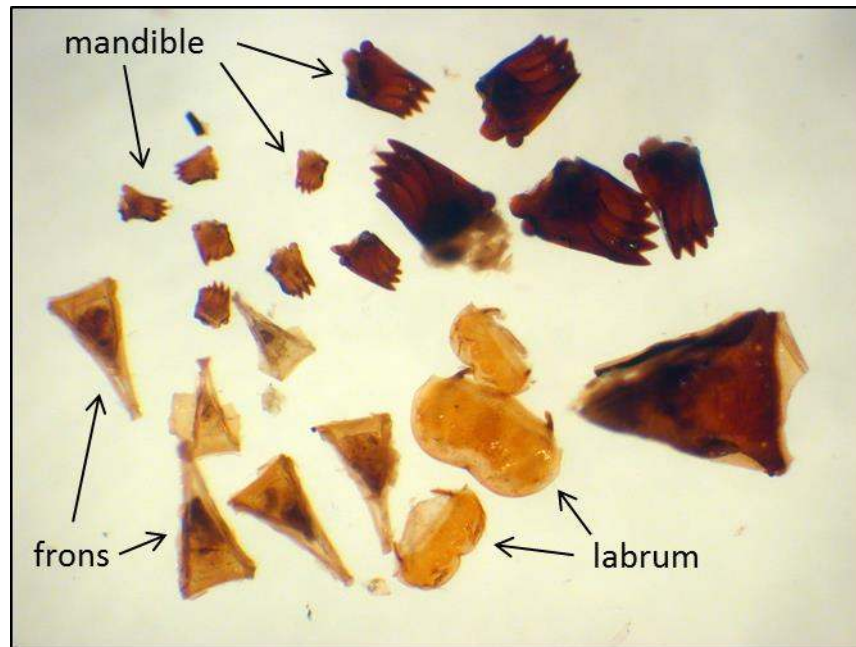
Figure 4. Insect fragments from a typical kiwikiu fecal sample include caterpillar mandibles, frons and labrums, all diagnostic parts of a caterpillar head.
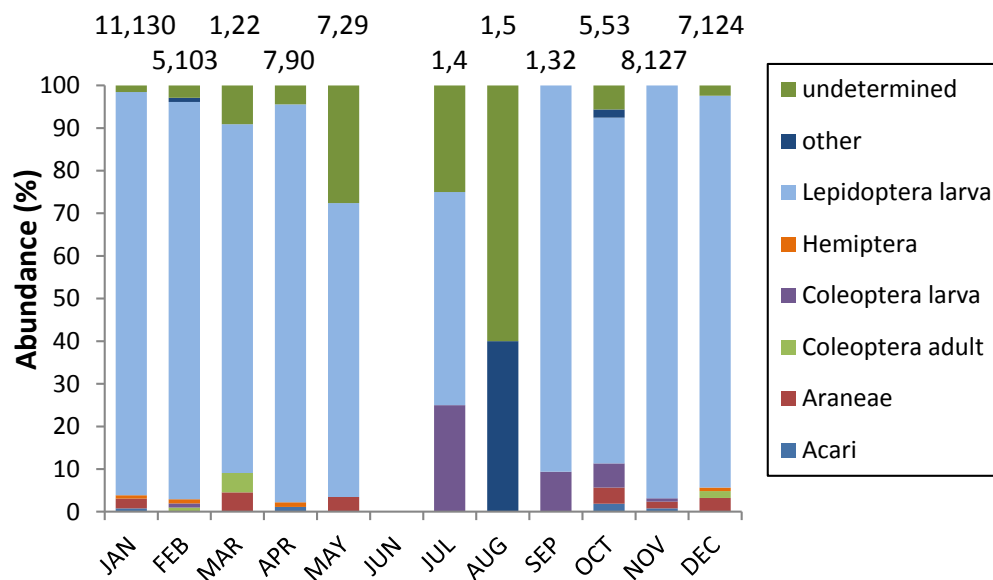
Figure 5. Percent abundance of the most common arthropods in kiwikiu fecal samples collected at Hanawi and Waikamoi (data combined). The values above each bar indicate the number of fecal samples analyzed followed by total number of arthropod prey identified during that month. Common names for arthropod groups can be found in Table 1.

Table 2. Percent abundance of arthropods from fecal samples of Maui ʻalauahio collected at Hanawi. Total numbers of fecal samples and prey items identified for each female, male and individuals of unknown sex are indicated in parentheses.

Prey taxon[1]	Female (3,22)	male (6,61)	unknown (92,794)	Total (101,877)
Acari	0.0	0.0	0.5	0.5
Araneae	9.1	11.5	16.8	16.2
Coleoptera				
Carabidae adult	0.0	3.3	3.4	3.3
Carabidae larva	4.5	0.0	1.6	1.6
Curculionoidea[2]	0.0	3.3	3.5	3.4
Nitidulidae	4.5	1.6	2.0	2.1
undetermined adult	0.0	8.2	1.4	1.8
undetermined larva	0.0	1.6	0.0	0.1
Diptera	4.5	0.0	1.5	1.5
Hemiptera				
Heteroptera				
Lygaeidae	0.0	0.0	0.5	0.5
Miridae	4.5	0.0	0.6	0.7
Nabidae	0.0	1.6	1.4	1.4
undetermined	0.0	0.0	0.3	0.2
Auchenorrhyncha				
Cicadellidae	0.0	0.0	0.9	0.8
Fulgoroidea[3]	13.6	1.6	3.9	4.0
Sternorrhyncha				
Psyllidae	0.0	0.0	5.3	4.8
Hymenoptera	4.5	0.0	2.5	2.4
Lepidoptera adult	0.0	1.6	3.1	3.0
Lepidoptera larva	40.9	47.5	43.1	43.3
Neuroptera adult	0.0	0.0	0.4	0.3
Neuroptera larva	0.0	3.3	0.4	0.6
undetermined	13.6	14.8	6.9	7.6

[1]Common names of prey taxa not included in Table 1 are: Heteroptera = typical bugs; Lygaeidae = seed bugs; Miridae = leaf bugs; Nabidae = assassin bugs; Auchenorrhyncha = suborder with no common name; Cicadellidae = leafhoppers; Neuroptera = lacewings. Auchenorrhyncha and Sternorrhyncha are collectively referred to as "Homoptera".

[2]The superfamily Curculionoidea includes the weevil families Aglycyderidae and Curculionidae.

[3]The superfamily Fulgoroidea includes the planthopper families Delphacidae (delphacid planthoppers) and Cixiidae (cixiid planthoppers).

The relative abundance of arthropod taxa in the diet of Maui 'alauahio was generally consistent over the course of the year, with caterpillars being most common, followed by spiders, adult beetles, hemipterans and psyllids (Figure 6). The incidence of caterpillars was 25% of the total in May, the only time it fell below 39%. Spiders were most frequently consumed during April when they made up 29% of all arthropods eaten.
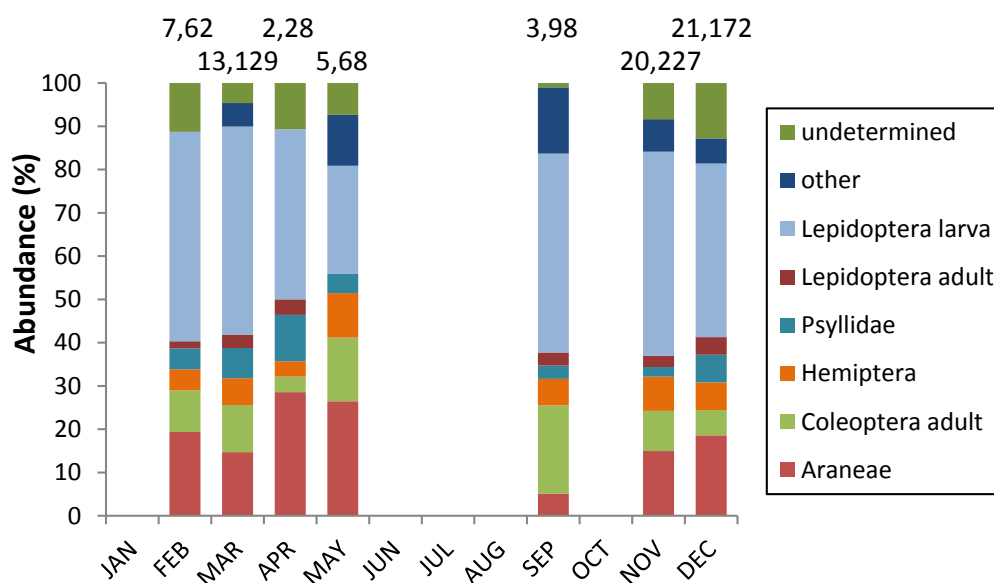

Figure 6. Percent abundance of the most common arthropods in Maui 'alauahio fecal samples collected at Hanawi. The values above each bar indicate the number of fecal samples analyzed followed by the total number of arthropod prey identified during that month. Psyllidae was separated from the rest of the Hemiptera because it was relatively abundant in the samples. Common names for arthropod groups can be found in Table 1.

Diet richness and diversity

The number of arthropod orders consumed by Maui 'alauahio and kiwikiu were similar (Tables 1, 2), and indices of diet richness were likewise similar for the species (Table 3). Nevertheless, the Maui 'alauahio diet proved to be richer than that of kiwikiu when rarefaction and extrapolation methods were applied to the data, the rarity of prey was accounted for, and the number of prey replaced the number of samples in the analysis (see Methods; Figure 7). Diet richness of kiwikiu nestlings was lower than for the adults of either species, despite the large number of individual prey expected in 100 samples (Table 3).

All commonly-used indices indicated that diet diversity was greater for Maui 'alauahio and least for kiwikiu nestlings (Table 4), although the method of combining multiple samples during each nest visit may have affected the results, especially for the high number of prey calculated to occur in 100 fecal samples.

Table 3. Richness estimators for arthropod orders found in Maui ʻalauahio and kiwikiu fecal samples. Fecal samples were collected from kiwikiu nestlings at one nest in 1995 (1 sample) and one nest in 1996 (11 samples); samples from both nests were pooled for analysis. Values calculated from EstimateS (v. 9.1.0; Colwell 2013). Individuals are the expected numbers of arthropod prey in 100 fecal samples as calculated using resampling methods. S(est) is the number of arthropod orders expected in the 100 fecal samples, given the reference sample. ACE is the Abundance Coverage-based Estimator and ICE is the Incidence Coverage-based Estimator. Bias-corrected forms of Chao1 (for abundance data) and Chao2 (for incidence data) were used. The high number of individual prey calculated to occur in 100 fecal samples from kiwikiu nestlings may be an artifact of combining samples at the nests, and other measures of richness may also be affected by sample pooling.

|	Fecal Samples	Individuals (computed)	S(est)	S(est) 95% CI Lower Bound	S(est) 95% CI Upper Bound	ACE Mean ± SD	ICE Mean ± SD	Chao 1 Mean	Chao 1 95% CI Lower Bound	Chao 1 95% CI Upper Bound	Chao 2 Mean	Chao 2 95% CI Lower Bound	Chao 2 95% CI Upper Bound
Maui ʻalauahio	69	657.48	9.00	9.00	9.00	9.08±0.34	9.07±0.29	8.98	8.98	9.62	8.98	8.98	9.64
kiwikiu	47	285.53	8.00	8.00	8.00	9.94±3.67	9.60±3.01	8.88	7.88	18.08	8.86	7.88	17.92
kiwikiu nestlings	12	3487.58	6.83	0.24	13.43	5.54±1.54	5.50±1.50	4.82	4.71	8.18	4.80	4.72	7.96
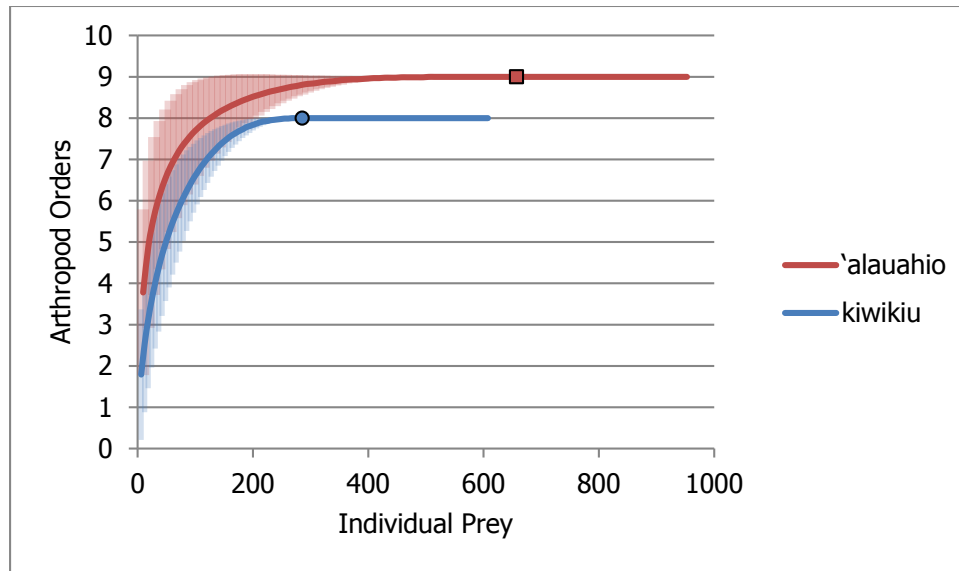
Figure 7. Estimated richness of arthropod orders from fecal samples from adult kiwikiu and Maui ʻalauahio. Values calculated from EstimateS (v. 9.1.0; Colwell 2013). Reference samples (Maui ʻalauahio = 69 samples; kiwikiu = 47 samples) are indicated by solid symbols, rarefaction by the lines to the left of the symbols, extrapolation by the continuation of the lines to the right of the symbols. Shading represents 95% CI around the accumulation curve. Asymptotes were reached by about the 530th (Maui ʻalauahio) and 270th (kiwikiu) prey items and the CIs converged to zero.

Table 4. Diversity estimators for arthropod orders found in Maui ʻalauahio and kiwikiu fecal samples. Values calculated from EstimateS (v. 9.1.0; Colwell 2013). Fecal samples were collected from kiwikiu nestlings representing one brood each in 1995 (1 sample) and 1996 (11 samples); samples from both nests were pooled for analysis.

	Fecal Samples	Fisher's Alpha Mean ± SD	Shannon Mean ± SD	Shannon Exponential Mean ± SD	Simpson Inverse Mean ± SD
Maui ʻalauahio	69	1.47 ± 0.20	1.48 ± 0.04	4.38 ± 0.16	3.15 ± 0.14
kiwikiu	47	1.45 ± 0.23	0.57 ± 0.08	1.78 ± 0.15	1.31 ± 0.06
kiwikiu nestlings	12	0.73 ± 0.13	0.13 ± 0.03	1.13 ± 0.04	1.04 ± 0.01

Arthropod prey assessment

Arthropods in koa and ʻōhiʻa foliage
Overall, caterpillars and moths were the dominant taxon on koa foliage at Waikamoi and Nakula during both spring and fall 2011, with the proportion of their total biomass ranging from 34% at Nakula during fall to 52% at Waikamoi during fall (Figure 8). Caterpillars were the dominant life stage, comprising 95% and 91% of Lepidoptera biomass at Waikamoi and Nakula, respectively. At Waikamoi, homopterans were second in biomass (17% during spring and fall combined), followed by beetles (9.4% during spring and fall combined) and hemipterans (7.1% during spring and fall combined). At Nakula, beetles comprised slightly greater biomass than did homopterans (18 and 15% during spring and fall combined, respectively).

In ʻōhiʻa foliage, spiders were the most abundant taxa at each site during each season, with their biomass ranging from 37% of the total biomass at Hanawi during spring to 58% of the biomass at Nakula during fall (Figure 9). Lepidoptera were generally second in abundance, ranging from 11% at Nakula during fall to 31% at Waikamoi during fall. Similar to koa, caterpillars were the dominant Lepidoptera life stage in ʻōhiʻa, comprising 53% of all Lepidoptera at Hanawi and 87% of all Lepidoptera at both Waikamoi and Nakula. Relative abundances of Coleoptera, Hemiptera, Homoptera and Psocoptera varied slightly among sites, but each comprised between 1 and 10% of the total biomass.
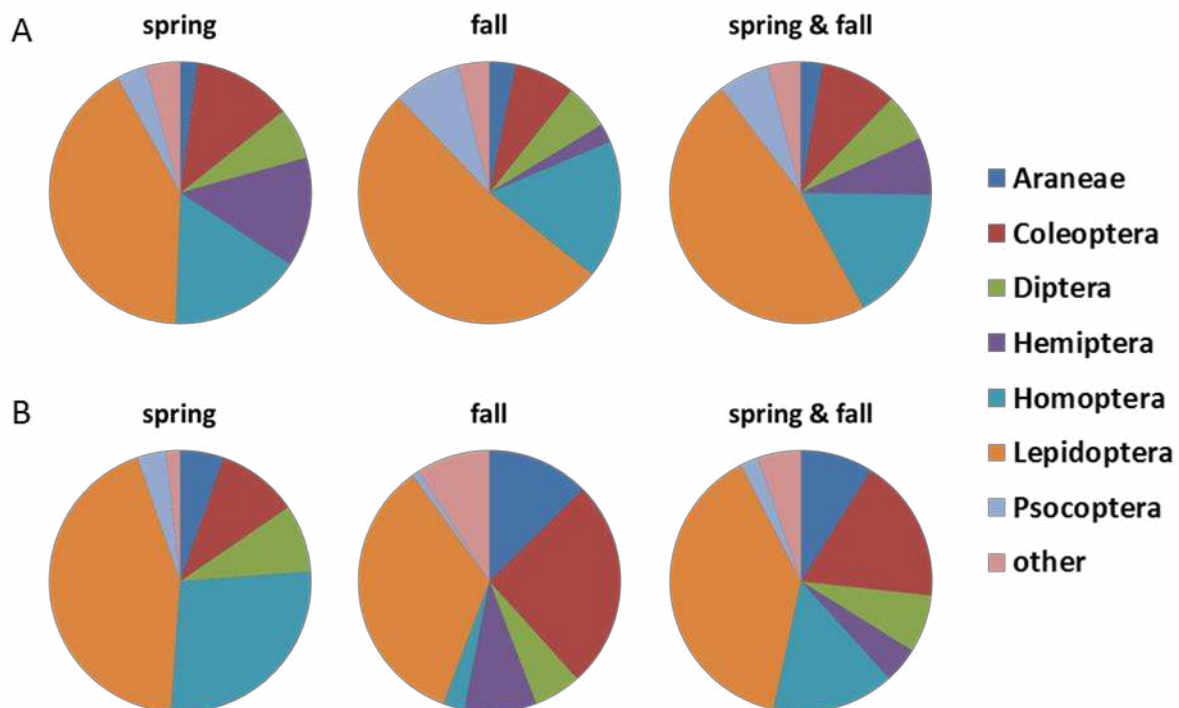

Figure 8. Relative abundance (mg arthropod/g foliage) of arthropod groups in koa foliage at Waikamoi (A) and Nakula (B) during spring, fall, and spring and fall combined. Common names for arthropod groups can be found in Tables 1 and 2.
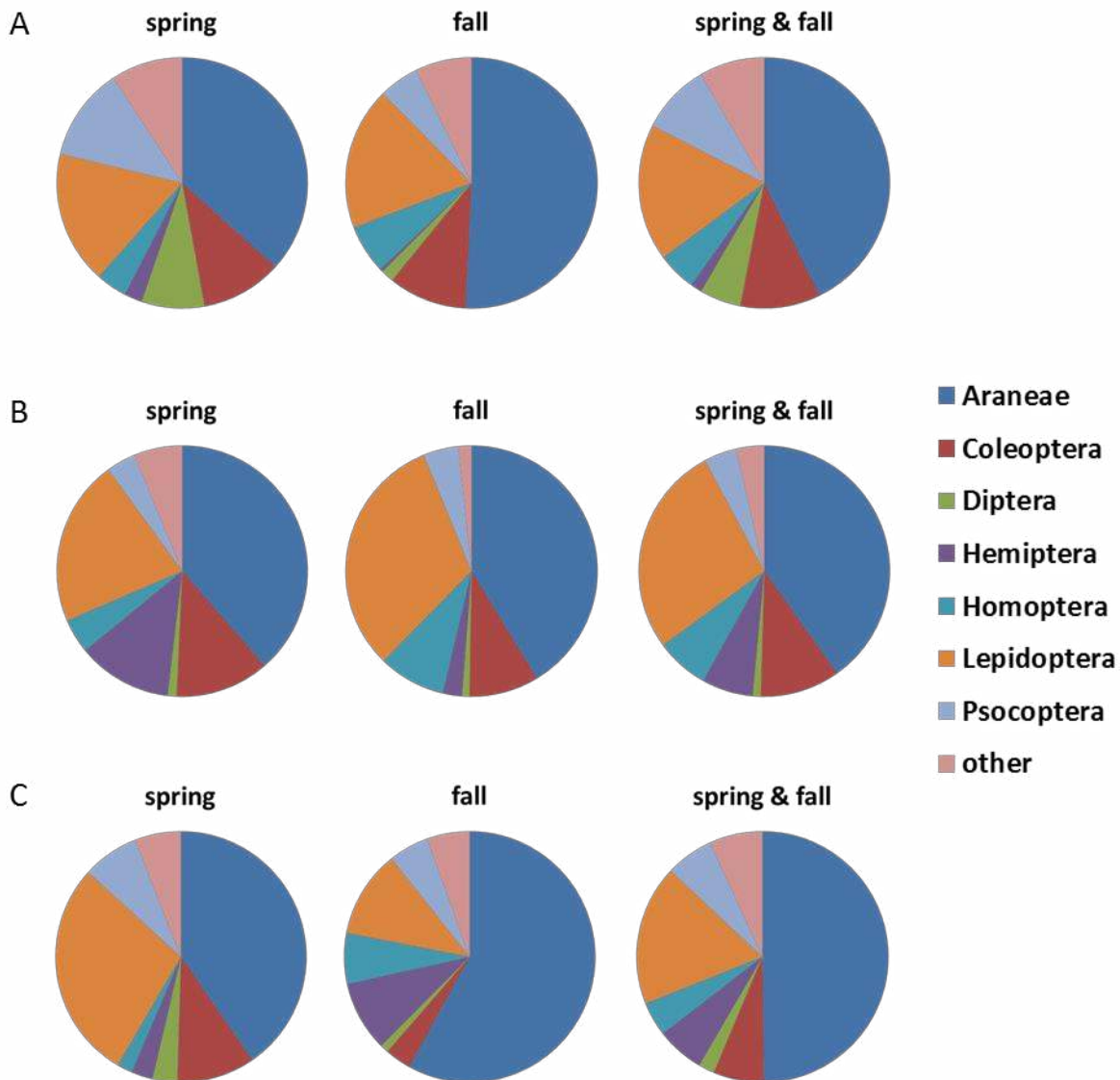
Figure 9. Relative abundance (mg arthropod/g foliage) of arthropod groups in ʻōhiʻa foliage at Hanawi (A), Waikamoi (B), and Nakula (C) during spring, fall, and spring and fall combined. Common names for arthropod groups can be found in Tables 1 and 2.

No difference was found in total arthropod biomass or the biomass of any individual taxon in koa foliage between spring and fall at Waikamoi or Nakula ($P > 0.020$ in all cases; $P < 0.0055$ required with Bonferroni correction). The pattern was similar in ʻōhiʻa foliage with no differences between spring and fall for any taxon at any site, except for spiders at Nakula, where their biomass was greater during fall than spring at Nakula.

Total arthropod biomass in koa foliage did not differ between sites during spring, fall, or for spring and fall combined (Figure 10). For arthropods in ʻōhiʻa foliage, a significant overall

difference was found among sites during fall and during spring and fall combined, with Waikamoi and Nakula being greater than Hanawi in both cases (Figure 10).
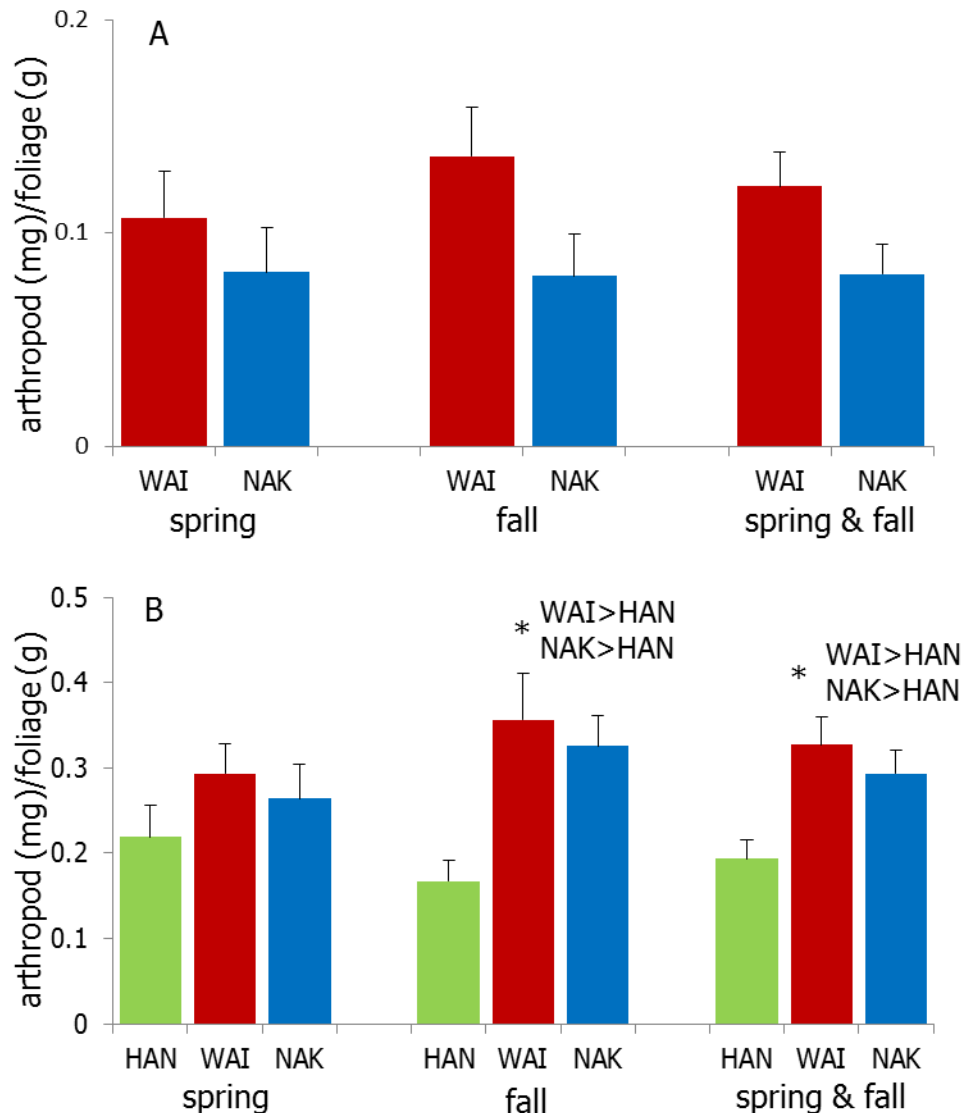

Figure 10. Total arthropod biomass (mean ± SEM) in foliage of koa (A) and ʻōhiʻa (B) at Hanawi (HAN), Waikamoi (WAI), and Nakula (NAK) during spring, fall, and spring and fall combined. Overall significant differences between sites are indicated by an asterisk. For ʻōhiʻa, significant between-site differences are shown above the bars.

On koa foliage, significant differences in arthropod biomass were detected between sites for flies, homopterans and barklice during fall, and for homopterans and barklice during spring and fall combined (Figure 11). In each instance, arthropod biomass was greater at Waikamoi than at Nakula. In ʻōhiʻa foliage, overall differences among sites were found for spiders, hemipterans,

and caterpillars and moths during fall, and spiders and hemipterans during spring and fall combined (Figure 11). The biomasses of spiders and hemipterans were greater at Waikamoi and Nakula than Hanawi during fall and during spring and fall combined. Caterpillar and moth biomass was greater at Waikamoi than Hanawi or Nakula during fall.

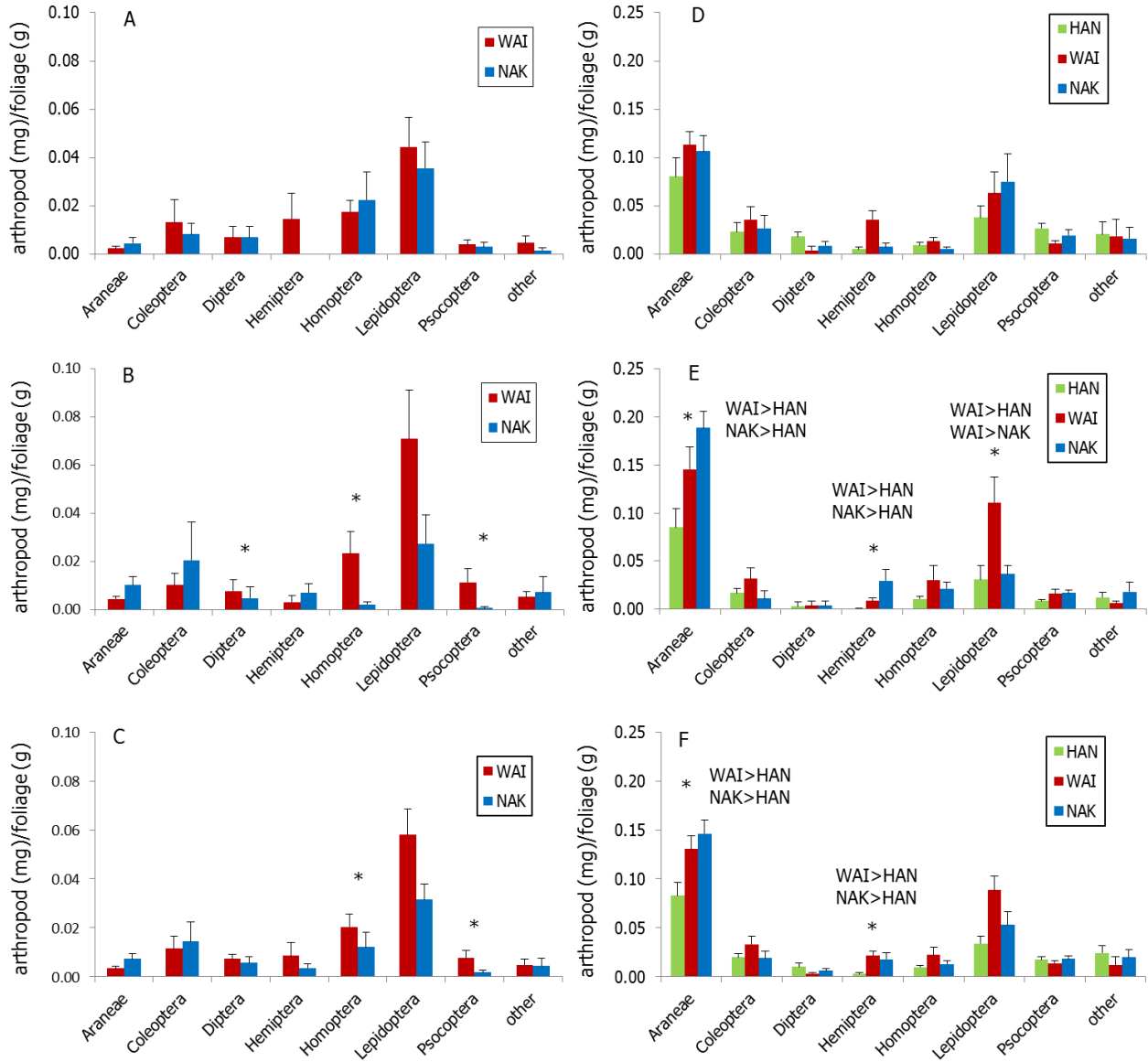Figure 11. Mean (± SEM) biomass of arthropods in foliage of koa during spring (A), fall (B), and spring and fall combined (C), and ʻōhiʻa during spring (D), fall (E), and spring and fall combined (F). Overall significant differences between sites are indicated by an asterisk. For ʻōhiʻa, significant between-site differences are shown above the bars. Common names for arthropod groups can be found in Tables 1 and 2.

Arthropods on koa and ʻōhiʻa bark

In bark traps set on koa, spiders comprised 46% and 92% of the arthropods sampled during the spring and fall combined at Waikamoi and Nakula, respectively (Figure 12). Seasonal differences were particularly large at Waikamoi where spiders comprised 76% of the total biomass during spring and 28% during fall. This difference was primarily due to proportionally larger numbers of isopods (33%) and millipedes (32%) collected during fall than during spring. At Nakula, the only taxon other than spiders to be relatively abundant during fall, comprising 19% of the total arthropod biomass, was Isopoda.
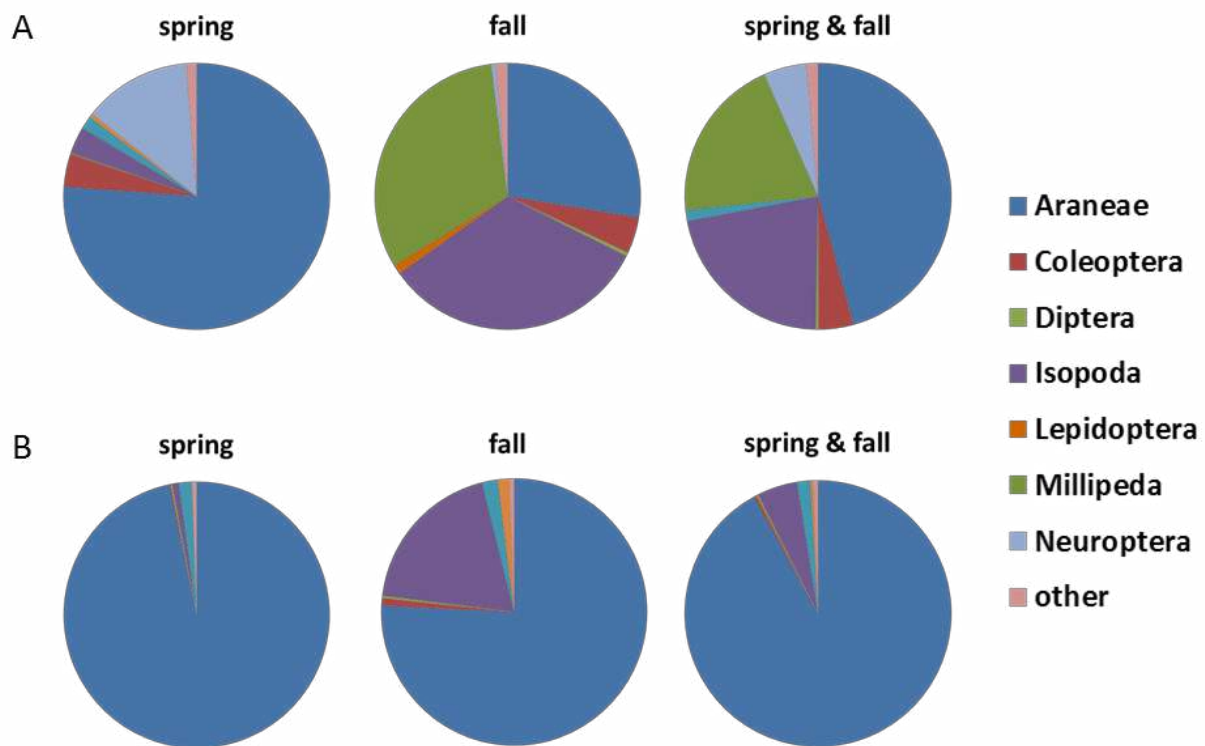

Figure 12. Relative abundance of arthropod groups collected in bark traps on koa at Waikamoi (A) and Nakula (B) during spring, fall, and spring and fall combined. Common names for arthropod groups can be found in Tables 1 and 2.

The bark fauna on ʻōhiʻa was dominated by spiders during spring at all three sites (> 65% in all cases) but comprised about 30% of the total arthropod biomass during fall at Waikamoi and Hanawi (28% and 32%, respectively; Figure 13). During fall, millipedes were the most abundant arthropod (40%) at Waikamoi while isopods (38%) comprised most of the arthropod biomass at Hanawi. Besides spiders, isopods were relatively common at Nakula during fall (16%). Caterpillars and moths comprised 8–9% of the biomass during fall at Waikamoi and Nakula.
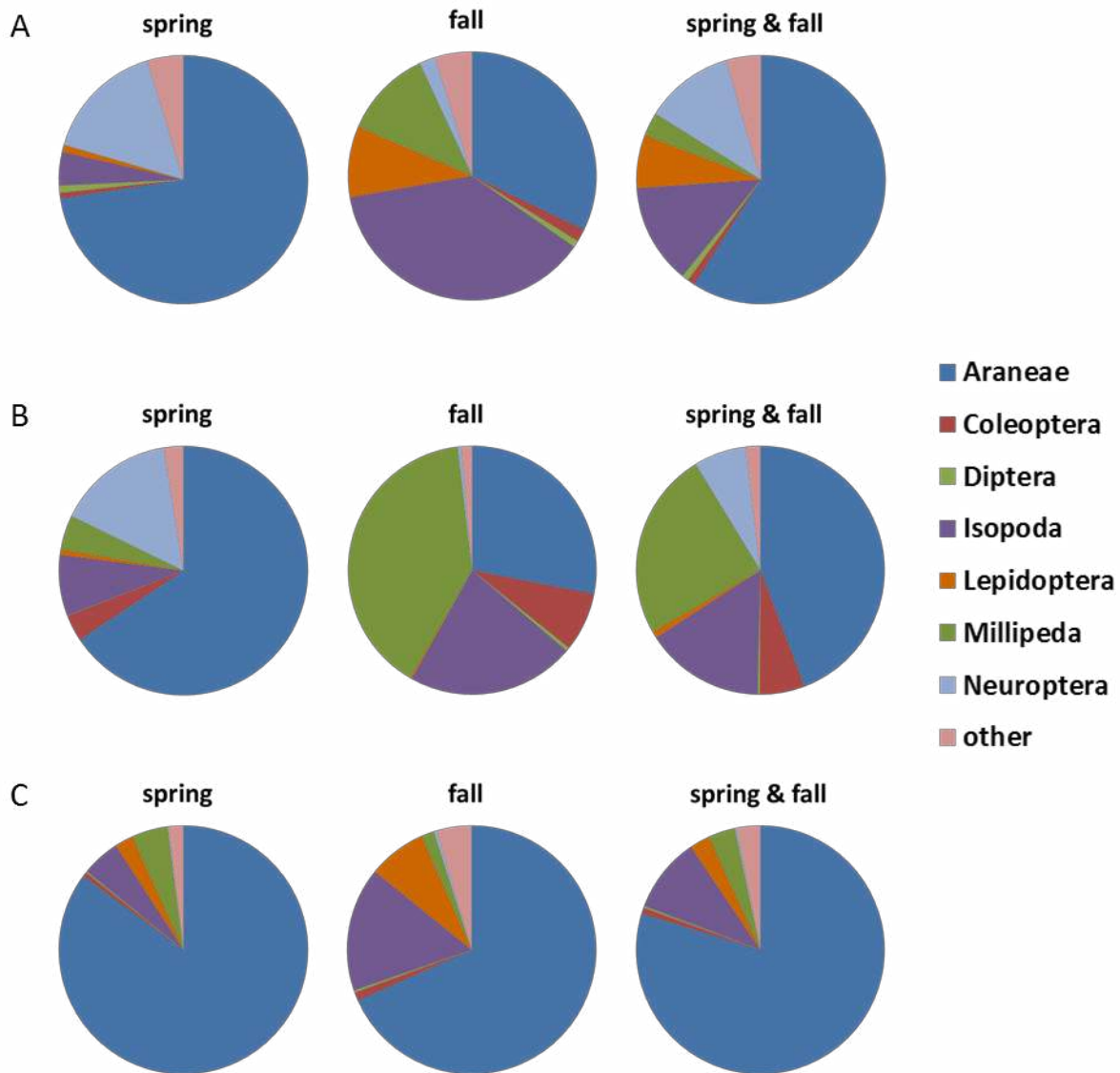
Figure 13. Relative abundance of arthropod groups collected in bark traps on ʻōhiʻa at Hanawi (A), Waikamoi (B), and Nakula (C) during spring, fall, and spring and fall combined. Common names for arthropod groups can be found in Tables 1 and 2.

A seasonal difference in total arthropod biomass was found on koa bark at Nakula (P = 0.002), where biomass was three times greater during spring than fall. This difference was primarily influenced by spiders, which showed the same temporal pattern (P = 0.001). At Waikamoi, no seasonal difference was found for total arthropod biomass although millipede biomass was greater during fall (P < 0.001) while lacewing biomass was greater during spring (P < 0.001). On ʻōhiʻa, a seasonal difference in total biomass was found only at Hanawi (P = 0.001), where biomass during spring was greater than fall. At Waikamoi, fly biomass was greater during fall than spring (P < 0.001) while the biomass of lacewings was greater during spring than fall (P < 0.001). The difference for spider biomass was marginally non-significant (P = 0.009; spring > fall). At Hanawi, total arthropod biomass and the biomass of lacewings were greater during

spring than fall ($P = 0.001$ and $P < 0.001$, respectively). Spider biomass was marginally greater during spring than fall ($P = 0.007$). No seasonal difference was found for any taxon at Nakula ($P > 0.065$ for all taxa).

Total arthropod biomass on koa bark was significantly greater at Waikamoi than at Nakula during fall and during spring and fall combined; the difference was marginally non-significant during spring ($P = 0.008$; Figure 14). On 'ōhi'a bark, total arthropod biomass differed significantly among sites during spring and during spring and fall combined, with the biomass at Waikamoi being greater than both Hanawi and Nakula in each instance.
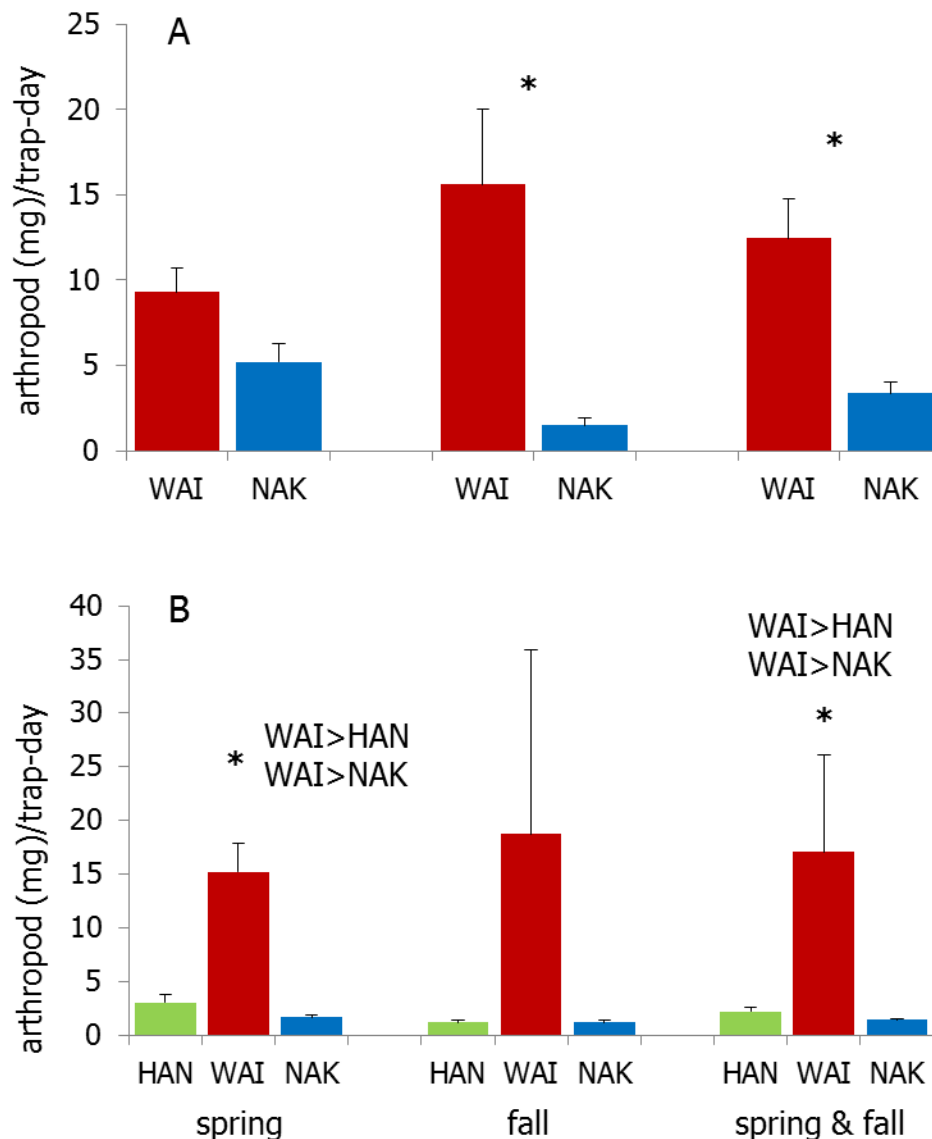

Figure 14. Total biomass of arthropods/trap-day (mean ± SEM) collected in bark traps on koa (A) and 'ōhi'a (B) at Hanawi (HAN), Waikamoi (WAI), and Nakula (NAK) during spring, fall, and spring and fall combined. Overall significant differences between sites are indicated by an asterisk. For 'ōhi'a, specific between-site differences are shown above the bars.

24

On koa bark, we found the biomass of numerous arthropod taxa to be significantly greater at Waikamoi compared to Nakula during each sample period (Figure 15). Beetle and lacewing biomass was greater during spring, fall, and spring and fall combined, while the biomass of spiders, flies, millipedes and other arthropods was greater during fall and during spring and fall combined. Caterpillar and moth biomass was greater at Waikamoi than Nakula during spring and during spring and fall combined. In no instance was the biomass of bark arthropods greater at Nakula than it was at Waikamoi.

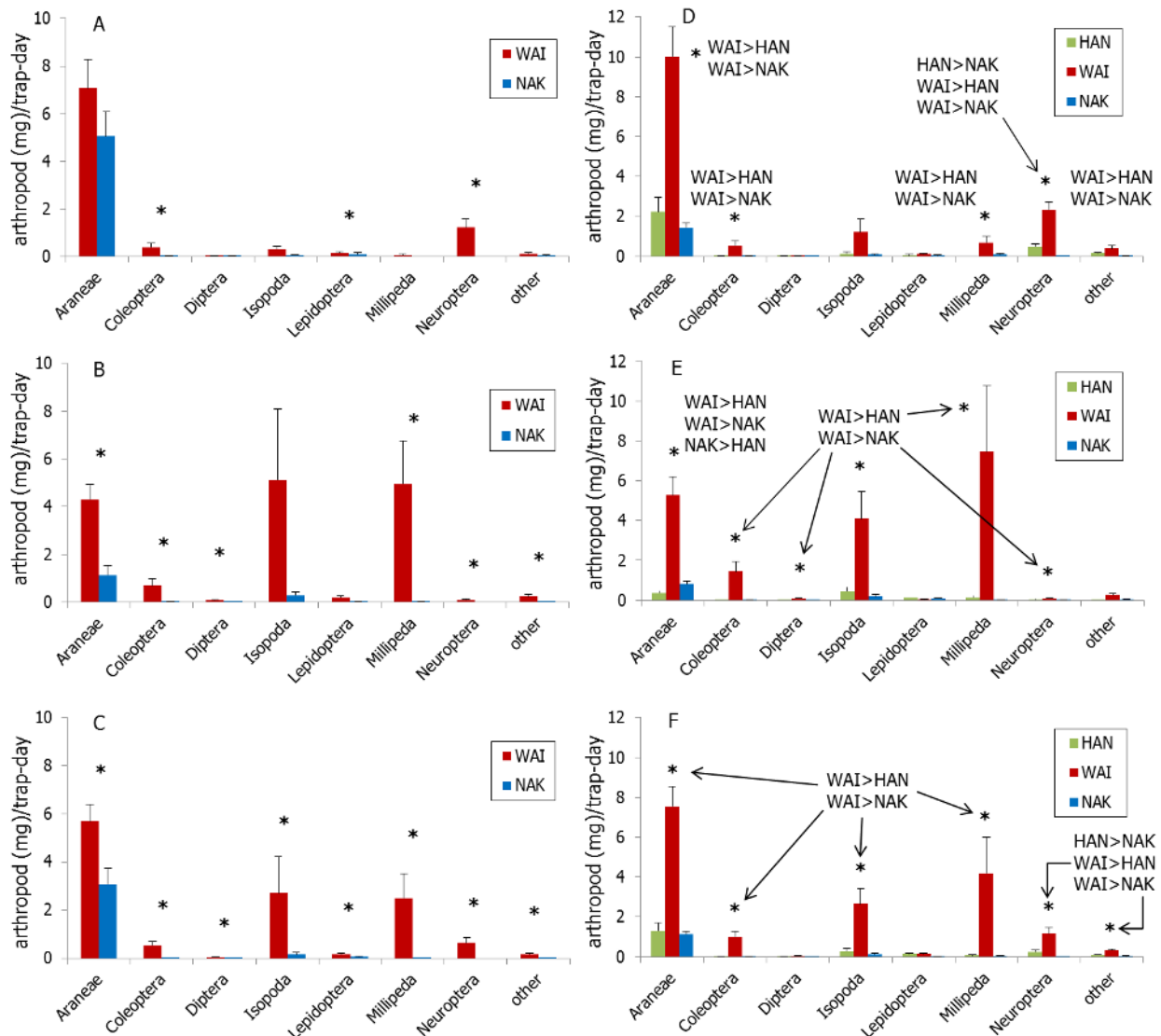Figure 15. Mean (± SEM) arthropod biomass from bark traps on koa during spring (A), fall (B), and spring and fall combined (C), and ʻōhiʻa during spring (D), fall (E), and spring and fall combined (F). Significant differences between sites are indicated by an asterisk. For ʻōhiʻa, specific between-site differences are shown above the bars. Common names for arthropod groups can be found in Table 1.

The pattern of arthropod biomass on ʻōhiʻa bark was similar to that found on koa with Waikamoi supporting greater biomass compared to the other sites for most taxa (Figure 15). Arthropod biomass at Hanawi was greater than it was at Nakula for other taxa during spring and lacewing biomass during spring and during spring and fall combined. Only for spider biomass collected during fall was Nakula greater than Hanawi.

Beetle activity in dead koa branches

The amount of bark surface examined for exit holes on dead koa branches (cm^2) was similar at Waikamoi and Nakula, indicating equal effort between sites (2.00 ± 0.23 m^2 and 2.56 ± 0.45 m^2, respectively; t-test, t = 1.01, P = 0.33).

Overall, there was a significant positive relationship between exit hole diameter and the diameter of the branch at each exit hole (y = 6.0283x + 21.771, R^2 = 0.1794; n = 503, F = 109.54, P < 0.001), but no difference existed in mean branch diameter at exit holes between sites (38.00 ± 2.08 mm and 38.28 ± 4.29 mm, respectively; t-test, t = 0.06, P = 0.95).

There was a large proportion of small exit holes (< 2 mm diameter) at Waikamoi compared to Nakula (121 of 286 or 42% vs. 14 of 351 or 4%, respectively; Figure 16). Because these exit holes likely represented small ambrosia beetles (Scolytidae; exit holes < 1.5 mm) that live deep within the branch (Hara and Beardsley 1979) and are probably not part of the kiwikiu's diet, they were excluded from further analysis. Subsequently, the mean density of exit holes > 2 mm diameter did not differ between Waikamoi and Nakula (5.96 ± 1.27 and 8.51 ± 1.27, respectively; t-test, t = 1.48, P = 0.15; Figure 17).
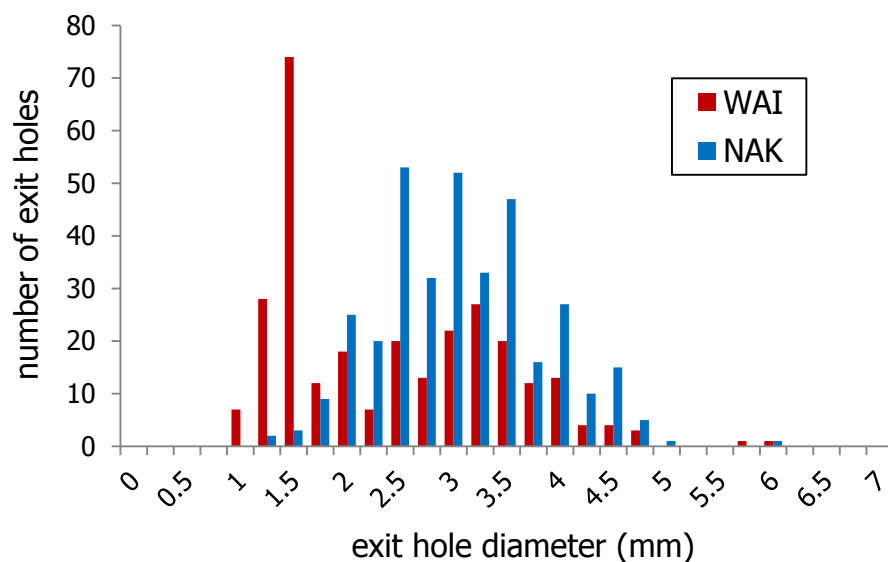

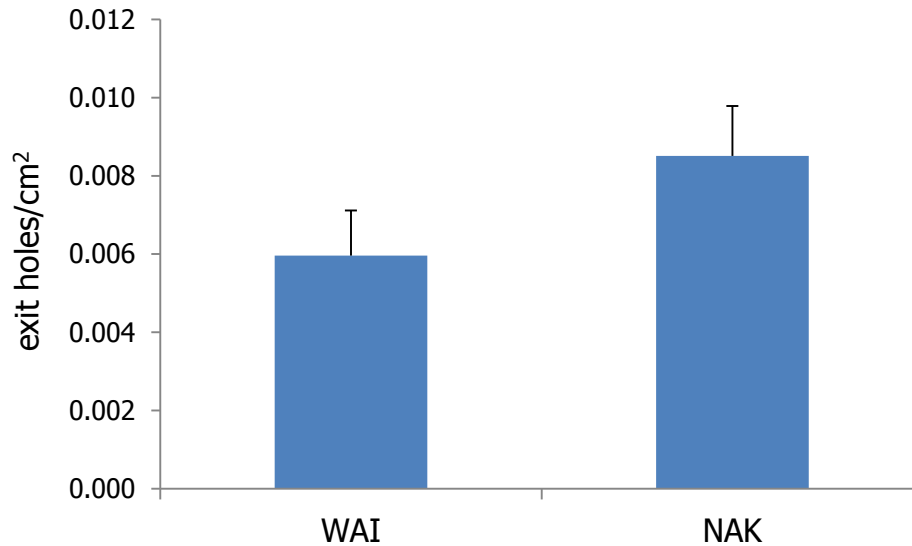Figure 16. Distribution of beetle exit hole diameters on the surface of dead koa branches at Waikamoi and Nakula.

Figure 17. Mean (± SEM) density of beetle exit holes > 2 mm diameter on the surface of dead koa branches at Waikamoi and Nakula.

Arthropods in ʻākala stems

The mean volume of ʻākala stems varied significantly among sites with Hanawi ($n = 8$; 743.5 ± 83.5) being significantly greater than Waikamoi ($n = 11$; 407.1 ± 41.4) and Nakula ($n = 7$; 232.8 ± 50.7) (Kruskal-Wallis Test, K-W test stat = 15.3, $P = 0.001$; $P < 0.02$ for all comparisons).

Overall, caterpillars and moth pupae were the dominant arthropod taxa identified in dead ʻākala stems at each site, comprising 87% of the fauna at Hanawi, 68% at Waikamoi and 100% at Nakula (Figure 18). Beetles (adults and larvae) were next in abundance, making up 9.1% of all arthropods at Hanawi (3.0% larvae and 6.1% adults) and 19% at Waikamoi (all adults); no beetles were found at Nakula. At Waikamoi, the remaining 14% of the fauna consisted of isopods (10.4%), millipedes (2.3%) and centipedes (1.1%). Adult beetles were primarily comprised of weevils (Curculionoidea; 27 of 30 individuals).

The density (number/cm^3) of all arthropods in ʻākala stems ranged from 0.006 (± 0.004) at Nakula to 0.012 (± 0.004) at Hanawi, but no difference was detected among sites ($P = 0.274$; Figure 19). Similarly, no difference was found in caterpillar and moth density among sites ($P = 0.331$; Figure 19). Arthropod abundance in stems was as high as 42 caterpillars and moth pupae in a single stem (0.0386 individuals/cm^3); the stem with the second most caterpillars and moth pupae contained 12 (0.018 individuals/cm^3). The mean diameter of all exit holes on ʻākala stems at all sites was 2.06 (± 0.18) with no difference detected among sites ($P = 0.863$; Figure 20).

27
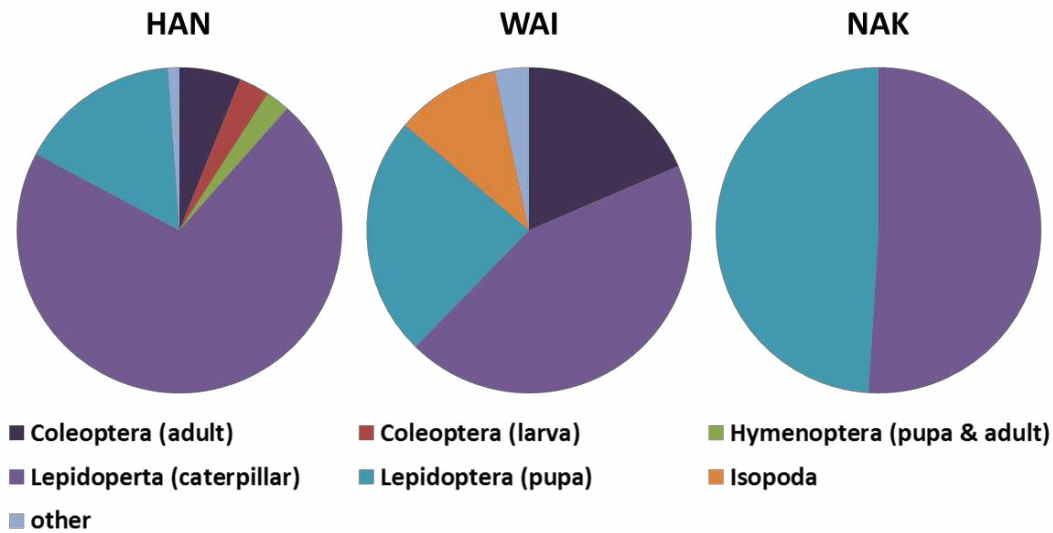
Figure 18. Relative abundance (number/cm^3 stem) of arthropod groups within dead 'ākala stems at Hanawi, Waikamoi, and Nakula. Proportions are based on mean values for multiple patches at each site. The "other" category contained millipedes and centipedes. Common names for arthropod groups can be found in Tables 1 and 2.
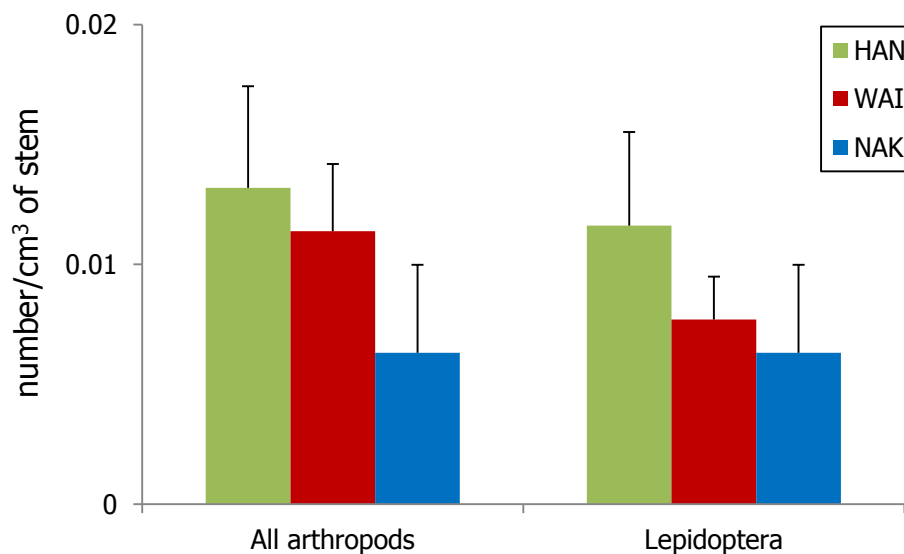
Figure 19. Mean (± SEM) density of all arthropods and Lepidoptera (caterpillars and moth pupae combined) in 'ākala stems at Hanawi, Waikamoi, and Nakula. No significant differences were found among sites for either group.

Figure 20. Distribution of exit hole diameters in ʻākala stems at Hanawi, Waikamoi and Nakula.

DISCUSSION

Diets of kiwikiu and Maui ʻalauahio

Caterpillars were the dominant prey of Maui ʻalauahio, and they were nearly the exclusive prey of kiwikiu, comprising 91% of the arthropods in adult fecal samples and 98% in nestling samples. Maui ʻalauahio displayed a more varied diet, which in addition to caterpillars (43% of the diet), also included significant numbers of spiders (16%) and adult and larval beetles (12%). In 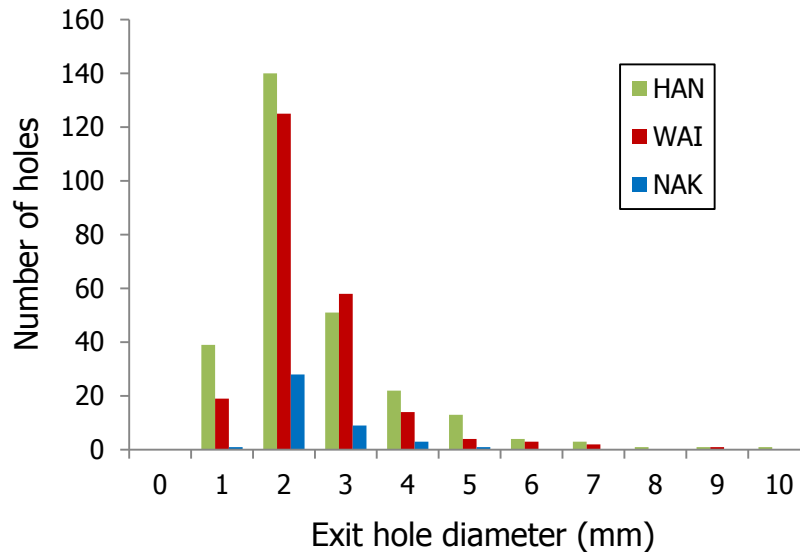general, the dominance of caterpillars in the diets of kiwikiu and Maui ʻalauahio is consistent with that found for other Hawaiian forest birds (Baldwin 1953, P. Banko and W. Banko 2009, USGS unpublished data). For example, at Hakalau Forest NWR, the prey base of all five native insectivorous bird species consisted of > 40% caterpillars (USGS unpublished data). Even birds that are not primarily insectivorous depend on caterpillars as a source of protein for themselves and their young (Perkins 1903, Baldwin 1953). "As key foods for nestlings, caterpillars may have facilitated the evolution of extreme feeding specialization among the Hawaiian honeycreepers (P. Banko and W. Banko 2009), and threats to caterpillars likely contributed to the historical decline of specialists and even some generalist bird populations (W. Banko and P. Banko 2009)."

In mesic, koa-dominated forests of the northwestern flank of Haleakalā, Perkins (1903) observed that the larvae, pupae, and teneral adults of cerambycid beetles (*Plagithmysus* [= *Clytarlus*]) living in wood were the preferred prey of kiwikiu. Koa is host to several species of cerambycid beetles (Swezey 1954, Gressitt and Davis 1969), which can be abundant in dead and dying branches (Goldsmith *et al.* 2007). Goldsmith (2007) found the density of cerambycid larvae, pupae, and adults to average 3.5 individuals per branch in small trees (6–8 m tall) supporting branches with a mean basal diameter of 25.1 ± 4.7 mm at about 1,650 m elevation at Hakalau. Intuitively, larger branches, such as those found on mature trees at Nakula, would be expected to have greater numbers of beetles. Although cerambycids were not identified in female kiwikiu fecal samples (*n* = 21) from either site, they comprised 16.7% of the remains

found in male samples (*n* = 15) at Waikamoi, where koa was common. At Hanawi, where koa is absent, the incidence of cerambycids in male samples (*n* = 3) was only 2.4%. In addition to beetles, however, Perkins (1903) recognized that looper caterpillars (most likely *Scotorythra* spp.) made up a significant proportion of the diet of young birds. Several species of *Scotorythra* caterpillars occur on koa (Swezey 1954) and can be very abundant during summer months (USGS unpublished data) when young kiwikiu are dependent upon their parents for food (Simon *et al.* 2000, Becker *et al.* 2010) and during rare population irruptions (Haines *et al.* 2009, Banko *et al.* 2014).

The number of fecal samples for each species supported a robust evaluation of diet richness and diversity because these primarily insectivorous species apparently consume many arthropod prey throughout the day. Nevertheless, we did not attempt to characterize differences between sexes, post-fledging age classes, study sites, seasons, or years, all of which would require more samples. The diet of the Maui ʻalauahio was richer and more diverse than the diet of the kiwikiu, as expected from differences in foraging behavior (Simon *et al.* 1997, Baker and Baker 2000) and beak morphology (P. Banko and W. Banko 2009). Caterpillars were the most common prey, but spiders, psyllids and planthoppers (primary Delphacidae) also were frequently consumed. All these taxa are often found in foliage, a primary foraging substrate used by Maui ʻalauahio (Baker and Baker 2000).

Diets of Hawaiian forest birds can be expected to track temporal and spatial fluctuations in arthropod prey. The abundance of some arthropods in tree foliage, such spiders on ʻōhiʻa (Fretz 2002) and psyllids on koa (Leeper and Beardsley 1973, Bridges *et al.* 1981), vary over the course of the year, but community-wide changes in arthropod prey availability, and how this is reflected in the diets of birds, is poorly known. Because most of the fecal samples from kiwikiu and Maui ʻalauahio analyzed in this study were collected during November–March, overall views of diets may be biased towards prey available at that time. However, our results indicate little change in overall diet composition throughout the study as caterpillars were dominant in all months except August for kiwikiu and May for Maui ʻalauahio; however, the number of samples was low during that time so deviations from the general pattern of caterpillar consumption should be viewed with caution. For Maui ʻalauahio, the abundances of adult beetles, hemipterans, and other arthropods were proportionally higher during May than during the rest of the year.

Arthropod food resources

Arthropods in foliage of koa and ʻōhiʻa

In general, the abundance of arthropods in the foliage of koa and ʻōhiʻa at Nakula was similar to that found at Waikamoi and Hanawi, suggesting a prey base that could be capable of supporting both bird species. In koa, the biomass of only the relatively minor dietary taxa, Homoptera and Psocoptera, was lower at Nakula than at Waikamoi. The overall pattern of arthropod biomass on ʻōhiʻa was similar to koa, except that caterpillar biomass was lower during fall at both Nakula and Hanawi compared to Waikamoi; no other taxon at Nakula was ever lower than at Waikamoi or Hanawi. Although hatch-year kiwikiu are still largely dependent on their parents for food during fall (Sept–Nov; Simon *et al.* 2000) lower caterpillar abundance during this time could result in greater energy expenditure to capture prey or a shift in prey preference.

Surprisingly, total arthropod biomass in ʻōhiʻa foliage was significantly lower at Hanawi during the fall and during the spring and fall combined compared to Waikamoi and Nakula. During both the spring and fall, arthropod biomass at Hanawi was 41% and 34% lower than at Waikamoi and Nakula, respectively. This difference was primarily driven by spiders, which on average comprised about 44% of overall arthropod biomass at Hanawi. Correspondingly, the proportion of spiders in the diet of Maui ʻalauahio was at its lowest point during September (5%), although it increased to 15% by November. Few spiders were detected in the diet of kiwikiu, which may be little affected by changes in spider abundance. It is unclear why spider biomass was lower at Hanawi compared to the other sites, but finer taxonomic resolution of the spider guild may help clarify this pattern.

The majority of the caterpillars collected in koa foliage were species of *Scotorythra*, generally the most common caterpillar genus found on koa. *Scotorythra* feed exposed on the faces and margins of phyllodes, and to a lesser extent true leaves, and are important prey for many Hawaiian forest birds (USGS unpublished data). *Scotorythra* were recognized by Perkins (1903) to be an important component of the diet of young kiwikiu. *Scotorythra* is one of the most diverse genera of Hawaiian macrolepidoptera with 43 species described, and their larvae are known to feed on at least 30 species of host plants (Heddle 2003). In addition to koa, at least 10 plant species known to host *Scotorythra* are found at Nakula suggesting a relatively rich host plant community at that site. *Scotorythra* populations can fluctuate considerably over time, as witnessed by *S. paludicola* which occasionally irrupts to levels capable of defoliating vast tracks of koa (Perkins 1913, Swezey 1926, Haines *et al.* 2009, Banko *et al.* 2014), resulting in a short-term plethora of food for birds. *Scotorythra* are generally less abundant on ʻōhiʻa, where species of *Carposina* (*Carposinidae*), *Hyposmocoma* (Cosmopterigidae) and *Thyrocopa* (Oecophoridae) are the most abundant (Swezey 1954). While the biomass of caterpillars was similar between ʻōhiʻa and koa (0.047 and 0.042 g caterpillar/g foliage, respectively, for all sites combined), most caterpillars found on ʻōhiʻa are somewhat concealed in the foliage, potentially making them difficult for kiwikiu to find. For example, *Thyrocopa* caterpillars often use silk to "tie" leaves together creating a protective envelope in which they feed, and *Hyposmocoma* caterpillars encase their bodies with various organic and inorganic particles for protection. Illustrating the challenge but also the benefits of obtaining concealed prey, slightly crossed bills have evolved in the ʻakepa (*Loxops coccineus*) and ʻakekeʻe (*L. caeruleirostris*) to extricate *Carposina* caterpillars concealed within developing ʻōhiʻa leaf buds (Lepson and Freed 1997, Lepson and Pratt 1997).

Arthropods captured via leaf gleaning comprised about 10% of all prey captures by kiwikiu at Hanawi (Mountainspring 1987). Although a relatively minor behavior for adult kiwikiu, foliage gleaning may be more important for young birds learning to feed on their own while transitioning to more complex adult foraging behaviors such as lifting epiphytes, probing wood and fruit, and splitting stems and wood (Simon *et al.* 1997, 2000). In contrast, about one-half (49%) of all foraging maneuvers of adult Maui ʻalauahio at Waikamoi consisted of gleaning, with 70% occurring on ʻōhiʻa foliage (Baker and Baker 2000). Gleaning over the foliage of koa and ʻōhiʻa, which are the dominant plant species at Nakula, may be particularly important for reintroduced Maui ʻalauahio.

Arthropods from bark of koa and ʻōhiʻa

Waikamoi supported a greater biomass of arthropods on bark than both Hanawi and Nakula. On koa bark, the biomass of all arthropods as well as all eight individual taxa analyzed, was

significantly greater at Waikamoi than at Nakula. The same pattern was found for six individual taxa on ʻōhiʻa bark. Significantly, however, few differences were found between Nakula and Hanawi in arthropod biomass on ʻōhiʻa bark; only lacewing biomass was greater at Hanawi during the spring and for the spring and fall combined.

Spiders were abundant on koa and ʻōhiʻa bark at all three sites, although isopods, millipedes, and lacewings were also common at Waikamoi and Hanawi. While the latter three groups are ecologically important, only small numbers of lacewings were found in Maui ʻalauahio fecal samples. In general, isopods and millipedes are rarely consumed by Hawaiian forest birds (USGS unpublished data), although Perkins (1903), referring generally to "*Oreomyzae*" (including Maui ʻalauahio), indicated that millipedes (= myriopods) were sometimes eaten. In contrast, lacewings, particularly the larval stage, are commonly consumed by Hawaiian forest birds (Baldwin 1953, USGS unpublished data). However, most of the lacewings collected in bark traps were adults, and it is unclear on which substrate lacewing larvae were most abundant.

Overall, caterpillars were uncommon on koa bark, suggesting that this is a relatively poor substrate for birds seeking this prey group. This was surprising because caterpillars of *Scotorythra* and other moths sometimes seek refuge from predators in well-developed bark crevices located on tree trunks (Moeed and Meads 1983, Majer et al. 2003, U.S. Geological Survey unpublished data). In contrast, caterpillars in ʻōhiʻa foliage that utilize concealment to avoid predation likely move little distance, making them less likely to be collected in traps placed on tree trunks. Despite generally low numbers in traps, caterpillars at Hanawi and Nakula were relatively more abundant in ʻōhiʻa during fall than spring.

Beetle activity in dead koa branches

Our data suggest that Nakula and Waikamoi support similar densities of wood-boring beetles in koa branches. Although we did not detect many beetle larvae in the diet of kiwikiu collected at Waikamoi (none from two females and about 17% from three males), beetle larvae, particularly cerambycids, are considered key prey for kiwikiu in habitat dominated by koa (Perkins 1903). Because koa is co-dominant with ʻōhiʻa at Nakula, beetle larvae in dying and dead koa branches would likely be an important food resource for reintroduced kiwikiu. A lack of discrete exit hole size classes prevented us from determining the specific types of beetles present in koa branches, but as many as six species of cerambycids, as well as several other wood- and bark-inhabiting species may have been present at each site (Swezey 1953, Gressitt 1978). Rearing of larvae collected from branches within earlier stages of decomposition would allow identification of the beetles present.

Arthropods in ʻākala stems

Dead ʻākala stems supported an abundant and diverse community of arthropods, with caterpillars and moth pupae being particularly common. Although there was no significant difference in the mean density of arthropods among sites, arthropod density was twice as great at Hanawi compared to Nakula, suggesting that additional sampling may yield significant differences among sites. Regardless, ʻākala at Nakula supported caterpillars, despite the small number of patches present (n = 7). Because the remaining patches of ʻākala at Nakula were restricted to the steep walls of gulches that were inaccessible to ungulates, we expect that ʻākala will be able to increase throughout the area after animals have been removed.

ʻĀkala is an important foraging substrate for kiwikiu. At Manawainui, on the eastern edge of kiwikiu's range, kiwikiu foraged on ʻākala and koa with similar intensity, despite ʻākala being a relatively rare component of the understory (Stein 2007). Surprisingly, Mountainspring (1987) rarely observed kiwikiu capturing prey from ʻākala at Hanawi. Simon *et al.* (1997) reported kiwikiu to primarily use ʻākala during fall and winter months when stems did not have leaves, but Stein (2007) found ʻākala to be utilized during all times of the year. We found caterpillars feeding in green ʻākala stems at Hanawi, although the extent to which this occurred was not quantified.

While caterpillars and moth pupae dominated the ʻākala arthropod community at all sites, adult weevils (primarily *Proterhinus* sp. [Aglycyderidae] and *Oodemas* sp. [Curculionidae]) were also present at Waikamoi and Hanawi. No weevils were found at Nakula during the spring, but a small pilot study during May 2011 revealed 10 weevils in one dead stem, indicating that they are present in the environment. It is possible that the timing of our collection at Nakula missed the time during which weevils were present in stems. The larvae of *Plagithmysus* beetles (Cerambycidae) also feed in ʻākala stems but were rarely collected; the few large exit holes found on stems at Hanawi and Waikamoi may have been created by these insects.

Conclusion

Our results indicate that caterpillars are the most important foods of kiwikiu and Maui ʻalauahio throughout the year. In general, the abundance of caterpillars and other frequent arthropod prey did not differ significantly between Hanawi and Waikamoi, the two sites in the current range of the birds, and Nakula, the site where these birds are targeted for reintroduction. In particular, caterpillars were at least as abundant across most substrates at Nakula as they were in Hanawi and Waikamoi. Only on the bark of koa were caterpillars significantly less abundant at Nakula than at Waikamoi. Despite generally similar prey abundances across sites, our results should be interpreted cautiously, with several points bearing consideration.

Our assessment of arthropod abundance is based on individual stems, branches, or trees, and does not represent arthropod abundance across the landscape. To make a more thorough comparison among the three sites, estimates of the density of each substrate should be made. In a comparison of prey densities between two study areas, Fretz (2002) found no statistical difference in arthropod biomass at the level of the individual branch, but when the results were scaled up to account for foliage density of trees and the density of trees within sites, arthropod abundances became significantly different between sites. This exemplifies how measurement scales can affect how arthropod resources are interpreted. For Nakula, the logical next step toward assessing the overall arthropod resource base is to extrapolate our findings to the landscape level by estimating the amount of each foraging substrate available at each site.

The diversity of foraging substrates at Nakula is lower compared to Hanawi and Waikamoi. Mountainspring (1987) observed kiwikiu capturing arthropod prey from 15 plant species on windward Haleakalā (80% of all observations were made at Hanawi), six of which are not found at Nakula. Plants used by kiwikiu that are absent from Nakula include pilo, kanawao, ʻoheʻohe (*Tetraplasandra kavaiensis*), hoʻawa (*Pittosporum confertiflorum*), naenae (*Dubautia* sp.), and manono (*Kadua affinis*). Of these, ʻōhelo, pilo and kanawao were most important at windward sites, comprising 35% of all prey captures. Of the seven foraging plants present at Nakula, koa, ʻōhiʻa, and pūkiawe are common while ʻōlapa, alani, kōlea, and ʻākala are primarily restricted to gulches and are uncommon or rare. Although pūkiawe is relatively common at Nakula, only a single arthropod prey item was captured at windward sites on this plant species

(Mountainspring 1987), suggesting it is relatively unimportant as a foraging substrate. It is unclear whether these "missing elements" were ever widespread at Nakula, but the dominance of only two foraging substrates, ʻōhiʻa and koa, underscores the need to restore a diverse plant community in order to sustain a robust population of kiwikiu.

Presumably, windward sites on Haleakalā represent more suitable habitat for kiwikiu than Nakula due to the greater diversity and abundance of foraging substrates. However, kiwikiu likely possess considerable plasticity in their foraging behavior and ability to procure food on different substrates. The range of habitats occupied by kiwikiu was once much greater than today, and included dry coastal and lowland habitats on Maui and Molokaʻi (Olson and James 1982). Considering the large variety of foraging substrates and prey available to kiwikiu across their former range kiwikiu may respond adaptively to varying food availability as long as minimum abundance thresholds are met. Although the arthropod prey base at Nakula is mostly supported by koa and ʻōhiʻa, the removal of ungulates will promote the recovery of other important foraging plants such as ʻākala.

Access by birds to diverse foraging substrates is important also if the reduced caterpillar abundance during fall that we observed at Nakula and Hanawi represents the longer-term trend. If so, kiwikiu at Hanawi might compensate for lower caterpillar availability by switching to other substrates. Some birds shift their use of foraging substrates and prey choice when primary foods becomes limited (Holmes and Schultz 1988). Although kiwikiu are territorial and do not track food resources outside their home range (Pratt *et al.* 2001), they also likely shift foraging substrates as arthropod prey abundances change over time. For example, ʻākala stems begin dying back during fall (Berlin *et al.* 2000) and are likely beginning to host caterpillars, beetles and other arthropods that kiwikiu consume. In addition, *Carposina* caterpillars within the fruit of kanawao are becoming increasingly available in the fall (Berlin *et al.* 2000) and are utilized by kiwikiu (Figure 21; Mountainspring 1987). We did not assess the abundance of caterpillars within kanawao because that plant species was not found at Nakula. The absence of kanawao and low abundance of ʻākala at Nakula could provide seasonal challenges to foraging for kiwikiu until the understory plant community is restored.

Arthropod abundance alone does not explain abundances of Hawaiian forest birds, even in areas where disease is not considered a limiting factor. For example, we found arthropod biomass to be significantly greater in ʻōhiʻa foliage and on ʻōhiʻa bark at Waikamoi compared to Hanawi, yet the highest densities of kiwikiu and other forest birds are found at Hanawi (Camp *et al.* 2009). Rather than overall abundance, it is likely that a minimum arthropod threshold interacts with other factors to sustain bird populations. Due to seasonal changes in prey availability, this minimum must be sustained over the course of the year.

Despite the challenges and uncertainty involved in reestablishing kiwikiu at Nakula, this area is important, particularly in the face of climate change, as warmer temperatures are likely to increase the elevation at which disease-carrying mosquitoes are expected to be found, reducing the extent of high-elevation habitat refugia free of mosquitoes (Benning *et al.* 2002, Atkinson and LaPointe 2009). As habitat conditions in windward montane forests change, restoring bird populations in leeward forests such as Nakula may be critically important in preventing additional extinctions of Hawaiian forest birds.

Figure 21. Ripe kanawao (*Broussaisia arguta*) berries showing feeding damage caused by kiwikiu. Caterpillars (*Carposina* sp.) that develop in the berries are likely the prey being targeted.

Acknowledgements

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