Technical Report HCSU-066

RICHNESS, DIVERSITY, AND SIMILARITY OF ARTHROPOD PREY CONSUMED BY A COMMUNITY OF HAWAIIAN FOREST BIRDS

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July 2015

This product was prepared under Cooperative Agreement G09AC00042 for the
Pacific Island Ecosystems Research Center of the U.S. Geological Survey.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

We evaluated the diet richness, diversity, and similarity of a community of seven endemic and two introduced passerine birds by analyzing the composition of arthropod prey in fecal samples collected during 1994–1998 at Hakalau Forest National Wildlife Refuge, Hawai'i Island. Most prey fragments were identified to order, but we also distinguished among morpho-species of Lepidoptera based on the shape of larval (caterpillar) mandibles for higher resolution of this important prey type. Diets were compared among feeding specialists, generalists, and "intermediate" species and among introduced and three endangered Hawaiian honeycreeper (Fringillidae) species. Lepidoptera (moths), especially the larval (caterpillar) stage, comprised the greatest proportion of prey in samples of all bird species except for the introduced Japanese white-eye (*Zosterops japonicus*; JAWE). Araneae (spiders) was the most abundant order in JAWE samples and the second most abundant order for most other species. The two specialist honeycreepers ranked lowest in the richness and diversity of arthropod orders, but only the 'akiapōlā'au (*Hemignathus munroi,* AKIP) was significantly lower than the three generalist or intermediate honeycreeper species. The diversity of arthropod orders was significantly lower for the three endangered honeycreeper species compared to the two introduced species. No significant differences were observed among the five honeycreepers with respect to the arthropod orders they consumed. The use of arthropod orders taken by endangered honeycreepers and introduced species was significantly different in all paired comparisons except for JAWE and 'ākepa (*Loxops coccineus*; AKEP). In terms of richness and diversity of caterpillar morpho-species in the diet, only the specialist, AKEP, was significantly lower than all three generalist and intermediate species. Both AKEP and AKIP consumed a significantly different diet of caterpillar morpho-species compared to at least one honeycreeper generalist or intermediate species. Among the endangered honeycreepers and introduced species, the richness and diversity of caterpillar morpho-species was significantly lower only for AKEP compared to both introduced species. Significant differences were not observed between endangered and introduced species in the distribution of caterpillar morpho-species in the diet. Only three morpho-species were heavily exploited, with one being consumed by all bird species. The heavy exploitation of very few morpho-species by specialists underscored their greater vulnerability to changes in forest food webs and threats to key arthropod prey. When evaluated together with data on overlap in foraging behavior, our results could be useful in evaluating competition between bird species at Hakalau. Nevertheless, invasive parasitoid wasps may impact key caterpillar prey more substantially than do introduced birds, highlighting the need for additional research to understand the ecology of caterpillar species and their interactions with both invertebrate and vertebrate consumers. The severe decline of specialist bird species historically and recently is a reminder of the importance of maintaining food web resilience, potentially through vigorous habitat restoration, to withstand the continuing and perhaps increasing threats from a diverse array of invasive species and climate change.

INTRODUCTION

Food availability and the variety of foraging strategies used by consumers to obtain resources are critical in shaping species adaptations and community structure. Not surprisingly, disruptions in food webs due to invasive species or changes in environmental conditions can lead to population decline and extinction, which may profoundly transform communities. This process contributed to the collapse of Hawai'i's once-rich native bird communities (W. Banko and P. Banko 2009). Nevertheless, remnants of communities dominated by native Hawaiian species persist in a few forests, allowing a glimpse into the feeding ecology of bird assemblages that were once far richer and complex. Understanding the diets and feeding niches of whole bird communities is relevant to conservation because trophic interactions, which are critical to species co-existence, can be complicated and easily disrupted by a variety of biotic and environmental factors.

The striking diversity of beak forms of the Hawaiian honeycreepers (formerly Drepanidinae but now further submerged within Frigillidae) illustrates the critical role of food and foraging in the ecology and evolution of Hawaiian passerines (Passeriformes; "perching birds," "songbirds," or often referred to herein as "forest birds;" P. Banko and W. Banko 2009). Unusual and even sometimes extraordinary beak adaptations evolved for exploiting nectar, fruit, seeds, and arthropods (Pratt 2005), but few of the most spectacular examples have survived to the present. Birds with highly divergent bill types and specialized feeding behavior were especially vulnerable to extinction after the arrival of humans (Pratt 2005), and specialists suffered faster rates of decline and a higher rate of extinction than did generalists (W. Banko and P. Banko 2009). Preserving the remaining species requires a detailed understanding of their contemporary feeding ecology because much of our knowledge comes from a time when many more bird species existed, populations were larger and more widely distributed, habitats were less fragmented, and resources were more abundant (Perkins 1903, 1913; Henshaw 1902, Munro 1944). Since the time of the early Hawaiian naturalists, habitat degradation by ungulates, rodents, and weeds has continued (Cuddihy and Stone 1990, Pratt and Jacobi 2009). Furthermore, food webs have been disrupted by a variety of invasive insects, including parasitoid wasps, some of which were introduced long ago to control agricultural pests (Perkins 1913; Swezey 1954, Zimmerman 1958, Howarth 1991, Henneman and Memmott 2001, P. Banko and W. Banko 2009). Climate change also is beginning to disturb habitat and food web stability, at least in the higher elevations of Hawai'i (Pratt *et al.* 2009, Banko *et al.* 2013, Atkinson *et al.* 2013).

Knowledge of the feeding ecology, including foraging behavior and diet, of Hawaiian forest birds is incomplete and seldom based on quantitative or systematic data. Although foraging behavior can be observed directly and in some detail (Ralph and Noon 1988, Ralph and Fancy 1996), understanding diet composition depends on examining stomach contents or fecal samples (Baldwin 1953, Ralph *et al.* 1985), which requires a substantial investment of time and expertise in identifying food items. Despite the wide array of foods eaten by Hawaiian forest birds, arthropods are critical in providing protein and other nutrients for breeding and feeding offspring (Perkins 1903). Because of their fundamental importance in bird diets, we examined the distribution of insects, spiders, and other arthropod prey among consumers. Our first objective was to quantify the consumption of arthropod prey by a diverse passerine community comprised of feeding specialists and generalists (*sensu* P. Banko and W. Banko 2009). In particular, we sought to identify arthropods that might stand out as key prey for consumers. Because we expected specialists to forage on fewer types of arthropods compared to generalists (Morse 1971, Schoener 1971), a second objective was to evaluate differences in diet richness and diversity within an entire community of birds to evaluate how specialized beaks and behaviors might constrain prey selection. Finally, we wanted to compare the similarity of diets of endangered and introduced species to identify potential competition and the vulnerabilities of diets and food webs to impacts from invasive species and other threats. Based on foraging behavior (Ralph and Noon 1988) and population distribution patterns (Mountainspring and Scott 1985), competition with the introduced Japanese white-eye (*Zosterops japonicus*; JAWE) may impact native bird populations. Based largely on demographic studies, competition with JAWE is asserted to be an important factor contributing to the decline of native bird populations (Freed and Cann 2009; 2010; 2012a, b; 2013a, b; 2014; Freed *et al.* 2008, 2009). Assessing competition is beyond the scope of our study, but knowledge of bird diets is an important step in evaluating the potential strength of competitive interactions.

METHODS

Study Area

The study took place on the Hakalau Forest Unit of Hakalau Forest National Wildlife Refuge (hereafter Hakalau; 19° 51′ N, 155° 18′ W), located on the windward slope of Mauna Kea Volcano, Hawaiʽi Island (Figure 1). The refuge supports one of the most intact communities of Hawaiian forest passerines remaining in Hawaiʽi, and it was established for the protection of three endangered Hawaiian honeycreeper species. Comprising 13,247 ha, Hakalau ranges in elevation from about 1,400 to 2,000 m and protects important habitat for eight species of endemic Hawaiian passerines (Scott *et al.* 1986; http://www.fws.gov/hakalauforest/). Fecal (diet) samples were collected from birds by the U.S. Geological Survey as part of routine mist-netting and banding at three sites, Maulua (northern), Nāuhi (central), and Puaʽākala (southern), between 1500 and 1640 m elevation and located within or adjacent to habitat supporting the highest densities of endangered bird species (Camp *et al.* 2010). This part of the refuge consists of mature forest dominated by ʻōhiʻa (*Metrosideros polymorpha*) and koa (*Acacia koa*) trees but also supports other common montane forest trees such kōlea (*Myrsine lessertiana*) and ʻōlapa (*Cheirodendron trigynum*); shrubs including ʻākala (*Rubus hawaiensis*), pūkiawe (*Leptecophylla tameiameiae*), and ʻōhelo (*Vaccinium calycinum*); and hāpuʽu (*Cibotium* spp.) tree ferns. Extensive habitat restoration and reforestation has been occurring at Hakalau (Hess *et al*. 2010, Camp *et al*. 2010), with over 400,000 native trees planted in former pasturelands by 2010 (U.S. Fish and Wildlife Service 2010). Fecal samples analyzed in this study were collected in forest that had previously been extensively disturbed by ungulates but where native trees were not planted. There were few differences in arthropod abundance were detected between tree species or sites at Hakalau (Peck *et al*. 2014). Arthropod biomass and densities per unit of ʽōhiʽa foliage are distributed relatively evenly across Hakalau, but differences in canopy density and forest cover affect the availability of arthropod prey to birds (Fretz 2002).

Bird Community

The study included eight endemic and three introduced passerine species commonly found at Hakalau (Table 1). Most species are generalists in terms of their foraging behavior, but the ʽakiapōlāʽau (*Hemignathus munroi,* AKIP) and ʽākepa (*Loxops coccineus,* AKEP) are highly specialized insectivores with modified beaks (Banko and Banko 2009). The beak of the AKIP is unprecedented among birds with its asymmetrical upper and lower mandibles, and it obtains prey by excavating dead wood and by probing and gleaning bark and other surfaces (Pratt *et al.* 2001). AKIP forage selectively but not exclusively in koa trees with males foraging more often on larger branches and trunks and females foraging more often on smaller branches and twigs, generally placing them higher in the canopy (Ralph and Fancy 1996). The beak of the AKEP is slightly twisted at the tip, which is a relatively rare trait among birds that allows them to feed on arthropods by prying open leaf and flower buds as well as koa phyllodes and seed pods bound together with spider silk (Lepson and Freed 1997). AKEP forage mostly on terminal leaf clusters of ʽōhiʽa and among koa phyllodes and seed pods, but they also forage among the leaves of other trees and shrubs (Lepson and Freed 1997). The third endangered species, the Hawaiʽi creeper (*Oreomystis mana,* HCRE), also is insectivorous, but does not possess a specialized bill. HCRE forage stereotypically along the large- and medium-sized branches primarily of ʽōhiʽa and koa in the middle and upper forest canopy, but they sometimes also glean from twigs and foliage from these and a few other trees and shrubs (Lepson and Woodworth 2002). The Hawaiʽi ʽamakihi (*Hemignathus virens virens,* HAAM), is an abundant, widespread honeycreeper with a non-specialized beak, and it

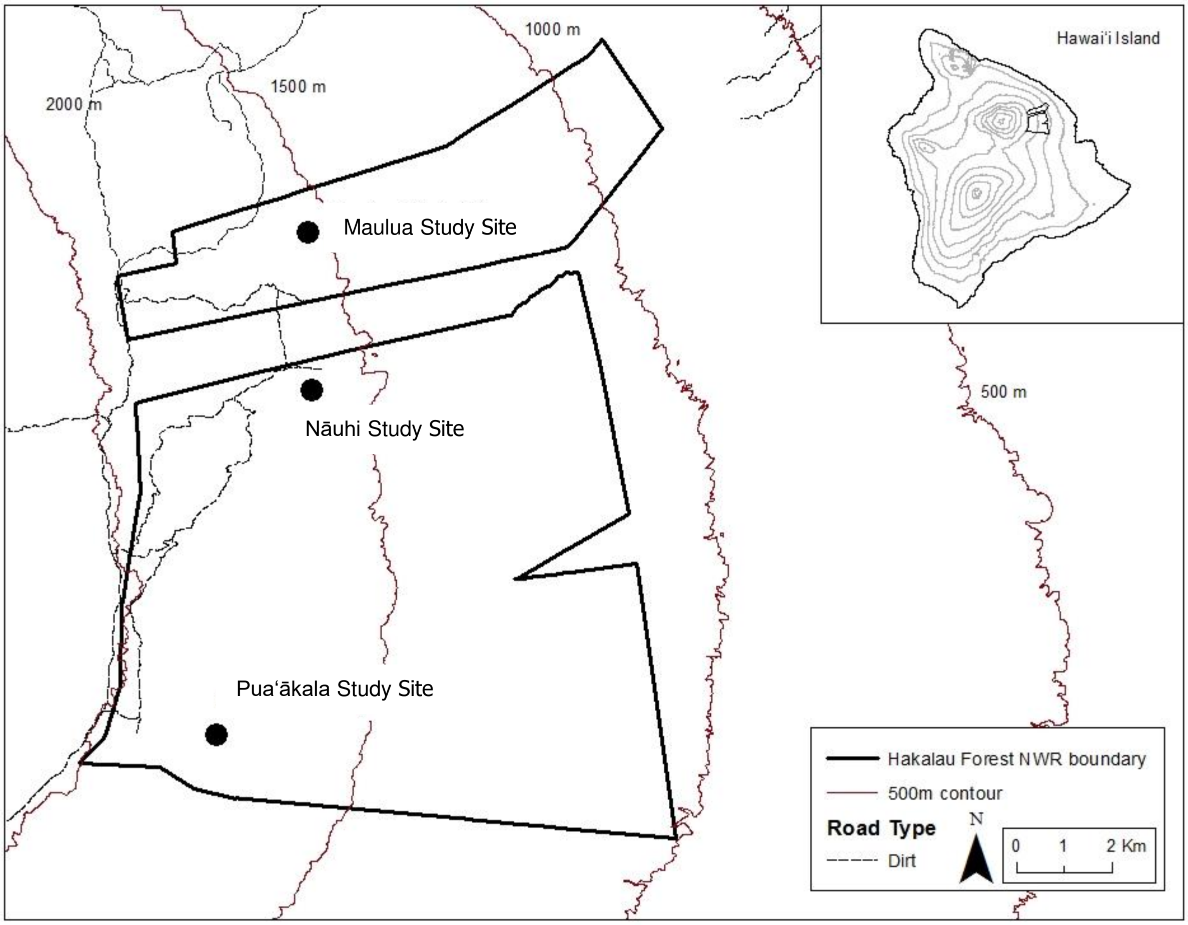

Figure 1. Three study sites where fecal samples were collected from forest birds at Hakalau Forest National Wildlife Refuge, Hawaiʽi Island, 1994–1998.

forages on arthropods, nectar, and occasionally small fruits in a variety of microhabitats at all levels of the forest canopy (Lindsey *et al.* 1998). Two honeycreeper species that feed mostly on nectar but also forage for arthropods are the ʽiʽiwi (*Vestiaria coccinea,* IIWI) and ʽapapane (*Himatione sanguinea,* APAP) (Fancy and Ralph 1997, 1998). The relatively long, decurved bill of the IIWI suggests a close association with endemic lobeliads (Campanulaceae), which possess floral and nectar characteristics attractive to generalist passerine nectarivores (Lammers and Freeman 1986; Pender 2013, Pender *et al*. 2014) and which have become rare or locally extinct. In recent times, IIWI obtain nectar mainly from ʽōhiʽa lehua, (*Metrosideros polymorpha*), the most abundant and widespread native tree at Hakalau and throughout the Hawaiian Islands. ʽŌhiʽa lehua nectar also is heavily exploited by the APAP, which has a relatively short, less decurved bill. The Hawaiʽi ʽelepaio (*Chasiempis sandwichensis*) is an endemic monarch flycatcher (Monarchidae) that forages on arthropods by aerial maneuvers and gleaning from a variety of sub-canopy microhabitats (VanderWerf 1998). The ʽōmaʽo (*Myadestes obscurus,* OMAO) is an endemic thrush (Turdidae) that forages mainly for small fruits and arthropods in the mid-canopy and understory (Wakelee and Fancy 1999).

Four species of introduced birds are found in appreciable numbers at Hakalau (Camp *et al.* 2010), and we examined the diets of three. The most abundant of these is the Japanese white-eye (*Zosterops japonicus;* Zosteropidae; JAWE), a generalist with a relatively short, straight beak that feeds opportunistically on arthropods, nectar, and small fruits throughout the forest canopy and understory (van Riper 2000). The red-billed leiothrix (*Leiothrix lutea;* Timaliidae; RBLE) is another common, widespread introduced species with a short, straight beak and generalized foraging behavior. It forages in the understory on arthropods and small fruits (Male *et al.* 1998). Northern cardinals (*Cardinalis cardinalis;* Cardinalidae; NOCA) are widespread but relatively uncommon, and they forage mainly on understory fruit and arthropods with their heavy, conical beak. Body weights of male forest birds at Hakalau range from 10.6 g (AKEP; Lepson and Freed 1997) to about 45 g (NOCA: North America; Halkin and Linville 1999). Reflecting the exceptional diversity in beak morphology, male beak lengths range from 11.6 mm (AKEP; Lepson and Freed 1997) to 27.5 mm (IIWI; Fancy and Ralph 1998). We undertook diet studies using fecal samples collected from birds captured for demographic studies during 1994−1998 (Woodworth *et al.* 2001). Our results, therefore, do not address diet composition of species across the strong environmental gradient extending downslope to forests with higher rainfall and lower native bird diversity (Scott *et al.* 1986).

Sampling Procedures and Specimen Identification

Fecal samples were collected from birds captured in the upper elevations of Hakalau at Maulua (*n* = 83), Nāuhi (*n* = 182), and Pua'ākala (*n* = 74), although they were not analyzed at the site level. The samples were obtained in all months of the year during 1994−1996; additional samples were collected from endangered birds in 1997 and 1998. Fecal material was obtained from cotton bags that held birds during banding. The samples were placed into plastic vials containing EtOH for long-term storage until they were analyzed during 2009−2010. Fragments of arthropod prey within the samples were carefully teased apart using forceps and pins until all identifiable parts were separated. Arthropod body parts were identified using Leica MZ-6 and MZ-12 stereomicroscopes at 10–40X magnification and were primarily based on comparisons to reference specimens collected at Hakalau and at several other comparable sites elsewhere on Hawai'i Island. Most identifiable parts were photographed using a Nikon Coolpix 995 digital camera mounted on a phototube.

Fragments of Coleoptera, Hemiptera, and Homoptera (now revised), were identified to family and most other taxa were identified to order or other higher-level taxon. Although some prey were identified only to class or subclass (e.g. Acarina, Diplopoda, Chilopoda), we instead use the term "order" throughout for convenience. Classification of the order Hemiptera has recently been revised to include four suborders, but here we use the traditional, more widely recognized, names Hemiptera (the "true bugs") and Homoptera (primarily leafhoppers, planthoppers, psyllids, aphids, and scales). Genus or species level determinations were made in many instances, but overall their occurrence was too infrequent for meaningful analysis and interpretation (Cooper *et al.* 1990). Caterpillar mandibles are often morphologically distinct among taxa (species, genera or families), so we identified caterpillar mandibles to the lowest taxonomic level possible, after which we assigned them to a morpho-species. Numerous arthropod fragments remained unidentified in the samples. In general, these were either fragments for which no match could be made to reference specimens, remnants that were too damaged to be identified confidently, or parts of previously identified specimens. Numbers of individual arthropod taxa within each sample were determined by counting body parts and are minimum abundance estimates. For example, if seven leg segments from the same insect taxon were found in a sample, the number of individuals counted within that sample was two, when in fact, there may have been more than two individuals. Seeds and other plant material were found in some samples but were not identified here.

Table 1. Classification and status of passerine species included in the diet study. Although once classified as an endemic family, the Hawaiian honeycreepers (formerly Drepanidinae) are now generally considered to be a subgroup of the finch family (Fringillidae). Species listed as endemic are found only on Hawai‘i Island, except the ‘ī‘iwi and ‘apapane, which occur on other Hawaiian islands. Feeding type (generalist, intermediate, or specialist) and major foods follow P. Banko and W. Banko (2009).

Family	Species	Common name	Code	Status	Feeding type (main foods)
Monarchidae	*Chasiempis sandwichensis*	Hawai‘i ‘elepaio	HAEL	endemic	generalist (arthropod)
Turdidae	*Myadestes obscurus*	‘ōma‘o	OMAO	endemic	generalist (fruit, arthropod)
Zosteropidae	*Zosterops japonicus*	Japanese white-eye	JAWE	endemic	generalist (arthropod, nectar, fruit)
Timaliidae	*Leiothrix lutea*	red-billed leiothrix	RBLE	introduced	generalist (arthropod, fruit)
Cardinalidae	*Cardinalis cardinalis*	northern cardinal	NOCA	introduced	specialist (fruit, arthropod)
Fringillidae	*Hemignathus virens virens*	Hawai‘i ‘amakihi	HAAM	endemic	generalist (arthropod, nectar, fruit)
Fringillidae	*Hemignathus munroi*	‘akiapōlā‘au	AKIP	endemic, endangered	specialist (arthropod),
Fringillidae	*Loxops mana*	Hawai‘i creeper	HCRE	endemic, endangered	intermediate (arthropod)
Fringillidae	*Loxops coccineus coccineus*	Hawai‘i ‘ākepa	AKEP	endemic, endangered	specialist (arthropod)
Fringillidae	*Vestiaria coccinea*	‘ī‘iwi	IIWI	endemic	intermediate (nectar, arthropod)
Fringillidae	*Himatione sanguinea*	‘apapane	APAP	endemic	generalist (nectar, arthropod)

Over the course of the study, numbered leg bands on birds indicated that several individuals were caught on two occasions. This happened five times for HAAM; 13 times for HAEL (plus one bird that was caught three times); and two times each for HCRE, JAWE and RBLE. Because none of the recaptured birds were caught on the same day, each fecal sample was considered to represent an independent sample. In addition to fecal samples collected from adult birds, four samples were collected on different days from a single nest containing an AKIP nestling between 23 February and 2 March 1995. It is unclear how many individual samples were represented in these four samples, but each was considered to be separate for analysis.

Analysis

Frequency of occurrence for each taxon was calculated by dividing the number of samples in which it was identified by the total number of samples for each bird species. We calculated diet richness and diversity indices from our prey abundance and incidence data using EstimateS (ver. 9.1.0 for Windows; Colwell 2013). For richness, EstimateS provided sample-based rarefaction and extrapolation methods for comparing richness based on equivalent numbers of samples (set to 100 in EstimateS). The richness index also accounted for the abundance and frequency of each prey type in the samples and used 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).

EstimateS calculated the diversity of prey in the fecal samples using rarefied subsamples of the reference sample to combine information on richness and evenness in different ways. We selected the Shannon Exponential Diversity index because of its balanced evaluation of prey richness and evenness in the fecal samples. We also included the Inverse Simpson Diversity index to evaluate diet diversity with a bias toward the more abundant, frequent prey types. Both richness and diversity are expressed here in units of equivalent, equally abundant taxa, allowing us to compare diets among species.

As in the case of richness estimators, EstimateS computed the 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) 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).

We evaluated the similarity of bird diets using a permutation test via the anosim function within the vegan (Oksanen *et al.* 2013) package running in the R (R Core Team 2014) statistics environment. A Chao distance index (Chao *et al.* 2005) was calculated between each sample, and similarities between the two species were compared to those between 999,999 random permutations of the samples. This approach used the variability of prey abundance in the samples in a way that was comparable with the richness and diversity indices. We use similarity and dissimilarity interchangeably throughout but note that the Chao distance index is usually reported as "dissimilarity."

We used our data to address two diet-related questions relevant to ecology and conservation:

- Are there differences between specialist (AKEP, AKIP) and non-specialist (HAAM, HCRE, IIWI) Hawaiian honeycreepers in richness, diversity, and similarity of arthropod orders and caterpillar morpho-species?

- Are there differences between endangered species (AKEP, AKIP, HCRE) and introduced species (JAWE, RBLE) in richness, diversity, and similarity of arthropod orders and caterpillar morpho-species?

We tested for significance ($P \leq 0.05$) between differences in richness and diversity of diets using Z-tests. For the two sets of comparisons (specialist v. generalist species and endangered v. introduced species), we adjusted the significance of the observed differences with a Holm (1979) correction for multiple comparisons (36 in each analysis). This relatively large number of pairwise comparisons may have obscured some dietary patterns. Due to limited sample sizes for many species, we did not evaluate differences in diet due to site, year, sex, or age. Instead, we pooled all data for each species. Nevertheless, we visually examined seasonal trends of Lepidoptera and Araneae in the samples.

Principal coordinates analysis (PCoA) was used to visualize the degree to which diets overlapped among six of the species, including the three endangered insectivores (AKEP, AKIP, HCRE), two of the best-represented native generalists (HAAM, HAEL), and the introduced generalist believed most likely to compete with native species (JAWE; Mountainspring and Scott 1985, Ralph and Noon 1988, Freed and Cann 2014 and references therein). JAWE was selected over RBLE due to assertions of intense competition with native forest birds (Freed and Cann 2014 and references therein). Other species were excluded from the analysis primarily to maintain the visual clarity and simplicity of the graphic. The PCoA was based on 41 categories of identifiable prey items found in more than one fecal sample. The canonical distances were reduced to a set of four dimensions that best preserved the relationships among samples. These new axes were then rotated to provide the two-dimensional perspective that best discriminated between the samples of the six bird species.

RESULTS

A total of 341 adult and four nestling fecal samples were examined from 11 bird species: 255 (74%) from native species and 90 (26%) from introduced species (Table 2). Bird species represented by 25 or more samples were: HAAM, HAEL, HCRE, IIWI, JAWE, and RBLE. Ten or fewer samples were available for adult endangered AKEP and AKIP, and all four nestling samples were collected from a single AKIP individual in one nest. The abundant APAP and relatively uncommon NOCA were represented by only four and three samples, respectively; therefore they were excluded from most analyses and discussion. Fecal samples were collected from all three study sites for all species except AKEP, but more samples were obtained from Nāuhi, the central site, than from Pua`ākala and Maulua combined (Table 2).

Abundance and Frequency of Arthropod Orders in Fecal Samples

Lepidoptera were the most abundant category of prey overall (34.1% of identified prey; Table 3), followed by Araneae (16.1%), Homoptera (13.3%), Coleoptera (10.8%), Hymenoptera (8.1%), Diptera (6.3%), and Hemiptera (6.1%; Table 4). Lepidoptera (moths only—no butterflies) comprised ≥ 40% of all prey for six bird species and 72% of prey identified in the four AKIP nestling samples. Lepidoptera, particularly caterpillars, were the most abundant prey in samples of all birds except APAP and JAWE, for which they were ranked second and third in abundance, respectively. Overall, caterpillars were three times more frequent and nearly seven times more abundant in samples than were adult moths. Caterpillars were found exclusively in samples from AKEP, AKIP, APAP, IIWI and NOCA (Table 5). In contrast, both adult moths and caterpillars were about equally frequent in HAEL and RBLE samples.

Table 2. Distribution of fecal samples collected from native and introduced bird species at three sites at Hakalau, 1994−1998. Data on location were missing from seven samples. See Table 1 for scientific and common names of birds.

	Study Site				
Bird species	Pua`ākala	Nāuhi	Maulua	Unknown	Total
AKEP	8	2	0	0	10
AKIP (adult)	1	3	3	0	7
AKIP (nestlings)	4	0	0	0	4
APAP	1	2	1	0	4
HAAM	4	36	26	5	71
HAEL	12	59	21	0	92
HCRE	8	17	6	1	32
IIWI	9	13	3	0	25
JAWE	11	13	5	0	29
NOCA	1	1	1	0	3
OMAO	2	5	3	0	10
RBLE	15	29	13	1	58
Total	76	180	82	7	345

We identified 2,942 individual prey distributed among 17 arthropod orders, but an additional 331 prey (10.1% of total) could not be identified (Table 3). Unidentifiable prey varied among species, ranging from 5.9% in OMAO to 30.0% in APAP (Table 4). In addition to arthropod prey, we detected fruit in five species: HAAM (1 seed in 1 sample), IIWI (1 seed in 1 sample), NOCA (1 seed in 1 sample), OMAO (10 seeds in 9 samples), RBLE (48 seeds in 34 samples).

Caterpillars were found in 76% of all samples and in ≥ 50% of samples of each of the 11 bird species. They were observed in 90% of AKEP samples and in all HCRE and AKIP samples, including all AKIP nestling samples. On average, 26% of the arthropods consumed by Hakalau birds consisted of caterpillars, and their consumption dropped below 22% only during August and September (Figure 2).

Caterpillars comprised 52% of the annual diet of the three endangered, insectivorous Hawaiian honeycreepers (AKEP, AKIP, HCRE), and their consumption of caterpillars dropped below 48% only during August−October (Figure 3). Araneae were found in samples of all species except NOCA. Araneae were the most abundant prey of APAP and JAWE, and they ranked second in abundance for six other species (Table 3). Araneae occurred in > 80% of samples of six species, and all four AKIP nestling samples contained them. On average, 19% of the annual bird diet consisted of Araneae, and their consumption never dropped below 12% (Figure 4). Araneae consumption was generally similar for the insectivorous honeycreeper species and other bird species (Figure 5).

Homopterans ranked third in abundance overall and were present in samples of all species except AKIP and NOCA (Table 3). They ranked second in abundance in samples of JAWE and constituted ≥ 10% of the identified prey of five bird species. The superfamily Fulgoroidea, which includes the morphologically similar families Delphacidae and Cixiidae, was the most commonly identified homopteran prey of APAP, HAEL, OMAO, JAWE, and RBLE. Psyllidae was more abundant in samples of AKEP, HAAM, and IIWI.

Table 3. Abundance of arthropod taxa consumed by bird species at Hakalau, 1994–1998.

			Native species									Introduced species			
			AKEP	AKIP	AKIP*	APAP	HAAM	HCRE	HAEL	IIWI	OMAO	JAWE	NOCA	RBLE	Total
Order	Family	*n*	10	7	4	4	71	32	92	25	10	29	3	58	345
Acarina[1]	Unidentified				3		4	3	3	2	3			8	26
Araneae	Unidentified		16	1	7	6	104	61	152	11	6	72		38	474
Coleoptera	Carabidae						5	23	32					26	86
	Larva							2	2						4
	Cerambycidae				1			1	2		1				5
	Larva			11	8										19
	Curculionidae				1		5	8	30		1	5		21	71
	Nitidulidae				2		3	1	25		1	9		15	56
	Staphylinidae								3						3
	Unidentified				2		1	5	49	1	3	5	2	4	72
	Coccinelidae larva							1							1
	unidentified pupa											1			1
	Coleoptera total			*11*	*14*		*14*	*41*	*143*	*1*	*6*	*20*	*2*	*66*	*318*
Diplopoda[2]	Unidentified													14	14
Diptera	Unidentified		1			2	14	5	91	5	3	5	0	60	186
Hemiptera	Lygaeidae							2	5			3			10
	Miridae		1				6	3	32	4	2	1		8	57
	Nabidae		2				2	4	52		2	14		14	90
	Scutellaridae											1	1	1	3
	Unidentified						1	6	7	1	1	1		1	18
	Hemiptera total		*3*				*9*	*15*	*96*	*5*	*5*	*20*	*1*	*24*	*178*
Homoptera	Aphididae						9							2	11
	Cicadellidae		2				9		15	2		6		6	40
	Fulgoroidea[3]		4			1	33	6	92	1	3	44		39	223
	Psyllidae		7				47	3	26	8		17		8	116
	Unidentified							1	1						2
	Homoptera total		*13*			*1*	*98*	*10*	*134*	*11*	*3*	*67*		*55*	*392*
Hymenoptera	Unidentified		1		1		10	3	124		6	12		80	237
Isopoda	Unidentified						2		30	1		3		3	39
Lepidoptera	Unidentified			2			1	6	64		3	2		49	127
	unidentified larva		37	46	73	5	295	128	112	27	13	42	7	89	874
	unidentified pupa			3											3
	Lepidoptera total		*37*	*51*	*73*	*5*	*296*	*134*	*176*	*27*	*16*	*44*	*7*	*138*	*1004*
Neuroptera	Unidentified							4	5						9
	unidentified larva		3		3		7	2	18	3		1			37
	Neuroptera total		*3*		*3*		*7*	*6*	*23*	*3*		*1*			*46*
Psocoptera	Unidentified		1				4	1	5	2		5		2	20
Other[4]	Unidentified						2		3					3	8
unidentified	Unidentified		11	10	3	6	69	34	85	25	3	20	4	61	331
Total identified			75	63	101	14	564	279	980	68	48	249	10	491	2942

*AKIP = AKIP nestling samples; [1]Acarina (mites) = taxonomic level Subclass (Class Arachnida); [2]Diplopoda (millipedes) = taxonomic level Class; [3]Superfamily Fulgoroidea includes Delphacidae and Cixiidae; [4]Other = Chilopoda (taxonomic level Class [centipedes]), Collembola, Isoptera, Pseudoscorpionida, and Thysanoptera.

Table 4. Proportion of arthropod taxa in fecal samples of birds at Hakalau Forest National Wildlife Refuge, Hawai'i Island, 1994–1998. Values are percentages calculated by dividing the number of a particular prey by the total number of identified prey for each bird species (based on prey abundances in Table 3).

			Native species									Introduced species			
			AKEP	AKIP	AKIP*	APAP	HAAM	HCRE	HAEL	IIWI	OMAO	JAWE	NOCA	RBLE	Overall
Order	Family	*n*	(10)	(7)	(4)	(4)	(71)	(32)	(92)	(25)	(10)	(29)	(3)	(58)	(345)
Acarina[1]	Unidentified				3.0		0.7	1.1	0.3	2.9	6.2			1.6	0.9
Araneae	Unidentified		21.3	1.6	6.9	42.9	18.4	21.9	15.5	16.2	12.5	28.9		7.7	16.1
Coleoptera	Carabidae						0.9	8.2	3.3					5.3	2.9
	Larva							0.7	0.2						0.1
	Cerambycidae				1.0			0.4	0.2		2.1				0.2
	Larva			17.5	7.9										0.6
	Curculionidae				1.0		0.9	2.9	3.1		2.1	2.0		4.3	2.4
	Nitidulidae				2.0		0.5	0.4	2.6		2.1	3.6		3.1	1.9
	Staphylinidae								0.3						0.1
	Unidentified				2.0		1.8	1.8	5.0	1.5	6.2	2.0	0.2	0.8	2.4
	Coccinelidae larva							1.4							0.03
	unidentified pupa											0.04			0.03
	Coleoptera total			*17.5*	*13.9*		*2.5*	*14.7*	*14.6*	*1.5*	*12.5*	*8.0*	*0.2*	*13.4*	*10.8*
Diplopoda[2]	Unidentified													2.9	0.5
Diptera	Unidentified		1.3			14.3	2.5	1.8	9.3	7.4	6.2	2.0	0	12.2	6.3
Hemiptera	Lygaeidae							0.7	0.5			1.2			0.3
	Miridae		1.3				1.1	1.1	3.3	5.9	4.2	0.4		1.6	1.9
	Nabidae		2.7				0.4	1.4	5.3		4.2	5.6		2.9	3.1
	Scutellaridae											0.4	0.1	0.2	0.1
	Unidentified						0.2	2.2	0.7	1.5	2.1	0.4		0.2	0.6
	Hemiptera total		*4.0*				*1.6*	*5.4*	*9.8*	*7.4*	*10.4*	*8.0*	*0.1*	*4.9*	*6.1*
Homoptera	Aphididae						1.6							0.4	0.4
	Cicadellidae		2.7				1.6		1.5	2.9		2.4		1.2	1.4
	Fulgoroidea[3]		5.3			7.1	5.9	2.2	9.4	1.5	6.2	17.7		7.9	7.6
	Psyllidae		9.3				8.3	1.1	2.7	11.8		6.8		1.6	3.9
	Unidentified							0.4	0.1						0.1
	Homoptera total		*17.3*			*7.1*	*17.4*	*3.6*	*13.7*	*16.2*	*6.2*	*26.9*		*11.2*	*13.3*
Hymenoptera	Unidentified		1.3		1.0		1.8	1.1	12.7		12.5	4.8		16.3	8.1
Isopoda	Unidentified						0.4		3.1	1.5		1.2		0.6	1.3
Lepidoptera	Unidentified			3.2			10.2	2.2	6.5		6.2	0.8		10.0	4.3
	unidentified larva		49.3	73.0	72.3	35.7	52.3	45.9	11.4	39.7	27.1	16.9	0.7	18.1	29.7
	unidentified pupa			4.8											30.1
	Lepidoptera total		*49.3*	*81.0*	*72.3*	*35.7*	*52.5*	*48.0*	*18.0*	*39.7*	*33.3*	*17.7*	*0.7*	*28.1*	*34.1*
Neuroptera	Unidentified							1.4	0.5						0.3
	unidentified larva		4.0		3.0		1.2	0.7	1.8	4.4		0.4			1.3
	Neuroptera total		*4.0*		*3.0*		*1.2*	*2.2*	*2.3*	*4.4*		*0.4*			*1.6*
Psocoptera	Unidentified		1.3				0.7	0.4	0.5	2.9		0.2		0.4	0.7
Other[4]	Unidentified						0.4		0.3					0.6	0.3
Unidentified[5]	Unidentified		12.8	13.7	2.9	3.0	10.9	10.9	8.0	26.9	5.9	7.4	28.6	11.1	10.1

*AKIP = AKIP nestling samples; [1]Acarina (mites) = taxonomic level Subclass (Class Arachnida); [2]Diplopoda (millipedes) = taxonomic level Class; [3]Superfamily Fulgoroidea includes Delphacidae and Cixiidae; [4]Other = Chilopoda (taxonomic level Class [centipedes]), Collembola, Isoptera, Pseudoscorpionida, and Thysanoptera; [5]Percentage of all prey that could not be identified to order (for all identified and unidentified prey combined – not to be included in summations of percentages of identified prey).

Table 5. Incidence of arthropod orders in fecal samples of birds at Hakalau Forest National Wildlife Refuge, Hawai‘i Island, 1994–1998. Only the most frequently consumed orders are included. Values are percentages and were calculated by dividing the number of samples in which each taxon was identified by the total number of samples.

	Native species									Introduced species			
	AKEP	AKIP	AKIP*	APAP	HAAM	HCRE	HAEL	IIWI	OMAO	JAWE	NOCA	RBLE	Mean
Order *n*	(10)	(7)	(4)	(4)	(71)	(32)	(92)	(25)	(10)	(29)	(3)	(58)	(345)
Araneae	100	14	100	100	82	84	84	40	50	97		53	67
Coleoptera		29	100		13	66	80	4	30	55	67	57	37
Diptera	10			25	15	16	74	20	20	17		66	26
Hemiptera	30				11	41	72	20	40	59	33	31	34
Homoptera	80			25	73	25	91	28	30	97		60	54
Hymenoptera	10		25		10	9	77		30	38		78	28
Lepidoptera (all)	90	100	100	50	80	100	79	52	60	79	67	91	81
adult				50	1	19	61		30	7		66	24
larvae	90	100	100		80	100	58	52	50	79	67	74	76
Neuroptera	20		50		10	13	21	12		3			9

*AKIP = AKIP nestling samples; [1]Means exclude *AKIP, APAP, NOCA

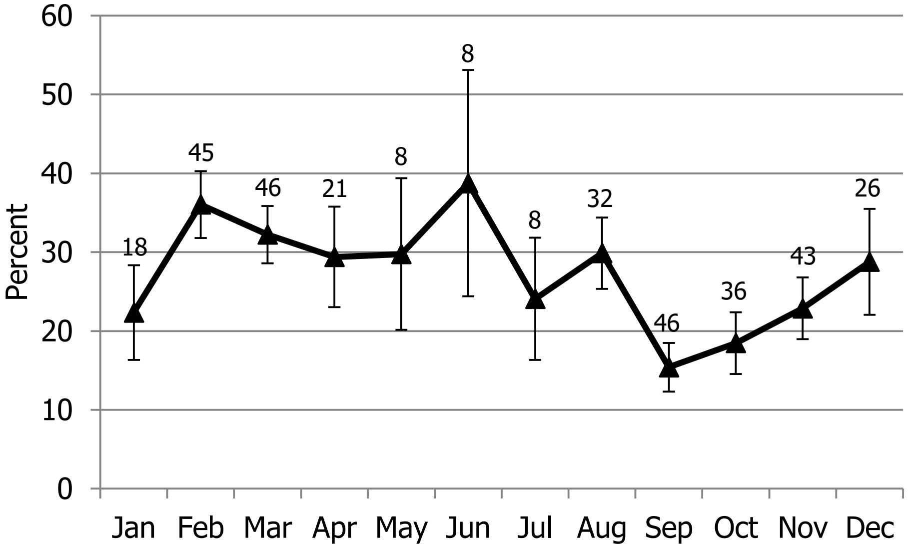

Figure 2. Mean percentage of caterpillars in fecal samples of all bird species for each month at Hakalau, 1994−1998. Sample sizes are shown with the SE bars for the monthly means.

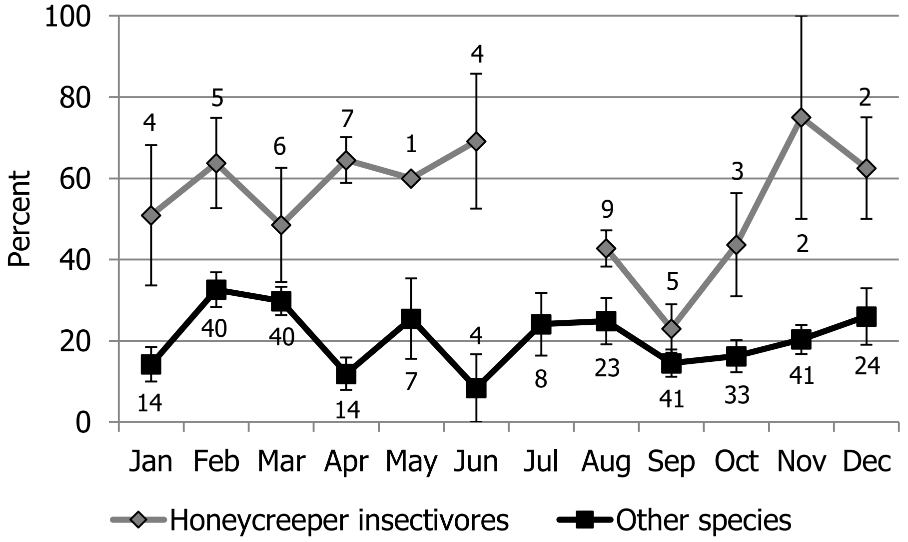

Figure 3. Mean percentage of caterpillars in fecal samples of the three endangered, insectivorous Hawaiian honeycreeper species (AKEP, AKIP, HCRE) and all other bird species for each month at Hakalau, 1994−1998. Sample sizes are shown with the SE bars for the monthly means.

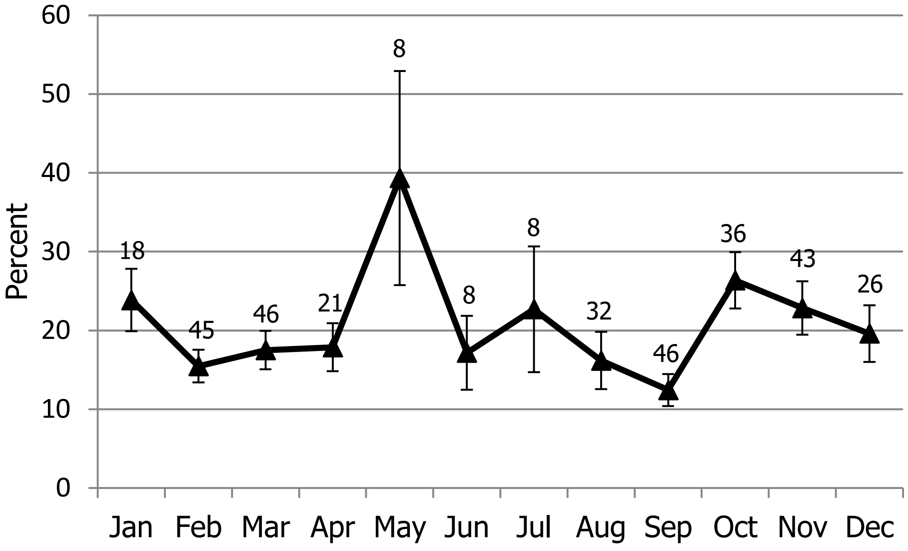

Figure 4. Mean percentage of Araneae (spiders) in fecal samples of all bird species for each month at Hakalau, 1994−1998. Sample sizes are shown with the SE bars of the monthly means.

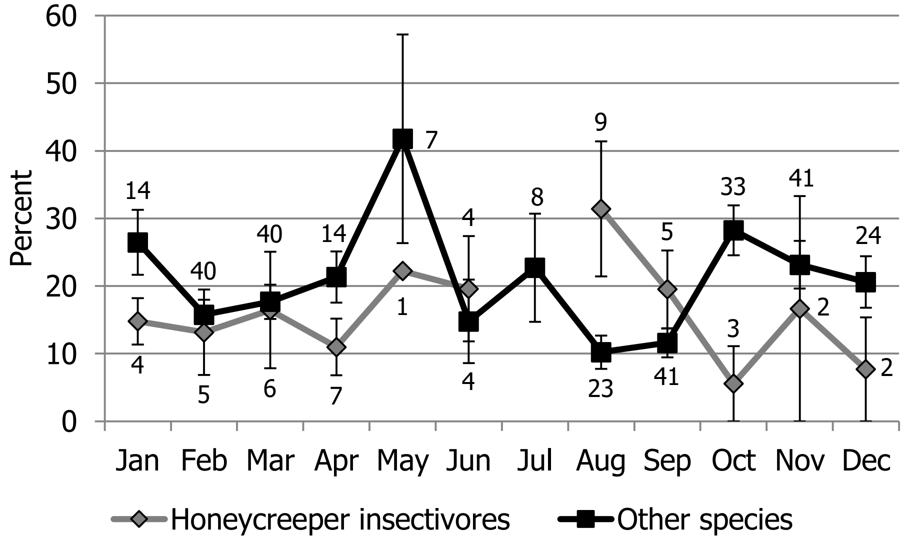

Figure 5. Mean percentage of Araneae (spiders) in fecal samples of the three endangered, insectivorous Hawaiian honeycreeper species (AKEP, AKIP, HCRE) and all other bird species for each month at Hakalau, 1994−1998. Sample sizes are shown with the SE bars for the monthly means.

Coleoptera ranked fourth in abundance overall and were identified in samples of all species except AKEP and APAP (Table 3). Coleoptera constituted 10–20% of the total number of identified prey of six species. Larval Cerambycidae were identified primarily in AKIP samples (both adult and nestling). Adult Carabidae were found primarily in HCRE and RBLE.

Most of the taxa found less frequently in the fecal samples were nonetheless consumed by many bird species. Hymenoptera (primarily Ichneumonoidea; no Formicidae) ranked fifth in abundance overall and were most commonly found in HAEL, OMAO, and RBLE samples, although four other species also consumed them (Table 3). Diptera, ranked sixth, were mostly found in APAP, HAEL, IIWI, OMAO, and RBLE samples. Hemiptera, ranked seventh, were primarily found in HCRE, HAEL, IIWI, and JAWE.

Richness, Diversity, and Similarity of Arthropod Orders in Fecal Samples

The richness and diversity of arthropods in species' samples ranged widely. Overall, richness and diversity were greatest for HAEL and RBLE, both widespread generalists (Table 6). Arthropod richness was also very high for HAAM, although arthropod diversity was low. In contrast, the OMAO was characterized by low arthropod richness and high diversity. Richness and diversity ranks for other species were relatively consistent.

Among the Hawaiian honeycreepers, arthropod richness was highest in the generalist, HAAM, followed by the two intermediate species, HCRE and IIWI, and then by the two specialists, AKEP and AKIP (Table 6). Arthropod richness was 3.4 times greater for HAAM than for AKIP, and the difference was highly significant (Table 7). HAAM samples were 1.5 times richer than AKEP samples, which was not significant. Arthropod diversity was highest in IIWI, followed by HCRE, HAAM, AKEP, and AKIP (Table 6). Arthropod diversity was 3.6 higher for IIWI than for AKIP, and this and other differences between AKIP and other non-specialists were highly significant (Table 7). Diversity was also significantly higher for IIWI than for AKEP. The composition of arthropod orders consumed by specialist and generalist Hawaiian honeycreepers did not differ significantly (Table 7).

Arthropod richness was 3.4 time greater for the introduced RBLE compared to the endangered AKIP, and the difference was significant (Table 7). Richness for the JAWE was also significantly greater than for AKIP. Arthropod diversity differed significantly between each pair of introduced and endangered species (Table 7). Similarly, differences in the arthropod orders consumed were significant between most species pairs but not between JAWE and AKEP.

Table 6. Richness and diversity of arthropod prey in fecal samples from forest birds at Hakalau, 1994−1998. Observed richness is the number of arthropod orders actually identified from the samples (*n*), and mean richness is the number of orders expected from 100 samples, given the reference sample (calculated from program EstimateS). Shannon Exponential and Simpson Inverse diversity indices are expressed in units of equivalent, equally abundant arthropod orders.

Bird Species	*n*	Observed Richness	Calculated Richness (95% CI)	Rank	Shannon Mean (SD)	Rank	Simpson Mean (SD)	Rank
AKEP	10	8	7.5 (5.1−9.8)	8	4.0 (0.29)	8	3.1 (0.20)	7
AKIP	7	3	3.4 (1.2−5.7)	9	1.6 (0.22)	9	1.4 (0.17)	9
HAAM	71	13	11.4 (8.9−13.8)	3	4.2 (0.39)	7	2.9 (0.34)	8
HAEL	92	14	13.2 (11.2−15.1)	1	8.3 (0.14)	1	7.5 (0.16)	1
HCRE	32	10	11.0 (7.8−14.1)	4	4.5 (0.35)	6	3.3 (0.28)	6
IIWI	25	10	9.5 (7.0−12.0)	6	5.8 (0.60)	5	4.4 (0.61)	5
JAWE	29	10	10.5 (8.0−12.9)	5	6.0 (0.24)	4	4.9 (0.23)	4
OMAO	10	8	8.9 (5.6−12.2)	7	6.2 (0.83)	3	5.1 (0.98)	3
RBLE	58	13	11.5 (9.2−13.9)	2	7.5 (0.28)	2	6.2 (0.30)	2

Table 7. Richness, diversity, and dissimilarity of arthropod orders in fecal samples of generalist versus specialist Hawaiian honeycreeper species and endangered versus introduced species. Z-test statistics for richness and diversity and the Chao distance statistic are presented with significance values with and without adjustment for multiple comparisons. Significance in dissimilarity indicates that the diets of two species are different. Numbers of fecal samples for each species were: AKEP = 10, AKIP = 7, HAAM = 71, HCRE = 32, IIWI = 25, JAWE = 29, RBLE = 58.

	Richness			Diversity			Dissimilarity		
Generalist vs. Specialist	Z statistic	*P*	*P*-adj.	Z statistic	*P*	*P*-adj.	Chao distance	*P*	*P*-adj.
AKEP-HAAM	2.266	0.0059	0.1233	0.453	0.1627	1.0000	-0.1474	0.9347	1.0000
AKEP-HCRE	1.741	0.0204	0.3266	1.166	0.0609	0.7103	0.2200	0.0105	0.1989
AKEP-IIWI	1.171	0.0604	0.7103	2.701	0.0017	0.0432	-0.1624	0.9968	1.0000
AKIP-HAAM	4.687	0.0000	0.0000	5.717	0.0000	0.0000	0.2717	0.0134	0.3124
AKIP-HCRE	3.796	0.0000	0.0011	6.942	0.0000	0.0000	0.2973	0.0039	0.0892
AKIP-IIWI	3.561	0.0001	0.0027	6.478	0.0000	0.0000	-0.0362	0.5763	1.0000
Endangered vs. Introduced									
AKEP-JAWE	1.756	0.0198	0.2572	2.784	0.0000	0.0000	0.1885	0.0308	0.3701
AKEP-RBLE	2.402	0.0041	0.0692	5.954	0.0000	0.0000	0.3975	0.0001	0.0024
AKIP-JAWE	4.167	0.0000	0.0002	0.254	0.0000	0.0000	0.8640	0.0000	0.0000
AKIP-RBLE	4.882	0.0000	0.0000	3.319	0.0002	0.0000	0.6353	0.0000	0.0001
HCRE-JAWE	0.230	0.2046	1.0000	1.872	0.0001	0.0028	0.3218	0.0000	0.0000
HCRE-RBLE	0.278	0.1953	1.0000	0.350	0.0000	0.0000	0.3805	0.0000	0.0000

Principal coordinates analysis (PCoA), based on 41 categories of identifiable prey items found in more than one fecal sample, revealed that the fecal samples of HAAM and AKEP overlapped to the greatest extent (Figure 6). Overlap was also apparent between HAAM and AKIP, HCRE, and JAWE. Besides overlapping with HAAM, the samples of the introduced JAWE also overlapped somewhat with HAEL and HCRE.

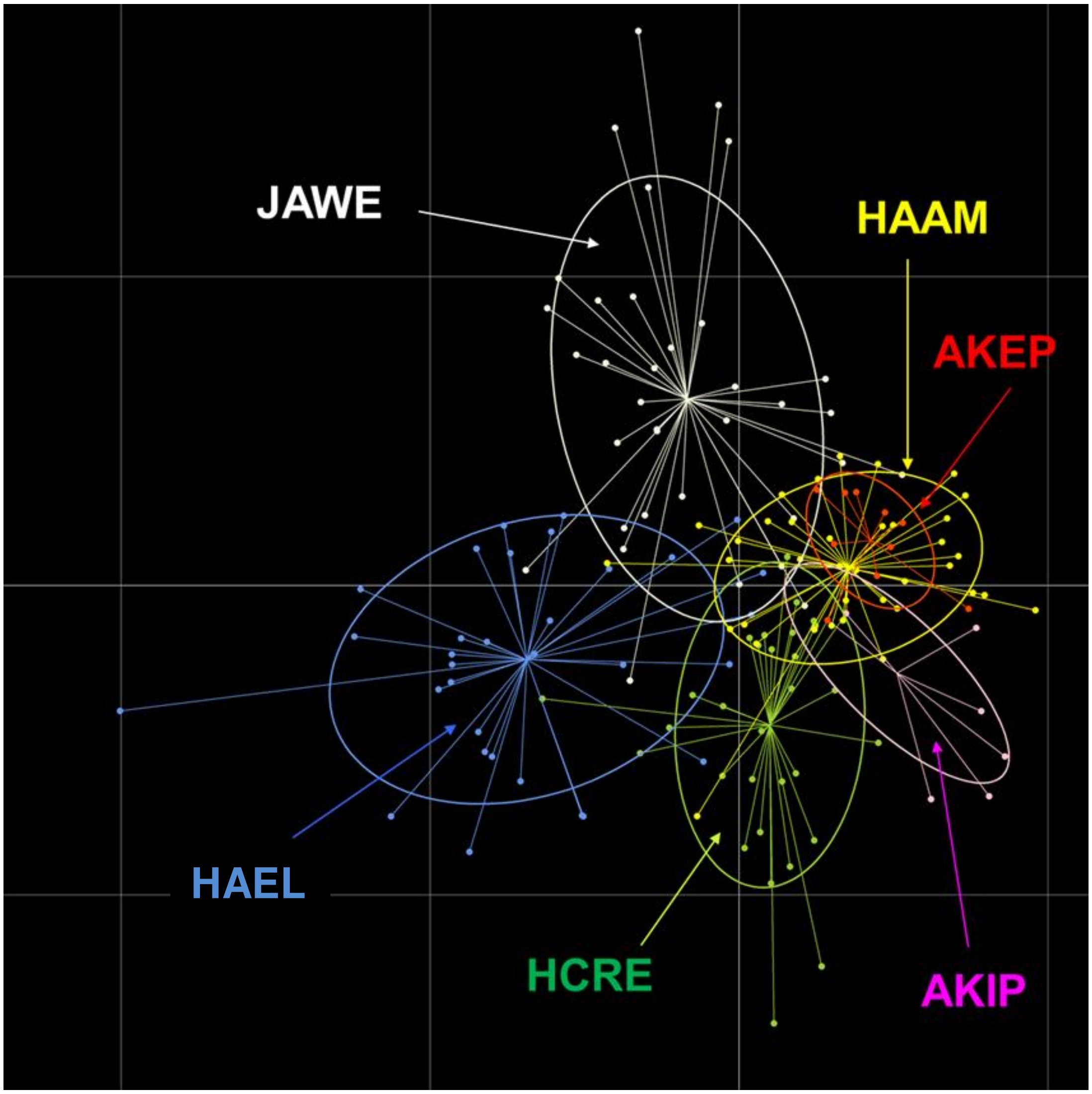

Figure 6. Principal Coordinates Analysis depiction of overlap in arthropod prey in fecal samples of birds at Hakalau, 1994–1998. Only six species are represented for visual clarity, but they include all three endangered species (AKEP, AKIP, HCRE), two abundant native species (HAAM, HAEL), and one abundant introduced species (JAWE).

Abundance, Richness, Diversity, and Similarity of Caterpillar Morpho-species in Fecal Samples

Nineteen morpho-species of caterpillars were identified from their mandibles in the fecal samples. Of 720 caterpillar prey items, 42% were of type K, 15% were of types G and J (Table 8, Figure 7). Other morpho-species each comprised less than 8% of the total. Type K was most abundant in the samples of AKEP, AKIP, HAAM, and IIWI. Type J was the most abundant in the samples of HAEL, while G was the most abundant type in HCRE and JAWE samples. Caterpillars fed to the AKIP nestling(s) were the same as those eaten by the adults but included types G and J; type E was more common in the nestling samples than in the adult samples.

HCRE ranked first in caterpillar richness and second in diversity, and RBLE ranked second highest in richness and highest in diversity (Table 9). The lowest ranked species in caterpillar richness and diversity were IIWI and AKEP. Among the Hawaiian honeycreepers, caterpillar richness was low for the two specialists, AKEP and AKIP, but also for IIWI. Richness for HCRE, the highest ranked honeycreeper, was 5.4 times greater than richness for AKEP, the lowest ranked, and the difference was significant (Table 10). Richness also differed significantly between HAAM and AKEP. The same pattern was observed for caterpillar diversity among the honeycreepers, and diversity for HCRE, the highest-ranked species, was 3.5 times greater than diversity for AKEP, the lowest ranked species. The only significant difference in the composition of caterpillar morpho-species between a specialist and non-specialist was between HCRE and AKEP (Table 10).

Between introduced and endangered species, caterpillar richness was significantly higher for the introduced RBLE in comparison to AKEP and AKIP but not HCRE (Table 10). Richness for the introduced JAWE was significantly greater only from AKEP. Although HCRE richness was 1.9 times greater than for JAWE, the difference was not significant. Caterpillar diversity was greater for both JAWE and RBLE than for AKEP, but diversity for JAWE was significantly less than for HCRE, the species with highest diversity (Table 10). There were no significant differences between introduced and endangered species in terms of the composition of caterpillar morpho-species in the fecal samples (Table 10).

Table 8. Abundance of caterpillar morpho-species in fecal samples of birds at Hakalau, 1994–1998. Morpho-species were determined by mandible morphology.

Caterpillar		Native species									Introduced species				
morpho-		AKEP	AKIP	AKIP*	APAP	HAAM	HCRE	HAEL	IIWI	OMAO	JAWE	NOCA	RBLE	Total	Percent
species	*n*	(10)	(7)	(4)	(4)	(71)	(32)	(92)	(25)	(10)	(29)	(3)	(58)	(345)	of total
A													1	1	0.14
B						1		2	1				1	5	0.69
C							1						1	2	0.28
D						1								1	0.14
E			2	12			6	2						22	3.06
F						46	3						1	50	6.94
G				1			53	17			17	5	12	105	14.58
H			1											1	0.14
I										1				1	0.14
J		7		7		26	10	34	8	3	4		11	110	15.28
K		25	26	36	2	163	7	13	13	1	7		9	302	41.94
L						1	1	3					11	16	2.22
M			9	11										20	2.78
N			1	1		2	4	2		3	2	1	2	18	2.50
O							4	1						5	0.69
P						3	21	27			2		3	56	7.78
Q						1		1						2	0.28
R			1				1							2	0.28
S									1					1	0.14
Total prey		32	40	68	2	244	111	102	23	8	32	6	52	720	
Total morpho-species		2	6	6	1	9	11	10	4	4	5	2	10	19	

*AKIP = AKIP nestling samples

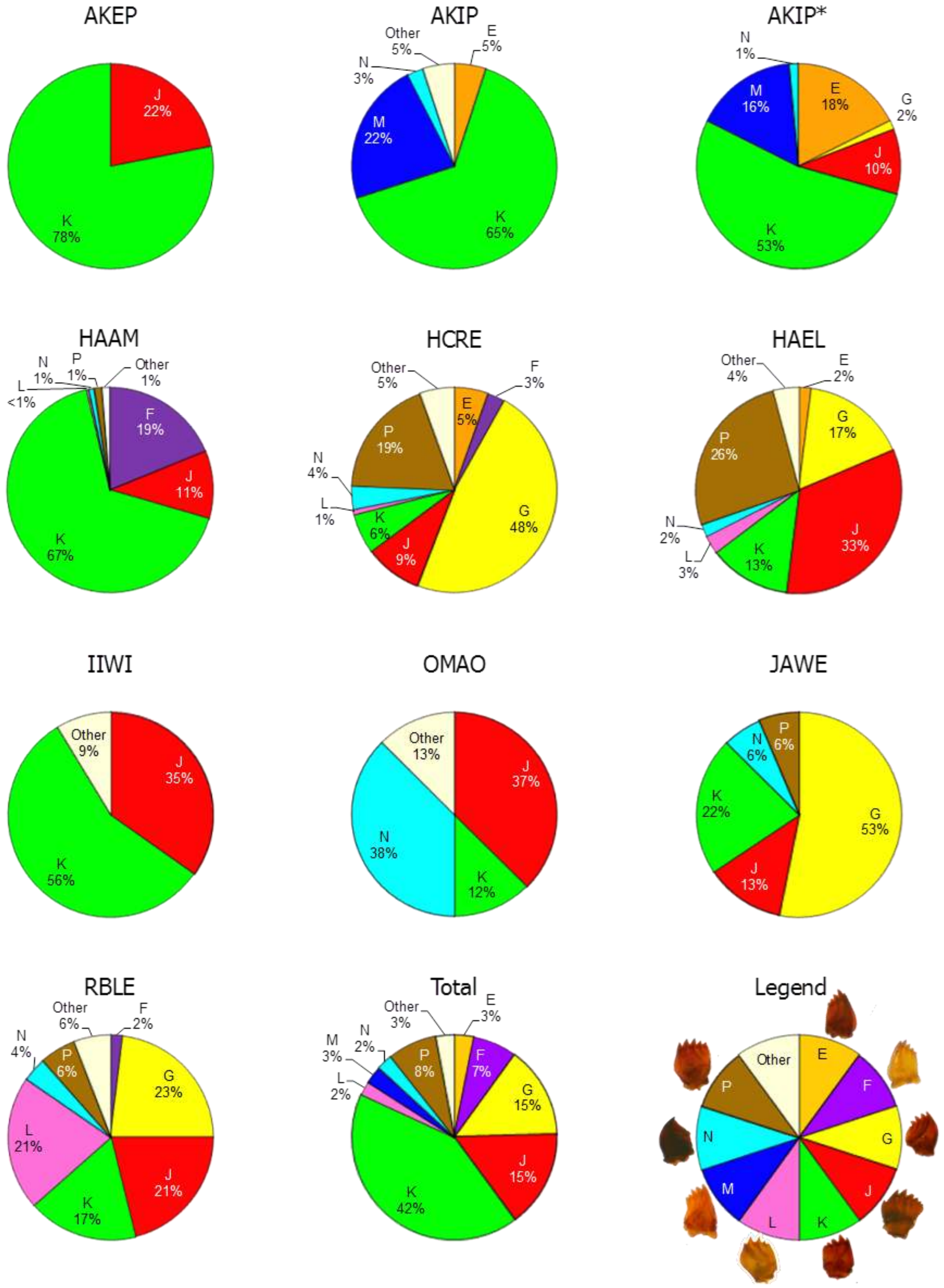

Figure 7. Distribution of the caterpillar morpho-species most frequently identified in fecal samples of bird species at Hakalau, 1994–1998. Each letter represents a different morpho-species and "Other" represents the remaining 10 morph-species. Mandibles of each major morpho-species are depicted in the legend. AKIP* = AKIP nestlings.

Table 9. Richness and diversity of caterpillar morpho-species in fecal samples of forest birds at Hakalau, 1994–1998. Caterpillar morpho-species were determined from mandible morphology. Observed richness is the number of morpho-species actually identified from the samples (*n*), and mean richness is the number of morph-species expected from 100 samples, given the reference sample (calculated from program EstimateS). Shannon Exponential and Simpson Inverse diversity indices are expressed in units of equivalent, equally abundant caterpillar morpho-species.

Bird Species	*n*	Observed Richness	Calculated Richness (95% CI)	Rank	Shannon Mean (SD)	Rank	Simpson Mean (SD)	Rank
AKEP	10	2	2.0 (2.0–2.0)	9	1.7 (0.11)	9	1.6 (0.13)	9
AKIP	7	6	5.1 (4.2–6.1)	7	3.5 (0.82)	5	3.0 (0.67)	5
HAAM	71	9	9.1 (5.1–13.0)	3	3.3 (0.32)	6	2.4 (0.26)	6
HAEL	92	11	7.1 (4.9–9.3)	4	5.0 (0.60)	3	4.0 (0.51)	3
HCRE	32	10	10.7 (5.8–15.7)	1	6.0 (0.60)	2	4.7 (0.59)	2
IIWI	25	4	3.5 (1.0–6.0)	8	2.4 (0.42)	8	2.1 (0.37)	8
JAWE	29	5	5.5 (3.0–7.9)	6	3.8 (0.51)	4	3.2 (0.61)	4
OMAO	10	4	5.7 (-0.8–12.2)	5	2.6 (0.80)	7	2.4 (0.74)	7
RBLE	58	10	9.7 (7.2–12.3)	2	6.0 (0.80)	1	5.0 (0.72)	1

Table 10. Richness, diversity, and dissimilarity of caterpillar morpho-species in fecal samples of generalist versus specialist Hawaiian honeycreeper species and endangered versus introduced species. Z-test statistics for richness and diversity and the Chao distance statistic are presented with significance values with and without adjustment for multiple comparisons. Significance in dissimilarity indicates that the diets of two species are different. Numbers of fecal samples for each species were: AKEP = 8, AKIP = 4, HAAM = 46, HCRE = 27, IIWI = 10, JAWE = 16, RBLE = 22.

	Richness			Diversity			Dissimilarity		
Generalist vs. Specialist	Z statistic	*P*	*P*-adj.	Z statistic	*P*	*P*-adj.	Chao distance	*P*	*P*-adj.
AKEP-HAAM	3.517	0.0001	0.0031	4.581	0.0000	0.0000	-0.1968	0.9973	1.0000
AKEP-HCRE	3.478	0.0001	0.0034	6.984	0.0000	0.0000	0.2695	0.0005	0.0121
AKEP-IIWI	1.175	0.0600	0.7103	1.474	0.0351	0.5267	0.0337	0.2335	1.0000
AKIP-HAAM	1.902	0.0143	0.2574	0.204	0.2095	1.0000	0.2988	0.0459	0.6421
AKIP-HCRE	2.187	0.0072	0.1435	2.490	0.0032	0.0766	0.3369	0.0005	0.1096
AKIP-IIWI	1.231	0.0546	0.7094	1.183	0.0592	0.7103	0.1515	0.1192	0.9538
Endangered vs. Introduced									
AKEP-JAWE	2.784	0.0013	0.0242	3.891	0.0000	0.0006	-0.0197	0.5200	1.0000
AKEP-RBLE	5.954	0.0000	0.0000	3.891	0.0000	0.0006	0.0180	0.3366	1.0000
AKIP-JAWE	0.254	0.1999	1.0000	2.252	0.0061	0.0973	0.0279	0.3181	1.0000
AKIP-RBLE	3.319	0.0002	0.0045	2.252	0.0061	0.0973	0.1082	0.0555	0.4992
HCRE-JAWE	1.872	0.0153	0.2141	2.832	0.0012	0.0220	0.0846	0.0354	0.3701
HCRE-RBLE	0.350	0.1815	1.0000	0.050	0.2400	1.0000	0.0609	0.0324	0.3701

DISCUSSION

Prey Selection

This study is the first to assess the richness and diversity of arthropods consumed by nearly all members of a community of montane Hawaiian passerines. Many birds were represented by at least 25 fecal samples, which were collected over multiple years and during all months across a diverse, native, montane rainforest. The clearest and most compelling result was that caterpillars comprised the largest portion of the arthropod component of the diet for most species. Caterpillars were the primary prey of the endangered insectivores (AKEP, AKIP, and HCRE) throughout the year, and they were the main food delivered to AKIP nestlings. Our findings corroborate the observation of early naturalists who worked at a time of presumably higher bird densities and more intact native prey communities, that caterpillars were the dominant prey of Hawaiian forest birds and were critically important to nestlings (Perkins 1903, 1913; Henshaw 1902). Our findings parallel those of a number of continental studies that have documented caterpillars as an important component of the breeding season diet of forest passerines (Holmes *et al*. 1992, Rodenhouse and Holmes 1992, Sample *et al*. 1993, Naef-Daenzer and Keller *et al*. 1999). We did not assess the abundance of caterpillars or other prey as part of this study, but surveys elsewhere on windward Hawai‘i Island suggest that caterpillars are not the most abundant arthropods or the group with the highest biomass at Hakalau (Fretz 2002, Gruner 2007, Peck *et al*. 2008, U.S. Geological Survey unpublished data). Heavy consumption of caterpillars by all species, therefore, is likely due to their nutritional value and relative ease of capture.

Although prey availability strongly affects the abundance and reproduction of some species (Burke and Nol 1998, Zanette *et al*. 2000), prey selection by insectivorous birds may be influenced more by the nutritional and energetic value of prey (Razeng and Watson 2015) and by prey size (Naef-Daenzer *et al*. 2000), although some species can easily switch from preferred prey with little documented effect on reproductive success (Sample *et al*. 1993, Nagy and Smith 1997). During breeding, when food may be a strong limiting factor for some species (Martin 1987), arthropods fed to nestlings may be selected for their nutritional value (Ramsay and Houston 2003; Arnold *et al*. 2007, 2010). Especially frequent and abundant in the samples of Hakalau birds were Lepidoptera and Araneae, which have been shown to provide consumers with high levels of calories, protein, lipids, carbohydrates, carotenoids, and other nutrients (Schroeder 1977, Robel *et al*. 1995, Banko *et al*. 2002, Ramsay and Houston 2003, Eeva *et al*. 2010, Egan *et al*. 2014, Razeng and Watson 2015) and can meet the growth requirements of birds (Studier *et al*. 1991). Both orders are important components of the diets of continental and other island passerines, especially during the breeding season (Lack 1966, Grant and Grant 1989, Perrins 1991, Holmes *et al*. 1992, Rodenhouse and Holmes 1992, Sample *et al*. 1993, Naef-Daenzer and Keller *et al*. 1999). Nevertheless, in some diet studies, Coleoptera, Hymenoptera, and a few other orders have been ranked higher in prevalence than Lepidoptera and Araneae (Rotenberry 1980, Robinson and Holmes 1982, Poulin *et al*. 1994, Poulin and Lefebvre 1996, Durães and Marini 2005, Razeng and Watson 2012). To some extent, dominant prey types in the diet likely reflect their availability in the environment. Coleoptera, Hemiptera, and Homoptera were often found in fecal samples of many Hakalau birds, and these orders are similarly rich in nutrients and calories (Robel *et al*. 1995, Razeng and Watson 2015). Psocoptera and Acarina also were eaten by many birds at Hakalau, but only occasionally and in small numbers. This suggests that most bird species, including specialists, can be opportunistic consumers of small, abundant prey, but there may also be unknown nutritional benefits of including some prey types occasionally. Diplopoda and Isopoda, for example, appeared infrequently in the fecal samples of Hakalau birds, but they are very rich in calcium compared to other arthropods and may be critical during eggshell and bone development (Graveland and van Gijzen 1994, Graveland

and Drent 1997). Diplopods seem to be uncommon on trees at Hakalau (Peck *et al.* 2014, U.S. Geological Survey unpublished data) and may not be readily obtainable by birds. In contrast, isopods can be abundant on tree bark surfaces at Hakalau and other wet forests (Peck *et al.* 2014, Peck *et al.* 2015), but they may be largely avoided by small birds due to their relatively large body size and high chitin content. We do not know whether isopods are eaten more frequently during the nesting season, when calcium requirements should be greatest (Graveland and van Gijzen 1994, Graveland and Drent 1997).

Diet Richness and Diversity

Diet richness is not necessarily a reliable indicator of specialization (Sherry 1990), but our results support the longstanding ecological maxim that generalists tend to feed on a greater variety of foods than do specialists. Although some patterns of richness and diversity may have been obscured by adjusting the level of statistical significance of observed differences between species with a correction for multiple comparisons, species rankings indicate trends that may prove significant with expanded sampling effort, especially among the endangered species. The two specialists, AKIP and AKEP, were ranked lowest in the richness and diversity of arthropod orders consumed due to the preponderance of caterpillars in their samples. Among the Hawaiian honeycreepers, arthropod richness was 3.4 times greater for the generalist, HAAM, than for AKIP. Diversity was 3.6 times greater for IIWI, a species with an intermediate level of specialization (P. Banko and W. Banko 2009), than for AKIP. Although many arthropod orders were consumed by HAAM, their heavy exploitation of caterpillars lowered the diversity estimate nearly to the rank of AKEP. In fact, HAAM was ranked slightly lower than AKEP by the Simpson index, which is more sensitive to unevenness in the abundance of prey types. Arthropods in samples of the top-ranked non-honeycreeper generalist, HAEL, were nearly four times richer and five times more diverse than arthropods in AKIP samples. In contrast, arthropod richness was relatively low for the OMAO, a frugivorous non-honeycreeper, but diversity was high because prey abundance and prevalence in the samples was not overwhelmingly dominated by just a few orders.

The two introduced species ranked high (RBLE) and intermediate (JAWE) in arthropod richness and diversity. JAWE were intermediate in rank for both indices due to their consumption of many orders but with some emphasis on Araneae and Homoptera. Although among the endangered species, richness of arthropod prey for HCRE was closest in rank to the introduced species, diversity was significantly greater for the introduced species compared to all three endangered birds. Diet diversity or generalization is a manifestation of behavioral flexibility, which is a key trait in the successful invasion of introduced bird species (Sol *et al.* 2002), and it likely increases the potential for competition with native species (Foster 2009).

Because caterpillars are the premier prey of most species at Hakalau, variation in their use may be a more important indicator than arthropod orders, of diet vulnerability among bird species. High richness and diversity of arthropod orders in the fecal samples did not consistently correspond to high richness and diversity of caterpillar morpho-species. The species with the greatest consistency was the RBLE, which ranked second in terms of arthropod richness and diversity as well as first in caterpillar diversity and second in caterpillar richness. Less consistent was the HAEL, which ranked first in arthropod order richness and diversity but only fourth in caterpillar richness and third in caterpillar diversity. Least consistent was the HCRE, which ranked first in caterpillar richness and second in caterpillar diversity but fourth and sixth in arthropod richness and diversity, respectively. The high diversity of caterpillars in the diet of HCRE might help explain their somewhat higher population abundance (Camp *et al.* 2010) relative to the other endangered species, assuming that caterpillars were limiting their populations.

Despite heavy use of caterpillars among all the Hawaiian honeycreepers, we observed low richness of caterpillar morpho-species among the two specialists, AKEP and AKIP, and the intermediate species, IIWI. Low caterpillar richness was not unexpected for birds with specialized beak shapes and suggests that the foraging substrates they typically use may not support a wide variety of species or that their repertoire of search images when foraging is limited to certain species. On the other hand, the non-specialists HCRE and HAAM ate a rich variety of caterpillar morpho-species. Caterpillar diversity likewise was low for the specialists and IIWI, which heavily utilized only two morpho-species, but diversity was also low for HAAM, which concentrated on only three morph-species. Low caterpillar diversity also resulted from the heavy exploitation of a single morpho-species (K) by all four honeycreeper species. In contrast, HCRE samples contained many individuals of morpho-species G, yet despite this strong bias its caterpillar diversity was 3.5 times higher than that of AKEP.

Generally, caterpillar richness and diversity was higher for the introduced species than for the endangered species. RBLE and HCRE both consumed a rich assortment of caterpillars, but JAWE ranked lower, which might be expected given its lower overall consumption of Lepidoptera. Caterpillar richness was generally similar for AKIP, whose samples contained the highest proportion of caterpillars of any species, and JAWE. Nevertheless, richness was higher for JAWE than for AKEP, whose samples yielded only two morpho-species. Compared to the introduced species, AKEP was significantly lower and AKIP ranked lower in caterpillar diversity. Nevertheless, caterpillar diversity was significantly greater for HCRE than for JAWE.

We found no clear community-wide patterns of diet richness and diversity distinguishing introduced and endemic bird species at Hakalau. Among native species, the richness of arthropod orders in diets ranged nearly four-fold (3.4–13.2) and arthropod diversity ranged over five-fold (1.6–8.3). The diet richness and diversity of the two introduced species, which successfully invaded a community already stocked with native generalist foragers, were nested within the ranges of the native birds. This might suggest that arthropod prey availability has not been limiting, at least to generalist foragers or species that may not overlap extensively in their use of foraging microhabitats. Nevertheless, should the number of generalists continue to increase, we would expect the potential for competition to increase (Moulton and Pimm 1983, Moulton 1993), at least among birds foraging extensively in the same microhabitats. Additional predatory pressure exerted on arthropod populations might reduce the already low diet richness and diversity among endangered species. On the other hand, arthropod populations will likely increase at Hakalau as habitats are restored, and improved foraging conditions might result in greater diet richness and diversity among native species. The establishment of new alien arthropod species could enrich diets if birds found them to be suitable prey, or they might diminish the abundance of existing prey through predation, parasitism, or competition.

Diet Similarity

Understanding diet similarity and the potential for competition among species may be important to the conservation of Hawaiian forest birds. Our results provide the first quantitative comparison of the similarity in arthropods consumed by birds at Hakalau, but we caution against using them to infer competition without also considering similarity in the use of foraging substrates. Although a number of species forage on at least some of the same substrates, there is also considerable separation in terms of vertical position in the canopy, frequency of substrates used, and types of foraging maneuvers employed (U.S. Geological Survey unpublished data). Important differences in foraging niche can also exist between the sexes of some species (Ralph and Fancy 1996).

Similarity in the use of arthropod orders by Hakalau birds offers a starting point for examining diet similarity at lower taxonomic levels, although it does not by itself indicate overlap in the use of species, genera, or even families of arthropods. No significant differences were seen in the arthropod orders consumed by specialist and generalist Hawaiian honeycreepers, and the only significant difference in caterpillar morpho-species consumed was between AKEP and HCRE. On the other hand, differences between introduced and endangered birds in the arthropod orders they consumed were significant for all pairs of species except AKEP and JAWE. Even so, no differences between species pairs were significant in the caterpillar morpho-species they consumed. Additional samples and a finer resolution of prey identification, particularly for the endangered species, are likely necessary to reveal differences in diet among species.

Methodological Considerations

Conducting richness and diversity analyses at the order level constrains the conclusions that can be drawn because the composition of prey species or even genera or families may differ among birds. Likewise, identifying species rather than morpho-species of caterpillars consumed by birds would provide much needed resolution about the richness, diversity, and similarity of the diets of birds at Hakalau. Some morpho-species might represent different life stages (instars) within a species, which, even if true, might represent an important aspect of resource partitioning among bird species. For example, younger caterpillar instars sometimes utilize different feeding or refuge substrates than do older instars, which could expose them to different bird predators. Furthermore, some morpho-species may represent taxa with different life histories, host plants, or microhabitat requirements, in which case the potential for competition among bird species may be reduced, depending on the results of foraging studies.

Fecal analysis is a useful method for determining gross diet composition without harming the birds (Ralph *et al.* 1985, Rosenberg and Cooper 1990, Burger *et al.* 1999, Deloria-Sheffield *et al.* 2001), but stomach samples permit identification of prey to finer taxonomic levels (Baldwin 1953). Nevertheless, results can be similar, as we found when we compared results from 308 JAWE samples from windward Hawai'i Island that were obtained by stomach flushing (lavage) with those from JAWE fecal samples from Hakalau (U.S. Geological Survey unpublished data). Furthermore, we identified similar numbers of arthropod orders in the diets of two species that Baldwin (1953) collected for analysis of stomach contents. Baldwin identified prey from 10 orders in stomachs of IIWI he collected, and we found the same number in IIWI fecal samples. Baldwin found 11 orders in HAAM stomachs, whereas we found 13 in fecal samples. Therefore, increasing the number of samples from APAP should yield about 11 arthropod orders, the number found by Baldwin, rather than only the four we found. Similarly, we did not find five insect orders in our seven adult AKIP fecal samples that were found in 39 fecal samples by Ralph and Fancy (1996), including Diptera, Hemiptera, Homoptera, Hymenoptera, and Neuroptera, although we did identify Hymenoptera and Neuroptera in AKIP nestling samples. Additional AKIP fecal samples would likely have revealed at least occasional consumption of these taxa. We also could expect to find more caterpillar morpho-species but perhaps few other arthropod orders with additional AKEP sampling. We found the same arthropod orders that Lepson and Freed (1997) identified most frequently in 87 fecal samples of AKEP on Mauna Loa Volcano, Hawai'i Island, and 'akeke'e (*Loxops caeruleirostris*) on Kaua'i Island, when they were classified as a single species.

Small samples sizes for some species also limited our ability to identify seasonal trends in the use of Lepidoptera and Araneae. Months with the fewest samples were May–July, during the latter part of the nesting season and when fledglings are becoming increasingly independent of parental care. Moreover, temporal trends in arthropod consumption by endangered species were driven by HCRE, which was overwhelmingly represented compared to AKEP and AKIP.

Implications for Conservation

Both the *Revised Recovery Plan for Hawaiian Forest Birds* (U.S. Fish and Wildlife Service 2006) and the *Hakalau Forest National Wildlife Refuge Comprehensive Conservation Plan* (U.S. Fish and Wildlife Service 2010) recognize the importance of investigating the foraging behavior and food requirements of native birds, determining the availability of key foods, and identifying threats from food depletion and competition with introduced species. Our results support the relevance of these recommendations and contribute to the understanding of the complex trophic interactions between birds and arthropods at Hakalau, the flagship for Hawaiian forest bird conservation. They also provide a benchmark for evaluating dietary shifts that may result from interactions with invasive species, forest succession (primarily through habitat restoration), variation in arthropod community structure, and climate change.

Our results also provide insights about other Hawaiian forest bird communities and may be helpful in understanding challenges in recovering populations of other endangered or declining species. Low arthropod diversity and exceedingly heavy exploitation of caterpillars (91% of prey from 55 fecal samples) were also hallmarks of the endangered specialist insectivore, kiwikiu or Maui parrotbill (*Pseudonestor xanthophrys*; MAPA), and its nestlings in high montane, wet forest on Maui (Peck *et al*. 2015). MAPA is the most specialized extant insectivore on Maui, and its beak is similarly asymmetrical in shape but much stouter compared to that of the AKIP on Hawaiʽi Island (P. Banko and W. Banko 2009). The diversity of arthropod orders for the two species was similar (1.8 MAPA vs. 1.6 AKIP), although arthropod richness was 2.4 times higher for MAPA (8.0 vs. 3.4). The Maui ʽalauahio (*Paroreomyza montana*; MAAL) also closely matched its ecological counterpart, HCRE, on Hawaiʽi Island in terms of the prevalence of caterpillars (43% MAAL vs. 48% HCRE) and Araneae (16% MAAL vs. 22% HCRE) in its diet (Peck *et al*. 2015). Arthropod richness (9.0 MAAL vs. 11.0 HCRE) and diversity (4.4 MAAL vs. 4.5 HCRE) were also similar. Symmetry in diet diversity between bird communities could indicate similarities in habitat structure and quality, arthropod availability, and the relative abundance and feeding behavior of specialists and generalists. Marked differences in diet diversity between bird communities might underscore the vulnerabilities of species to competition or food web disruption, which could help managers develop ways for improving habitat quality.

Birds, particularly generalist insectivores, can impact forest arthropod communities in Hawaiʽi through top-down trophic interactions (Gruner 2004), but soil nutrient levels and other bottom-up factors also affect arthropod community structure and the population dynamics of species that may compete (e.g., Araneae) with birds for prey or that are the prey (e.g., caterpillars) of birds. Seasonal changes in arthropod populations are often subtle, or at least difficult to detect (Peck 1993, U.S. Geological Survey unpublished data), but we had a rare opportunity to observe a massive increase in caterpillar abundance and the resulting changes in the foraging behavior, diet, and body weight of birds at Hakalau. During 2013–2014, the native koa moth (*Scotorythra paludicola*; Geometridae) irrupted in massive numbers, defoliating many koa trees across windward Hawaiʽi Island (Banko *et al*. 2014). It was the largest outbreak ever recorded and the first on Hawaiʽi Island in 60 years (Davis 1955, Haines *et al.* 2009). We documented increased bird activity in koa trees as caterpillar numbers increased, then decreased activity after koa defoliation and the crash of caterpillar numbers. Diet analyses indicated that HAAM and JAWE greatly increased their consumption of caterpillars during the outbreak, both shifting from predominantly Psyllidae (Homoptera) to caterpillars during the outbreak. Moreover, the caterpillar component of the HAAM diet shifted strongly to the irrupting *S. paludicola*. Most common bird species gained weight during the outbreak, with significant gains for the four small insectivores (JAWE, HAAM, HAEL, and HCRE). Due to their low numbers, we could not evaluate the response of the two specialists, AKEP and AKIP, to the superabundance of caterpillars, but the outbreak revealed how Hawaiian forest birds generally, like some continental birds responding to insect outbreaks (McMartin *et* *al.* 2002), shift their diets and benefit, at least in the short-term, from increased caterpillar abundance. Understanding the ability of specialists to switch to alternative prey has conservation significance because it can help to predict their responses to changes in arthropod populations due to a variety of environmental factors and because dietary shifts may require changes in foraging behavior (Sample *et al.* 1993) and incur energetic costs (Whitmore *et al.* 1993), which may affect future reproduction (Marshall *et al.* 2002).

Additional research is needed to resolve critical trophic relationships among all the bird species at Hakalau. In particular, results of our diet study are insufficient to support the view that JAWE pose the major threat to endangered and other native bird species at Hakalau through competition for food (Freed and Cann 2009; 2010; 2012a, b; 2013a, b; 2014; Freed *et al.* 2008, 2009), despite some overlap of arthropod prey types and a generally increasing population (Camp *et al.* 2010). Moreover, AKEP forage "almost exclusively on terminal leaf clusters of ʻōhiʻa and among koa leaves and seedpods" (Lepson and Freed 1997), which distinguishes them from JAWE (van Riper 2000). On the other hand, we believe that concern about the overall impact of introduced birds and other predators on arthropod populations is warranted, considering, for example, the generalized diet of RBLE. Moreover, a new invasive, generalist insectivore, the Japanese bush-warbler (*Cettia diphone*; Cettiidae) is spreading at Hakalau and many other areas of Hawaiʻi Island (Pyle and Pyle 2009). Like the RBLE, it is a denizen of the forest understory and is unlikely to forage in the middle or upper canopy. Even so, impacts to arthropods in the understory might have repercussions higher in the canopy, and the ecology of Lepidoptera species throughout the forest understory and canopy should be investigated. In addition to invasive bird species, the native generalist, HAAM, which is more abundant than JAWE and RBLE combined in open forest habitats (Camp *et al.* 2010) and which heavily exploits caterpillars, might exert at least as much pressure on arthropod populations as the introduced birds. Forest birds can affect populations of their arthropod prey, especially when they occur at relatively low levels (Otvos 1979, Holmes 1990, Glen 2004). Therefore, to identify competitive interactions and understand the dynamics of forest food webs and arthropod populations in the disturbed forest community of Hakalau, it is necessary to determine how multiple, small insectivores and other factors may limit the availability of arthropod prey that are critical to endangered or other native species.

Whatever degree of competition may exist among birds at Hakalau, specialized species are most vulnerable to food web disruption (Perkins 1903, P. Banko and W. Banko 2009), and many more specialists than generalists became extinct or declined historically from the combined impacts of a wide variety of food competitors, predators, diseases, and habitat changes (reviewed in W. Banko and P. Banko 2009). One of the principle threats to caterpillar prey at Hakalau may come from alien parasitoid wasps, which kill about 25% of their hosts (U.S. Geological Survey unpublished data). Alien parasitoids are abundant, diverse, and widely distributed in low and mid elevation forests, but they are also commonly found in upper montane and even subalpine forests (Henneman and Memmott 2001, Brenner *et al.* 2002, Oboyski *et al.* 2004, Peck *et al.* 2008, Kaufman and Wright 2010). Alien parasitoids also attack spiders (Perkins 1913), another key prey group of Hawaiian birds, although there is no information about their primary host species or impacts on host populations. *Vespula pensylvanica,* or the Western yellowjacket wasp, is another potential threat to a wide range of arthropod prey important to Hawaiian birds, including caterpillars, spiders, and Hemiptera (including Homoptera; Gambino 1992, Wilson *et al*. 2009). Arthropods are the primary protein source from which *Vespula* provision their brood, and the number of prey items harvested by foragers from single, large, two-year old colony in Hawaiʻi Volcanoes National Park was estimated to have been in the million (Gambino 1991, 1992). *Vespula* populations are relatively scarce at Hakalau in wet years, but numbers increase in dry years (U.S. Fish and Wildlife Service 2010). A more detailed understanding of the ecology of these invasive threats as well as the feeding ecology of Hawaiian birds has been a longstanding conservation need, because both native and alien predators and parasitoids attack the arthropod prey of native forest birds. R. C. L. Perkins, the preeminent naturalist of Hawai`i when it supported much greater biodiversity, acknowledged the importance of arthropods to birds not only as their prey but also as their competitors (in this case native competitors) when he noted over a century ago (Perkins 1903), "For many of these hidden larvae [caterpillars] they [`ākepa, referring generally to taxa on all islands] compete rather with the native wasps than with other birds."

ACKNOWLEDGEMENTS

This research was funded by the Hawai`i Division of Forestry and Wildlife with the assistance of Scott Fretz, the Science Support Program of the U.S. Fish and Wildlife Service, and the Wildlife Program of the U.S. Geological Survey. We are grateful to Bethany Woodworth for making the fecal samples available to us. We thank M. Euaparadorn, J. Cappadonna, and M. Grove for field and lab assistance. We also thank J. Jeffrey, J. Glynn and R. Wass of Hakalau Forest NWR for logistical support. We are grateful to Steve Kendall and Steve Hess for helpful comments on an earlier draft of the manuscript.

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