THESIS

I. SEED DISPERSAL BY THE CRITICALLY ENDANGERED ALALA (*CORVUS HAWAIIENSIS*) II. INTEGRATING COMMUNITY VALUES INTO ALALA (*CORVUS HAWAIIENSIS*) RECOVERY

Submitted by

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ABSTRACT

I. SEED DISPERSAL BY THE CRITICALLY ENDANGERED ALALA (*CORVUS HAWAIIENSIS*) II. INTEGRATING COMMUNITY VALUES INTO ALALA (*CORVUS HAWAIIENSIS*) RECOVERY

Species loss can lead to cascading effects on communities, including the disruption of ecological processes such as seed dispersal. The endangered Alala (*Corvus hawaiiensis*), the largest remaining species of native Hawaiian forest bird, was once common in mesic and dry forests on the Island of Hawaii, but today exists solely in captivity. Prior to its extinction in the wild, the Alala may have helped establish and maintain native Hawaiian forest communities by dispersing seeds of a wide variety of native plants. In the absence of Alala, the structure and composition of Hawaii's forests may be changing and some large-fruited plants may be dispersal limited, persisting primarily as ecological anachronisms. I fed captive Alala a variety of native fruits, documented behaviors relating to seed dispersal, and measured the germination success of seeds that passed through the gut of Alala relative to the germination success of seeds in control groups. Alala ate and carried fourteen native fruits and provided germination benefits to several species by ingesting their seeds. My results suggest that some plants rely heavily on Alala for these services. In captivity, juvenile birds displayed seed

dispersal behaviors more often than adult birds for most fruiting plants in my study. I introduced captive Alala to two large-fruited, dry forest plants, not previously recorded as Alala food resources, but which may have once been part of their natural diet. The seed dispersal behavior that Alala displayed towards these species supports the inclusion of dry and mesic forests in Alala habitat restoration plans and adds weight to the idea that plant dispersal limitation may contribute to the rarity of these plants. My study provides evidence that Alala 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 Alala to their former range.

Incorporating community values and perspectives into endangered species recovery programs is generally underutilized but can be an important tool for achieving conservation success. Species recovery programs adjacent to human communities can particularly benefit from integrating local perspectives on nature into program goals and practices. The Alala or Hawaiian Crow (*Corvus hawaiiensis*) is currently extinct in the wild but once possessed great cultural value to ancient Hawaiians and may have played a pivotal role as a seed disperser in Hawaii's forests. Past efforts to restore this charismatic bird to its historical range failed in part due to human conflict. I conducted focus group interviews in two communities bordering Alala historical range to assess participants' ability to recognize the Alala, and to understand how these community members value natural resources. I found that although very few participants recognized the Alala, many expressed curiosity and concern for the species. Participants demonstrated predominantly utilitarian views towards natural resources but these value orientations were steeped with cultural significance. Alala recovery efforts will benefit through emphasis of both the utilitarian and cultural value of this species. Reintroduction projects in Hawaii and elsewhere should dedicate a portion of their resources towards understanding the perspectives of the human communities surrounding future reintroduction sites. This approach will help avoid potential conflicts before they arise and maximize the likelihood of success by building programs based on shared values.

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Introduction

In addition to biodiversity loss, species extinction can have cascading impacts on entire communities through the disruption of ecological processes. The replacement of 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 (*Bison 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 rainforest plants but are threatened by overharvest from humans (Anderson et al. 2009).

When influential species like these 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 & Martin 1982; Guimaraes et al. 2008). Extending this 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 & Galetti 2009). In oceanic island ecosystems, birds are often the sole native animal seed disperser of native plants.

Birds facilitate plant dispersal by moving seeds away from the parent plant and thus decreasing intra-specific competition between parent plants and progeny (Malmborg & Willson 1988), placing seeds in favorable locations through caching behavior (McKinney et al. 2009) and increasing seed germination success by removing fleshy fruit

(Paulsen & Hogstedt 2002) or scarifying the seed coat (Paulsen & Hogstedt 2002; Rodriguez-Perez et al. 2005). The decline or extinction of these bird dispersers can thus lead to cascading negative effects on the plant community (Sekercioglu et al. 2004; McKinney et al. 2009; Babweteera & 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 Hawaii's native fruiting flora to the islands (Carlquist 1967; Price & Wagner 2004) and has evolved in several additional plant lineages whose ancestors used externally adhesive seed dispersal (Price & Wagner 2004). Large-scale extinction and endangerment of native Hawaiian plant species (Olson & James 1982; Steadman 1995; Boyer 2008) is likely to have fundamentally altered bird-plant mutualisms in Hawaii (Pau et al. 2009). On the Big Island of Hawaii, only two native frugivorous forest birds are extant today: the Omao or Hawaiian Thrush (*Myadestes obscurus*) and the Alala or Hawaiian Crow (*Corvus hawaiiensis*). Omao, although extirpated from the southern mesic and dry forests (vanRiper & Scott 1979), remain relatively common in forests on the eastern slopes of the island. The Alala, the last remaining species from a small evolutionary radiation that included at least two other Hawaiian corvids (James & Olson 1991), is genetically closer to the Common Raven (*Corvus corax*) of North America and Eurasia than to typical crows (Fleischer & McIntosh 2001) and also resembles the Common Raven in size, vocal repertoire and intelligence (Banko et al. 2002).

Early western naturalists documented Alala as a common species in the southern mesic and dry forests of the Big Island of Hawaii (Perkins 1903; Figure 1) and fossil evidence places this species on the island of Maui up through, though not beyond, the first stages of Polynesian colonization of that island (James et al. 1987; Figure 2). The Alala’s decline and eventual extinction in the wild, despite the protection afforded by its status as one of the first species on the 1967 precursor to the U.S. Endangered Species List, is attributed to several factors including persecution, habitat loss, and predation and disease transmission by invasive species (Henshaw 1902; Perkins 1903; Munro 1960; Giffin et al. 1987). Following an unsuccessful re-establishment attempt involving captive-bred birds in the 1990s, as well as the continued loss of wild birds (USFWS 2003; Walters 2006), the last sighting of a wild Alala occurred in 2002. This species is classified as endangered in the United States and is now considered extirpated in the wild (USFWS 2009; IUCN 2010). The remaining Alala population currently persists in two captive propagation facilities: the Maui Bird Conservation Center (MBCC) in Olinda on the island of Maui, and the Keauhou Bird Conservation Center (KBCC) in Volcano on the island of Hawaii (Figure 1) and consists of a total of 95 individuals as of September 2011. The goals of the captive breeding program are to maintain a self-sustaining captive Alala population and to one day begin the re-establishment of Alala populations within their native range (Lieberman & Kuehler 2009).

In the absence of Omao and Alala in the southeastern mesic and dry forests on the island of Hawaii, some 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 & Robinson 2007). However, due to their substantially smaller body and bill sizes (Figure 3; vanRiper 2000; Male et al. 1998) compared with the Alala (Banko et al. 2002) these birds may alter forest communities

(Wheelwright 1985; Jordano et al. 2007; Babweteera & Brown 2009) and drive the selective dispersal of small-seeded native and exotic invasive plants in Hawaii's forests (Chimera & Drake 2010). The Alala, as the largest remaining native Hawaiian frugivore, may therefore have once played a major, and now unfulfilled, ecological role in maintaining the diversity and structure of native forests within its historic range through dispersing native seeds of varying sizes (Figure 3).

Our understanding of how Alala once dispersed seeds within these Hawaiian forest communities is incomplete and limited to observations by early naturalists (e.g. Henshaw 1902; Perkins 1903; Rock 1913), or from studies in sites that have been substantially modified by human activities (Tomich 1971; Sakai et al. 1986; Sakai & Carpenter 1990). Knowledge regarding the connection between many native fruit-bearing plants and the Alala is therefore dependent on the spatial distribution of pollen and fossil records (Olson & James 1982; James et al. 1987; James & Olson 1991; Pau et al. 2009). Although Alala have not been observed consuming most dry forest plants, characteristics of these plants such as large fruit size and lack of current seed dispersers lead some researchers to reason that the large-billed and large-bodied Alala was one possible seed disperser for these plant species (J. Price, L. Pratt, T. Pratt, pers. comm.; Figure 3). On the island of Hawaii and elsewhere in the island chain, extinct avifauna such as other corvid species (Figure 2) and flightless rails could have also once functioned as seed dispersers for native plants, though diet information is largely unknown for these birds. Some of these large-fruited dry forest plants, such as loulu palms (*Pritchardia* sp) and halapepe (*Pleomele hawaiiensis*), are rare or endangered today. These plants, hereafter "large fruited plants", if indeed they represent possible food sources for wild Alala, could be included in habitat restoration plans for Alala release sites and may in turn benefit from Alala 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.

My objective is to document the Alala's potential role in maintaining and restoring Hawaii's forests through seed dispersal. I used feeding trials with captive Alala to determine 1) the dispersal potential of captive Alala for native Hawaiian fruiting plant species; 2) whether bird characteristics such as age and sex influence the probability of these behaviors, as a bird's age may inform their openness to new experiences and a bird's sex may have determined foraging choices in the wild; and 3) whether Alala ingestion results in increased seed germination success, as the avian digestive process may chemically prepare seeds for germination. In testing these objectives, I also make a substantive contribution to the hypothesis that some of Hawaii's native plants persist in nature primarily as anachronisms. To this end, I included several species of large fruited plants in the feeding trials that Alala had not previously been observed to consume in the wild.

Methods

Study sites & sample size

I 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 Alala (Figure 1). These sites included The Nature Conservancy preserves of Kona Hema and Kaiholena; Kaupulehu dryland forest; Kipuka Ki, Kipuka Puaulu, Kilauea summit and Naulu Forest in the Hawaii Volcanoes National Park; the Amy B.H. Greenwell Ethnobotanical Garden;

and the forests immediately surrounding KBCC. I clipped whole branches with fruits still attached unless this practice would have excessively harmed the plant, as was often the case with the large-fruited plants, and then I instead collected single fruits. I refrigerated all fruits and branches 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, which is located in Volcano, Hawaii on land leased from Kamehameha Schools. Fruit feeding trials and collection of ingested seeds took place within Alala aviaries. All aviaries are mosquito-, bird-, and mammal-proof, are open to air and weather via mosquito netting, and are generally 12m x 3m x 4.2-6m high, with inter-connecting hatches, cinder floors, sparse live vegetation and dead logs, and have cut-limb perches bracketed to the walls (Figure 4a), with primary sentinel perches located high in the aviary (at approximately 4.8m). During the course of my study, KBCC housed 61 Alala either singly, together with a mate, or in peer groups of 4, 8, or 10, though all birds were within sight of another; no bird was completely isolated. I classified individuals into two groupings, based on Alala typically reaching reproductive maturity at age three: “juvenile” if they were less than three years of age and “adult” if three years or older. I included 57 Alala in our trials (13 juvenile males, 9 juvenile females, 16 adult males, 19 adult females), and excluded the remaining four Alala due to aberrant behaviors as a result of imprinting and/or aggression towards humans. During the course of this study, one adult female died and one juvenile male was moved to the Maui facility. I included these two birds in my study, as I took the number of times each bird received various plant species into account in my analyses. All Alala were cared for daily by KBCC staff and fed an omnivorous diet of commercial (de-seeded) fruits, animal protein and proprietary feeds such as pellets. These captive Alala had not previously experienced native fruits as a regular food source, although they had occasionally been offered native fruits as enrichment.

Foraging behavior & seed dispersal

I selected plant species for use in feeding trials based on a list of 26 native Hawaiian plants that wild Alala had been observed to consume (Tomich 1971; Sakai et al. 1986; Sakai & Carpenter 1990; Banko et al. 2002). Due to the limitations of fruiting phenology, abundance, and access to collecting sites, I obtained enough fruits from 11 of these species to conduct feeding trials with all 57 Alala. I included the following plants in the flock-wide study (hereafter I refer to common names only): olapa (*Cheirondendron trygnum*), oha kepau (*Clermontia hawaiiensis*), pilo (*Coprosma rhynocarpa*), kawau (*Ilex anomala*), naio (*Myoporum sandwicensis*), kolea (*Myrsine lanaiensis*), mamaki (*Pipturus albidus*), hoawa (*Pittosporum hosmeri*), pukiawe (*Styphelia tameiameiae*), ohe mauka (*Tetraplasandra hawaiiensis*), and ohelo (*Vaccinium reticulatum*) (Table 1). I 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 I offered these species to a smaller subset of Alala (Table 1).

Additionally, I chose 5 large-fruited plants that wild Alala had never before been observed eating and conducted preliminary trials with adult non-reproductive Alala to ensure these species were not toxic, by monitoring bird health following observed ingestion. The adult, non-reproductive Alala ingested two of these plants, loulu

(*Pritchardia schattaueri*) and halapepe (*Pleomele hawaiiensis*), with no negative impacts, and I included these plants in the flock-wide feeding trials. I tested and subsequently included loulu fruits in two forms: the black, hard mature form ("black loulu") and the green, soft immature form ("green loulu"). I did not observe the adult non-reproductive Alala ingesting the three other species of large-fruited plants I offered them: maile (*Alyxia oliviformis*), olopua (*Nestegis sandwicensis*) and alaa (*Pouteria hawaiiensis*), and therefore I was unable to safely offer these plants to the rest of the flock (Table 1).

For three consecutive days within a week, I offered each Alala in the flock-wide study fruits or fruiting branches from 3-7 native plant species at a time, based on fruiting availability in the wild. If Alala were housed with a mate or peers, I offered multiple fruits for each bird, and observed both or all birds concurrently. I placed fruits on a log or the cement aviary curbing within view of an observation vantage point outside the aviary. I observed each Alala's immediate reaction to the fruits from behind a one-way glass window for five minutes (Figure 4b) and recorded eating, carrying, and caching behaviors. After approximately 24 hours, I returned to the aviary and removed any of the fruits or branches I found, and offered the Alala fresh fruits and branches to repeat the trial for a total of three consecutive days per week. I repeated these trials over the two field seasons and the birds in the study were exposed to each fruiting plant species 12 times on average (Table 1; Figure 5; Figure 6). The variation in the number of replicate trials for each plant species given to each bird was due to fruit availability at collection sites and is taken into account in my analysis.

Seed germination

Ingested seeds can either pass through the digestive system and are defecated by Alala, or can be regurgitated by Alala in the form of a pellet (Figure 4c & d) – a phenomenon common in a diverse array of birds ranging from raptors as large as Great-horned Owls (Houston et al. 1998) to small passerines such as Black Phoebes (Wolf 1997). Squares of plexiglass placed under Alala primary perches (Figure 4a) amassed samples of fecal droppings and regurgitated pellets, which I then collected approximately 18 hours following each feeding trial, for subsequent use in germination trials. Depending on the number of seeds found, I used at least 10 and up to 50 ingested seeds per plant species in 3-5 germination trials. In the greenhouse I planted three treatment groups ("fecal", "pellet", "cleaned"), as well as a control group ("whole"). I planted seeds found within droppings in the treatment group "fecal" and seeds within pellets in the treatment group "pellet". I planted seeds within whole fruits in the treatment group "whole" and seeds that I cleaned manually of fruit pulp in the treatment group "cleaned". Each group mimics a potential seed treatment in the wild: seeds ingested by wild Alala (fecal and pellet), seeds with fruit pulp removed by wild Alala but that remain un-ingested (cleaned), and seeds within fruits that Alala 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 Alala but which remained un-ingested were counted and removed but not included in germination trials with the exception of loulu seeds that showed evidence of external scarification. I chose planting media and watering schedules for each species based on advice given by native plant experts and these conditions did not vary between the treatments. I tracked germination success for as long as the project allowed (31-75 weeks depending on the species).

Data analysis

I conducted my analyses of bird behavior and seed germination trials separately for each plant. I used logistic regression to model the proportion of times I observed birds eating each plant and carrying each plant as a function of age and sex, weighted by the number of times I gave each plant species to each bird. I 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. I conducted all statistical modeling in program R (version 2.13.0) using the Multi-model Inference (MuMIN) package. I did not observe caching behavior often enough to perform statistical analysis.

I constructed a set of *a priori* models to test for the effects of a bird's age and sex on two observed Alala dispersal behaviors (eating and carrying), and to test for the effect of treatment on seed germination. First, for each dispersal behavior, I 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, I tested for differences in the proportion of seeds germinated between treatment groups (*Treatment*), separately for each plant species. I used the corrected Akaike's Information Criterion (AICc) for small sample sizes for model selection to assess which variables or combination of these variables had the most support from my data for contributing to observed eating and carrying behaviors and seed germination success (Burnham & 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 I present models with at least 10% support. I present model-averaged estimates weighted by Akaike weights (w_i), and unconditional standard errors.

Results

Foraging behavior & seed dispersal

I observed Alala eating the fruits of all plant species in my study, although the probability of observing eating behavior varied among plant species (Figure 5). I 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; Figure 5). Two of these plants (oha kepau and mamaki) 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 similar levels of support as the intercept-only model (Table 2; Figure 5).

I observed Alala carrying the fruits of all plant species, and the probability of carrying varied among plant species (Figure 6). I found support for an age effect on carrying behavior in 8 of the 14 plants. Seven of these 8 plants 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; Figure 6). I did not find support for an age effect for pilo or for ohelo, plants that had an age effect on eating, but found support for an age effect with hoawa, a plant that did not have an age effect on eating behavior, and shows a different pattern with juvenile birds having a lower probability of carrying than adult birds (Table 3; Figure 6). I found slight support for an additive affect of sex and age in two plants (oha kepau and hoawa), which suggested similar patterns of males, juvenile and adult, having a higher probability of eating relative to juvenile and adult females, respectively (Table 3; Figure 6). The remaining 4 plants did not have support for age and sex effects on the probability of carrying (Table 3). The effect sizes of Alala age and sex on the probability of observing eating and carrying behaviors and complete model results for eating and carrying behaviors appear in the appendix (Appendix Table 1; 2).

The third observed dispersal behavior, caching, did not occur as frequently as other types of seed dispersal and as a result I did not obtain sufficient data for statistical analysis, although this behavior was observed for all fruit species (Table 1). Three plants were limited from inclusion in the flock-wide study by low fruit collection availability and I report only anecdotal observations of a subset of Alala eating and carrying these plants (Table 1). Additionally, three large-fruited plants were never eaten by Alala in these fruits' preliminary non-toxicity trials using a subset of non-reproductive birds (and therefore these plants were not included in the flock-wide trials) but I did observe this subset of Alala carrying and caching each of these fruits (Table 1).

Seed germination

Among the thirteen plant species included in the flock-wide feeding trials, I obtained intact ingested seeds of 12 species from within fecal droppings and/or pellet material (Table 1). For the 13^{th} species, loulu, I found pieces of green loulu endosperm, partially digested and regurgitated within Alala pellets, but this does not represent seed dispersal *per se* and may instead be better characterized as seed predation. I found no evidence of whole ingested black loulu seeds in pellets or fecal droppings, though Alala manipulation of this mature form of loulu sometimes resulted in removal of the fruit's fibrous outer husk, leaving the seed itself intact. I collected the Alala-husked loulu for germination trials without sufficient replication for statistical analysis, and two out of twelve of the Alala-husked loulu sprouted within the time period of my study.

Of the 12 species for which I obtained actual ingested seeds, I was able to conduct 3 or 5 replicate trials to analyze germination results for 6 plants: olapa, oha kepau, mamaki, pilo, hoawa, and ohelo. I found support for a treatment effect with three species (Oha kepau, Hoawa and Ohelo) (Table 4) and germination success for ingested seeds (fecal & pellet) was higher than seeds in whole fruits for these plants (Figure 7). For the remaining three species I did not find support for a treatment effect on germination success, with ingested seeds germinating in similar percentages to seeds in whole fruits (Table 4; Figure 7). The effect size of seed treatment on the germination success and complete model selection results appear in the appendix (Appendix Table 3; 4).

Discussion

The captive Alala cached, ate, and carried all 14 fruits in this study, including two rare and endangered plant species, loulu and halapepe, that have no known seed disperser in the wild. One of the 13 plant species, hoawa, relied entirely on Alala manipulation or ingestion for germination and the germination success for two other species increased in response to Alala ingestion compared to seeds in whole fruits. This strong response, using multiple mechanisms to disperse all fruiting plant species offered and enhancing germination success in a subset of species, suggests that Alala once played a pivotal role as a seed disperser in the mesic and dry forests on the Big Island of Hawaii. As a result, it is reasonable to propose that Hawaii's forest communities may have undergone substantial changes in the time since Alala and other large-bodied native birds functionally disappeared from the island chain. My results contribute evidence that loss of these large bird species from the wild may be the basis for some ecological anachronisms in Hawaii's forests. Restoring the ecological processes that support Hawaii's native ecosystems will rely on the reciprocal restoration of birds and plants. Importantly, my study provides additional reason beyond "intrinsic value" to reintroduce Alala to their original range on the Big Island of Hawaii. I also suggest that establishing populations of Alala on other islands, where other native crows once existed (Figure 7), could serve to restore dispersal services to those communities, utilizing Alala as ecological analogues for now extinct local frugivores. Recreating seed dispersal services with extant native species has a precedent, as demonstrated by the Aldabran giant tortoise (*Aldabrachelys gigantea*). This species was introduced to Mauritius as a non-indigenous but functional substitute for extinct native seed dispersers that played a crucial role in maintaining plant diversity (Griffiths & Harris 2010; Griffiths et al. 2010).

My models indicate an influence of age on seed dispersal behaviors in the captive flock. Although wild Alala parents selectively fed nestlings fruits high in protein content (Sakai & 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 Alala that I observed in my study could be a result of behavioral differences perhaps compounded by captivity. Juvenile captive Alala show greater curiosity than adults towards novel items such as enrichment toys (natural and unnatural), which have no nutritional value (R. Switzer, pers. obs). 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 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 Alala 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 I observed in adult Alala 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 Alala, particularly those who are potential candidates for release. This practice could increase the likelihood of young released Alala obtaining sufficient food resources; as a result, the age of Alala at release could also be a significant factor in post-release survivability.

My models suggested a potential additive influence of sex for a few plants on the probability of seed dispersal behavior by the captive birds, but I did not have enough support from the data to detect a strong effect. Knowledge regarding differences between male and female foraging behavior in the wild is extremely limited. During the nesting season in the wild, observers noted that female Alala ate olapa more often than males, and that males often fed olapa to females (Banko et al. 2002). Although my study took place during the non-breeding season, the suggested differences in seed dispersal behaviors between males and females could be a function of underlying residual behaviors that in the wild manifested as divergent foraging strategies. Alternatively, the divergence in foraging behaviors between captive Alala of different sexes may again be an artifact of their captivity.

The wide range of fruits the captive birds in my study selected is consistent with the generalist diet of native fruits observed in wild Alala (Sakai et al. 1986; Sakai & Carpenter 1990; Banko et al. 2002) and contributes additional information on Alala diet plants that could be used to select and prepare prospective Alala reintroduction sites. Within the context of my study, plants that Alala 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 Alala foraging behaviors should not justify excluding these species from restoration efforts.

My observations of captive Alala eating and carrying loulu and halapepe increases the list of known Alala diet plants and challenges the assumptions that currently define Alala habitat. The interest the captive Alala showed towards these two large-fruited dry forest plants may support including dry forest in Alala recovery plans and may support increasing connectivity between forest types in Hawaii's highly fragmented landscape. This step could help restore the species' previously observed seasonal elevation movements (Perkins 1903) and boost resiliency in the face of climate change. Managers utilizing the results of my study to aid in Alala 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. The phenology and availability of fruiting plants at different elevations and in different seasons will also likely 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 like predator abundance, forest cover and density and disease vectors will also be important considerations for habitat plans and release site selection.

Alala 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 loulu. Although caching did not occur as often as eating and carrying behaviors, I observed all fruiting plant species cached by Alala over the course of the study and this is consistent with documentation of caching behavior in wild Alala (Sakai et al. 1986; Banko et al. 2002). This intriguing behavior, auspiciously still present in the captive Alala, 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, Alala could place developing seedlings out of reach of destructive ungulates. Beyond carrying and caching, eating behavior results first in the removal of fruit pulp and then typically in the ingestion of seeds which become part of a regurgitated pellet or pass completely through the digestive tract, processes which may provide further benefits to some plants.

The germination benefits associated with Alala ingestion varied among the plant species in my study. The plants pilo, olapa, and mamaki do not appear to receive germination benefits from passing through Alala and therefore do not appear to rely on Alala specifically for germination preparation. Although Alala ingestion does not appear to harm the seeds, and the large-bodied Alala 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 kepau and hoawa, two large fruited plants with no known remaining native seed dispersers, received germination benefits from Alala ingestion. Alala appear to increase seed germination in oha kepau by cleaning the seeds of fruit pulp. Alala probably enable seed germination in hoawa by first removing the seeds from the capsules and then further through ingestion, perhaps through chemical scarification of the endocarp (Figure 4d). Documentation from early naturalists, biogeography, and the results of this study suggest that Alala once played a key role in dispersing these two species.

Oha kepau 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 & 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 & McIntosh 2001). 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 kepau I used in my study, *Clermontia hawaiiensis,* is not endangered, but two similar species, *C. lindseyana* and *C. pyrularia*, are both endangered and historically found within Alala range. The large fruit size of oha kepau and closely related species may limit the ability of the smaller introduced birds to access oha kepau seeds; no seed dispersers other than the Alala have been documented for this group of species. In addition to gaining a germination advantage through Alala ingestion, these plants are particularly sensitive to ungulate herbivory, and Alala caching behavior may prove critical to seedling survival and the persistence of this remarkable group of plants.

Hoawa, a plant whose fruit is a woody capsule filled with oily seeds, emerged from my study as the species with the most convincing evidence of an ecological anachronism in the Hawaiian archipelago. An ancestor to hoawa, carried by a bird internally or externally (Carlquist 1966), arrived in Hawaii relatively recently and subsequently radiated into 11 species, 9 of which are endemic to Hawaii and 7 of which are single-island endemics (Gemmill et al. 2001). These Hawaiian endemics developed larger seeds and a tougher capsule than species in this genus that are found elsewhere in the Pacific (Carlquist 1967). Early naturalists note that Alala appear to be important for hoawa dispersal, but seem to assume that dispersal occurred via external adhesion of the oily sticky seeds (Rock 1913; Carlquist 1967). Later researchers found hoawa seeds in wild Alala droppings (Sakai et al. 1986) and I confirm that Alala ingestion does not impair seed germination and instead enhances germination success even beyond the simple removal of the seeds from the capsule. Germination did not occur in our study in the absence of seed removal from capsules.

The species of hoawa used in my study, *P. hosmeri*, and others in this genus may be Hawaiian forest anachronisms, persisting for now while their probable primary seed dispersers, the Alala and other Hawaiian corvids, are extinct or restricted to captivity. Corvid species are known or speculated to have inhabited all main islands in the Hawaiian archipelago prior to human arrival (James et al. 1987), and *Pittosporum* species on other islands may have relied on other crows, in addition to, or instead of, Alala as seed dispersal vectors (Figure 2). Passive seed rain for this genus appears absent in nature (Drake 1988), and while rats do feed on hoawa seeds and it is possible that their foraging could result in some seed dispersal (Shiels & Drake 2011), this activity more likely results in seed predation (L. Pratt pers. comm; pers. obs.) as evidenced by the general lack of seedlings or saplings in the wild today. Important questions emerging from my research include how hoawa seed dispersal occurs in contemporary Hawaiian forests, whether hoawa species persist primarily as older or out-planted populations, and whether the secondary dispersal vectors that may exist are sufficient for maintaining these plants' short- and long-term survival.

My sample size prevented us from including the large-fruited dry forest plants halapepe and loulu in my germination analysis but I also consider the possibility that these are additional examples of Hawaiian anachronisms, as they were dispersed by Alala in my captive trials and their likely dispersal limitation in the wild may contribute to their status as endangered species (Pau et al. 2002). Although previous observers did not consider these species to be part of the Alala diet, Alala likely frequented dry forests in the past, evidenced by their probable lowland extirpation due to agricultural activities by the ancient Hawaiians (Olson & James 1982), their observed seasonal movements (Perkins 1903) that may have included forays into lowland dry forests, and their documented consumption of lama fruits (Tomich 1971), a primarily dry forest plant that also extended into the mesic forests historically documented as typical Alala habitat. Halapepe has no known seed disperser but its fleshy fruit implies bird dispersal, and the captive Alala exhibited some interest in the bright red fruits and pearly round seeds. I did collect a few halapepe seeds in Alala pellets and fecal droppings but did not obtain substantial replication for inclusion in my germination trials.

The species of loulu used in my 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 a seed's movement to the immediate vicinity of habitat that has already proven beneficial to its parent plant. Bird dispersal, perhaps with Alala as the sole remaining vector, is another possibility. The captive Alala 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 represents seed predation and has no reproductive benefit to the plant. The Alala in my study almost never actually 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 Alala to eat the green fruit and perhaps the plant gains a dispersal benefit when the birds sometimes move or husk the black mature fruits by accidentally dropping them or through manipulative play behaviors.

Halapepe and loulu are two examples of the diverse yet highly threatened Hawaiian dry forest plants that may have historically relied on Alala for seed dispersal services and today seem to persist solely as Hawaiian anachronisms. Other possible dry forest plants that may exist as Hawaiian anachronisms include alaa (*Pouteria hawaiiensis*) and maua (*Xylosma hawaiiensis*), both of which are endangered with large fruits and no known seed dispersal vector. Reconstructing these potential mutualistic relationships could benefit Alala by increasing their spatially and temporally available food resources, 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 hoawa and loulu have persisted despite the decline, extirpation and extinction of native fruit-eating birds is an intriguing and critical question that arises from my 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 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 & 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 likely 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 & 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 on-going conservation efforts of humans. Restoring a functional population of Alala as primary seed dispersers for these plants could save thousands of dollars in restoration costs, undo ecological anachronisms such as those exemplified by hoawa and other plants in this study, and help restore and maintain Hawaii's natural and cultural heritage (Culliney et al. *unpublished data*). Alala recovery efforts ultimately face significant challenges from numerous factors, and the successful establishment of a sustainable and ecologically functioning wild Alala population will take concerted and cooperative effort over an extended timeline. However, the results of my study add another reason to restore critically endangered species to the wild that goes beyond "intrinsic value". Globally, many native species such as Alala 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.

Table 1. Native fruiting plant species used in the flock-wide feeding trials and in those trials that involved a subset of the flock. These species were chosen based on prior documentation of Alala diet in the wild or based on overlap with the historic range of Alala (J Price, T Pratt, L Pratt, pers. comm.). Average fruit and seed sizes are presented. The number of times we gave each plant species to each bird varied based on availability in nature. Results of the feeding trials (note that numbers are not model averaged estimates) are presented on bird behaviors relating to seed dispersal (eating, carrying, caching) as well as the number of ingested seeds compared to the approximate number of seeds given.

Trial Type	*Plant species used in feeding trials* — *Hawaiian name*	*Scientific name*	*Mean Fruit size (mm)*	*Mean Seed size (mm)*	*Number of times given to each bird*	*Number of Alala*	*Number times observed eating**	*Number times observed carrying**	*Number times observed caching*	*Approx. number of seeds given***	*Number seeds found ingested****
Flock-wide	Hoawa[1,2]	*Pittosporum hosmeri*	55[A]	9[A]	3-25	57	12	140	17	14688	257
	Kawau[1]	*Ilex anomala*	9[A]	3[B]	10-29	57	35	40	10	99957	510
	Kolea[1]	*Myrsine lanaiensis*	7[A]	6[B]	3	57	25	31	6	1609	72
	Mamaki[1,2]	*Pipturus albidus*	20[A]	1[B]	12-18	57	123	54	6	251856	209
	Naio[1]	*Myoporum sandwisense*	6[A]	2[A]	15-24	57	64	41	11	6019	411
	Oha kepau[1,2]	*Clermontia hawaiiensis*	31[A]	0.5[B]	6	57	54	55	4	167620	1513
	Ohe mauka[1]	*Tetraplasandra hawaiiensis*	7[A]	6[B]	12-25	57	74	63	14	28017	305
	Ohelo[1,2]	*Vaccinium reticulatum*	12[A]	0.5[B]	12-19	57	193	78	19	419520	848
	Olapa[1,2]	*Cheirodendron trigynum*	75[A]	5[B]	10-23	57	89	39	4	49812	813
	Pilo[1]	*Coprosma rhynocarpa*	10[A]	7[B]	12-18	57	350	181	20	13166	1523
	Pukiawe[1]	*Styphelia tameiameiae*	5[A]	3[B]	10-27	57	111	32	2	6505	336
	Loulu[5]	*Pritchardia schattaueri* (black)	40[A]	40[A]	4-12	57	2	57	2	360	0
	Loulu[5]	*Pritchardia schattaueri* (green)	31[B]	*N/A*	3-9	57	8	107	3	366	2.75[§]
	Halapepe[5]	*Pleomele hawaiiensis*	12[A]	7[A]	6-13	57	4	88	20	1064	13
Subset of flock	Kopiko[1]	*Psychotria hawaiiensis*	7[A]	7[B]	3-5	39	8	14	5	604	4
	Lama[3]	*Diospyros sandwicensis*	17[A]	13[A]	1-3	21	0	17	1	67	1
	Oha wai[1,2]	*Clermontia parviflora*	19[A]	0.5[B]	6	39	8	8	4	72090	316
Non-toxicity	Alaa[5]	*Pouteria sandwicensis*	33[A]	24[A]	5-10	2	0	2	2	*N/A*[‡]	*N/A*
	Maile[5]	*Alyxia oliviformis*	*Unknown*	13[B]	4-5	2	0	2	1	70	0
	Olopua[5]	*Nestegis sandwicensis*	19[A]	*Unknown*	5	1	1	3	3	5	0

Alala diet sources: [1]Sakai et al. 1986, [2]Sakai & Carpenter 1990, [3]Tomich 1971, [4]Perkins 1903, [5]Speculated based on range overlap.

Fruit and seed size sources: [A]Wagner et al. 1999, [B]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 Alala pellets.

[‡]Alaa used in these pre-trials were small unfertilized fruits without seeds

Table 2. Model selection results ($w_i \geq 10\%$) for regressions of Alala characteristics (age and sex) on the probability of Alala eating behavior for 13 native Hawaiian plants; results include Akaike information criterion corrected for small sample size (*AICc*), relative AICc (*ΔAICc*), Akaike weight (w_i), and number of parameters in the model (*k*).

Plant species	*Model*	*AICc*	*ΔAICc*	w_i	*k*
Pilo	Age	9.74	0	0.75	3
	Age+sex	12.00	2.26	0.24	4
Ohelo	Age	-7.09	0	0.75	3
	Age+sex	-4.90	2.18	0.25	4
Oha kepau	Age+sex	-48.24	0	0.68	4
	Age	-46.76	1.49	0.32	3
Kolea	Age	5.06	0	0.73	3
	Age+sex	7.11	2.05	0.26	4
Mamaki	Age+sex	-65.40	0	0.52	4
	Age	-65.26	0.15	0.48	3
Pukiawe	Age	-122.31	0	0.76	3
	Age+sex	-120.05	2.27	0.24	4
Ohe mauka	Age	-117.31	0	0.62	3
	Age+sex	-116.35	0.96	0.38	4
Naio	Age	-139.90	0	0.71	3
	Age+sex	-138.10	1.80	0.29	4
Kawau	Age	-161.17	0	0.57	3
	Age+sex	-160.61	0.55	0.43	4
Olapa	Age	-15.90	0	0.41	3
	Age+sex	-15.25	0.65	0.30	4
	Intercept only	-14.33	1.57	0.19	2
	Sex	-13.06	2.84	0.10	3
Hoawa	Intercept only	-242.46	0	0.37	2
	Age	-241.82	0.64	0.27	3
	Sex	-241.42	1.04	0.22	3
	Age+sex	-240.56	1.90	0.14	4
Loulu-green	Intercept only	-260.97	0	0.44	2
	Sex	-259.90	1.07	0.26	3
	Age	-259.22	1.75	0.18	3
	Age+sex	-258.32	2.65	0.12	4
Halapepe	Intercept only	-195.83	0	0.52	2
	Sex	-194.09	1.73	0.22	3
	Age	-193.76	2.06	0.19	3
Loulu-black	Intercept only	-260.97	0	0.44	2
	Sex	-259.90	1.07	0.26	3
	Age	-259.22	1.75	0.18	3
	Age+sex	-258.32	2.65	0.12	4

Table 3. Model selection results ($w_i \geq 10\%$) for regressions of Alala characteristics (age and sex) on the probability of Alala carrying behavior for 13 native Hawaiian plants; results include Akaike information criterion corrected for small sample size (*AICc*), relative AICc (*ΔAICc*), Akaike weight (w_i), and number of parameters in the model (k).

Plant species	*Model*	*AICc*	*ΔAICc*	w_i	k
Kolea	Age	-0.18	0	0.76	3
	Age+sex	2.14	2.32	0.24	4
Ohe mauka	Age	-132.59	0	0.72	3
	Age+sex	-130.72	1.87	0.28	4
Naio	Age	-169.88	0	0.74	3
	Age+sex	-167.75	2.13	0.26	4
Kawa'u	Age	-163.27	0	0.69	3
	Age+sex	-161.66	1.61	0.31	4
Pukiawe	Age	-195.26	0	0.62	3
	Age+sex	-194.23	1.02	0.37	4
Mamaki	Age+sex	-119.49	0	0.70	4
	Age	-117.12	2.37	0.21	3
Ohelo	Age	-62.19	0	0.56	3
	Age+sex	-60.13	2.06	0.20	4
	Intercept only	-59.75	2.43	0.17	2
Oha kepau	Age+sex	-18.21	0	0.58	4
	Age	-17.34	0.87	0.37	3
Pilo	Intercept only	-31.04	0	0.56	2
	Age	-28.95	2.09	0.20	3
	Sex	-28.83	2.21	0.18	3
Olapa	Sex	-86.95	0	0.48	3
	Intercept only	-85.58	1.37	0.24	2
	Age+sex	-85.16	1.80	0.19	4
Hoawa	Age+sex	-3.16	0	0.58	4
	Age	-2.42	0.73	0.40	3
Halapepe	Intercept only	-15.29	0	0.44	2
	Sex	-14.09	1.20	0.24	3
	Age	-13.88	1.41	0.22	3
	Age+sex	-12.44	2.84	0.11	4
Loulu-green	Intercept only	1.91	0	0.41	2
	Sex	2.26	0.35	0.35	3
	Age	4.13	2.22	0.14	3
	Age+sex	4.58	2.67	0.11	4
Loulu-black	Sex	-22.99	0	0.40	3
	Age+sex	-22.39	0.59	0.30	4
	Age	-21.11	1.88	0.16	3
	Intercept only	-20.98	2.01	0.15	2

Table 4. Model selection results ($w_i \geq 10\%$) for regressions of seed treatment on seed germination success; results include Akaike information criterion corrected for small sample size (*AICc*), relative AICc (*ΔAICc*), Akaike weight (w_i), and number of parameters in the model (k).

Plant species	*Model*	*AICc*	*ΔAICc*	w_i	k
Oha kepau	Treatment	-9.22	0	0.99	4
Hoawa	Treatment	-3.87	0	0.99	5
Ohelo	Treatment	-15.81	0	0.99	4
Pilo	Intercept only	14.23	0	0.56	2
	Treatment	14.68	0.44	0.44	5
Olapa	Intercept only	-13.60	0	0.68	2
	Treatment	-12.06	1.54	0.32	5
Mamaki	Intercept only	-3.54	0	0.96	2

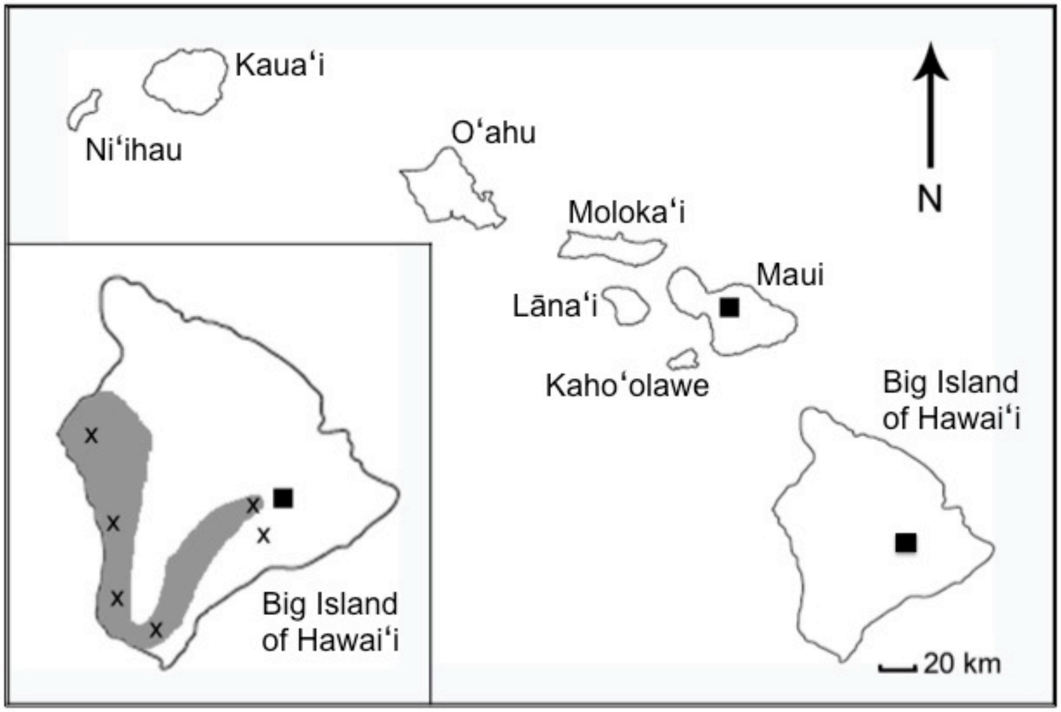

Figure 1. Alala breeding facilities in the Hawaiian Islands include the Keauhou Bird Conservation Center on the Big Island of Hawaii in Volcano, HI and the Maui Bird Conservation Center in Makawao, HI on the island of Maui (black squares). The historic range of Alala (grey shading) is shown on the Island of Hawaii (after Banko et al. 2002) as well as the locations of fruit collection sites (x).

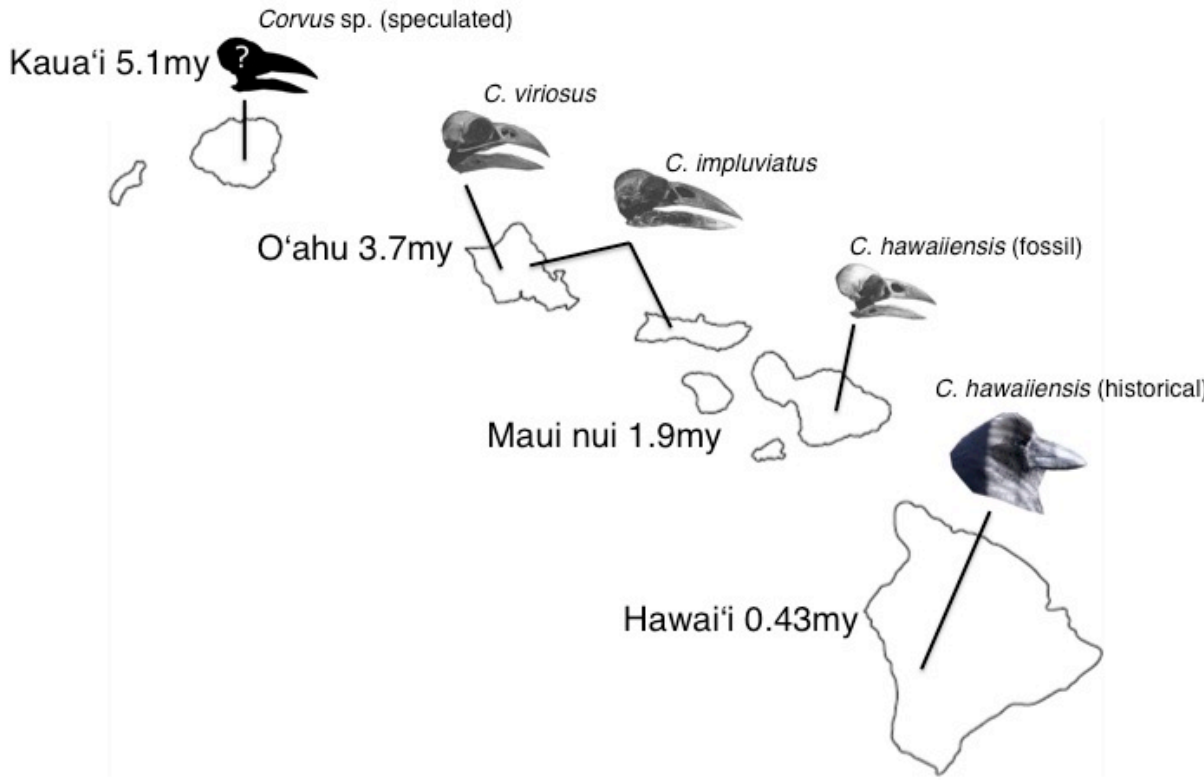

Figure 2. Alala were documented historically on the Island of Hawaii (Henshaw 1902; Perkins 1903) and in the fossil record on Maui (James et al. 1987); two other *Corvus* species fossils were discovered on Maui nui and Oahu, and likely existed on Kauai as well (James & Olson 1991).

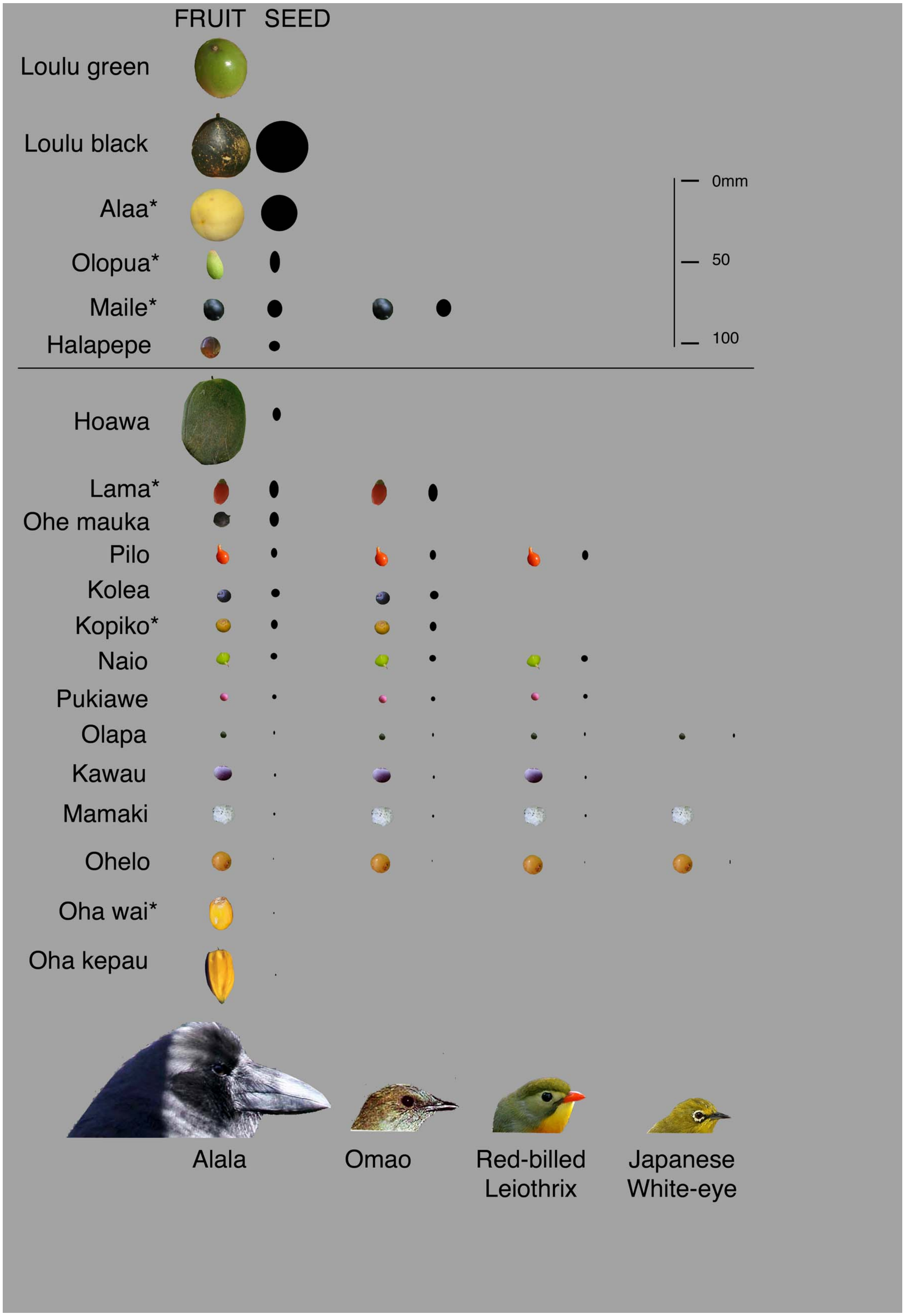
FRUIT
SEED
Loulu green
Loulu black
Alaa*
Olopua*
Maile*
Halapepe
0mm
50
100
Hoawa
Lama*
Ohe mauka
Pilo
Kolea
Kopiko*
Naio
Pukiawe
Olapa
Kawau
Mamaki
Ohelo
Oha wai*
Oha kepau
Alala
Omao
Red-billed Leiothrix
Japanese White-eye

Figure 3. Native fruits and seeds consumed (in order of seed size) by Alala (*Corvus hawaiiensis*; native, extinct in the wild), Omao (*Myadestes obscurus*; native, extirpated from Alala historic range), Red-billed Leiothrix (*Leiothrix lutea*; exotic introduced, common), and Japanese White-eye (*Zosterops japonicus*; exotic introduced, common) (Tomich 1971, Sakai et al. 1986, Sakai & Carpenter 1990, Male et al. 1998, Wakelee and Fancy 1999, vanRiper 2000, Wagner et al. 2000, Banko et al. 2002, Foster and Robinson 2007, L. Pejchar unpublished data, and S. Culliney unpublished data). Only the 14 fruits and seeds used in the flock-wide study and the six fruits used in the trials involving a subset of Alala (*) are shown. The top five species (placed above the horizontal line) are speculated to have been part of the Alala diet based on possible prehistoric range overlap (J Price, T Pratt, L Pratt, pers. comm.).

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

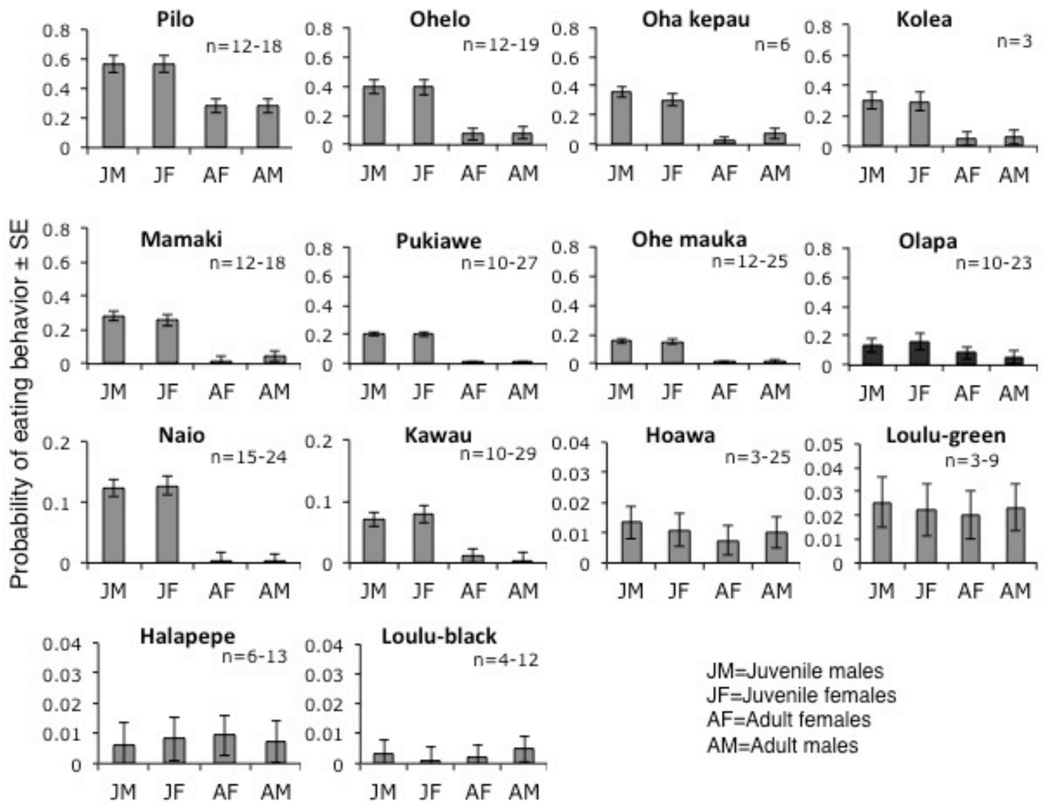

Figure 5. Model averaged estimates of probabilities of observing Alala eating behavior ± SE (note differing scales) for 13 species of native Hawaiian plants (loulu represented twice with fruits in black mature form and green immature form), separated by bird age and sex classes. The number of times each bird was given each plant varied, as indicated by sample size (n).

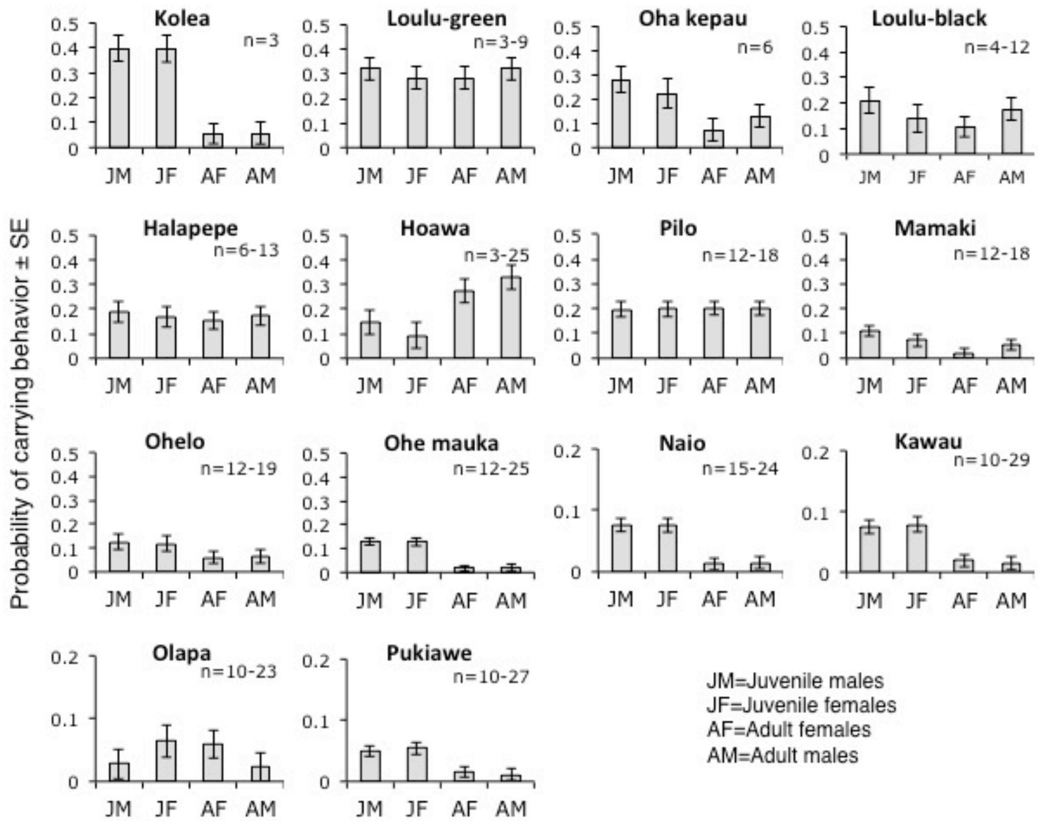

Figure 6. Model averaged estimates of probabilities of observing Alala carrying behavior ± SE (note differing scales) for 13 species of native Hawaiian plants (loulu represented twice with fruits in black mature form and green immature form), separated by bird age and sex classes. The number of times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

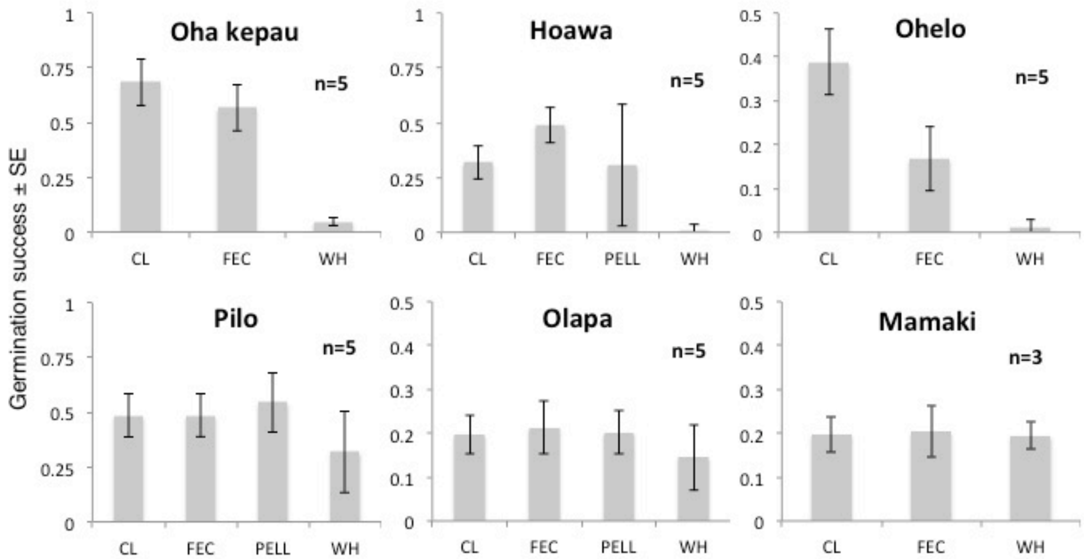

Figure 7. Model averaged estimates of proportion of seeds germinated ± SE (note differing scales) between seeds cleaned by hand (CL), Alala ingested seeds from fecal droppings (FEC), pellets (PELL), and seeds in whole fruits (WH) for 6 species of native Hawaiian plants. Number of replicate trials was either 3 or 5, as indicated by sample size (n).

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Appendix

Appendix Table 1. Effect size for age and sex variables from model averaging for each of the 14 plants.

Behavior	*Plant species*	*Effect*	*Size*	*Adjusted SE*	*Lower CL*	*Upper CL*
Eating	Olapa	Age	-0.1110	0.0565	-0.2220	-0.0002
		Sex	-0.0642	0.0556	-0.1730	0.0447
	Oha kepau	Age	-0.2810	0.0426	-0.3650	-0.1980
		Sex	0.0775	0.0411	-0.0030	0.1580
	Pilo	Age	-0.2870	0.0704	-0.4250	-0.1490
		Sex	-0.0163	0.0699	-0.1530	0.1210
	Kawau	Age	-0.0665	0.0152	-0.0963	-0.0367
		Sex	-0.0193	0.0152	-0.0490	0.0104
	Naio	Age	-0.1240	0.0183	-0.1600	-0.0878
		Sex	-0.0126	0.0184	-0.0486	0.0234
	Kolea	Age	-0.2430	0.0690	-0.3790	-0.1080
		Sex	0.0340	0.0675	-0.0984	0.1660
	Mamaki	Age	-0.2400	0.0358	-0.3110	-0.1700
		Sex	0.0532	0.0353	-0.0159	0.1220
	Hoawa	Age	-0.0083	0.0070	-0.0220	0.0053
		Sex	0.0071	0.0070	-0.0065	0.0208
	Halapepe	Age	0.0044	0.0115	-0.0181	0.0268
		Sex	-0.0075	0.0111	-0.0293	0.0143
	Loulu-black	Age	0.0048	0.0066	-0.0082	0.0178
		Sex	0.0066	0.0061	-0.0055	0.0186
	Loulu-green	Age	-0.0076	0.0165	-0.0400	0.0247
		Sex	0.0111	0.0162	-0.0207	0.0430
	Pukiawe	Age	-0.2000	0.0215	-0.2420	-0.1580
		Sex	0.0045	0.0216	-0.0379	0.0468
	Ohe mauka	Age	-0.1480	0.0222	-0.1910	-0.1040
		Sex	0.0246	0.0220	-0.0185	0.0677
	Ohelo	Age	-0.3160	0.0601	-0.4330	-0.1980
		Sex	0.0207	0.0599	-0.0967	0.1380
Carrying	Olapa	Age	-0.0187	0.0309	-0.0792	0.0419
		Sex	-0.0551	0.0295	-0.1130	0.0027
	Oha kepau	Age	-0.1570	0.0554	-0.2650	-0.0480
		Sex	0.0931	0.0538	-0.0123	0.1980
	Pilo	Age	0.0176	0.0502	-0.0807	0.1160
		Sex	-0.0057	0.0491	-0.1020	0.0906
	Kawau	Age	-0.0597	0.0149	-0.0890	-0.0305
		Sex	-0.0121	0.0150	-0.0415	0.0174
	Naio	Age	-0.0619	0.0141	-0.0895	-0.0343
		Sex	0.0058	0.0142	-0.0220	0.0336
	Kolea	Age	-0.3400	0.0658	-0.4690	-0.2110
		Sex	-0.0007	0.0645	-0.1270	0.1260
	Mamaki	Age	-0.0585	0.0224	-0.1020	-0.0145
		Sex	0.0468	0.0221	0.0034	0.0902
	Hoawa	Age	0.1860	0.0564	0.0752	0.2960
		Sex	0.0938	0.0558	-0.0157	0.2030
	Halapepe	Age	-0.0482	0.0571	-0.1600	0.0636
		Sex	0.0531	0.0556	-0.0558	0.1620
	Loulu-black	Age	-0.0733	0.0550	-0.1810	0.0346
		Sex	0.0984	0.0509	-0.0015	0.1980
	Loulu-green	Age	-0.0033	0.0658	-0.1320	0.1260
		Sex	0.0848	0.0640	-0.0406	0.2100
	Pukiawe	Age	-0.0388	0.0113	-0.0610	-0.0166
		Sex	-0.0122	0.0113	-0.0343	0.0099
	Ohe mauka	Age	-0.1100	0.0194	-0.1480	-0.0717
		Sex	0.0124	0.0193	-0.0255	0.0503
	Ohelo	Age	-0.0775	0.0371	-0.1500	-0.0049
		Sex	0.0203	0.0373	-0.0528	0.0935

Appendix Table 2. Complete model selection results for regressions of Alala characteristics (age and sex) on the probability of Alala eating and carrying behavior for 13 native Hawaiian plants; results include Akaike information criterion corrected for small sample size (*AICc*), relative AICc (*ΔAICc*), Akaike weight (w_i), and number of parameters in the model (k).

Response	*Plant species*	*Model*	*AICc*	*ΔAICc*	w_i	k
Eating	Olapa	Age	-15.90	0	0.41	3
		Age+sex	-15.25	0.65	0.30	4
		Intercept only	-14.33	1.57	0.19	2
		Sex	-13.06	2.84	0.10	3
	Oha kepau	Age+sex	-48.24	0	0.68	4
		Age	-46.76	1.49	0.32	3
		Sex	-15.66	32.58	0.00	3
		Intercept only	-13.72	34.52	0.00	2
	Pilo	Age	9.74	0	0.75	3
		Age+sex	12.00	2.26	0.24	4
		Intercept only	23.21	13.47	0.00	2
		Sex	25.36	15.62	0.00	3
	Kawau	Age	-161.17	0	0.57	3
		Age+sex	-160.61	0.55	0.43	4
		Intercept only	-146.06	15.11	0.00	2
		Sex	-144.15	17.02	0.00	3
	Naio	Age	-139.90	0	0.71	3
		Age+sex	-138.10	1.80	0.29	4
		Intercept only	-106.54	33.36	0.00	2
		Sex	-104.31	35.59	0.00	3
	Kolea	Age	5.06	0	0.73	3
		Age+sex	7.11	2.05	0.26	4
		Intercept only	15.11	10.05	0.00	2
		Sex	16.64	11.58	0.00	3
	Mamaki	Age+sex	-65.40	0	0.52	4
		Age	-65.26	0.15	0.48	3
		Sex	-32.35	33.06	0.00	3
		Intercept only	-31.31	34.10	0.00	2
	Hoawa	Intercept only	-242.46	0	0.37	2
		Age	-241.82	0.64	0.27	3
		Sex	-241.42	1.04	0.22	3
		Age+sex	-240.56	1.90	0.14	4
	Halapepe	Intercept only	-195.83	0	0.52	2
		Sex	-194.09	1.73	0.22	3
		Age	-193.76	2.06	0.19	3
		Age+sex	-191.89	3.93	0.07	4
	Loulu-black	Intercept only	-260.97	0	0.44	2
		Sex	-259.90	1.07	0.26	3
		Age	-259.22	1.75	0.18	3
		Age+sex	-258.32	2.65	0.12	4
	Loulu-green	Intercept only	-260.97	0	0.44	2
		Sex	-259.90	1.07	0.26	3
		Age	-259.22	1.75	0.18	3
		Age+sex	-258.32	2.65	0.12	4
	Pukiawe	Age	-122.31	0	0.76	3
		Age+sex	-120.05	2.27	0.24	4
		Intercept only	-68.55	53.76	0.00	2
		Sex	-66.99	55.33	0.00	3
	Ohe mauka	Age	-117.31	0	0.62	3
		Age+sex	-116.35	0.96	0.38	4
		Intercept only	-84.46	32.85	0.00	2
		Sex	-83.81	33.50	0.00	3
	Ohelo	Age	-7.09	0	0.75	3
		Age+sex	-4.90	2.18	0.25	4
		Intercept only	14.99	22.08	0.00	2
		Sex	16.50	23.58	0.00	3

Carrying	Olapa	Sex	-86.95	0	0.48	3
		Intercept only	-85.58	1.37	0.24	2
		Age+sex	-85.16	1.80	0.19	4
		Age	-83.55	3.40	0.09	3
	Oha kepau	Age+sex	-18.21	0	0.58	4
		Age	-17.34	0.87	0.37	3
		Sex	-12.61	5.60	0.03	3
		Intercept only	-10.88	7.33	0.01	2
	Pilo	Intercept only	-31.04	0	0.56	2
		Age	-28.95	2.09	0.20	3
		Sex	-28.83	2.21	0.18	3
		Age+sex	-26.64	4.40	0.06	4
	Kawau	Age	-163.27	0	0.69	3
		Age+sex	-161.66	1.61	0.31	4
		Intercept only	-150.42	12.85	0.00	2
		Sex	-148.23	15.04	0.00	3
	Naio	Age	-169.88	0	0.74	3
		Age+sex	-167.75	2.13	0.26	4
		Intercept only	-154.12	15.76	0.00	2
		Sex	-152.50	17.38	0.00	3
	Kolea	Age	-0.18	0	0.76	3
		Age+sex	2.14	2.32	0.24	4
		Intercept only	21.04	21.21	0.00	2
		Sex	23.04	23.22	0.00	3
	Mamaki	Age+sex	-119.49	0	0.70	4
		Age	-117.12	2.37	0.21	3
		Sex	-114.91	4.58	0.07	3
		Intercept only	-111.54	7.95	0.01	2
	Hoawa	Age+sex	-3.16	0	0.58	4
		Age	-2.42	0.73	0.40	3
		Intercept only	5.53	8.68	0.01	2
		Sex	5.82	8.98	0.01	3
	Halapepe	Intercept only	-15.29	0	0.44	2
		Sex	-14.09	1.20	0.24	3
		Age	-13.88	1.41	0.22	3
		Age+sex	-12.44	2.84	0.11	4
	Loulu-ripe	Sex	-22.99	0	0.40	3
		Age+sex	-22.39	0.59	0.30	4
		Age	-21.11	1.88	0.16	3
		Intercept only	-20.98	2.01	0.15	2
	Loulu-green	Intercept only	1.91	0	0.41	2
		Sex	2.26	0.35	0.35	3
		Age	4.13	2.22	0.14	3
		Age+sex	4.58	2.67	0.11	4
	Pukiawe	Age	-195.26	0	0.62	3
		Age+sex	-194.23	1.02	0.37	4
		Intercept only	-186.19	9.07	0.01	2
		Sex	-184.38	10.87	0.00	3
	Ohe mauka	Age	-132.59	0	0.72	3
		Age+sex	-130.72	1.87	0.28	4
		Intercept only	-107.60	24.98	0.00	2
		Sex	-106.17	26.42	0.00	3
	Ohelo	Age	-62.19	0	0.56	3
		Age+sex	-60.13	2.06	0.20	4
		Intercept only	-59.75	2.43	0.17	2
		Sex	-58.09	4.10	0.07	3

Appendix Table 3. Effect size for the treatment variable from model averaging for the six plants included in germination trials.

Plant species	*Effect*	*Size*	*Adjusted SE*	*Lower CL*	*Upper CL*
Olapa	Cleaned (intercept)	0.197	0.0469	0.105	0.289
	Fecal	0.0508	0.0928	-0.131	0.233
	Pellet	0.0166	0.0904	-0.161	0.194
	Whole	-0.164	0.0854	-0.331	0.00339
Oha kepau	Cleaned (intercept)	0.684	0.119	0.451	0.917
	Fecal	-0.118	0.166	-0.443	0.207
	Whole	-0.637	0.12	-0.873	-0.401
Pilo	Cleaned (intercept)	0.483	0.105	0.278	0.688
	Fecal	0.00435	0.178	-0.345	0.354
	Pellet	0.14	0.186	-0.224	0.504
	Whole	-0.369	0.186	-0.733	-0.00513
Mamaki	Cleaned (intercept)	0.198	0.0475	0.105	0.291
	Fecal	0.132	0.199	-0.258	0.522
	Whole	-0.119	0.135	-0.383	0.145
Hoawa	Cleaned (intercept)	0.318	0.0825	0.157	0.48
	Fecal	0.169	0.119	-0.0641	0.403
	Pellet	-0.011	0.318	-0.635	0.613
	Whole	-0.319	0.092	-0.499	-0.138
Ohelo	Cleaned (intercept)	0.388	0.0833	0.224	0.551
	Fecal	-0.222	0.114	-0.446	0.0019
	Whole	-0.377	0.0831	-0.54	-0.214

Appendix Table 4. Complete model selection results for regressions of seed treatment on seed germination success; results include Akaike information criterion corrected for small sample size (*AICc*), relative AICc (*ΔAICc*), Akaike weight (w_i), and number of parameters in the model (k).

Plant species	*Model*	*AICc*	*ΔAICc*	w_i	k
Oha kepau	Treatment	-9.22	0	0.99	4
	Intercept only	10.01	19	0.00	2
Hoawa	Treatment	-3.87	0	0.99	5
	Intercept only	9.36	13	0.00	2
Ohelo	Treatment	-15.81	0	0.99	4
	Intercept only	-4.49	11	0.00	2
Pilo	Intercept only	14.23	0	0.56	2
	Treatment	14.68	0.44	0.44	5
Olapa	Intercept only	-13.60	0	0.68	2
	Treatment	-12.06	1.54	0.32	5
Mamaki	Intercept only	-3.54	0	0.96	2
	Treatment	2.96	6.50	0.04	4

Part II. Integrating community values into Alala (*Corvus hawaiiensis*) recovery

Introduction

Each year millions of conservation dollars go towards endangered bird restoration programs, a large portion of which is dedicated to captive breeding and release programs (Restani & Marzluff 2001). These programs utilize the finest captive rearing and ecological science available to contribute to reintroduction and recovery efforts. A critical but often neglected step in these efforts is understanding and incorporating the knowledge, values, and perspectives of the people living in communities in and adjacent to the sites where species are reintroduced. Research into the human dimensions of natural resources can provide managers with strategies to describe conservation in terms relevant to stakeholders with differing underlying values (Decker et al. 2004). For example, consideration of the human dimensions surrounding a European bison reintroduction program enabled the species' conservation to move forward more effectively (Decker et al. 2010). Insight into the values underlying stakeholder perspectives can allow managers to proactively implement more effectual and cost-effective reintroduction programs.

The state of Hawaii, a vulnerable island system characterized by high endemism, is a hotspot for endangered species and home to a culturally diverse human population. Hawaii provides numerous examples of how conservation efforts can come into conflict with human activities. Habitat needs for the critically endangered Palila (*Loxioides balleuei*), for example, are at odds with the desires of many recreational hunters who would like to maintain populations of introduced ungulates (Juvik & Juvik 1984; Banko et al. 2009). The nocturnal dispersal of endangered Newell's Shearwaters (*Puffinus newelli*), a seabird that navigates by the moon and becomes disoriented by artificial lights, has recently clashed with Kauai residents who value their evening sporting events (Associated Press 2010). Wildlife restoration programs such as these and others around the world that currently focus on the natural sciences to inform successful restoration of endangered species could also benefit from research on the human dimensions surrounding the target species or ecosystem. Greater understanding of this under-appreciated dimension of reintroduction efforts prior to project commencement could alleviate social, economic and political roadblocks and facilitate the implementation of critical ecological recovery strategies.

I will use the terms *utilitarian* and *mutualist* to describe how a person's underlying values orient them to regard wildlife as a resource (Bright et al. 2000) or wildlife as members of one's own community (Teel & Manfredo 2009). Prior research indicates that the state of Hawaii as a whole exhibits a mutualist value orientation toward wildlife (Tanger & Laband 2008; Teel & Manfredo 2009). However, these findings neither considered value orientations at a local level nor investigated the nuances of the cultural motivations behind the utilitarian and mutualist mindsets. The utilitarian value orientation is particularly associated with conservative values typically found in rural ranching and hunting communities in the American West (Bright et al. 2000). I will explore how the definitions of each value orientation may change in light of cultural distinctions and how these distinctions can inform and clarify discussions of endangered species recovery. I use the Alala, or Hawaiian Crow (*Corvus hawaiiensis*), as a case study to show how understanding community values might contribute to the ultimate success of native species recovery programs.

Study species

Alala are large, charismatic, omnivorous crows that held great significance to the ancient Hawaiians (Cook 1796; Pukui 1983) and were once readily found in the mesic forests on the south-facing slopes of Mauna Loa on the Big Island of Hawaii (Fig. 1) (Henshaw 1902; Perkins 1903; Banko et al. 2002). Their population declined through the 20th century, despite being among the first species federally protected by the 1967 precursor to the U.S. Endangered Species List. Although the primary reasons behind the wild Alala decline and an unsuccessful attempt at re-establishment using captive-bred birds are ecological in nature (Giffin et al. 1987; Work et al. 2000; Banko et al. 2002; USFWS 2003), human dimensions also played a prominent contributing role (Walters 2006). Antagonistic shooting of Alala by humans in the historical period was recorded but poorly understood and quantified by neither early explorers (Henshaw 1902; Perkins 1903) nor later biologists (Munro 1960; Giffin et al. 1987). More recently, discord between private landowners and biologists over site access to Alala habitat was further exacerbated by the long-standing rift between these stakeholders regarding mishandling of scientific inquiry, property rights, and cultural differences (Walters 2006).

The last wild Alala was observed in 2002, and biologists consider the species extinct in the wild (USFWS 2009; IUCN 2010). Two breeding facilities administered by the San Diego Zoo house the entire remaining Alala population; 95 fledged individuals as of September 2011. A partnership between the Hawaii Endangered Bird Conservation Program, the San Diego Zoological Society, the U.S. Fish and Wildlife Service (USFWS) and the state of Hawaii's Department of Forestry and Wildlife (DOFAW) intends to release captive-reared Alala into the wild in the future, with the ultimate goal of establishing a viable wild population (USFWS 2003). To avoid a repetition of past tragedies, I reason that considering the human dimensions of Alala conservation and understanding attitudes towards the Alala in particular, and Hawaii's ecosystems more broadly, will contribute substantially to a future Alala reintroduction.

Methods

Focus group interviews

As part of a larger study investigating wildlife value orientations and how children interact with nature in six U.S. states (Teel & Bruyere unpublished data), and alongside a parallel study investigating the ecological role of the Alala (S.C., L.P., R. Switzer & V. Ruiz-Gutierrez, unpublished data), researchers conducted focus group interviews in December 2009 in Honoka'a and Pahala, two rural communities on the Big Island of Hawaii (Fig. 1). Focus groups have been well-established as an appropriate approach to collecting qualitative data on societal attitudes and values (Creswell 1994). In Honoka'a researchers interviewed a group of 8 educators (hereafter "Honoka'a educators", or "HE") and a group of 11 parents (hereafter "Honoka'a parents" or "HP"). Researchers conducted one interview in Pahala with a group of 3 community members (hereafter "Pahala community" or "PC"). Researchers recruited participants for all three interviews by distributing flyers to parents and teachers, and offered food, childcare, and a monetary stipend as a reimbursement for time and attendance, following standard protocol for focus groups (Creswell 1994).

The procedure for assessing wildlife value orientations lasted approximately 30 minutes for each of the focus group sessions. Other topics within the focus group sessions included discussion of barriers to participation in environmental education programs, but I do not report those findings here. Each focus group included one local moderator, trained onsite in interview methods, and two researchers acting as observers. Researchers recorded audio and transcribed comments for all three focus groups. An assistant transcribed and analyzed focus group discussions using a two-step open and axial coding method (Creswell 1994).

Photo assessment

The moderator showed the participants six photographs, each depicting a different human-wildlife situation. The photos (Fig. 2) represent major wildlife value orientations and depict: (1) waterfowl hunters with rifles, (2) a man holding a fawn, (3) animal rights protesters marching against a rodeo, (4) a feral pig in a degraded forest, (5) Alala in native habitat (photo credit Zoological Society of San Diego), and (6) a fisherman casting a net. The researchers intended the content in the photos 1-4 and 6 to elicit utilitarian and mutualist value orientations, and intended photo 5 to reveal recognition and reaction towards Alala.

To gauge reactions to each photograph, researchers first asked participants to individually rate whether they liked and whether they could relate to the photograph. These questions prepared participants for vocally rating and discussing the photographs as a group and served as a way to check initial individual assessments against participants' group statements. The moderator then showed the photographs a second time to the group, one at a time, and participants vocally responded to and discussed the photos.

Results

I found that the focus group interviews uncovered three key findings: 1) Very few participants recognized the Alala but all participants expressed a positive reaction towards the species; 2) Participants held a predominantly utilitarian orientation towards natural resources but with emphasis on sustainable stewardship and the ethical use of animals; 3) Value orientations were suffused with cultural significance.

Key Finding #1: Very few participants recognized the Alala but all participants expressed a positive reaction towards the species.

Pahala community: One of the three participants guessed the bird depicted in the photo was a raven, while another person tentatively identified the Alala. Once the moderator affirmed the species, these participants asked several questions, indicating their interest in the Alala and its situation:

> *PC 1: How did they get extinct? Was it their food source? Did it get depleted? ... I mean people don't really hunt ravens.*
>
> *...*
>
> *PC 2: So where's the [breeding facility]? Can the public go there?*
>
> *PC 3: Are they succeeding with the birds now? How long do they live?*

Honoka'a parents: No participant among the 11 Honoka'a parents recognized the Alala, although one participant knew that the bird was a crow species. When the moderator identified the bird, these parents indicated murmurs of comprehension and one parent expressed appreciation at the idea of a wild animal living without human interference:

> *HP 1: I like this photo. It's eating the natural [berries]. It's almost like people [are] on-looking but we're not really there.*

Honoka'a educators: Among these educators, 2 out of 8 recognized the Alala and were able to name the species. One of these participants, a well-informed cultural practitioner, also expressed his regard for the Alala and knowledge about its history of decline:

> *HE 1: LOVE this photo. It's a sad photo, but it's a good photo. Just by knowing there are only two of them left in the wild, not even?*

Other participants who did not immediately recognize the Alala were still familiar with its current status and natural history of the Alala:

> *HE 1: That's the one they are feeding them with the puppets to get them so that they could release them into the wild.*
>
> *HE 2: And they protect the forest. There's a connection.*

The cultural practitioner then shared a *mo'olelo* about the Alala, a tale that is passed down in Hawaiian tradition through generations. Two other educators expressed the thrill they experienced from listening to his story:

> *HE 1: It's a sad part of history, the story of this bird, because the Alala has always been known culturally. When people used to walk in the forest, he would go off, "alalalala!" to let everything know. I remember from when Kupuna ["grandparent" or "elder"] telling us when the waiting ships weren't too heavy, they want a lot of salted pork. So to go into the forest they need to guarantee they get their pig. So the Alala start going off and the animals would run. The hunters would shoot the Alala to keep the forest quiet…[But] the Alala would warn of danger, of spiritual negative energy coming toward them. Without the call of the Alala anymore, no one hears the crying of the forest. We don't see the problem and don't hear the message.*
>
> *HE 2: All chicken skin! [An expression that literally means, "shivering", but further conveys an intense emotional connection.]*
>
> *HE 3: Beautiful.*

Among the participants in the three focus groups, few were able to identify the Alala, however, those who did not immediately recognize the species were somewhat familiar with the bird after having the photo identified for them. Once identified, the responses to the Alala were positive, inquisitive, and included cultural subtext.

Key Finding #2: Participants held a predominantly utilitarian orientation towards natural resources but with qualifications for sustainable stewardship and the ethical use of animals.

Pahala community: When responding to the waterfowl hunting photo, one participant expressed disapproval at what the participant supposed were hunting activities purely for sport:

> *PC 1: I don't like it because it's just for game purposes. They're not hunting to eat or anything…If you're going to go on a hunt, if you're going to shoot something like a pig or something, for the purpose of taking it home, then yes. These guys are just shooting it for a trophy.*

Other respondents noted that hunting, while acceptable, should be subject to harvest regulation:

> *PC 1: I like the picture, I just think that hunting should be regulated. It needs to be controlled.*
>
> *PC 2: I think there should be a balance between how many animals humans consume.*

These participants reiterated this position in response to the photo depicting net fishing, lamenting their observations of over-harvest in an era of increasing scarcity:

> *PC 1: Even though my grandpa used to [net fish], you know, when fish was in abundance, I didn't mind it. But now today I don't look at it that way anymore. Because the netting has been cleaning out the fish…there was an abundance of fish back then; there isn't anymore…because I can go out there and fish for three hours and don't catch anything…*

Overall these community members had little inclination towards the mutualist orientation. In response to the photo showing animal rights protestors, one participant labeled animal rights as the responsibility of the human community, but characterized humans not as equals to animals, but as their guardians:

> *PC 1: I like what the sign says. She's right; animals do have rights. Because they don't have a voice, we're the voice for the animals.*

Honoka'a parents: These participants echoed the Pahala community members' sentiment that hunting is acceptable if the goal is to obtain food, and not purely sport, in response to the waterfowl hunting photo:

> *HP 1: I didn't like it because it doesn't look like they're hunting for food. It looks like they're hunting for sport.*
>
> *HP 2: I don't have a problem with other people [hunting] as long as they're not throwing the animals away and they're actually eating them, and also if the animals aren't endangered.*

Within the context of the photo depicting net fishing, the parents further qualified their views of wild population harvest to include sustainable methods:

> *HP 1: I sometimes have a hard time with net fishing because it can take too much I think; it can be wasteful.*
>
> *HP 2: But throw-net is an art…And if you're good enough to catch anything you deserve it."*
>
> *HP 3: I guess it just has to be done carefully…that you don't…overfish."*

These participants also demonstrate their respect for animals while still expressing a clear utilitarian value orientation towards the purpose of human use of animals:

> *HP 1: I do believe that animals have rights and that we should respect them for it …but I think that God put them here for us to be able to continue living. And so I think that if we continue on respectfully knowing that and whatever we take, we utilize it.*

Honoka'a educators: These educators spoke in line with the other focus groups about the importance that harvest should occur with an objective for survival, not sport. This viewpoint was taken somewhat to the extreme when one educator described someone they knew shooting a monk seal (*Monachus schauinslandi)*, a federally protected endangered species. Although there was initially mild distress in the speaker's subtext over the monk seal mother herself, the emerging opinion is not one of concern over the harm to an endangered species, but disgust over the wastefulness of a hunting act that was not for human consumption:

HE 1: There was that monk seal, they killed the monk seal; I think it was a pregnant mother.

HE 2: Did he eat it?

HE 1: No they just left the body there!

In addition to the importance of only harvesting animals for food, these educators also expressed agreement with treating animals with respect. One educator described a practice of hunting a female goat and taking the kids to raise for food and approved of the simultaneous resource extraction and the humane care of the young animals:

HE 1: You see people doing that here with goats…you shoot the mama goat and that's what families eat. And then they take the babies home and they raise them. Okay, they will be eaten but at least they're taken care of.

In general, participants in all focus groups approved of hunting that harvested wildlife for human consumption. Participants deemed hunting and fishing acceptable within a sustainable context and approved of respecting animals harvested for food. The Honoka'a educators also pointed out correctly that the waterfowl hunting photo was not necessarily relevant in Hawaii, where native waterfowl are protected from hunting and exotic game birds represent the only bird hunting opportunities. Furthermore, because Hawaii lacks native wildlife appropriate for hunting, the natural alliance between hunters and conservationists that can occur on the mainland do not exist, and tensions between the groups cannot be ameliorated with the demarcation of common resource conservation goals.

Key Finding #3: Utilitarian views were suffused with cultural significance.

<u>Pahala community members:</u> One participant mentioned an ancient Hawaiian concept of *kapu* law regulating the harvest of terrestrial and marine wildlife populations, in which authorities set harvest limits and designate species as off limits for portions of the year

(coinciding with species' natural history). This concept provides an example of how culture can inform a sustainable utilitarian value orientation:

> *PC 1: Hawaii used to have the kapu law, the kapu system, you can't hunt so many pigs or whatever. I think we should go back to that – that would be way better than what we do now.*

Honoka'a educators: The controversy surrounding feral pigs and hunting in Hawaii is beyond the scope of this project. However, the cultural and symbolic value held by one participant for both pigs and plants indicates that culture plays a major role in how people contemplate complex conservation issues.

In response to the feral pig photo, the cultural practitioner who had demonstrated his knowledge about the Alala noted that the pig (called *Pua'a* in Hawaiian) holds a special status in native Hawaiian culture.

> *HE 1: As a native Hawaiian, we honor the Pua'a. The pig is highly regarded in our culture.*

Within the same discussion, this participant also stated that he has value for culturally-significant native plants and he shares this value with the children in his community:

> *HE 1: A big thing I share with a lot of my kids in the forestry program is that when I used to hunt [pigs] when I was little, my family and I, we were out there also hunting. We were the shepherds of the forest. We know where the maile [an understory vine used to make leis for celebrations such as weddings and graduations] patches are, the koa trees. We know how to bend the maile down so that it grows and spreads. It was [our] responsibility.*

He then went on to relate a past controversy where native plant conservation required fencing out feral pigs, and the cultural interests of plants and pigs came into direct conflict. Another educator explicitly brought up the importance of native species conservation:

> *HE 1: In the 80s or 90s there was a pig on Kohala Mountain, where forestry conservation [was happening]…they fenced off the forest on the top of Kohala mountain and caused a huge uproar in the community.*

> *HE 2: But it's protecting certain native species that are only found in that area. You have to look at it both ways.*

The cultural practitioner agreed and identified several of the perspectives involved, including people who gather forest plants, the hunters, and the symbolism of the pig to the native Hawaiians:

> *HE 1: Yeah, that's why it's controversial, because we have native people [who] need to go up there and gather there. You used to have hunters who are used to going up there to go and hunt the pigs. You have the pig itself, which is a very important symbol for our people.*

Deep-rooted culture plays a considerable role for some of these participants in informing how they approach natural resource issues such as sustainability, exotic species and native species restoration. Often, these values can conflict both between stakeholders and within individuals. For example, people may simultaneously value mutually exclusive elements of the forest such as Alala and native plants, and the feral pigs that have led to their decline.

Discussion

Few individuals in the focus groups were able to positively identify the Alala in the photo. This overall low level of recognition among people living in communities flanking Alala historical range is discouraging to Alala restoration efforts. This alarming disparity calls for managers to increase awareness of Alala among those people who live in the immediate vicinity of Alala range, on par with the goals of restoring Alala habitat and increasing the captive population. Once the Alala was identified for them, however, some participants recalled knowledge of Alala conservation, and all reactions were animated, positive and inquisitive. One participant expressed appreciation for seeing a native species in the wild, an important basis on which to build support within local communities.

The *mo'olelo* shared by the cultural practitioner, about the Alala as the voice of the forest, hints that more indigenous knowledge may exist than is recorded in historical documents. It is possible that this story and others like it persist in the local consciousness, despite the Alala's extinction in the wild. Uplifting cultural stories about a critically endangered species could become important tools for generating interest and recognition in the Alala despite its absence from the contemporary experience.

The utilitarian value orientation emerging from these focus groups is consistent with the association of this orientation with people who live in rural areas (Manfredo et al. 2003) and suggests that managers should plan to approach local community discussions of Alala restoration within a primarily utilitarian framework. However, I also uncovered an emphasis on cultural values that is often lacking from traditional utilitarian views. Conservation scientists should seek support and common ground for Alala restoration in areas surrounding Alala release sites using a predominantly utilitarian approach infused with cultural significance. For instance, outreach describing how the Alala provides a service by dispersing seeds for lama (*Diospyros sandwicensis*), a plant species traditionally used to symbolize the Hawaiian hula goddess Laka, could resonate with utilitarian minded people who retain great esteem for indigenous culture.

The participants in the focus groups expressed approval for hunting game animals, such as pigs and fish, for food, and disapproval for activities that wasted the meat of the harvested animals. In the context of forest bird conservation, the unfortunate paradox is that Hawaii has no native terrestrial wildlife with populations fit for harvest. As a result, the natural alliances between hunters and conservationists that can occur on the mainland United States do not form easily in Hawaii. The most extreme cases of conflict are often between conservation scientists who support ungulate eradication in sensitive natural areas and those citizens and their associated organizations that unilaterally oppose ungulate eradication or hunting restrictions of any kind.

One potential means of addressing this conflict is to envision a future in which native species are sustainably harvested if threats to these species are curtailed and populations once again become self-sustaining. Regulated harvest of native wildlife, as successfully conducted by the indigenous New Zealand Maori with shearwaters (Taiepa et al. 1997), may achieve common ground between conservationists and hunters. Although the Hawaiians apparently never harvested Alala for food (Teauotalani 1859-1960 *in* Banko et al. 2002), they were likely valued for their feathers by the ancient Hawaiians who used the feathers of many wild native bird species in a variety of practical, decorative and spiritual ways (Brigham 1899 *in* Banko et al. 2002; Malo 1951; Munro 1960). Currently, the captive flock generates many naturally molted feathers, which are discarded. In the same way that Native American tribes hold permits to utilize properly collected hawk and eagle feathers for cultural customs, Alala feathers could be made available to cultural practitioners.

Describing the Alala's role in dispersing the seeds of culturally significant plants could also illustrate their value to utilitarian- and culturally-minded people. As a generalist frugivore, the Alala disperses seeds for numerous native plants (Sakai et al. 1986; Sakai & Carpenter 1990; S.C., L.P., R. Switzer & V. Ruiz-Gutierrez, unpublished data). Among these, many hold cultural significance (Malo 1951), such as mamaki (*Pipturus albidus*), a plant used traditionally for cloth-making and medicinal tea, and ohe mauka (*Tetraplasandra hawaiiense*), berries from which produce a blue pigment for dying cloth. Emphasizing the connections between Alala and plants that cultural practitioners still use today could engage people who hold culturally-informed utilitarian value for natural resources.

The utilitarian value orientation uncovered in my analysis also has implications for other aspects of Alala conservation. Successful eradication and control of exotic ungulates within Alala habitat will be a critical tool in this species' reintroduction. Disapproval towards conservation efforts to eradicate ungulates from native forest tracts may often be due to concerns over wasted meat, and not necessarily fundamentally antagonistic towards conservation goals. Partnering with local hunters or community members to discuss the options for game animal control and the fate of the carcasses could alleviate some of the potential animosity towards the fencing and ungulate eradication that is necessary well in advance of future Alala releases. The high cultural regard that the ancient Hawaiians held for the pig may also play a role in the conflict local people today feel between feral pigs and native species and this symbolic value may interfere with conservation efforts. Recognizing this deep-rooted regard for pigs and incorporating this knowledge into discussions with community members could ultimately benefit Alala recovery efforts.

The mutualist value orientation did not surface prominently in the interviews. However, the documented spiritual value the ancient Hawaiians had for the Alala and the possible mutualist value that contemporary people have for this species argue for incorporating mutualist values into a strategy for engaging communities in restoration projects. The ancient Hawaiians regarded the Alala highly, attributing spiritual connotations (Cook 1796) and human characteristics (Pukui 1983) to this extremely enigmatic species. Some contemporary Hawaiian families may consider the Alala an *aumakua* (Walters 2006), a physical manifestation in nature of one's deceased ancestors that have become family gods (Pukui et al. 1972). A local microbrewery, Mehana Brewing Company, uses a caricature of an Alala on the label of their Alala Hawaiian Crow Porter. Local community members who help select given names for the season's newest captive Alala chicks may view these individual birds as extended members of their community. Additional research into historical documents, especially Hawaiian language newspapers, which are only beginning to be translated, and interviews with *kupuna*, or elders, could uncover more indigenous knowledge on Alala natural history, additional ancient and historical perspectives on the species, and other *mo'olelo* from a time when the Alala were common on the landscape.

Although the Alala currently persists only in captivity, and efforts for a future release are only in the planning stages, understanding the community values and perspectives in regards to this species and associated recovery efforts is critical. The limited recognition of Alala among focus groups is discouraging, but participants did express enthusiasm about learning more about the species, a promising platform for species restoration. Some of the complex social obstacles facing Alala recovery might be alleviated by approaching these primarily utilitarian and culturally minded community members with information of this species' past use for feathers, their role as a seed disperser for Hawaiian plants, and their symbolism within ancient and modern culture. This framework, which describes native species restoration within a context of local value orientations, could also be applied to numerous other restoration projects in Hawaii.

Research that leads to deeper understanding of the human dimensions surrounding ecological restoration projects in Hawaii and elsewhere will allow conservation scientists and practitioners to preemptively navigate community issues, which may otherwise impede progress, towards a positive outcome for both the species and society. Sharing of findings from diverse communities faced with reintroduction projects in their backyards could produce general guidelines to inform recovery efforts elsewhere. Encouraging this discussion of how human values and culture are linked to local native species will be vital for sustaining and restoring global biodiversity.

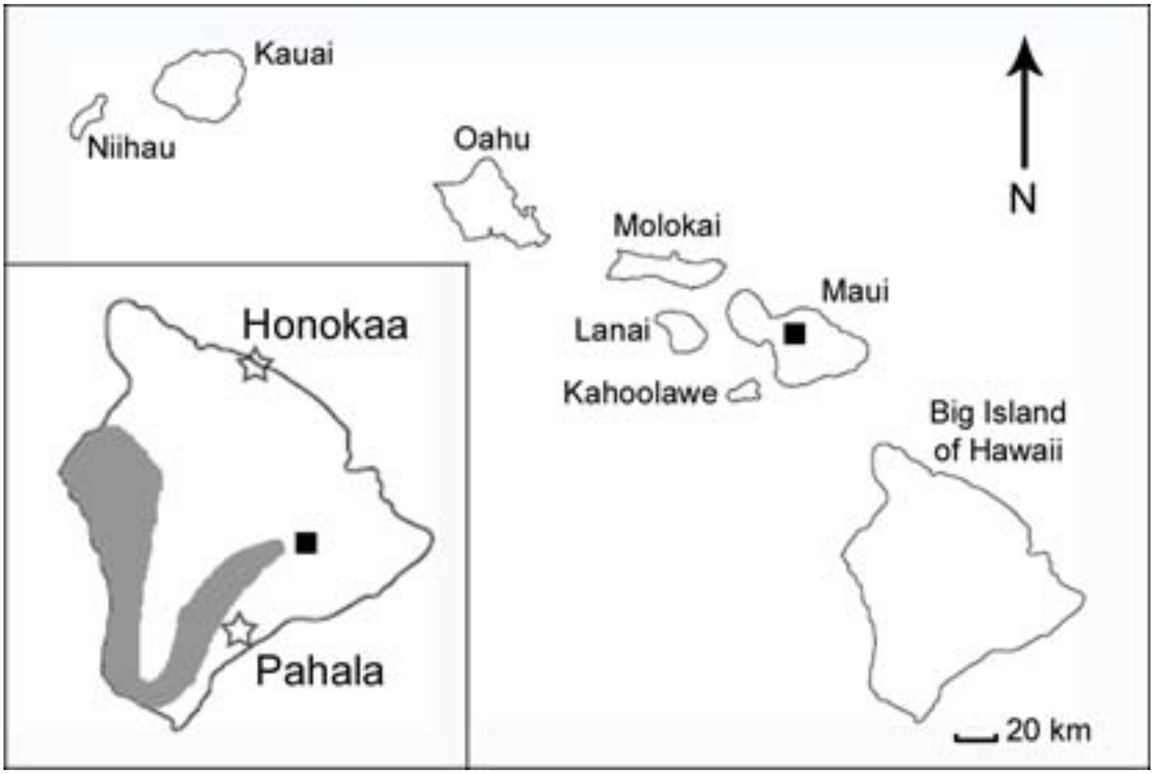

Figure 1. Alala historical range (grey shading; Banko et al 2002). Current Alala flock housed in the Keauhou Bird Conservation Center in Volcano on the Big Island of Hawaii and in the Maui Bird Conservation Center in Makawao on Maui (black squares). We conducted focus group interviews in the communities of Honokaa and Pahala on the Big Island of Hawaii (grey stars).

Figure 2. Photos used in focus group interviews to elicit value orientations and attitudes towards Alala and natural resources. Photos 1, 4, 5, 6 originally appeared to participants in color. Photo credit for Photo 5: Zoological Society of San Diego.

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