

# Seed dispersal by a captive corvid: the role of the ‘Alalā (*Corvus hawaiiensis*) in shaping Hawai‘i’s plant communities

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**Abstract.** Species loss can lead to cascading effects on communities, including the disruption of ecological processes such as seed dispersal. The endangered ‘Alalā (*Corvus hawaiiensis*), the largest remaining species of native Hawaiian forest bird, was once common in mesic and dry forests on the Big Island of Hawai‘i, but today it exists solely in captivity. Prior to its extinction in the wild, the ‘Alalā may have helped to establish and maintain native Hawaiian forest communities by dispersing seeds of a wide variety of native plants. In the absence of ‘Alalā, the structure and composition of Hawai‘i’s forests may be changing, and some large-fruited plants may be dispersal limited, persisting primarily as ecological anachronisms. We fed captive ‘Alalā a variety of native fruits, documented behaviors relating to seed dispersal, and measured the germination success of seeds that passed through the gut of ‘Alalā relative to the germination success of seeds in control groups. ‘Alalā ate and carried 14 native fruits and provided germination benefits to several species by ingesting their seeds. Our results suggest that some plants rely heavily on ‘Alalā for these services. In captivity, juvenile birds displayed seed dispersal behaviors more often than adult birds for most fruiting plants in our study. We introduced captive ‘Alalā to two large-fruited, dry-forest plants, not previously recorded as ‘Alalā food resources, but which may once have been part of their natural diet. The seed dispersal behavior that ‘Alalā displayed toward these species supports the inclusion of dry and mesic forests in ‘Alalā habitat restoration plans and adds weight to the idea that plant dispersal limitation may contribute to the rarity of these plants. Our study provides evidence that ‘Alalā have the capacity to play a vital role in maintaining the diversity of fruiting plants in native Hawaiian forests through seed dispersal and enhanced seed germination, thus adding greater urgency to efforts to restore ‘Alalā to their former range.

**Key words:** ‘Alalā; anachronism; captive breeding; *Corvus hawaiiensis*; dispersal limitation; endangered species; foraging behavior; frugivory; germination success; Hawaiian Crow; restoration; seed dispersal.

## INTRODUCTION

In addition to biodiversity loss, species extinction can drive cascading impacts on entire communities through the disruption of ecological processes and partnerships (Diamond et al. 1989). The replacement of bison (*Bison bison*) with domestic cattle on North America’s grasslands does not support the same diversity of plant species that once thrived in and adjacent to bison wallows (McMillan et al. 2011). Other species remain extant in the wild but significant and ongoing anthropogenic activities threaten their survival and ecological function. Frugivorous Amazonian fishes provide remarkably effective and long-distance seed dispersal for rain forest plants but are threatened by overharvest by

humans (Anderson et al. 2009). Alarming, although species with close parasitic or mutualistic partners are predicted to be especially vulnerable to coextinction, examples are rarely observed in nature (Dunn et al. 2009).

When influential species disappear completely, communities may be left with “ghosts of past mutualisms” (Guimaraes et al. 2008). Classic examples of such anachronisms are the large-fruited plants that persist in South America despite the loss of their putative primary seed dispersers, the Pleistocene megafauna (Janzen and Martin 1982, Guimaraes et al. 2008). Extending this  $\bar{x}$  concept to island ecosystems, where lower overall species diversity means fewer secondary dispersal options for plants, demonstrates the degree to which island species are vulnerable to becoming anachronisms following the extinction of primary dispersal agents (Hansen and Galetti 2009). In oceanic island ecosystems, birds are often the sole native animal seed disperser of native plants.

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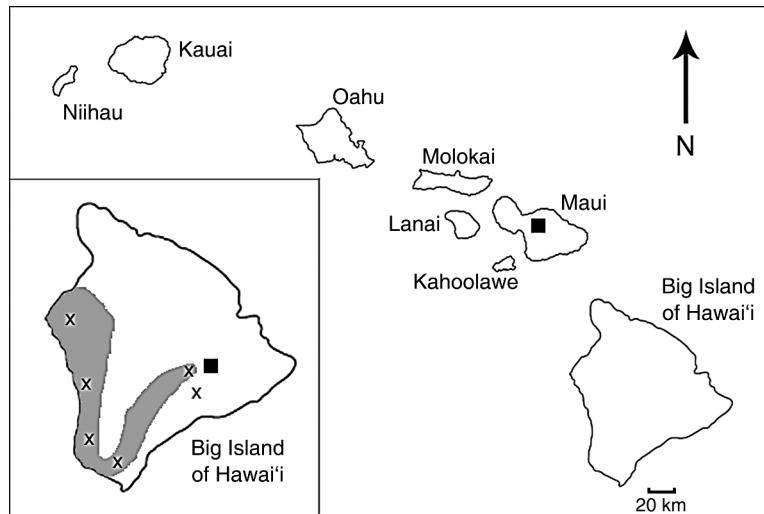


FIG. 1. 'Alalā (*Corvus hawaiiensis*) breeding facilities in the Hawaiian Islands include the Keauhou Bird Conservation Center on the Big Island of Hawai'i in Volcano, Hawaii, USA, and the Maui Bird Conservation Center in Makawao, Hawaii, USA (black squares). The historic range of 'Alalā (gray shading) is shown on the Big Island of Hawai'i (after Banko et al. [2002]) as well as the locations of fruit collection sites (×).

Birds facilitate plant dispersal by moving seeds away from the parent plant and thus decreasing intraspecific competition between parent plants and progeny (Malmberg and Willson 1988), placing seeds in favorable locations through caching behavior (McKinney et al. 2009), and increasing seed germination success by removing fleshy fruit (Paulsen and Hogstedt 2002) or scarifying the seed coat (Paulsen and Hogstedt 2002, Rodriguez-Perez et al. 2005). Population declines or extinctions of these bird dispersers can thus lead to cascading negative effects on the plant community (Sekercioglu et al. 2004, McKinney et al. 2009, Babweteera and Brown 2010).

The Hawaiian archipelago is a model system for studying the impact of bird extinctions on plant communities. Internal bird dispersal played a prominent role in transporting the ancestors of Hawai'i's native fruiting flora to the islands (Carlquist 1967, Price and Wagner 2004) and has evolved in several additional plant lineages whose ancestors used externally adhesive seed dispersal (Price and Wagner 2004). Large-scale extinction and endangerment of native Hawaiian bird species (Olson and James 1982, Steadman 1995, Boyer 2008) is likely to have fundamentally altered bird-plant mutualisms in Hawai'i (Pau et al. 2009). Excluding the 'Ō'ū (*Psittirostra psittacea*), which is listed as critically endangered and possibly extinct (IUCN 2011), only two primarily frugivorous native forest birds remain extant on the Big Island of Hawai'i: the 'Ōma'o or Hawaiian Thrush (*Myadestes obscurus*) and the 'Alalā or Hawaiian Crow (*Corvus hawaiiensis*). 'Ōma'o, although extirpated from the southern mesic and dry forests (van Riper and Scott 1979), remain relatively common in forests on the eastern slopes of the island. The 'Alalā, the last remaining species from a small evolutionary

radiation that included at least two, and perhaps four, other Hawaiian corvids (James and Olson 1991; H. James, *personal communication*), is genetically closer to the Common Raven (*Corvus corax*) of North America and Eurasia than to typical crows (Fleischer and McIntosh 2001) and also resembles the Common Raven in size, vocal repertoire, and intelligence (Banko et al. 2002).

Early western naturalists documented 'Alalā as common in the southern and western mesic and dry forests of the Big Island of Hawai'i (Henshaw 1902, Perkins 1903; see Fig. 1) and fossil evidence probably places this species on Maui as well, but only until early Polynesian colonization (James et al. 1987; see Fig. 2). Throughout the 1900s and into the 21st century, 'Alalā populations declined and became increasingly fragmented due to multiple factors including persecution, habitat loss, and predation and disease transmission by invasive species (Henshaw 1902, Perkins 1903, Munro 1960, Giffin et al. 1987, Banko et al. 2002). Despite the protection afforded by its status on the U.S. Endangered Species List (USFWS 2009) and restoration efforts involving captive-bred birds in the 1990s (USFWS 2003, Walters 2006), the wild population dwindled to the last sighting of a wild 'Alalā in 2002 (Banko 2009). As of December 2011, the captive population of 95 individuals persists in two propagation facilities: the Maui Bird Conservation Center (MBCC) and the Keauhou Bird Conservation Center (KBCC); see Fig. 1. The goals of the captive breeding program are to maintain a self-sustaining captive 'Alalā population and to reestablish 'Alalā populations within their native range (Lieberman and Kuehler 2009).

The 'Alalā undoubtedly played an important, and now unfulfilled, ecological role in maintaining forest

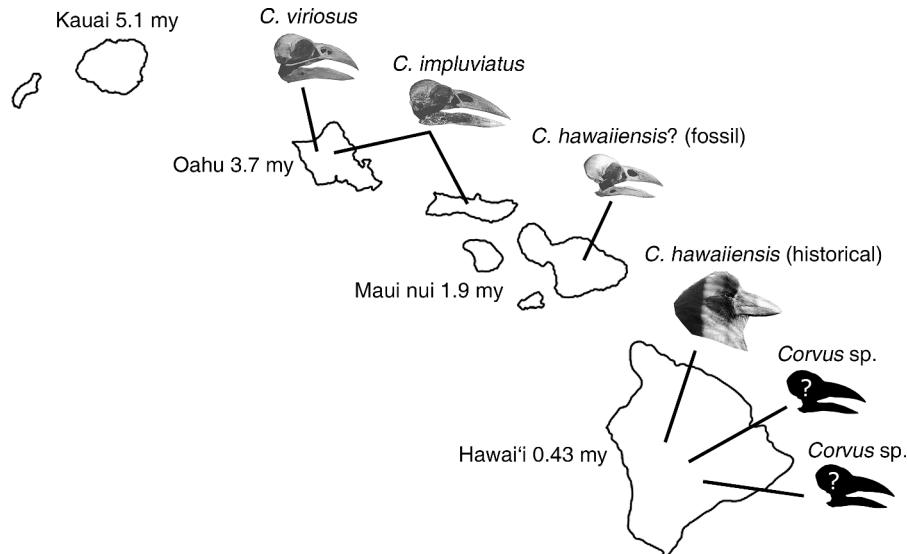


FIG. 2. Age of formation of Hawaiian islands (my, million years) and distribution of fossil *Corvus* species as well as *C. hawaiiensis*. 'Alalā were documented historically on the Big Island of Hawai'i (Henshaw 1902, Perkins 1903), and the fossil record indicates that two unnamed *Corvus* species once shared this island with 'Alalā (H. James, *personal communication*). A species tentatively identified as *C. hawaiiensis* appears in the fossil record on Maui (James et al. 1987). Two other *Corvus* species fossils were discovered on Maui nui and O'ahu (James and Olson 1991). The continued absence of crows in the fossil record on Kauai probably indicates that crows did not exist on this island (H. James, *personal communication*). Images of corvid skulls are from James and Olson (1991), reprinted with permission.

diversity and structure by dispersing native seeds over a broad range of sizes (Fig. 3). In the absence of 'Alalā, 'Ōma'o, and other native birds, some Hawaiian plants may now rely entirely on small, introduced bird species such as the Red-billed Leiothrix (*Leiothrix lutea*) and the Japanese White-eye (*Zosterops japonicus*) for seed dispersal (Foster and Robinson 2007). However, due to their substantially smaller body and bill sizes (Fig. 3; Male et al. 1998, van Riper 2000), these birds may alter forest communities (Wheelwright 1985, Jordano et al. 2007, Babweteera and Brown 2009) and drive the selective dispersal of small-seeded native and exotic invasive plants in Hawai'i's forests (Chimera and Drake 2010).

Our understanding of seed dispersal by 'Alalā is incomplete and based on limited observations by early naturalists (e.g., Henshaw 1902, Perkins 1903, Rock 1913) and later studies in highly modified habitats (Tomich 1971, Sakai et al. 1986, Sakai and Carpenter 1990, Banko et al. 2002). Knowledge regarding the connection between many native fruit-bearing plants and the 'Alalā is therefore dependent on the spatial distribution of pollen and fossil records (Olson and James 1982, James et al. 1987, James and Olson 1991, Pau et al. 2009). Although 'Alalā have not been observed consuming most dry-forest plants, the large fruit size of most dry-forest plants and their lack of current seed dispersers has led some researchers to suggest that 'Alalā and other corvids (Fig. 2) were probably important seed dispersers in dry and mesic forests throughout the archipelago (J. Price, L. Pratt, and T. Pratt, *personal*

*communication*; Fig. 3). Some dry-forest plants, such as loulou palms (*Pritchardia* spp.) and halapepe (*Pleomele hawaiiensis*) (hereafter "large-fruited plants") are rare or endangered today, and could be included in habitat restoration plans for 'Alalā release sites; they may in turn benefit from 'Alalā recovery. Identifying these possible anachronisms in Hawaiian forest plants could provide incentive for restoring past mutualisms using extant flora and fauna to avoid further secondary extinctions.

Our objective is to document the 'Alalā's potential role in maintaining and restoring Hawai'i's forests through seed dispersal. We used feeding trials with captive 'Alalā to determine (1) the dispersal potential of captive 'Alalā for native Hawaiian fruiting plant species; (2) whether bird age and sex influence foraging choices and seed dispersal; and (3) whether 'Alalā ingestion results in improved seed germination, as the avian digestive process may chemically prepare seeds for germination. Because we were also interested in the hypothesis that some Hawaiian native plants persist in nature as anachronisms, we included in the feeding trials several species of large-fruited plants that had never before been reported as being consumed by wild 'Alalā.

## METHODS

### *Study sites and sample size*

We collected native Hawaiian fruits in the months of August to December 2009 and June to December 2010 from sites within the historic range of the 'Alalā (Fig. 1). Sites included The Nature Conservancy preserves of

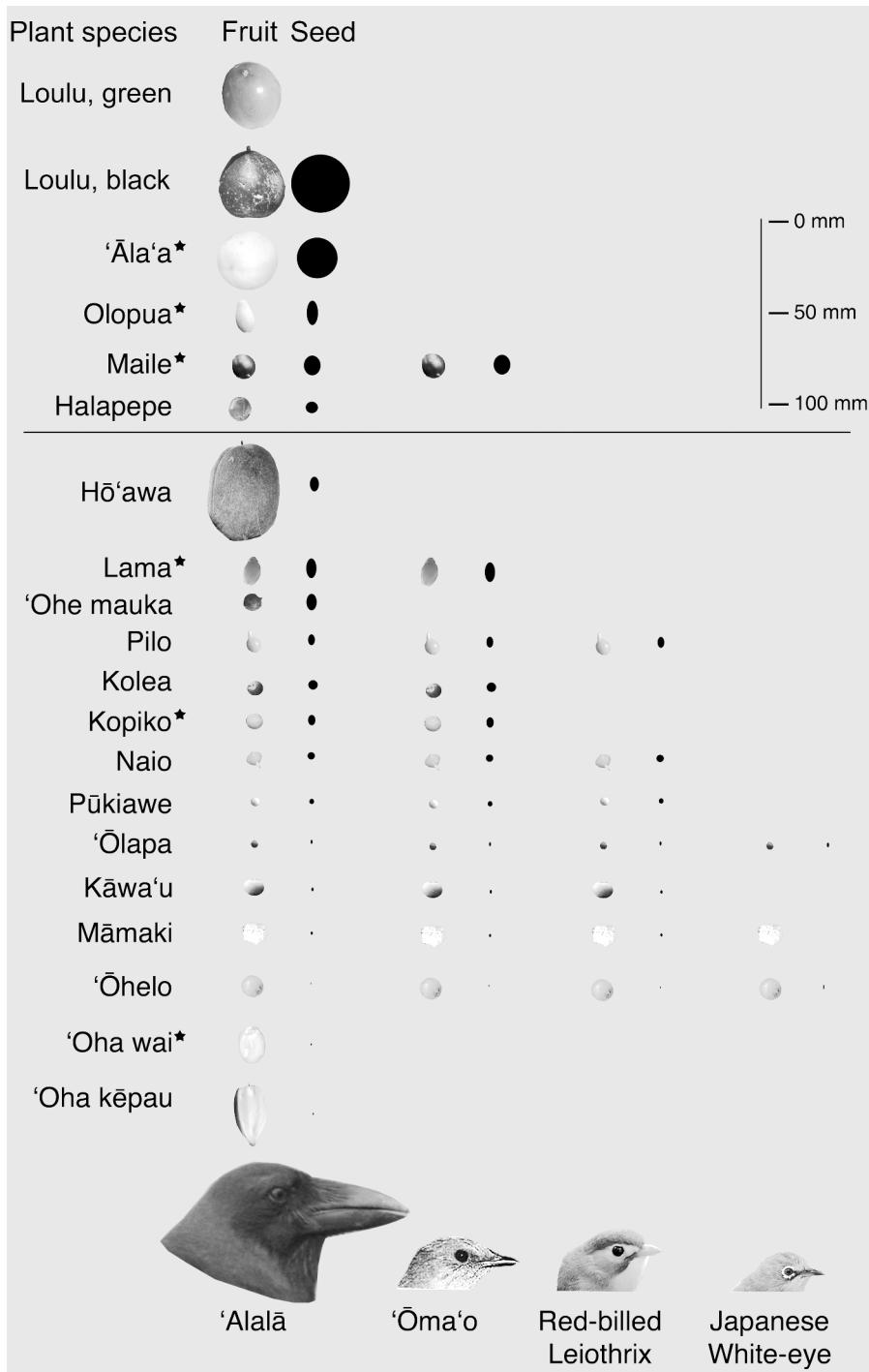


FIG. 3. Native fruits and seeds consumed (in order of seed size) by 'Alalā (*Corvus hawaiiensis*; native, extinct in the wild), 'Ōma'o (*Myadestes obscurus*; native, extirpated from 'Alalā historic range), Red-billed Leiothrix (*Leiothrix lutea*; exotic introduced, common), and Japanese White-eye (*Zosterops japonicus*; exotic introduced, common) (data sources: Tomich 1971, Sakai et al. 1986, Sakai and Carpenter 1990, Male et al. 1998, Wagner et al. 1999, Wakelee and Fancy 1999, van Riper 2000, Banko et al. 2002, Foster and Robinson 2007; L. Pejchar, *unpublished data*; S. Culliney, *unpublished data*). Only the 14 fruits and seeds used in the flock-wide study and the six fruits (with star symbol) used in the trials involving a subset of 'Alalā are shown. The top five species (placed above the horizontal line) are speculated to have been part of the 'Alalā diet, based on possible prehistoric range overlap (J. Price, T. Pratt, L. Pratt, *personal communication*).

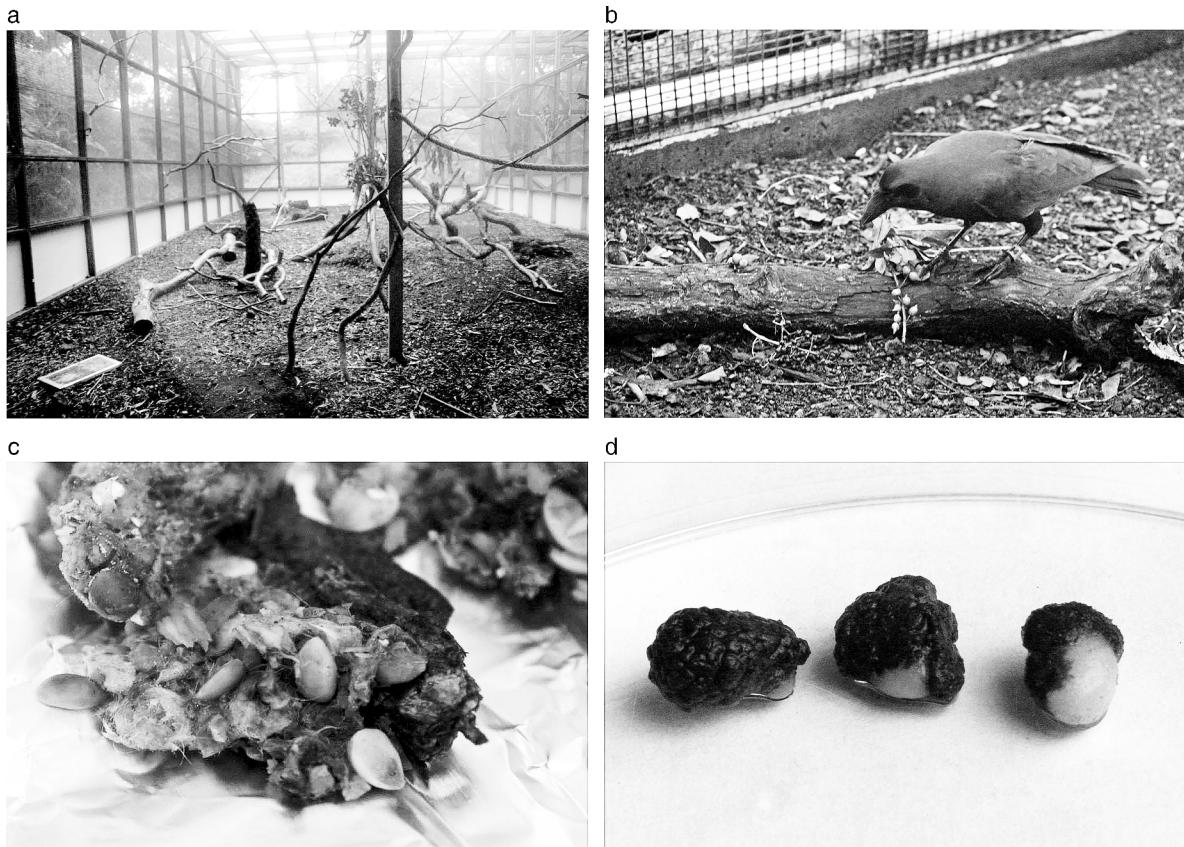


FIG. 4. Clockwise from upper left: (a) an 'Alalā aviary with a plexiglass square for collection of droppings and pellets at bottom left, (b) an adult female 'Alalā selects fruits, (c) pilo (*Coprosmma rhynocarpa*) seeds in an 'Alalā pellet, (d) partially scarified hō'awa (*Pittosporum hosmeri*) seeds removed from an 'Alalā pellet.

Kona Hema and Kaiholena, Ka'ūpūlehu dryland forest, Kīpuka Kī, Kīpuka Puauolu, Kīlauea summit and Nāulu Forest in the Hawai'i Volcanoes National Park, the Amy B. H. Greenwell Ethnobotanical Garden, and the forests immediately surrounding KBCC. We normally collected whole branches with fruits. When this practice would have harmed the plant, as was the case with large-fruited plants, we collected only single fruits. Fruits and branches were refrigerated to preserve freshness for at least 24 hours and no longer than two weeks before use in feeding and germination trials.

Seed germination trials took place in a greenhouse at the KBCC facility. Fruit feeding trials and collection of ingested seeds took place within 'Alalā aviaries. These mosquito-, bird-, and mammal-proof aviaries are open to air and weather, generally measure  $12 \times 3 \times 4.2\text{--}6$  m high, have interconnecting hatches and cinder floors, with sparse live vegetation and dead logs, and cut-limb perches bracketed to the walls including high ( $\sim 4.8$  m) sentinel perches (Fig. 4a). During our study, 61 'Alalā were held at KBCC singly, as pairs, or in groups of 4, 8, or 10 birds. All birds were in visual and vocal contact with conspecifics, and all individuals were identifiable by their color bands. 'Alalā reach sexual maturity at about

three years of age, and therefore we classified birds less than three years as "juveniles" and those older than three years as "adults." Our trials included 57 'Alalā (13 juvenile males, 9 juvenile females, 16 adult males, 19 adult females); 4 birds were excluded due to aberrant behaviors as a result of imprinting and/or aggression toward humans. Because our analyses accounted for the number of times each bird received each plant species, we included data collected on an adult female that died and a juvenile male that was transferred to MBCC during our study. All 'Alalā were cared for daily by KBCC staff and were fed an omnivorous diet of commercial (de-seeded) fruits, animal protein, and proprietary feeds such as pellets. Although the birds at KBCC did not receive native fruits as part of their regular diet, all had been exposed to some species of native fruits occasionally as enrichment items.

#### *Foraging behavior and seed dispersal*

We selected plant species for use in feeding trials based on a list of 26 native Hawaiian plants that wild 'Alalā had been observed to consume (Tomich 1971, Sakai et al. 1986, Sakai and Carpenter 1990, Banko et al. 2002). Unfortunately, due to limitations of fruiting

TABLE 1. Native fruiting plant species used in the flock-wide feeding trials and in those trials that involved a subset of the flock of 'Ālālā (*Corvus hawaiiensis*).

Feeding trial type, plant species used, and source of data	Mean size (mm)		No. 'Ālālā	Number of times			Number of seeds		
	Fruit	Seed		Given to each bird	Bird observed eating†	Bird observed carrying†	Bird observed caching	Given‡	Found ingested§
<b>Flock-wide</b>									
Hō'awa <sup>1,2</sup> ( <i>Pittosporum hosmeri</i> )	55 <sup>A</sup>	9 <sup>A</sup>	3–25	57	12	140	17	14 688 257	
Kāwa'u <sup>1</sup> ( <i>Ilex anomala</i> )	9 <sup>A</sup>	3	10–29	57	35	40	10	99 957 510	
Kolea <sup>1</sup> ( <i>Myrsine lanaiensis</i> )	7 <sup>A</sup>	6	3	57	25	31	6	1 609 72	
Māmaki <sup>1,2</sup> ( <i>Pipturus albidus</i> )	20 <sup>A</sup>	1	12–18	57	123	54	6	251 856 209	
Naio <sup>1</sup> ( <i>Myoporum sandwicense</i> )	6 <sup>A</sup>	2 <sup>A</sup>	15–24	57	64	41	11	6 019 411	
'Oha kēpau <sup>1,2</sup> ( <i>Clermontia hawaiiensis</i> )	31 <sup>A</sup>	0.5	6	57	54	55	4	167 620 1513	
'Ohe mauka <sup>1</sup> ( <i>Tetraplasandra hawaiiensis</i> )	7 <sup>A</sup>	6	12–25	57	74	63	14	28 017 305	
'Ōhelo <sup>1,2</sup> ( <i>Vaccinium reticulatum</i> )	12 <sup>A</sup>	0.5	12–19	57	193	78	19	419 520 848	
'Ōlapa <sup>1,2</sup> ( <i>Cheirondendron trigynum</i> )	75 <sup>A</sup>	5	10–23	57	89	39	4	49 812 813	
Pilo <sup>1</sup> ( <i>Coprosma rhynocarpa</i> )	10 <sup>A</sup>	7	12–18	57	350	181	20	13 166 1523	
Pūkiawe <sup>1</sup> ( <i>Styphelia tameiameia</i> )	5 <sup>A</sup>	3	10–27	57	111	32	2	6 505 336	
Loulu, black <sup>5</sup> ( <i>Pritchardia schattaueri</i> )	40 <sup>A</sup>	40 <sup>A</sup>	4–12	57	2	57	2	360 0	
Loulu, green <sup>5</sup> ( <i>Pritchardia schattaueri</i> )	31	NA	3–9	57	8	107	3	366 2.75¶	
Halapepe <sup>5</sup> ( <i>Pleomele hawaiiensis</i> )	12 <sup>A</sup>	7 <sup>A</sup>	6–13	57	4	88	20	1 064 13	
<b>Subset of flock</b>									
Kopiko <sup>1</sup> ( <i>Psychotria hawaiiensis</i> )	7 <sup>A</sup>	7	3–5	39	8	14	5	604 4	
Lama <sup>3</sup> ( <i>Diospyros sandwicensis</i> )	17 <sup>A</sup>	13 <sup>A</sup>	1–3	21	0	17	1	67 1	
'Oha wai <sup>1,2</sup> ( <i>Clermontia parviflora</i> )	19 <sup>A</sup>	0.5	6	39	8	8	4	72 090 316	
<b>Non-toxicity</b>									
'Āla'a <sup>5</sup> ( <i>Pouteria sandwicensis</i> )	33 <sup>A</sup>	24 <sup>A</sup>	5–10	2	0	2	2	NA# NA	
Maile <sup>5</sup> ( <i>Alyxia oliviformis</i> )	unk.	13	4–5	2	0	2	1	70 0	
Olopuā <sup>5</sup> ( <i>Nestegis sandwicensis</i> )	19 <sup>A</sup>	unk.	5	1	1	3	3	5 0	

Notes: Plants species were chosen based on prior documentation of 'Ālālā diet in the wild or overlap with the historic range of 'Ālālā (J. Price, T. Pratt, and L. Pratt, *personal communication*). The number of times we gave each plant species to each bird varied based on availability in nature. Results of feeding trials (note that numbers are not model-averaged estimates) show behaviors related to seed dispersal (eating, carrying, caching) as well as the number of ingested seeds compared to the approximate number of seeds given. "NA" means not applicable and "unk." means unknown. Numbered 'Ālālā diet sources: 1, Sakai et al. (1986); 2, Sakai and Carpenter (1990); 3, Tomich (1971); 4, Perkins (1903); 5, speculated based on range overlap. Fruit and seed size sources: A, Wagner et al. (1999); all other data are authors' observations and measurements.

† Raw data; not numbers from model averaging.

‡ Estimated using an average based on number of seeds within fruit as documented in Wagner et al. (1999) and our own observations.

§ Includes seeds found in fecal and pellet samples.

¶ Pieces of green loulu endosperm found in 'Ālālā pellets.

# 'Āla'a used in these pretrials were small unfertilized fruits without seeds.

phenology, abundance, and access to collecting sites, we were unable to include some plants, such as 'ie'ie (*Freycinetia arborea*), that early naturalists recorded as an important part of 'Ālālā diet (Perkins 1903). Instead, we obtained enough fruits from 11 species to conduct feeding trials with all 57 'Ālālā. We included the following plants in the flock-wide study (hereafter we refer to common names only): 'ōlapa (*Cheirondendron trigynum*), 'oha kēpau (*Clermontia hawaiiensis*), pilo (*Coprosma rhynocarpa*), kāwa'u (*Ilex anomala*), naio (*Myoporum sandwicense*), kolea (*Myrsine lanaiensis*), māmaki (*Pipturus albidus*), hō'awa (*Pittosporum hosmeri*), pūkiawe (*Styphelia tameiameia*), 'ohe mauka (*Tetraplasandra hawaiiensis*), and 'ōhelo (*Vaccinium reticulatum*) (Table 1). We obtained a limited number of fruits from three additional species on the list: lama (*Diospyros sandwicensis*), 'oha wai (*Clermontia parviflora*), and kopiko (*Psychotria hawaiiensis*) and we

offered these species to a smaller subset of 'Ālālā (Table 1).

We also conducted trials on five large-fruited plants never documented as being consumed by wild 'Ālālā. To test for possible toxicity, we gave these fruits to nonreproductive adult 'Ālālā and closely monitored their health following observed ingestion. Fruits of two of these plants, loulu (*Pritchardia schattaueri*) and halapepe (*Pleomele hawaiiensis*), were ingested without ill effects, and were included in the flock-wide feeding trials. We tested both the soft, immature ("green") and hard, mature ("black") loulu fruits. Because the adult, nonreproductive 'Ālālā did not ingest the fruits of maile (*Alyxia oliviformis*), olopuā (*Nestegis sandwicensis*), or 'āla'a (*Pouteria hawaiiensis*), we did not use these fruits in the flock-wide trials (Table 1).

During each feeding trial, we offered 'Ālālā the fruits or fruiting branches from 3–7 native plants, based on fruit availability. During each trial, we placed multiple

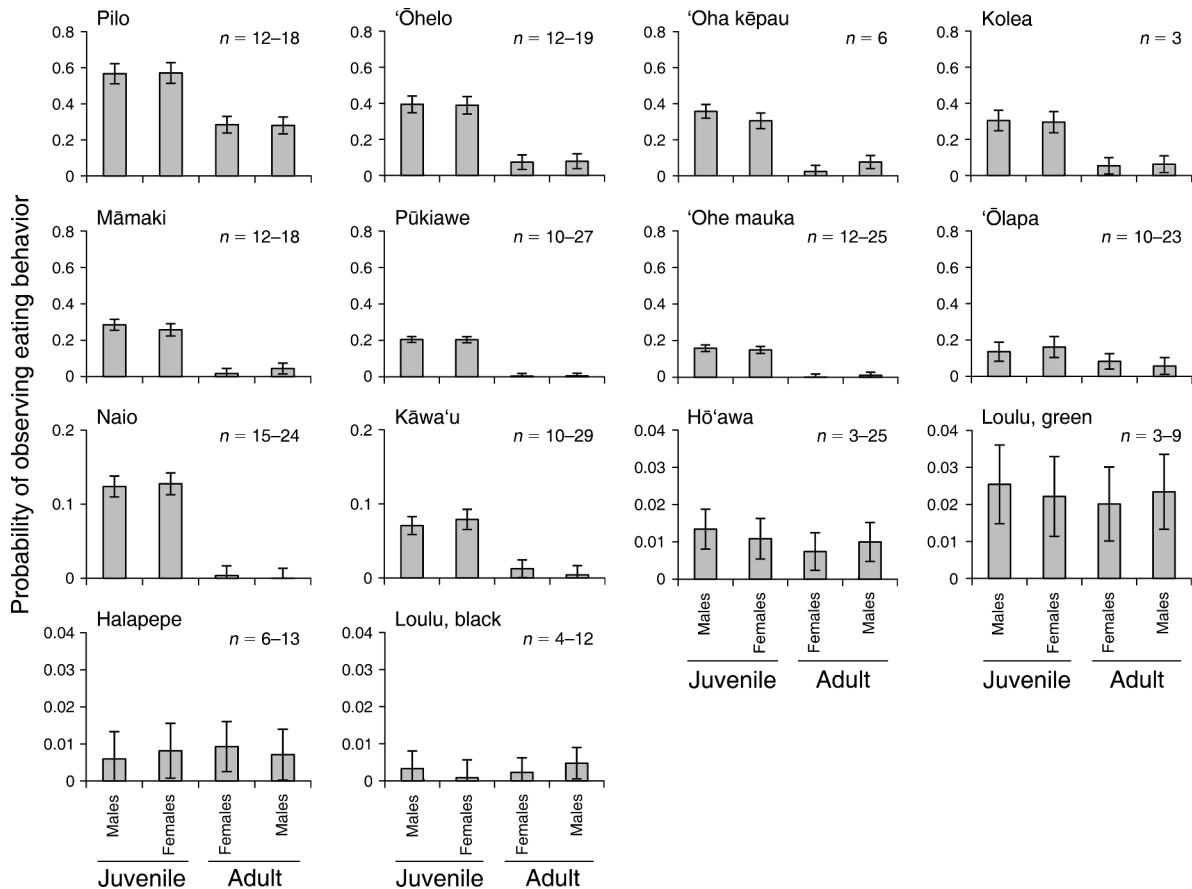


FIG. 5. Model-averaged estimates ( $\pm$ SE) of probabilities of observing 'Alalā eating behavior (note differing scales) for 13 species of native Hawaiian plants (loulou is represented twice with fruits in black mature form and green immature form), separated by bird age and sex classes. The number of times that each bird was given each plant varied, as indicated by sample size ( $n$ ).

fruits for each bird in the pair or flock on a log or the cement curbing in the aviary. From behind a one-way glass window (Fig. 4b), we then recorded the eating, carrying, and caching behaviors of all birds for 5 minutes. We removed remaining fruits and fruiting branches after  $\sim$ 24 hours, and replaced them with fresh fruits and branches. We repeated this procedure for three consecutive days each week. We repeated these trials over the two field seasons; the birds in the study were exposed to each fruiting plant species 12 times on average (Table 1, Figs. 5 and 6). The number of replicate trials for each plant species given to each bird varied due to fruit availability and was taken into account in our analysis.

#### Seed germination

Seeds ingested by 'Alalā are passed through the digestive tract and defecated or are regurgitated as a pellet (Fig. 4c, d), a phenomenon common in birds from raptors (Great-horned Owl *Bubo virginianus*; Houston et al. 1998) to small passerines (Black Phoebe *Sayornis nigricans*; Wolf 1997). Droppings and pellets were collected from squares of plexiglass placed under

sentinel perches (Fig. 4a) about 18 hours after each feeding trial. We used seeds recovered from droppings and pellets in subsequent germination trials. Depending on the number of seeds found, we used at least 10 and up to 50 ingested seeds per plant species in 3–5 germination trials. In the greenhouse we planted three treatment groups (i.e., "fecal" seeds retrieved from droppings; "pellet" seeds retrieved from pellets; and "cleaned" seeds cleaned manually of fruit pulp), as well as a control group (i.e., "whole," seeds planted within whole fruits). Each group mimics a potential seed treatment in the wild: seeds ingested by wild 'Alalā (fecal and pellet), un-ingested seeds with fruit pulp removed by wild 'Alalā (cleaned), and seeds within fruits that 'Alalā drop or cache without manipulation or seeds within fruits that fall from the parent tree to the forest floor in the absence of any seed disperser (whole). Seeds found scattered by the captive 'Alalā but that remained un-ingested were counted and removed but not included in germination trials, with the exception of loulou seeds that showed evidence of external scarification. We chose planting media and watering schedules for each species based on advice given by native plant experts and these conditions

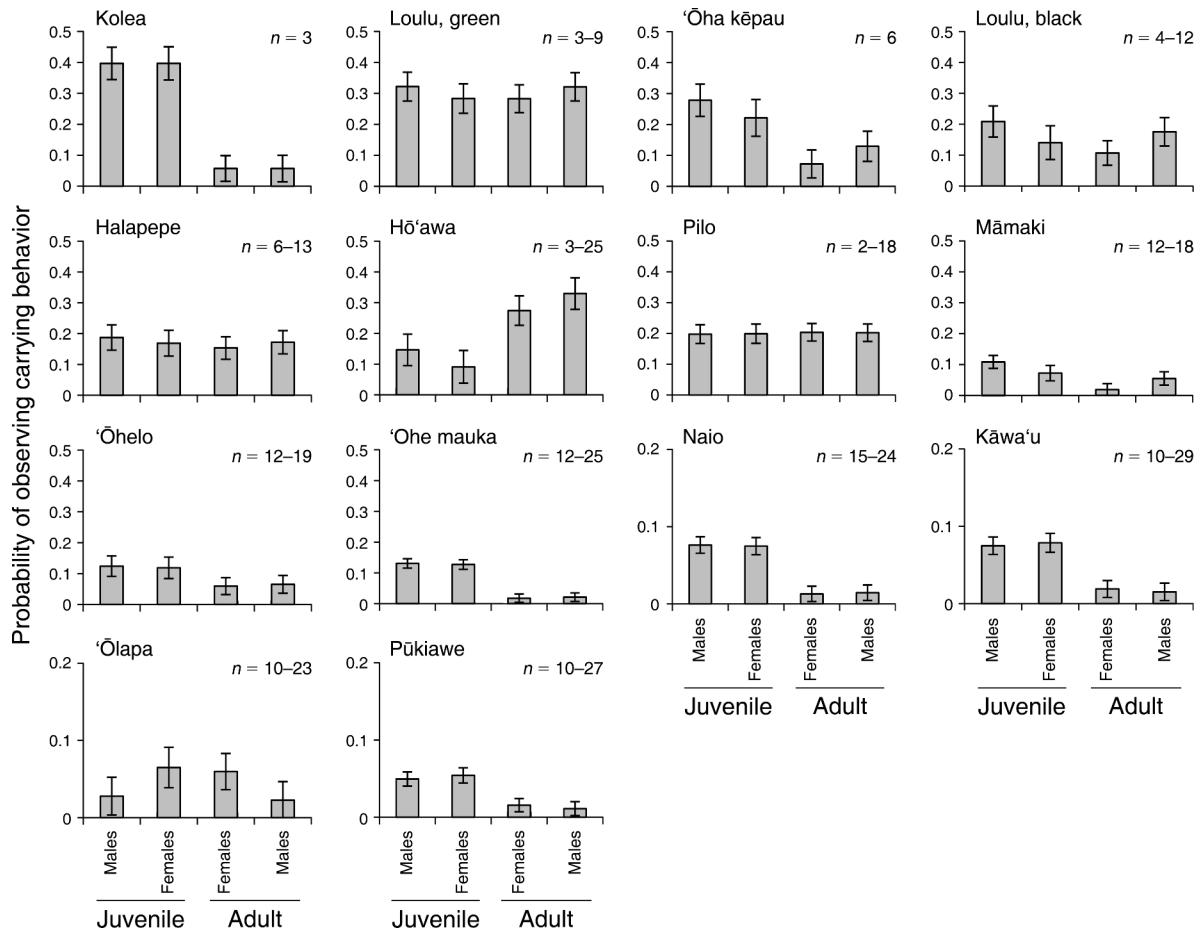


FIG. 6. Model-averaged estimates ( $\pm$ SE) of probabilities of observing 'Alalā carrying behavior (note differing scales) for 13 species of native Hawaiian plants (loulu is represented twice with fruits in black mature form and green immature form), separated by bird age and sex classes. The number of times that each bird was given each plant varied, as indicated by sample size ( $n$ ).

did not vary between the treatments. We tracked germination success for as long as the project allowed (31–75 weeks, depending on the species).

#### Data analysis

We conducted our behavior analyses and germination trials separately for each plant species. We used logistic regression to model the proportion of times that we observed birds eating each plant and carrying each plant as a function of age and sex, weighted by the number of times that we gave each plant species to each bird. We analyzed germination data using logistic regression to model the proportion of seeds germinated as a function of treatment group, weighted by the number of seeds in that group. We conducted all statistical modeling in program R version 2.13.0 (R Development Core Team 2011) using the multi-model inference (MuMIN) package. We did not observe caching behavior often enough to perform statistical analysis.

We constructed a set of a priori models to test for the effects of a bird's age and sex on two observed 'Alalā

dispersal behaviors (eating and carrying), and to test for the effect of treatment on seed germination. First, for each dispersal behavior, we tested for differences between juvenile and adult (Age) and between males and females (Sex), as well as additive effects (Age + Sex), separately for each plant species. Second, for seed germination, we tested for differences in the proportion of seeds germinated between treatment groups (Treatment), separately for each plant species. We used the corrected Akaike's Information Criterion ( $AIC_c$ ) for small sample sizes for model selection to assess which variables or combination of these variables had the most support from our data for contributing to observed eating and carrying behaviors and seed germination success (Burnham and Anderson 2002). The Akaike weights ( $w_i$ ) indicate the weight of evidence from the data that supports the hypothesis represented by each model, relative to the other tested models, and we present models with at least 10% support. We present model-averaged estimates weighted by Akaike weights ( $w_i$ ), and unconditional standard errors.

TABLE 2. Model selection results ( $w_i \geq 10\%$ ) for regressions of 'Alalā characteristics (age and sex) on the probability of 'Alalā eating behavior for 13 native Hawaiian plants.

Plant species	Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	$w_i$
Pilo	age	9.74	0	0.75
	age + sex	12.00	2.26	0.24
'Ōhelo	age	-7.09	0	0.75
	age + sex	-4.90	2.18	0.25
'Ōha kēpau	age + sex	-48.24	0	0.68
	age	-46.76	1.49	0.32
Kolea	age	5.06	0	0.73
	age + sex	7.11	2.05	0.26
Māmaki	age + sex	-65.40	0	0.52
	age	-65.26	0.15	0.48
Pūkiawe	age	-122.31	0	0.76
	age + sex	-120.05	2.27	0.24
'Ohe mauka	age	-117.31	0	0.62
	age + sex	-116.35	0.96	0.38
Naio	age	-139.90	0	0.71
	age + sex	-138.10	1.80	0.29
Kāwa'u	age	-161.17	0	0.57
	age + sex	-160.61	0.55	0.43
'Ōlapa	age	-15.90	0	0.41
	age + sex	-15.25	0.65	0.30
	intercept only	-14.33	1.57	0.19
	sex	-13.06	2.84	0.10
	intercept only	-242.46	0	0.37
Hō'awa	age	-241.82	0.64	0.27
	sex	-241.42	1.04	0.22
	age + sex	-240.56	1.90	0.14
Loulu, green	intercept only	-260.97	0	0.44
	sex	-259.90	1.07	0.26
	age	-259.22	1.75	0.18
	age + sex	-258.32	2.65	0.12
Halapepe	intercept only	-195.83	0	0.52
	sex	-194.09	1.73	0.22
	age	-193.76	2.06	0.19
Loulu, black	intercept only	-260.97	0	0.44
	sex	-259.90	1.07	0.26
	age	-259.22	1.75	0.18
	age + sex	-258.32	2.65	0.12

Note: Results include Akaike information criterion corrected for small sample size (AIC<sub>c</sub>), relative AIC<sub>c</sub> (ΔAIC<sub>c</sub>), and Akaike weight ( $w_i$ ).

## RESULTS

### *Foraging behavior and seed dispersal*

We observed 'Alalā eating the fruits of all plant species in our study, although the probability of observing eating behavior varied among plant species (Fig. 5). We found support for an age effect on eating behavior in 9 out of the 14 plants, with juvenile birds showing higher probabilities of eating fruits (Table 2, Fig. 5). Two of these plants ('oha kēpau and māmaki) showed slight support for an additive affect of age and sex, suggesting that adult males might have a higher probability of eating than adult females (Table 2). For the remaining five plants, models containing age and sex effects had levels of support similar to those of the intercept-only model (Table 2, Fig. 5). Data and R code are available in the Supplement.

We observed 'Alalā carrying the fruits of all plant species, and the probability of carrying varied among plant species (Fig. 6). We found support for an age

effect on carrying behavior in 8 of the 14 plants. Of these 8 plants, 7 were among the 9 plants that also had age effects on eating behavior, and showed a similar pattern of juvenile birds having higher probabilities of carrying fruits (Table 3, Fig. 6). We did not find support for an age effect for pilo or 'ōhelo, plants that had an age effect on eating, but found support for an age effect with hō'awa, a plant that did not have an age effect on eating behavior, and that showed a different pattern, with juvenile birds having a lower probability of carrying than adult birds (Table 3, Fig. 6). We found slight support for an additive effect of age and sex for 'oha kēpau and hō'awa, with juvenile and adult males having a higher probability of ingestion than juvenile and adult females (Table 3, Fig. 6). The remaining 4 plants did not have support for age and sex effects on the probability of carrying (Table 3). The effects of age and sex on the probability of observing eating and carrying behaviors, and complete model results for eating and carrying behaviors appear in Appendix C (Tables C1 and C2).

TABLE 3. Model selection results ( $w_i \geq 10\%$ ) for regressions of 'Alalā characteristics (age and sex) on the probability of 'Alalā carrying behavior for 13 native Hawaiian plants.

Plant species	Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	$w_i$
Kolea	age	-0.18	0	0.76
	age + sex	2.14	2.32	0.24
'Ohe mauka	age	-132.59	0	0.72
	age + sex	-130.72	1.87	0.28
Naio	age	-169.88	0	0.74
	age + sex	-167.75	2.13	0.26
Kāwa'u	age	-163.27	0	0.69
	age + sex	-161.66	1.61	0.31
Pūkiawe	age	-195.26	0	0.62
	age + sex	-194.23	1.02	0.37
Māmaki	age + sex	-119.49	0	0.70
	age	-117.12	2.37	0.21
'Ōhelo	age	-62.19	0	0.56
	age + sex	-60.13	2.06	0.20
'Ōha kēpau	intercept only	-59.75	2.43	0.17
	age + sex	-18.21	0	0.58
Pilo	age	-17.34	0.87	0.37
	intercept only	-31.04	0	0.56
'Ōlapa	age	-28.95	2.09	0.20
	sex	-28.83	2.21	0.18
Hō'awa	sex	-86.95	0	0.48
	intercept only	-85.58	1.37	0.24
Halapepe	age + sex	-85.16	1.80	0.19
	age	-3.16	0	0.58
Loulu, green	age	-2.42	0.73	0.40
	intercept only	-15.29	0	0.44
	sex	-14.09	1.20	0.24
	age	-13.88	1.41	0.22
Loulu, black	age + sex	-12.44	2.84	0.11
	intercept only	1.91	0	0.41
	sex	2.26	0.35	0.35
	age	4.13	2.22	0.14
Loulu, black	age + sex	4.58	2.67	0.11
	sex	-22.99	0	0.40
	age + sex	-22.39	0.59	0.30
	age	-21.11	1.88	0.16
intercept only	-20.98	2.01	0.15	

Note: Results include Akaike information criterion corrected for small sample size (AIC<sub>c</sub>), relative AIC<sub>c</sub> (ΔAIC<sub>c</sub>), and Akaike weight ( $w_i$ ).

TABLE 4. Model selection results ( $w_i \geq 10\%$ ) for regressions of seed treatment on seed germination success.

Plant species	Model	AIC <sub>c</sub>	$\Delta$ AIC <sub>c</sub>	$w_i$
'Oha kēpau	treatment	-9.22	0	0.99
Hō'awa	treatment	-3.87	0	0.99
'Ōhelo	treatment	-15.81	0	0.99
Pilo	intercept only	14.23	0	0.56
	treatment	14.68	0.44	0.44
'Ōlapa	intercept only	-13.60	0	0.68
	treatment	-12.06	1.54	0.32
Māmaki	intercept only	-3.54	0	0.96

Note: Results include Akaike information criterion corrected for small sample size (AIC<sub>c</sub>), relative AIC<sub>c</sub> ( $\Delta$ AIC<sub>c</sub>), and Akaike weight ( $w_i$ ).

The third observed dispersal behavior, caching, did not occur as frequently as eating or carrying. Although we did not obtain sufficient data for statistical analysis, caching was observed for all fruit species (Table 1). We were limited in the testing of kopiko, lama, and 'oha wai by low fruit availability, but we observed some 'Alalā eating, carrying, and caching the fruits of each of these species (Table 1). Similarly, although the adult, nonreproductive 'Alalā did not ingest the large fruits of 'āla'a, maile, and olopua during toxicity testing, we did observe these birds carrying and caching the fruits of each species (Table 1).

#### Seed germination

Of the 13 plant species included in the flock-wide trials, we collected ingested seeds of 12 species from droppings and/or pellets (Table 1). For the 13th species, loulu, we found pieces of green loulu endosperm, partially digested and regurgitated within 'Alalā pellets,

but this does not represent seed dispersal per se and may instead be better characterized as seed predation. We found no evidence of whole ingested black loulu seeds in pellets or fecal droppings, though 'Alalā manipulation of this mature form of loulu sometimes resulted in removal of the fruit's fibrous outer husk, leaving the seed itself intact. Although we lacked sufficient replicates for statistical analysis, 2 (17%) out of 12 'Alalā-husked loulu seeds subsequently sprouted after planting.

We were able to conduct 3–5 replicate germination trials for 6 of 12 plants for which we obtained ingested seeds: 'ōlapa, 'oha kēpau, māmaki, pilo, hō'awa, and 'ōhelo. We found support for a treatment effect with 'oha kēpau, hō'awa, and 'ōhelo (Table 4), with germination success for ingested seeds (fecal and pellet) higher than for seeds in whole fruits (Fig. 7). For 'ōlapa, māmaki, and pilo, we did not find a treatment effect on germination success, with ingested seeds germinating in percentages similar to those of seeds in whole fruits (Table 4, Fig. 7). The effect size of seed treatment on the germination success and complete model selection results appear in Appendix C (Tables C3 and C4).

#### DISCUSSION

Captive 'Alalā cached, ate, and carried all 14 fruits in this study, including those of loulu and halapepe, two endangered plants that presently lack known seed dispersers. Our results indicate that hō'awa relies entirely on 'Alalā ingestion or manipulation for germination, and that the germination of 'ōhelo and 'oha kēpau seeds was increased by 'Alalā ingestion as compared to seeds of whole fruits. These findings suggest that 'Alalā was once an important seed disperser in mesic and dry forests on the Big Island of Hawai'i and

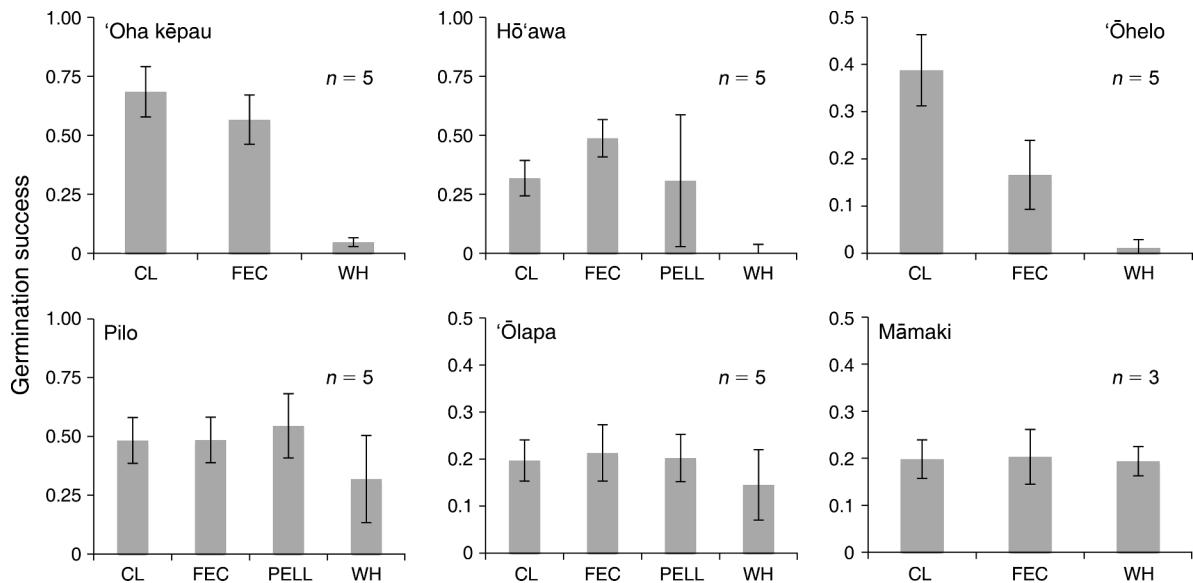


FIG. 7. Model-averaged estimates ( $\pm$ SE) of the proportion of seeds germinated (note differing scales) for seeds cleaned by hand (CL), 'Alalā-ingested seeds from fecal droppings (FEC), pellets (PELL), and seeds in whole fruits (WH) for six species of native Hawaiian plants. The number of replicate trials was either 3 or 5, as indicated by sample size ( $n$ ).

probably on Maui. The extinction of 'Alalā and other Hawaiian birds has influenced plant communities and accounts for some ecological anachronisms in Hawai'i's forests. Restoring the ecological processes that support Hawai'i's native ecosystems will rely on the reciprocal restoration of native birds and plants, in concert with efforts to reduce other serious threats such as invasive species. Importantly, our study provides additional reason beyond "intrinsic value" to reintroduce 'Alalā to their original range. We also suggest that establishing populations of 'Alalā on other islands, where 'Alalā or other native crows once existed (Fig. 2), could restore dispersal services to those communities, utilizing 'Alalā as ecological analogues for now extinct local frugivores. Recreating seed dispersal services with analogue species has a precedent, as demonstrated by the Aldabran giant tortoise (*Aldabrachelys gigantea*). This species was introduced to Mauritius as a nonindigenous but functional substitute for extinct native seed dispersers that played a crucial role in maintaining plant diversity (Griffiths and Harris 2010, Griffiths et al. 2010).

Our models indicate an influence of age on seed dispersal behaviors in the captive flock. Although wild 'Alalā parents selectively fed nestlings fruits high in protein content (Sakai and Carpenter 1990), no information exists on whether the diet of adult birds differed from juvenile birds no longer fed by their parents. The differences between the juvenile and adult captive 'Alalā that we observed in our study could be a result of behavioral differences perhaps compounded by captivity. Juvenile captive 'Alalā show greater curiosity than adults toward novel items such as enrichment toys (natural and unnatural), which have no nutritional value (R. Switzer, *personal observation*). Additionally, older birds kept alone or in compatible pairs may have lower energy expenditure than younger birds in an active flock situation. Receiving the entire nutritional intake that they may require from their routine daily diet, the older birds may be less likely to forage for and consume the additional native fruits. Consequently, an 'Alalā that had been frequently exposed to a wide variety of native fruits as a juvenile may not be any more likely to forage or consume native fruits in later years as a captive adult. However, in the event that the lower probability of eating and carrying native fruits that we observed in adult 'Alalā was indeed a result of a missed opportunity to introduce these birds to native fruits when they were young, aviculturalists should capitalize on this period of youthful interest and include native fruits regularly in the diet of young 'Alalā, particularly those that are potential candidates for release. This practice could improve foraging efficiency and increase post-release survivorship.

Our models suggested an additive influence of sex on seed dispersal behavior for a few plants, but we did not have enough support to detect a strong effect. It is unclear whether the differences that we detected in male and female seed dispersal behaviors reflect actual

differences between the sexes in foraging strategies or are simply an artifact of captivity. However, although knowledge of 'Alalā foraging behavior in the wild is quite limited, observers have noted that, during the breeding season, females ate more 'ōlapa than males, and males often fed 'ōlapa to females (Banko et al. 2002).

The wide range of fruits that the captive birds in our study selected is consistent with the generalist diet of native fruits observed in wild 'Alalā (Sakai et al. 1986, Sakai and Carpenter 1990, Banko et al. 2002) and contributes additional information on 'Alalā diet plants that could be used to select and prepare prospective 'Alalā reintroduction sites. Within the context of our study, plants that 'Alalā ate and carried may be especially suitable candidates for use in site selection and restoration and should be of conservation priority. However, the fact that some plants lacked strong evidence of 'Alalā foraging behaviors should not justify excluding these species from restoration efforts.

Managers utilizing the results of our study to aid in 'Alalā habitat decisions should also consider other factors. Possible differences in the nutritional demands of captive birds and future wild birds, which will eventually no longer be fed by human caretakers, could mean that fruits not often selected in captivity are still important for survival in the wild, and vice versa. Carrying and caching behaviors may also be accentuated in captivity, regardless of nutrition potential, although this may have been mitigated in part over time, as the birds lost interest in some fruits while retaining interest in others, resulting in higher overall probability of carrying behavior for some plants. The phenology and availability of fruiting plants at different elevations and in different seasons probably will also influence what fruits are important in the survival of future wild birds. Other critical diet items such as invertebrates, small birds, and mammals, and habitat factors such as predator abundance, forest cover and density, and disease vectors will also be important considerations for habitat plans and release site selection. Restoration plans will also be incomplete without consideration of certain plants, such as 'ie'ie (*Freycinetia arborea*), which early naturalists recorded as closely associated with wild 'Alalā foraging behaviors (Perkins 1903), but which we were unable to include in our study due to limitations in fruit availability.

'Alalā disperse native plant seeds through a range of foraging behaviors. Carrying behavior benefits plants through seed movement and perhaps seed manipulation, exemplified by the husking of the black loulou. Although caching did not occur as often as eating and carrying behaviors, we observed 'Alalā caching the fruits of all plant species in our study, consistent with the general caching behavior documented in the wild (Sakai et al. 1986, Banko et al. 2002). This intriguing behavior, auspiciously still present in the captive 'Alalā, may eventually benefit the forest plant community through

vertical dispersal by released birds. Many of the plant species in this study are able to grow epiphytically in Hawaiian forests. By moving seeds high in the canopy, 'Alalā could place developing seedlings out of reach of destructive ungulates. Beyond carrying and caching, eating behavior results in processes (i.e., fruit pulp removal and seed ingestion) that also provide germination benefits to some plants.

The germination benefits associated with 'Alalā ingestion varied among the plant species in our study. The plants pilo, 'ōlapa, and māmaki do not appear to receive germination benefits from passing through 'Alalā and therefore do not appear to rely on 'Alalā specifically for germination preparation. Although 'Alalā ingestion does not appear to harm the seeds, and the large-bodied 'Alalā could perhaps influence the relative abundance of these and other common plants through dispersing a large volume of seeds, ingestion by other bird species and simply falling to the forest floor may be other viable options for these plants. 'Oha kēpau and hō'awa, two large-fruited plants with no known remaining native seed dispersers, received germination benefits from 'Alalā ingestion. 'Alalā appear to increase seed germination in 'oha kēpau by cleaning the seeds of fruit pulp. 'Alalā probably enable seed germination in hō'awa by first removing the seeds from the capsules and then further through ingestion, perhaps through chemical scarification of the endocarp (Fig. 4d). Documentation from early naturalists, biogeography, and the results of this study suggest that 'Alalā once played a key role in dispersing both species.

'Oha kēpau is a member of the lobelioids, a large plant group of several endemic genera that arrived in the Hawaiian archipelago around 16 million years ago (Price and Wagner 2004). Most species in this group have fruits containing hundreds of tiny seeds, a characteristic that may have facilitated bird dispersal among islands along the archipelago's "conveyor belt" of geologic time (Fleischer and McIntosh 2001), even as the bird community in the archipelago has changed. The early botanist Joseph Rock describes walking through extensive forests of lobelioids (Rock 1913), but today even the common species are increasingly rare. The species of 'oha kēpau that we used in our study, *Clermontia hawaiiensis*, is not endangered, but two similar species, *C. lindseyana* and *C. pyrularia*, are both endangered and historically found within 'Alalā range. Although no seed dispersers other than the 'Alalā have been documented in the literature for this group of plants, anecdotal accounts suggest that some small, nonnative birds may currently be serving as seed dispersers for some 'oha kēpau species. In addition to gaining a dispersal and germination advantage through 'Alalā ingestion, these plants are particularly sensitive to ungulate herbivory, and 'Alalā caching behavior may prove critical to seedling survival and the persistence of this remarkable group of plants.

Hō'awa, a plant whose fruit is a woody capsule filled with oily seeds, emerged from our study as the species with the most convincing evidence of an ecological anachronism in the Hawaiian archipelago. An ancestor to hō'awa, carried by a bird internally or externally (Carlquist 1966), arrived in Hawai'i relatively recently and subsequently radiated into 11 species, 9 of which are endemic to Hawai'i and 7 of which are single-island endemics (Gemmil et al. 2001). These Hawaiian endemics developed larger seeds and a tougher capsule than other *Pittosporum* species found elsewhere in the Pacific (Carlquist 1967). Early naturalists noted that 'Alalā appear to be important for hō'awa dispersal, but assumed that dispersal occurred via external adhesion of the oily, sticky seeds (Rock 1913, Carlquist 1967). Sakai et al. (1986) found hō'awa seeds in wild 'Alalā droppings, and our findings indicate that 'Alalā ingestion enhances germination success even beyond the simple removal of the seeds from the capsule. In our study, germination only occurred when hō'awa seeds were removed from capsules.

The species of hō'awa used in our study, *P. hosmeri*, and others in this genus, may be Hawaiian forest anachronisms, persisting for now while their probable primary seed dispersers, the 'Alalā and other Hawaiian corvids, are extinct or restricted to captivity. Corvid species are known to have inhabited all main islands except Kaua'i in the Hawaiian archipelago prior to human arrival (James et al. 1987), and *Pittosporum* species on other islands may have relied on other crows as seed dispersal vectors, in addition to, or instead of, 'Alalā (Fig. 2). Passive seed rain for this genus appears to be absent in nature (Drake 1988), and although rats could provide some seed dispersal (Shiels and Drake 2011), the current absence of wild hō'awa seedlings or saplings suggests that rat foraging results primarily in seed predation (L. Pratt, *personal observation*). Important questions emerging from our research include how hō'awa seed dispersal occurs in contemporary Hawaiian forests, whether hō'awa species persist primarily as older or out-planted populations, and whether the secondary dispersal vectors that may exist are sufficient for sustaining these plant populations.

Sample sizes prevented us from including the large-fruited dry-forest plants halapepe and loulu in our germination analysis, but we suspect that these are additional examples of Hawaiian anachronisms. Both plants were dispersed by 'Alalā in our study, and dispersal limitations in the wild may contribute to their status as endangered (Pau et al. 2009). Although previous observers did not document these species as part of the 'Alalā diet, 'Alalā probably frequented dry forests in the past, as evidenced by their probable lowland extirpation due to agricultural activities by the ancient Hawaiians (Olson and James 1982), their observed seasonal movements (Perkins 1903) that may have included forays into lowland dry forests, and their documented consumption of the fruits of lama (Tomich

1971), a primarily dry-forest plant that also extended into the mesic forests historically documented as typical 'Alalā habitat. Halapepe has no known seed disperser, but its fleshy fruit implies bird dispersal, and the captive 'Alalā exhibited some interest in the bright red fruits and pearly round seeds. We did collect a few halapepe seeds in 'Alalā pellets and fecal droppings, but did not obtain substantial replication for inclusion in our germination trials.

The species of loulu used in our study, *Pritchardia schattaueri*, is an endangered member of an extensive genus of rare native palms whose ancestor arrived in the islands either by water or in a bird's gut (Carlquist 1966). Seed dispersal mechanisms for contemporary loulu species are also ambiguous; current hypotheses include very strong wind gusts, rolling downhill, and the theory of "precinctiveness" (Carlquist 1967), which proposes that extremely low dispersability actually benefits the plant by limiting seed movement away from suitable habitat near the parent plant. Bird dispersal, perhaps with 'Alalā as the sole remaining vector, is another possibility. Captive 'Alalā responded differently to the mature black and the immature green loulu fruits. The captive birds ate the immature endosperm contained within the green fruits (also a source of famine food for the ancient Hawaiians; Malo 1951) but this consumption probably represents seed predation. Captive 'Alalā rarely ate the tough, mature fruits, but did move, cache, and husk them, and these manipulated fruits retained the ability to sprout. The enormous quantity of fruit mast in these native palm trees may attract 'Alalā to eat the green fruit, and perhaps the plant gains a dispersal benefit when 'Alalā move, husk, and drop the mature black fruits through accident or play behaviors.

Halapepe and loulu are two examples of the diverse, yet highly threatened, Hawaiian dry-forest plants that historically may have relied on 'Alalā for seed dispersal services and that persist today as Hawaiian anachronisms. Other large-fruited, dry-forest plants in this category include 'āla'a (*Pouteria hawaiiensis*) and maua (*Xylosma hawaiiensis*), which are endangered and lack known seed dispersers. Reconstructing these potential mutualistic relationships could benefit 'Alalā by increasing their spatially and temporally available food resources, particularly in the face of climate change, and could benefit the dry-forest plants by restoring the bird-mediated dispersal and germination, both perhaps factors in their endangerment.

How native Hawaiian plants such as hō'awa and loulu have persisted despite the decline, extirpation, and extinction of native fruit-eating birds is an intriguing and critical question that arises from our results. In South America, prehistoric people may have functioned as secondary seed dispersers for some plant species that had lost their primary dispersers, the Pleistocene megafauna, and this may help to explain the endurance of some of those large-fruit anachronisms (Guimaraes et

al. 2008). The arrival of humans in the Hawaiian archipelago coincides with an approximately 50% loss in avifauna diversity (Olson and James 1982), including bird species that may have functioned as seed dispersers for native plants. However, the native Hawaiian people have historically documented expertise in the material, medicinal, and cultural uses of many native plants, including the species in this study (Malo 1951). This contemporary knowledge probably stems from the natural resource extraction methods practiced by the ancient Hawaiians, and this past use could have represented a form of secondary dispersal for plants that had lost their primary avian dispersers. Rats may also play an unexpected role in seed dispersal for some native Hawaiian plants (Shiels and Drake 2011). Exploring these and other possible secondary dispersal mechanisms for extant Hawaiian plant species could provide insight into their current status and the degree to which these species are likely to persist without human interference.

Today, many culturally and ecologically valuable plants may survive solely due to the ongoing conservation efforts of humans. Restoring a functional population of 'Alalā as primary seed dispersers for these plants could save thousands of dollars in restoration costs, undo ecological anachronisms such as those exemplified by hō'awa and other plants in this study, and help to restore and maintain Hawai'i's natural and cultural heritage (S. Culliney, B. Bruyere, T. Test, and L. Pejchar, *unpublished data*). 'Alalā recovery efforts ultimately face significant challenges from numerous factors, and the successful establishment of a sustainable and ecologically functioning wild 'Alalā population will take concerted and cooperative effort over an extended timeline (Banko et al. 2002, Banko 2009, USFWS 2009). However, the results of our study add another reason to restore critically endangered species to the wild that goes beyond "intrinsic value." Globally, many native species such as 'Alalā have been extirpated from the wild but persist in captivity or in a fragment of their former range. Given successful captive breeding, sufficient conservation funding, suitable restoration sites, and appropriate reintroduction techniques, these species could once again be functioning members of their former ecosystems.

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## SUPPLEMENTAL MATERIAL

### Appendix A

Color version of Fig. 3 showing bird species and the corresponding fruits and seed sizes that each bird is known to disperse (*Ecological Archives* A022-092-A1).

### Appendix B

Color version of Fig. 4 showing four methods photos (*Ecological Archives* A022-092-A2).

### Appendix C

Tables containing variable effect sizes and complete model selection results for both germination success and bird foraging behaviors (*Ecological Archives* A022-092-A3).

### Supplement

Data files and R code for both germination success and bird foraging behaviors (*Ecological Archives* A022-092-A4).