MANIPULATING SOCIAL INFORMATION TO PROMOTE FRUGIVORY BY BIRDS ON A HAWAIIAN ISLAND

BY

SEAN ERROLL MACDONALD

THESIS

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Adviser:

Adjunct Assistant Professor Jinelle H. Sperry

ABSTRACT

Animals across a range of taxa use social information when foraging. Fruit-eating vertebrates are no exception and use social information to find fruit, which may ultimately affect plant populations via seed dispersal. In many systems, mutualistic relationships between fruiting plants and frugivores are critical to maintain ecosystem functioning, especially in the tropics. On the island of Oʻahu, Hawaiʻi, all native, fruit-eating birds are extinct and several plant species are experiencing reduced recruitment likely due to a lack of seed dispersal. Over the years, numerous bird species have been introduced to the island many of which are frugivorous. Yet, introduced birds may not recognize native fruits as a resource and social information may be needed for introduced frugivores to target and feed on native fruits. We investigated if social information, in the form of broadcasted bird vocalizations, of introduced birds could increase visitations and more importantly frugivory on focal fruiting plants. We also tested if the visitation rates to focal plants were influenced by conspecific and/or heterospecific vocalizations. We conducted 80 playback experiments at native and introduced fruiting plants, and compared responses to silent control periods. Four times as many frugivores were detected and 10 times more frugivory events were recorded at plants during periods of broadcast vocalizations compared to control periods. The Japanese white-eye (*Zosterops japonicus*) exhibited the strongest response to both conspecific and heterospecific playbacks. Japanese white-eyes also consumed the most fruit from the widest array of plant species during trials. Introduced birds that use social information and readily identify novel resources may more effectively colonize new areas. We suggest that the white-eye's use of social information may help to support their robust population on Oʻahu. Ecosystems throughout the world are affected by the loss of mutualistic relationships, many of which provide valuable ecological services. As humans continue to modify environments, novel conservation approaches may be required to maintain important ecological functions.

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CHAPTER 1

CURRENT STRATEGIES FOR CONSERVATION OF HAWAII’S FLORA: A LITERATURE REVIEW

Introduction

The tropical Hawaiian archipelago is the most remote island chain in the world with 137 islands spanning some 2400 km (Wagner et al. 1999), with the closest continental land mass being 3600 km away. The eight main islands possess significant physiographic (0 – 4205 m a.s.l) and climatic variation (204 – 10271 mm precipitation) and exhibit sequentially older geological ages from southeast to northwest (Eldridge and Miller 1994). Consequently, Hawaii possesses a diversity of habitat types that played host to some of the most remarkable examples of adaptive radiation known including Hawaiian lobeliads (Campanulaceae), honeycreepers (*Carduelinae*), and terrestrial snails (*Achatinell*a). It comes as no surprise then that the archipelago is characterized by high levels of endemism with almost 9,000 species found nowhere else on the planet (Eldredge and Miller 1994).

After Polynesian settlement, Hawaiian ecosystems were radically modified through fire, agricultural development, and the introduction of plants, pigs, dogs, and rodents. With European colonization came grazing and browsing animals (i.e. goats, sheep, cattle, horses, European pigs) which fundamentally altered the naive native plant communities through herbivory and depredation (Viousek et al. 1987). Biological invasions such as these disrupt vital ecological interactions altering the basic structure and function of ecosystems (Traveset & Richardson 2006). Seed dispersal is one such ecosystem function, requiring a complex assemblage of multiple dispersers operating at several scales in order to be functional (Tsoar et al. 2010). In oceanic island ecosystems, birds are often the only animal disperser of native plant seeds (Culliney et al. 2012). Hawaii is no exception; native flora independently evolved fleshy fruits for bird-mediated dispersal at least four times (Foster and Robinson 2007). Historically, there were roughly 30 bird species, if not more, that consumed and transported seeds of native flora. With the exception of three species (*Myadestes, Corvus hawaiiensis*), all native frugivorous (fruit-eating) bird species in Hawaii have become extinct (Walther and Hume 2016).

For most plants, animal dispersers greatly influence the persistence, structure, and dynamics of plant populations and communities (Cousens et al. 2008; Nathan et al. 2009). Consequently, seed dispersal is one of the most vulnerable ecological processes in the life history of plants and the disruption of this mutualistic interaction is a fundamental threat to plant regeneration in forest ecosystems (Neuschulz et al. 2016). Therefore, it comes as no surprise that numerous rare plant taxa are experiencing recruitment bottlenecks across the Hawaiian archipelago due in part to a degraded seed dispersal network (Erwin 2007). Currently, more than 10 percent of Hawaii’s native flora have become extinct and over 40 percent of the remaining plant species are being threatened or endangered with extinction (Weisenberger and Keir 2014; USFWS 2012). An important contributing factor behind the precipitous decline in native plant communities can be linked to competitive displacement (Wilcove et al. 1998) and altered microclimates (Vitousek et al. 1993) caused by the more than 900 exotic plants that have become naturalized throughout the island chain (Eldredge and Miller 1994). To compound this problem, more birds have been introduced to Hawaii (> 150 species) than anywhere else in the world, many of which are frugivorous (Moulton and Pimm 1983). Several exotic fruit-eating birds disperse seeds of exotic over native plants, thereby facilitating the dominance and expansion of exotic plants (Vizentin-Bugoni et al. 2019). This shift in the composition of frugivore assemblages from native (i.e. *Corvus* spp., *Myadestes* spp., *Moho* spp.) to exotic dispersers (i.e. rodents, ungulates, birds) may negatively affect fruit removal (Albrecht et al. 2012, Schupp et al. 2010) and consequently the survival and recruitment of dependent plant species (Erwin and Young 2010).

Nearly, 42% of rain forests and 90% of dry forests across Hawaii have disappeared (Bruegmann 1996). Tropical dry forests are some of the most diverse communities in Hawaii hosting more native tree species than any other habitat in the state (Cabin et al. 2000). Nowhere is this more evident than on the island of Oʻahu where its lowlands are now almost entirely dominated by exotic plant species (D. Drake, pers. Comm). This is in large part due to the fact that Oahu is the most urbanized and populated island in the archipelago, hosting nearly 70% of the entire states population of 1.4 million (World Population Review 2019). The maintenance of native forests on Oahu is economically important considering that the Koolau mountain range alone is estimated to provide between $7.2 to 14 billion dollars' worth of ecosystem services to local residences (Kaiser et al. 1999). The key threats to native Hawaiian plants are feral animals, loss of pollinators and seed dispersers, fire, invasive plants, and human activity (Kawelo et al. 2012). To help combat the numerous threats facing native plant populations, habitat managers employ three main strategies that include: 1) protection and maintenance of critical habitat, 2) control exotic threats (i.e. ungulates, slugs, rodents, & plants), and 3) plant rare flora in suitable habitats (OANRP 2016). These approaches vary in effectiveness and cost with each providing their own set of challenges for implementation.

Protection and maintenance of critical habitat

The assessment, procurement, and maintenance of high quality habitats is essential for long-term restoration efforts aimed at regenerating rare plant populations. Before the protection of critical habitat can occur, there must be a habitat quality assessment to determine if a given parcel of land possesses the habitat requirements critical for the target species. After this stage, land is purchased either by private citizens, land trusts, non-governmental agencies, or by the state or federal governments. Once acquired, the land is enrolled, at the state or federal level, for protection along with a set of regulations as to how that land can be used, if at all, by the public for its natural resources. However, military lands come with their own set of regulations imposed by the federal government. All military lands must prevent the loss of biodiversity in accordance with federal statutes such as the Endangered Species Act, Fish and Wildlife Coordination Act, Migratory Bird Treaty Act, and the Sikes Act (OANRP 2016). The management of rare plant species on military lands can be substantial in certain states like Hawaii, where the military owns roughly 80,000 acres on the island of Oahu, which is roughly 21% of the island's land area (Kelly 1998). Much of the military lands that harbor rare plant species are in the remote highlands, which are often zoned as ranges for military munition exercises and communication stations. As a result, military ranges are sporadically located throughout Oahu and patchy across the landscape. Several management units have been designated within these fragmented ranges and receive continual restoration efforts by the Oahu Army Natural Resources Program.

Critical habitat for rare plant species is often highly fragmented, which by nature can increase edge effects that can include facilitating the introduction of exotic plants and animals, a modified fire regime (e.g. increased fire frequency and intensity), soil erosion, and increased predatory and competitive interactions (Murcia 1995; Fahrig 2003). Seedling recruitment is often reduced in fragments due to modified environmental conditions (i.e. microsites) or inbreeding depression (Burna 2003). Microsites are small-scale environments (e.g. disturbance regime, precipitation, canopy cover, presence of nurse plants) that are deemed safe for the successful replacement of one generation with the next. To compound the problem, there is good evidence that fruit production can be reduced in fragmented habitats due to lower pollinator abundance, modified pollinator visitation rates, or decreased pollen transfer (Bruna 2003). Furthermore, fragmented habitats can have reduced primary and secondary seed dispersal, and increased seed depredation via seed predators from the surrounding habitat (Bruna 2003). The disruption of all of these life stages for plants will eventually reduce recruitment, which can quickly lead to local extinctions of plant populations (Cardoso da Silva and Tabarelli 2000). Therefore, the protection and management of critical habitat as well as the factors necessary for the successful completion of all life stages (i.e. seed, seedling, adult, flower, and fruit) of sensitive plant species is vital for their continued existence.

Habitat managers also have to consider the implications of climate change for established natural areas and the persistence of rare plant populations (Halpin 1997; Walck et al. 2011). To address climate change, numerous management plans for continental species recommend reintroducing plants to sites that reside within the northern most latitudes of a species' range (United Nations Environment Program 2009). However, this strategy is not practical for many island ecosystems, Hawaii included. The vast majority of Hawaiian Islands do not have a northern island to relocate plants to and if there were, they would lay outside the species' narrow distribution range as many species evolved in isolated valleys or gulches (Kawelo et al. 2012). Therefore, habitat managers would have to establish sites higher in elevation to offset changes in temperature and precipitation gradients caused by climate change. Yet even this strategy is not ideal for Hawaii, as restoration sites available for plant reintroductions are extremely limited in size and number, which would increase interspecific competition (Kawelo et al. 2012). Moreover, moving plants outside their distribution ranges may create unnatural hybrids thereby reducing the genetic integrity of both species involved (Kawelo et al. 2012). It is hard to predict how climate change will affect many rare plants as the historic distribution, biology, and ecological roles for most species is relatively unknown (Kawelo et al. 2012). Despite these challenges, the protection of critical habitat is paramount in the recovery and continued conservation of rare plant species (Martin et al. 2016).

Exotic species control

Traditional biological control involves the importation, colonization, and establishment of natural adversaries (predators, parasites, and pathogens) to reduce exotic pest populations to densities that are economically negligible (McFadyen, 1998). In Hawaii, these exotic pests come in many forms from microscopic protist (e.g. avian malaria) to large animals (e.g. wild boar) with each causing a cascade of negative impacts throughout the fragile island ecosystems. Arguably, the most destructive invasive species across Hawaii are plants. Typically, introduced plants become invasive because they are no longer restricted by the herbivores or plant competitors that regulated their abundance and distribution within their native range (Hoddle 2004). One particular species that has caused considerable habitat degradation on the island of Oahu is strawberry guava (*Psidium cattleianum*). This small tree in the Myrtle family (*Myrtaceae*) is able to flourish under a variety of ecological conditions allowing it to form dense, monotypic stands in Hawaiian ecosystems (Huenneke and Vitousek 1989). Furthermore, this species outcompetes native species for sunlight, nutrients, water, and even dispersers. It does this by utilizing an extensive root system, rapid secondary growth, large fruit yields with high seed counts, and potentially even allellochemical compounds (Smith 1985). To control strawberry guava, habitat managers have begun testing Brazilian Scale (*Tectococcus ovatus*) a potential biological control agent in experimental plots on Oahu (K. Kawelo, Personal observation and communication). Brazilian Scale is an insect that is found in the native range of strawberry guava in South America and has been shown to be host-specific (DLNR 2010). However, more testing is needed as one of the most important native tree species in Hawaiian forests is Ohia (*Metrosideros polymorpha*), which is also in the Myrtle family, and so potentially at risk by the scale. In the past, the use of biological controls in Hawaii has yielded disastrous results. For example, several introduced rat species (*Rattus spp*.) are common seed predators of Hawaiian plants, and to control these invaders sugarcane farmers introduced the predatory small Indian mongoose (*Herpestes javanicus*; Simberloff et al. 2000). However, the small Indian mongoose is diurnal and rats nocturnal. This difference in activity period along with the mongoose's omnivorous diet led to the drastic decline in native bird species due in part to nest predation (Simberloff et al. 2000). Similarly, the accidental introduction of the giant African land snail (*Achatina fulica*) into Hawaii habitat managers again used a biological control approach by introducing the rosy wolfsnail (*Euglandina rosea*) in the hope that this species would depredate the giant African land snail (Gerlach 1994). Unfortunately, the predatory rosy wolfsnail inadvertently targeted native, tree snail species (*Achatinell*a, Achatinellidae). As a result, eight tree snail species have become extinct with the remaining 41 registered as federally endangered (Regnier et al. 2009). Therefore, the use of biological controls to increase native plant regeneration is a promising tool, but one that must be employed with care and the utmost certainty of its inability to negatively impact native flora and fauna.

The physical exclusion and elimination of exotic species is arguably the most common management tool to control introduced species in Hawaii. Classic methods of control typically include erecting fences around critical habitat and deploying traps to capture or kill exotic pests. In Hawaii, these established tactics are quite effective to control exotic ungulates and rodents for the benefit of native plant populations (Nelson et al. 2002, Hawaii Conservation Alliance 2005). Feral pigs cause tremendous ecological damage to Hawaiian forest ecosystems by increasing soil erosion and runoff, dispersal of exotic seeds that compete with native seeds, and consume or uproot native plants causing direct mortality (Nogueria-Filho et al. 2009). Similarly, feral goat populations negatively affect native grassland communities via staggering levels of herbivory on native seedlings, grasses, sedges, and shrubs (Coblentz 1978). Rodents (*Rattus* spp. and *Mus* spp.) are particularly damaging to naïve island ecosystems, because the flora have no adapted defense mechanisms such as noxious secondary compounds or thorns (Drake and Hunt 2009). Consequently, introduced rodents in Hawaii can indirectly reduce native plant recruitment via seed predation (Grant-Hoffman and Barboza 2010). In addition to vertebrates, twelve introduced slug species (e.g. *Stylommatophora* spp.) pose a serious threat to 22% of the threatened or endangered plant species across Hawaii (Joe and Daehler 2008). Exotic terrestrial slugs can be voracious herbivores of seedling leaves and have severely hampered the recovery of several endangered plant species (e.g. *Cyanea superba* and *Schiedea obovate*) on Oahu (Joe and Daehler 2008). Managers have had success creating fenced off sections of critical habitat from exotic snails, but these fenced areas have drawbacks, as they are extremely susceptible to weather events (i.e. hurricanes) in Hawaii (Kawelo et al. 2012). Exotic invasive plants often require mechanical controls as well including hand pulling, mowing, girdling, or felling, with some used in conjunction with herbicides to kill root systems.

The use of synthetic herbicides, such as photosynthesis inhibitors, lipid biosynthesis inhibitors, cell division inhibitors, and respiration inhibitors, is a critical part of exotic species control in small-scale settings for the restoration and maintenance of critical habitats. Herbicide use can be an effective measure to prevent the spread of invasive weeds into sensitive habitats that are accessible to the public. For instance, hiking trails are common introduction points of noxious weeds and often require herbicidal application. However, due to inherent risks to non-target plants the application of herbicides in Hawaii is restricted in high-quality habitats. Additional drawbacks for herbicides are that they are expensive, hazardous to human and wildlife health, labor intensive in remote regions, and can involve repeated applications in areas with a constant seed source. Furthermore, almost 200 weed species have evolved resistance to herbicides and their active ingredients (Heap 2005). Despite these challenges, herbicides still and will continue to remain a critical tool for managers of plant populations as its benefits can outweigh its risks in certain situations.

Seed sowing and seedling planting

To compensate for low flower and seed production of rare plants across Hawaii, intervention is often the only means to prevent a species from becoming extinct. Land managers achieve this by harvesting seeds or cuttings from wild individuals across the genetically representative populations for a given species. In Hawaii, rare plants produce very few seeds naturally therefore collecting propagules for seed sowing can be difficult. Moreover, unknown or sporadic fruiting times, accessibility to sites with seed-bearing plants, or even accessibility to seeds on the plants themselves are common obstacles that must be overcome to successfully harvest seeds or cuttings from dwindling populations (Kawelo et al. 2012). Traditionally, harvested seeds are cultivated in a nursery to produce seedlings that will be planted in suitable habitat or produce mature, fruiting-bearing adults whose seed will be sown in suitable habitats. These nursery plants can be used to supplement an existing population, restore a new population within its historic range, or even establish a new population outside its historic range. On Oahu, managers employ nursery grown cuttings, because they grow larger than wild plants and produce more fruit with higher seed-set (Kawelo et al. 2012). Unfortunately, the germination, growth, and pollination requirements for most rare plant species are unknown. Therefore, learning the environmental conditions required for the successful cultivation of rare plants often involves a trial and error approach, which is inherently time intensive. Additionally, nursery managers must take care to prevent the hybridization of congeners to ensure genotypic variation remains intact. Incidental artificial selection via hand pollination is an obstacle nursery managers must overcome as well as extremely limited space to grow plants (Kawelo et al. 2012). Despite the challenges associated with growing and planting seedlings it is a widely accepted and effective management tool to increase recruitment of rare plant populations in Hawaii.

Conclusion

Current management strategies to maintain and restore native plant communities are effective, but they come with inherent limitations in Hawaii. Protecting critical habitat throughout Hawaii's island communities is the foundation of conservation and considerable strides have ensured the persistence of numerous species. However, protected habitats represents a small fraction of the total land acreage in Hawaii, particularly on Oahu. Exotic species control is by far one of the most important steps habitat managers can take to promoting the regeneration of native species including plants. The potential of biological controls for invasive trees, the current use large-scale fences and trapping grids, and small-scale herbicide treatments are powerful means to improving the quality of critical habitats. Yet, eliminating exotics without harming native species can be difficult, which isn't made any easier by cultural ties to introduced species (i.e. pigs and hunting property lines, 'canoe' species) by Polynesians or the continual introductions of new species as global transportation increases. Planting seeds or seedlings is the most direct method habitat managers possess to create self-sustaining populations of native plants. Restoration efforts via planting seed or seedlings by government agencies, non-profits, local schools, or conservation groups has led to some amazing comebacks for species that were once threatened with extinction. The housing, growing, pollinating, and planting of plants is labor and time intensive requiring untold work hours of volunteer time. Additionally, many nurseries use limited numbers of seeds from an even more limited set of individuals bringing about a myriad of genetic problems. Not one tactic will remedy the growing problem of reduced recruitment of native plant populations, but the more tools a habitat manager has the more effective their efforts can be.

Despite considerable strides in habitat management across Hawaii, native plant communities continue to struggle to survive. In the conservation literature, there is a growing, global, seed dispersal crisis with Hawaii being just one example (McConkey et al. 2012). Therefore, innovative methods are drastically needed to restore and maintain native plant communities around the world. Considering that almost all native seed dispersers are extinct, one potential method may be to utilize current exotic bird species as surrogate seed dispersers. Many successful invaders are habitat generalists, which have the potential to maintain connectivity of isolated habitat patches through seed dispersal services (Albrecht et al. 2012). Furthermore, the importance of isolated fruiting individuals cannot be ignored as they may generate ‘stepping stone’ effects that support population expansion, recolonization of historic sites, and increased gene flow (Antonovics and Levin 1980; Morales et al. 2012). Therefore, attracting resident frugivorous birds into areas of native plants may increase recruitment rates until larger, self-sustaining populations become established.

Birds select habitat based upon a combination of direct resource cues such as the quality and quantity of food resources (Cody 1985), and indirect social cues such as the presence of conspecifics or heterospecifics (Danchin et al. 2004). Conspecific attraction is the tendency for individuals of the same species to settle near one another (Ward and Schlossberg 2004) and is often exhibited by bird species as it improves their ability to locate food or reduce predation. For decades, conservation practitioners have been exploiting this behavior in order to augment colonial seabird populations (Kress 1983; Ahlering and Faaborg 2006). Common methods of attracting avian conspecifics are visual cues (i.e. decoys), audio cues (i.e. playback of song), or a combination of the two. Recently, managers discovered that territorial songbirds respond to social cues as well and they have begun attracting migratory species into previously unoccupied, suitable habitat to establish breeding territories (Hahn and Silverman 2007; Ward and Schlossberg 2004). Moreover, Betts et al. (2008) showed that conspecific cues override habitat cues under certain conditions highlighting the influence and potential management implications of conspecific attraction. Recently, there has been a growing body of literature surrounding social information and habitat selection in birds, yet knowledge in this area is still rudimentary and its application to conservation issues limited (Ahlering et al. 2010). In order to improve our ability to incorporate behavioral ecology into restoration management it is imperative to drive advancement in experimental studies of conspecific attraction (Bayard and Elphick 2012). It has been suggested that playbacks of recorded feeding frenzies of arboreal animals and/or falling fruits could be used to lure frugivores to select plants in novel environments (Corlett 2011). To date, no study has investigated the efficacy of attracting birds into an area using audio lures with the sole purpose of consuming fruit of a specific plant species.

CHAPTER 2

MANIPULATING SOCIAL INFORMATION TO PROMOTE FRUGIVORY BY BIRDS ON A HAWAIIAN ISLAND[1]

Introduction

Animals make decisions throughout their lifetime, including habitat selection, mate choice, and food resource acquisition (Valone & Templeton 2002). These decisions can be informed either by trial and error interactions with their environment (personal information) or by acquiring information from other individuals (social information; Danchin et al. 2004). Although most research on social information has focused on its use for habitat selection, such as selecting a breeding location (e.g., Ward & Schlossberg 2004; Buxton et al. 2015), foraging animals may also use social information to acquire food resources (Danchin et al. 2004; Bonnie & Earley 2007). The importance of social information for finding food resources has been shown for a variety of taxa including bees (Visscher & Seeley 1982), fish (Pitcher et al. 1982), birds (Sullivan 1984), and bats (Wilkinson 1992). Social information can be particularly important when food resources, such as fruit, are spatially or temporally variable (Pöysä 1992; Marzluff et al. 1996; Thiebault et al. 2014).

For fruit eating animals (frugivores), the ability to locate food resources has important implications for both the forager and the fruiting plant. Up to 90% of woody plants in tropical forests are dependent on animals for seed dispersal (Howe & Smallwood 1982; Herrera 2002), and lack of effective dispersal can lead to a cascade of negative consequences affecting both

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community structure and ecosystem functioning (Bond 1994; Nathan & Muller-Landau 2000; McConkey et al. 2012). Recent research highlights that dispersal failure is a growing problem throughout temperate and tropical forests (Ozinga et al. 2009; Chimera & Drake 2010; Markl et al. 2012), and has been attributed to a decline of frugivorous species in certain systems (Temple 1977; Kirika et al. 2008). Current management efforts to increase seed dispersal involve planting seedlings or seeds, but have varying levels of success and require significant resources in both time and money (Lamb et al. 2005). Promoting frugivory through the manipulation of social information, if effective, could be a promising management tool for dispersal limited plant species.

Oceanic island ecosystems are fragile and have undergone numerous an untold number of mass extinction events upon human settlement, especially in regards to avifauna (Boyer 2008; Banko and Banko 2009; Boyer 2010; Szabo et al. 2012; Duncan et al. 2013). A classic example is the Hawaiian Archipelago, where bird extinctions have not only led to severe losses in the community level functional diversity, but also many of the ecological functions supported by these species (Boyer and Jetz 2014). In particular, nearly every endemic frugivorous bird species (i.e. *Corvus* spp., *Moho* spp., *Myadestes* spp.) has become extinct in the wild with the two remaining species (*Myadestes obscurus* on Hawai‘i; *M. palmeri* on Kaua‘i) being vulnerable to and critically endangered of extinction, respectively (Walther 2016; IUCN 2018). The extirpation or severe contraction of frugivore populations can have cascading effects on communities by disrupting mutualisms such as seed dispersal (Markl et al. 2012). The functional loss of this ecological guild could be disastrous to persisting native plant populations considering that over half are at risk of endangerment or extinction (Wagner et al. 1999) and of those that are trees almost 80% are reliant on bird mediated seed dispersal in dry forests (Pau et al. 2009). Not surprisingly, many rare, fleshy-fruited plants are experiencing recruitment bottlenecks throughout the Hawaiian Archipelago (Erwin & Young 2010) with the loss of vertebrate dispersers a likely factor (Loiselle & Blake 2003; Wonton & Kelly 2011).

Concurrent with the extinction of native frugivores, roughly 60 bird species, including many frugivorous species, have been introduced and become naturalized across the Hawaiian Islands (Pyle 2002). Studies have found that introduced frugivores can be effective seed disperses in Hawaiʻi (Foster & Robinson 2007; Chimera & Drake 2010; Pejchar 2015). While introduced frugivores can disperse seeds, we do not know how they locate fruits and how social information may facilitate frugivory. Gaining a better understanding of how social information between available to frugivores influences fruit consumption and seed dispersal could aid in the maintenance and restoration of native forests in Hawaiʻi, and other degraded ecosystems around the world.

Applying a playback experiment, we investigated if social information from four introduced bird species would increase visitations by these frugivores to focal fruiting plants. Many studies have found that individuals will respond to vocalizations of conspecifics, however simply attracting a frugivorous species to a fruiting tree is of little value to the plant, if the fruit is not consumed. We also tested if the addition of social information increased frugivory on focal fruiting plants. Finally, vocalizations may attract a conspecific to a fruiting plant, but the vocalization of heterospecific frugivores should also provide information on the presence of fruit. Therefore, we investigated if the visitation rates of introduced bird species to focal fruiting plants where influenced by both conspecific and heterospecific vocalizations.

Methods

Study sites

We collected all data within the montane, mesic forests of the Waiʻanae range on the island of Oʻahu, Hawaiʻi, USA (21° 32’ N, 158° 11’ W). Field sites spanned the length of the Waiʻanae range from Mokulēʻia to Nanakuli Forest Reserves. The majority of our study sites (365-731 meters a.s.l.) were on military lands managed by the Oʻahu Army Natural Resources Program, U.S. Army, Hawaiʻi for native plant preservation via planting of rare plant species and the control of introduced plant and animal species. Both native and introduced tree and shrub species are present within managed sites with the surrounding matrix being dominated by introduced species (e.g., *Psidium cattleianum*). The density of native plant species within managed sites varies, but is generally higher in comparison to the surrounding, unmanaged forest.

Study species

The four bird species we used in this study were the red-billed leiothrix (*Leiothrix lutea*), Japanese white-eye (*Zosterops japonicus*), red-whiskered bulbul (*Pycnonotus jocosus*), and red-vented bulbul (*Pycnonotus cafer*). All four species are moderately to highly frugivorous (i.e., diet comprised of 45% - 96% fruit; Corlett 1998; Foster & Robinson 2007; Linnebjerg et al. 2010; Spotswood et al. 2012; Pejchar 2015). Most of these frugivores were introduced to the islands at different times since European settlement and the species do not co-occur in their native ranges (van Riper 1979; Williams & Giddings 1984; Ralph et al. 1998).

Red-billed leiothrix (hereafter leiothrix) were introduced to Oʻahu in 1928 from the Himalayas and have exhibited cyclic population fluctuations until the 1980s when since their introduction and only since the late-1980’s have their population’s stabilized in the highlands (Simberloff & Gibbons 2004). Leiothrix can form feeding flocks of 20-100 individuals and typically forage in the understory among dense thickets (Fisher & Baldwin 1947). Japanese white-eye (hereafter white-eye) were introduced to Oʻahu in 1929 from eastern Asia and quickly became one of the most abundant and widespread birds across all of Hawaiʻi being found from sea level to the tree line (Guest 1973). White-eye frequently forage in flocks at all heights and vegetation densities (Berger 1981). Red-whiskered bulbuls were introduced to Oʻahu in 1965 from tropical Asia and did not become widespread until the 2000s being previously restricted to Honolulu (Williams & Giddings 1984). Originally from India, red-vented bulbuls were first documented in 1966 on Oʻahu and quickly spread across the island’s lowland agricultural areas (Williams & Giddings 1984). Both bulbul species are gregarious, regularly forming large communal roosts (Islam & Williams 2000).

Field methods

To estimate abundances of bird species, we conducted 238 avian surveys within study sites from December 2015 to May 2017 (Appendix A. Table A.1). We utilized belt transect surveys due to restricted access by the military and the small size (<0.02 ha) of the planting sites. We performed surveys for 20 minutes along a 150 meter transect. We established 16 belt transects at least 250 meters apart with eight within restoration sites and another eight in the surrounding forest along a similar aspect and slope. We conducted paired surveys to determine if avian frugivore communities within restoration sites significantly differed from those outside the restoration sites in unmanaged forest. We did not conduct surveys during intense wind, rain, or military activity. We recorded all birds within an unlimited distance within four hours of sunrise for each survey.

To determine if social information could attract introduced frugivorous birds to native fruiting plants and entice individuals to consume fruit, we ran playback experiments manipulating using vocalizations of our four focal bird species. We conducted all trials roughly once per week from 1 May 2016 to 31 July 2017 in order to account for differences in response during frugivore breeding and non-breeding seasons. On average, trials were conducted within four hours of sunrise. However, due to variable weather conditions several trials fell outside this time constraint. We chose focal plants opportunistically, biasing choices towards native species with mature fruit. Trials consisted of 18 native and seven introduced plant species, all of which have fleshy fruits likely evolved for animal-mediated seed dispersal (Appendix A. Table A.2). Eighty trials were completed in total with 73 trials on different days, but the seven that were conducted on the same day were >250m apart to prevent double sampling of the frugivore population. All surveys and trials were conducted by one person (S. E. MacDonald) to account for observer bias.

A trial included two components, each one hour long: 1) a silent control period (no broadcast of vocalizations) and 2) a treatment period (broadcast of vocalizations). We choose trial length. Thus, a trial had a total length of two hours, which was chosen in order to limit the influence of variability in weather experienced throughout a trial. We conducted a silent control period to estimate the level of frugivory that naturally occurs in this system. Treatment periods immediately followed control periods to avoid biasing species diversity and abundance estimates. For the treatment period we deployed a speaker (FoxPro model NX4, Pennsylvania, USA) within or near a focal plant and broadcasted vocalizations of our four bird species (74-80 dB). The speaker was elevated ≥ 1m to increase detectability by the local frugivore community. A 15-min playlist was created for each species using personal recordings of foraging birds on

Oʻahu (Sennheiser ME 66 microphone, Wedemark, Germany; Sony PCM-M10 recorder, Tokyo, Japan) as well as 17 recordings downloaded from Xeno-canto (Anderson et al. 2018). Unedited versions of personal recordings were uploaded to Xeno-canto (listed under Sean Erroll MacDonald). Greater than five exemplars were included for each playlist to account for individual variation in dialect and to reduce the potential of pseudoreplication (Kroodsma 1989). We filtered exemplar recordings for non-focal bird species vocalizations and low-frequency noise, and combined these to create playlists with Adobe Audition 2015 (California, USA). We randomly assigned exemplar order in each playlist. Playlists were interspersed with silence to mimic natural song rates for each species. In addition to these, we created a 15-min playlist of white-eye and leiothrix alarm vocalizations. When threatened these two species regularly participated in mobbing behavior together, attracting the attention of the immediate bird community. Therefore, we included this playback in the experimental design. Of the five playlists created, we randomly assigned four for broadcast for each trial. During trials, we broadcasted playlists immediately after one another, for a total of one hour.

We recorded bird activity (i.e., responsiveness) during each trial (control and treatment periods) for each individual detected within 10 m of the focal plant. More specifically, we noted the distance a bird was from the focal plant, its height in the vegetation, its total time spent within 10m of a focal plant, the plant species the bird foraged on, and the type of foraging behavior it exhibited for each trial. We defined a frugivory event as a conspicuous pecking and/or removal of fruit from a focal plant by a bird. Birds were not color-banded and thus individuals could not identified. Consequently, we did not count birds that persisted in the area during the transition from one playback to the next as being attracted during subsequent playbacks. If an individual left the area and another individual of the same species arrived >10 seconds later, we considered it a different individual, although great care was given to tracking individual birds within 10 m of the plant. Lastly, the observer was motionless and wore camouflage for the duration of a given trial to minimize detection.

Statistical analyses

We conducted all analyses in the program R version 3.4.3 (2017). For the purposes of this study, the term ‘frugivore’ only included the four focal bird species. We included only frugivores detected within 30 m of the transect due to detection probability limitations. Each survey was confined to a 30 m x 150 m belt transect allowing for the comparison of a localized bird community within and around restoration sites. We conducted all data collection in both restoration sites and the surrounding, unmanaged forests and found no significant difference between the two frugivore communities, so we pooled data from all avian surveys.

We used Pearson’s Chi-square test to compare the distribution of frugivore species that were observed during the treatment period to the distribution that would be expected for the treatment period based on avian survey data. The distribution of frugivores observed during the entire experiment (control and treatment) was then compared to the distribution that was actually observed across all avian surveys. We compared the observed frequency of frugivore species detected during control periods to the observed frequency of species detected during the treatment with Pearson’s Chi-Squared statistic. We conducted this test to determine if the frequency of frugivore species detected during the control periods significantly differed from treatment periods. Additionally, we used Wald’s odds ratio test for each focal frugivore species to compare the observed frequency of a given species detected during the playback experiment to the expected frequency of a given species derived from avian survey data.

We applied a generalized linear mixed effect model (GLMM) with a Poisson-distribution to raw abundance data from all trials of the playback experiment to compare the total number of frugivores present during control and treatment periods to determine if frugivores were attracted during treatment periods. The response variable was the total number of frugivores detected, the type of experimental period (i.e. control or treatment) as the sole fixed effect, and trial (i.e. 1, 2, 3…) as the random effect. We included trial as a random effect, because trials occurred at different plant species, sites, and times of the year and day.

Since individual birds were unmarked, there is the possibility of individuals being double counted, thus we used an additional approach to determine if frugivore abundances differed between control and treatment periods of the playback experiment. We compared the amount of time frugivores spent at the focal plant between treatment and control periods. Although we cannot determine how many individuals were present, the time spent near plants likely represents foraging opportunities and, from the plant perspective, opportunity for seed dispersal. We applied four GLMMs with a Poisson-distribution to raw data from all trials to compare the total number of minutes, for each focal frugivore species, within 10 meters of a focal plant between the control and treatment periods. The response variable was the total number of minutes a frugivore was detected, the type of experimental period (i.e. control or treatment) as the sole fixed effect, and trial (i.e. 1, 2, 3…) as the random effect. We included trial as a random effect because trials occurred at different plant species, sites, and times of the year and day.

To determine if specific species' frugivory rates varied during the treatment period, we applied GLMM with a Poisson-distribution to raw abundance data from all trials (treatments and controls). The response variable for this model was the number of frugivory events; the fixed effect was set as an interaction between frugivore species and period, and trial as the random effect. Again, we included trial as a random effect because trials occurred at different plant species, sites, and times of the year and day. We used a Tukey's pairwise comparison test to find means that were significantly different from each other based on the summary of coefficients for the GLMM.

Lastly, we used GLMM for each focal frugivorous bird species, to evaluate a frugivore's behavioral response to conspecific and heterospecific social information. We converted raw abundance counts to presence-absence, binomial data to increase model robustness due to limited detections during controls. We used binomially distributed errors (with a logit link function) for each GLMM. Out of the 80 trials conducted, we included 56 since all the playbacks in these trials had an equal length of 15 minutes available for comparison. For each model, the presence of a given species was the response variable, frugivore species of broadcasted playback was the fixed effect, and trial and playback order were the random effects. Trial was included as a random effect because trials occurred at different plant species, sites, and times of the year and day. Track order was a random effect because birds attracted to the first playback may have influenced subsequent playbacks conducted during treatment periods. For a given trial, the treatment period comprised four, 15-min playbacks. In order to control for effort per playback, we separated 60-minute control periods into four, 15-minute silent periods in the model to allow for comparison. We removed time of year, site, and plant species, because these did not significantly explain variation in any model by themselves. We set the control period as the intercept in all models. Results below are presented as means with standard error (SE).

Results

Avian surveys

We observed a total of nineteen bird species during surveys, 63% of which were the four focal species (2319 out of 3663 detections; Appendix A. Table A.1). The three most common bird species were, in descending order, red-billed leiothrix (5.18 ± 0.24 birds / transect), Japanese white-eye (3.80 ± 0.17 birds / transect), and red-whiskered bulbul (2.31 ± 0.16 birds / transect). Red-vented bulbul (0.83 ± 0.09 birds / transect) was the seventh most common bird species.

Playback experiment

Across all trials, we detected more frugivores during treatments (12.5 ± 0.91 birds detected /trial) compared to control periods (3.2 ± 0.37 birds detected/trial; Fig. 1a and Appendix A. Table A.3). During control periods, frugivores represented 62% (256 of 412) of all birds detected, which increased to 81% (1003 of 1235) during treatment periods. White-eye exhibited the largest increase, with more than 5x the number of detections during treatment than control periods (Fig. 2). Of all frugivores attracted 56% (563 of 1003 individuals) were white-eye followed by red-whiskered bulbul at 17% (173 of 1003 individuals), leiothrix at 17% (169 of 1003 individuals), and red-vented bulbul at 10% (98 of 1003 individuals). Due to individuals being unmarked the exact proportional increase of bird abundance cannot be estimated. However, the total number of minutes spent within 10 meters of a focal plant by each frugivore species mirrored abundance estimates (Fig. 3 and Appendix A. Table A.4). Again, white-eye displayed the largest increase, with almost 10x the number of minutes in the area during treatment periods compared to controls (Fig. 3). Furthermore, of the 3942 minutes frugivores occupied the area during treatment periods, Japanese white-eye constituted 58% (2302 of 3942 min) followed by red-whiskered bulbul at 17% (637 of 3942 min), leiothrix at 16% (636 of 3942 min), and red-vented bulbul at 9% (367 of 3942 min).

The frequency of observed detections during the treatment periods of the playback experiment differed from the expected frequency estimated from avian surveys ($\chi2 = 189.32,16$, df = 3, P-value = < 0.001; Fig. 2). Similarly, the frequency of observed detections differed between control and treatment periods of the playback experiment (Pearson's test; $\chi2= 32.9329$, df = 3, P-value= < 0.001; Fig. 2). The frequency of white-eye detected during the playback experiment was almost twice as high as expected based on avian survey detections (314 expected vs. 563 observed; Wald's odds ratio=1.41, P-value= 0.004; Table 1). Conversely, the frequency of leiothrix detected during the playback experiment was 50% less than what was expected based on avian survey detections (428 expected vs. 169 observed; Wald's odds ratio=0.86, P-value= 0.005; Table 1). There was not a significant difference between the frequency of observed detections during the playback experiment and expected detections based on avian surveys for red-whiskered bulbuls (191 expected vs. 173 observed; Wald's odds ratio=0.672, P-value= 0.065) or red-vented bulbul (69 expected vs. 98 observed; Wald's odds ratio=1.42, P-value= 0.351; Table 1).

Collectively, more frugivores consumed fruit during treatments (1.61 ± 0.49 birds consuming fruit / trial) compared to control periods (0.11 ± 0.08 birds consuming fruit / trial; Fig. 1b and Appendix A. Table A.3). For all frugivores detected during treatment periods, the frequency of those that consumed fruit from focal plant species compared to control periods was substantially greater for white-eye (17.5% vs. 6.9%, P-value= < 0.001; Fig. 4) and red-whiskered bulbul (11.7% vs. 3%, P-value= < 0.001; Fig. 4). Yet, only 6% (6 ate/98 attracted) of red-vented bulbul and 4% (6 ate/163 attracted) of leiothrix that responded to broadcasted vocalizations consumed fruit, and neither of these species consumed fruit during control periods (Fig. 4).

Focal frugivore species were more likely to visit the fruiting plants where their vocalizations were being broadcast (Fig. 5 and Appendix A. Table A.5). White-eye was the only species to visit fruiting plants where heterospecific vocalizations were broadcast, in particular this species responded to leiothrix and red-vented bulbul vocalizations (Fig. 5a). Interestingly, white-eye and leiothrix responded to the duet playback that contained both of their vocalizations as strongly as their respective solo conspecific vocalizations when compared to control periods (Fig. 5a, 5b). The two bulbul species did not visit fruiting plants where heterospecific vocalizations were broadcast (Fig. 5c, 5d). Anecdotally, all bird species elicited a greater response to alarm call portions of broadcasted tracks compared to song.

Discussion

Biological invasions have the potential to cause severe economic and ecological impacts to a country (Vitousek et al. 1997). The functional removal of introduced species from novel ecosystems is often impractical if not impossible in many tropical parts of the world such as Hawaiʻi. Therefore, understanding the behavioral characteristics (e.g. foraging) of introduced species' is important in determining their impact (positive, negative, or neutral) as well as their invasion success (Holway and Suarez 1999). If positive, certain species or behavioral traits could be manipulated augmented to enhance their ecosystem value with the aid of conservationists (Schlaepfer et al. 2011). Recent work has highlighted the necessity of innovative methods in attracting frugivorous animals into restoration sites to enhance seed dispersal (McConkey et al.

2012), such as using essential oils of fruits to attract bats (Biancoi et al. 2007). We demonstrate that social information of introduced, frugivorous birds can be manipulated to recruit individuals, which in turn stimulates foraging behavior allowing for increased seed dispersal. Additionally, the propensity of certain frugivores on Oahu to utilize social stimuli in foraging may indicate their ability to successfully invade insular ecosystems.

Our findings suggest that, in this system, playbacks cannot only attract recruit frugivores, but also drive their foraging decisions. For example, Japanese white-eye responded the strongest and consumed the most fruit regardless of the fruiting plant species or playback used in a trial. Conversely, leiothrix exhibited a relatively weak response to playbacks and consumed almost no fruit despite the fact that they were the most abundant species within the study sites. Equally surprising is that white-eye exhibited a slightly stronger response to the duet playback (white-eye + leiothrix) than to its conspecific vocalization. In a study of interspecific interactions in their native range, white-eye exhibited the same pattern (i.e., greater visitation rates) when exposed to both playbacks of conspecific vocalizations vs. a combination of heterospecific frugivore vocalizations (Gu et al. 2017). These findings suggest that white-eyes may rely on social information when foraging in this system. With respect to Hawaiʻi, Berger (1981) stated, “The white-eye is an example par excellence of the success of an exotic bird released in a foreign environment.” Therefore, the phenomenal success white-eye has had invading the Hawaiian Islands and other oceanic islands (Guest 1973) may be correlated to their use of social information when foraging. In contrast, leiothrix has had variable success invading the Hawaiian archipelago, becoming extirpated on Kauaʻi and exhibiting extreme population fluctuations since its introduction to the islands of Hawaiʻi and Oʻahu (Male et al. 1998). Consequently, the limited use of social information by leiothrix may be negatively affecting their ability to successfully forage and establish stable populations. For instance, faster rates of novel environment exploration have been associated with increased use of social information in great tits (*Parus major*; Marchetti & Drent 2000) and faster acoustic learning in black-capped chickadees (*Poecile atricapillus*; Guillette et al. 2009). Additionally, Morse (1971) argued that the degree to which birds respond to new food resources would determine their ability to colonize islands. If this is true, than our findings may suggest that how well a species can utilize social information can influence their ability to forage in and successfully invade novel ecosystems. Therefore, information on how well a bird exploits social information when foraging could help assess its potential invasiveness.

All four frugivores consumed fruit unevenly across plant species suggesting that plant characteristics are vital when considering the implementation of a playback experiment to promote frugivory. White-eye constituted the overwhelming majority of frugivory events (104 of 138) and consumed fruit from both native and introduced plant species. Not surprisingly, white-eye have been documented dispersing invasive plant species on other Hawaiian islands as well (Foster & Robinson 2007; Pejchar 2015). Conversely, all other focal frugivore species ate fruit from only a select few plant species. The two most consumed plant species were native (i.e. *Pipturus albidus, Myrsine lessertiana*) followed closely by several exotic species (i.e. *Psidium guajava, Rubus rosifolious, P. cattleanium*). Therefore, the manipulation of social information could be an effective tool to promote the frugivory of native plant species over introduced plant species (Simberloff & Von Holle 1999). Factors that need to be considered when evaluating which fruits introduced bird species feed on include but is not limited to fruit nutrition, fruit color, spatial distribution, and fruit morphology (Wheelwright & Janson 1985; Jordano 2000).

Conservation Implications

Although these results present a promising first step for increasing seed dispersal of rare plants, successful seed dispersal is a multistep process that can be influenced, among others, by the seed size, scarification during gut passage, or microhabitat of the deposited seed (Wheelwright & Janson 1985; Schupp 1995; Traveset et al. 2001). For example, although white-eyes were the most responsive frugivore their average gape width is significantly smaller than that of red-vented bulbul (Gleditsch et al. in review). Consequently, the attributes of fruit as well as surrogate frugivores need to be considered. We did not directly test seed fate, however increased frugivory likely leads to enhanced seed dispersal and ultimately improved recruitment within plant populations (Janzen 1970; Connell 1971; Wonton & Kelly 2011). We recognize that more work is needed, across the Hawaiian archipelago, on fruit preference and seed fate for the suite of endangered or at-risk plant species that are dependent on frugivore dispersal.

Throughout the tropics, many plant species are experiencing alarming rates of depressed recruitment with the loss of native frugivores a likely factor (Loiselle & Blake 2003; Kirika et al. 2008). In addition to plants, native bird species that experience recruitment failure could benefit from facilitated frugivory. On the island of Hawaiʻi, the ʻAlalā / Hawaiian crow (*Corvus hawaiiensis*) is extinct in the wild, but has the potential to shape Hawaiian plant communities through enhanced seed dispersal (Culliney et al. 2012). In the 1990's, managers attempted to reintroduce the species, which failed due to depredation and disease. Recently, conservationists have begun reintroducing captive-reared individuals into the wild with success. However, several individuals have died due in part to their inability to locate adequate food resources prompting managers to provide supplemental food for released individuals (DLNR 2019). Subordinate crows learn from alpha birds within their social hierarchy to develop foraging behaviors

(Chiarati et al. 2012). If this holds true for the Hawaiian crow, then the broadcast of non-territorial crow vocalizations near suitable foraging sites may provide the social information needed to increase recruitment of juvenile crows. The likelihood of promoting frugivory would most likely diminish as crows mature and form pair bonds, but the necessary associations with native fruits could be established and quite possibly transmitted to their offspring.

Introduced bird species are often not considered in conservation planning, and if anything are thought of as compounding a problem (Simberloff & Von Holle 1999), but in situations such as Oʻahu introduced species may play an important function in the dispersal of native seeds. More research is needed to understand the role of introduced bird species in ecosystem functions, and conservation may require novel approaches. A variety of methods are needed to effectively manage bird and plant species within degraded ecosystems, and promoted frugivory may be a valuable tool for the conservation of island communities and the unique bird-plant mutualisms that occur there.

SUMMARY

Many rare plant species are experiencing recruitment bottlenecks across the Hawaiian archipelago. The key threats to native Hawaiian plants are exotic species, loss of mutualisms (i.e. seed dispersal), and human-caused disturbances (e.g. fire, habitat loss). To help combat the numerous threats facing native plant populations, habitat managers typically use the following strategies: 1) protection and maintenance of critical habitat, 2) control exotic threats, and 3) plant rare flora in critical habitats. These approaches vary in effectiveness and cost with each providing their own set of challenges for implementation. The protection of critical habitat as well as the factors necessary for the successful completion of all life stages (i.e. seed, seedling, adult, flower, and fruit) of sensitive plant species is vital for their continued existence. The use of biological controls to increase native plant regeneration is a promising tool, but one that must be employed with care to avoid negatively affecting native flora and fauna. The exclusion and elimination of exotic species is arguably the most common management tool to control introduced species in Hawaii. The use of synthetic herbicides is a critical part of exotic species control for the restoration and maintenance of critical habitats. Lastly, growing and planting seedlings it is a widely accepted and effective management tool to increase recruitment of rare plant populations in Hawaii. All of these methods are valuable tools, but they come with inherent limitations in terms of scale and cost. Not one tactic will remedy the problem of reduced plant recruitment in Hawaii, but the more tools a habitat manager has the more effective their efforts can be. Therefore, innovative methods are needed to restore and maintain native plant populations, especially in areas of high concentrations of threatened or endangered species. One potential method may be attracting resident frugivorous birds into areas of native plants may increase recruitment rates until larger, self-sustaining populations become established.

For my thesis, I investigated if the use of social information could be used to attract exotic, frugivorous birds into restoration sites with the intent to increase fruit consumption and ultimately seed dispersal of rare native plant species. The social information used was the broadcast of songs and calls as these stimuli has been shown to attract conspecifics to a general area for breeding. I studied the effects of these playback experiments primarily in the restoration sites along the northwestern Waianae Mountains on the island of Oahu, Hawaii, USA in 2016 and 2017. I also conducted avian surveys within the restoration sites to determine the abundance and diversity of birds utilizing the restoration sites, especially with regards to the introduced frugivorous birds. The avian surveys conducted revealed that my focal bird species, Japanese white-eye, red-billed leiothrix, red-vented bulbul, and red-whiskered bulbul, comprise the majority of the bird communities around these restoration sites suggesting that they heavily influence seed dispersal of rare plants within the sites as well as the exotic species around its boundaries. The playback experiment revealed that the response strength to conspecific and heterospecific playlists were species-specific implying that not all species use social information to the same degree and care must be taken when choosing potential surrogates for artificially induced seed dispersal. More importantly, the experiment revealed that introduced birds, in this system, could be used to successfully increase bird presence and increase fruit consumption of nearby plants including those of target species. Fruit consumption across plant and bird species was not uniform highlighting that habitat managers must take the natural history of focal species into consideration, if this technique is to be implemented. I conclude that although these are promising results, more research is needed in determining this techniques efficacy in other systems and its potential drawbacks such as the accidental introduction of invasive seeds from birds that are attracted into sensitive habitats where threatened or endangered species reside.

FIGURES

Figure 2.1. Comparison of the mean number of frugivore detections and frugivory events between control and treatment periods. a) Mean number of frugivore detections (with standard error) per trial and b) the mean number of frugivory events (with standard error) per trial during control (silence) and treatment (broadcast of vocalization) periods across all trials (n = 80) of the playback experiment from May 2016 to July 2017 conducted on O‘ahu, Hawai‘i, USA. Significance was determined by applying a generalized linear mixed model to raw abundance data. Control periods were significantly different treatment periods with respect to the mean number of detections and the mean number of frugivory events.

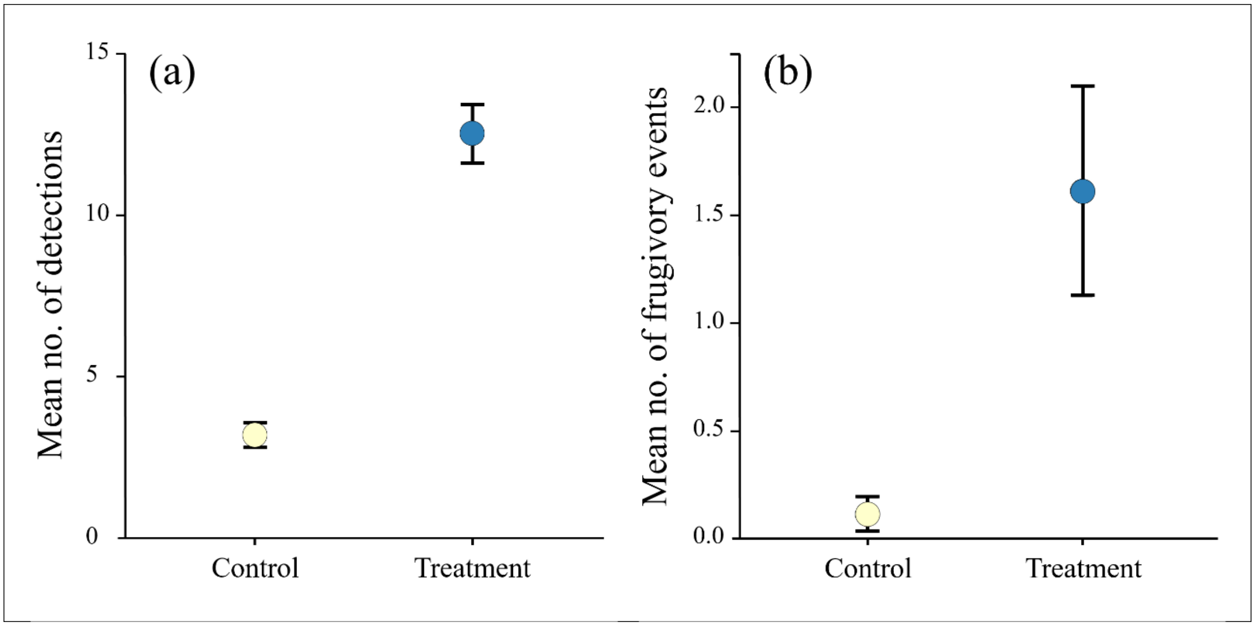


Figure 2.2. Comparison of the observed vs. expected number of frugivores detected during the control and treatment periods. Pearson's Chi-Squared test output comparing the expected frequency of frugivore species detected during all avian surveys (n = 238; white) to the observed frequency of frugivore species detected during the treatment periods (n = 80; blue bars). Additionally, the frequency of observed detections across all species of control and treatment periods of the playback experiment (grey bars) were compared and found to be different. The observed number of Japanese white-eye (JAWE), red-billed leiothrix (RBLE), red-whiskered bulbul (RWBU), and red-vented bulbul (RVBU) detected during the playback experiment were compared to expected values. Expected values were created by multiplying the frequency of a given frugivore species detected during avian surveys by the total number of frugivores observed during the playback experiment.

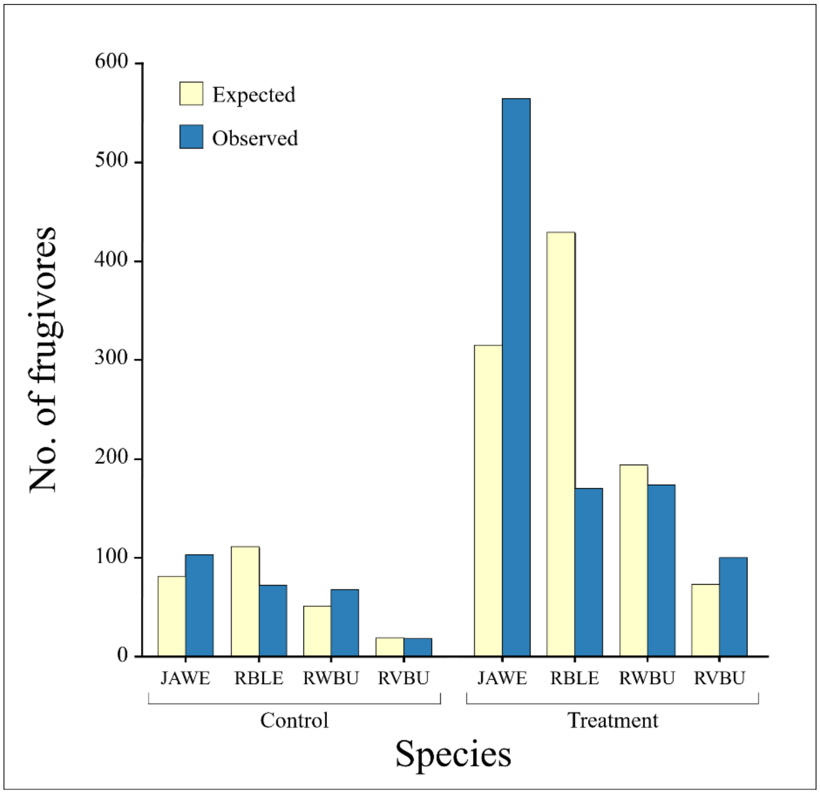


Figure 2.3. Total number of minutes all frugivorous birds spent around fruiting plants. The total number of minutes focal bird species were within 10 meters of the focal fruiting plants comparing control (silent) and treatment (playback) periods during experiments across trials (n = 78) from 2016 – 2017 on O‘ahu, Hawai‘i, USA. Focal bird species include Japanese white – eye, red – billed leiothrix, red – vented bulbul, and red – whiskered bulbul.

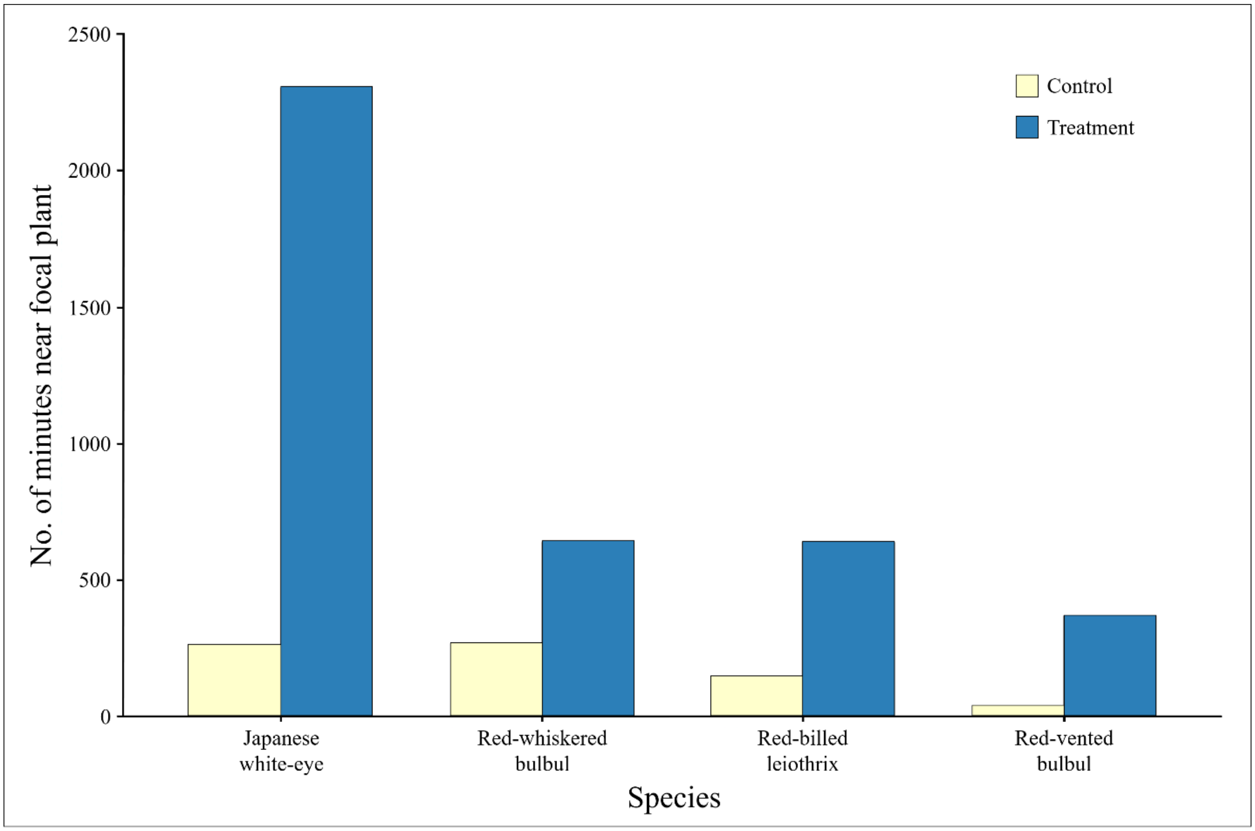


Figure 2.4. Comparison of the mean number of frugivores across bird species during treatment periods. Mean number of frugivory events (with standard error) by bird species during control (white bars) and treatment (blue bars) periods across all trials (n = 80) of the playback experiment from May 2016 to July 2017 conducted on O‘ahu, Hawai‘i, USA. Letters above bars denote significance, which were determined by applying a generalized linear mixed model to raw abundance data.

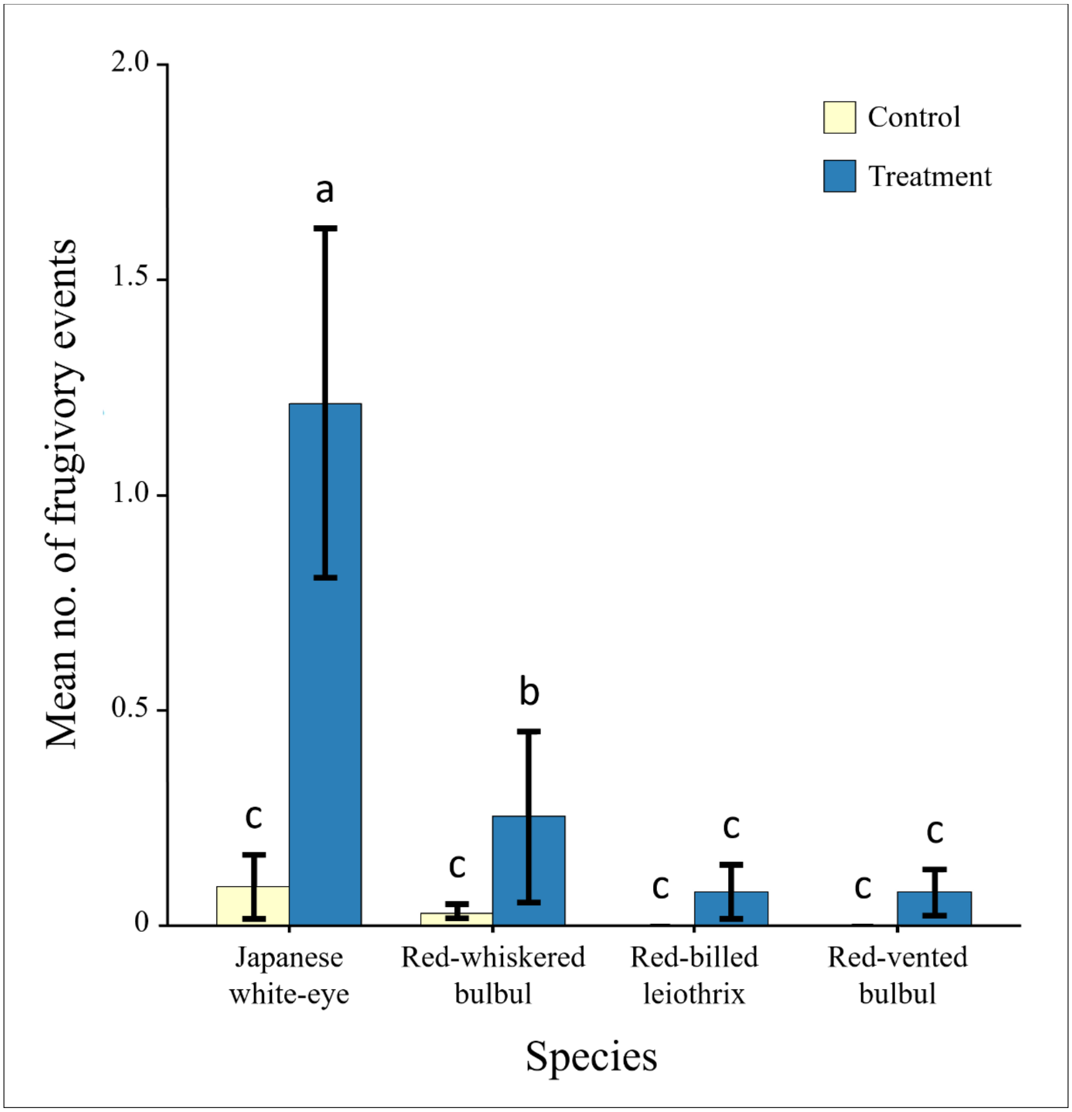
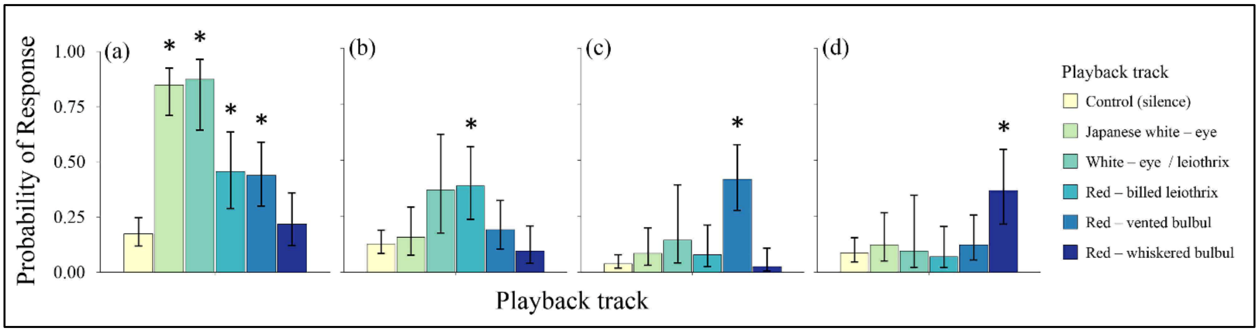


Figure 2.5. Probability of frugivore response to various playback tracks. The predicted probability (with 95% confidence intervals) of response to the broadcast of conspecific and heterospecific vocalizations (treatment) in comparison to silence (control) across trials (n = 56) from 2016 – 2017 on O‘ahu, Hawai‘i, USA. Probabilities were derived from four generalized linear mixed models denoted by a) Japanese white – eye, b) red – billed leiothrix, c) red – vented bulbul, and d) red – whiskered bulbul. Asterisks (*) indicate behavioral responses that were significantly different from the silent control period (yellow bars), which were set as the intercept in all models.



TABLE

Table 2.1. Comparison of odd ratios between playback experiment and avian surveys. Wald's odd ratio test outputs comparing the observed number of detections during the playback experiment and the expected number of detections based on avian surveys for all focal frugivore species. Frugivore species, odds ratio with 95% confidence intervals (CI), and associated *P*-values are shown.

Species	Odds ratio	Lower CI	Upper CI	*P* - value
Japanese white-eye*	1.406	1.018	1.944	0.038
Red-billed leiothrix*	0.606	0.428	0.858	0.005
Red-vented bulbul	1.420	0.678	2.975	0.351
Red-whiskered bulbul	0.672	0.441	1.027	0.065

* Denotes significance

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APPENDIX A. Summary statistics of all species and models utilized during study

Table A.1. All bird species detected during avian surveys. Total and mean number of detections (with standard errors) within 30 meters of belt transects by bird species (bold indicates focal frugivorous species) across 238 avian surveys from December 2015 to May 2017 in the Waiʻanae range of the island of Oʻahu, Hawaiʻi, USA.

Common name	Scientific name	Ave. no. detections / survey (± SE)	No. of detections
Red-billed leiothrix*	*Leiothrix lutea*	4.055 ± 0.215	961
Japanese white-eye*	*Zosterops japonicus*	3.494 ± 0.165	828
Red-whiskered bulbul*	*Pycnonotus jocosus*	1.608 ± 0.137	381
Common waxbill	*Estrilda astrild*	1.241 ± 0.153	294
ʻApapane	*Himatione sanguinea*	0.937 ± 0.105	222
White-rumped shama	*Copsychus malabaricus*	0.823 ± 0.065	195
Red-vented bulbul*	*Pycnontus cafer*	0.629 ± 0.079	149
Oʻahu ʻamakihi	*Chlorodrepanis flava*	0.586 ± 0.085	139
Japanese bush warbler	*Horornis diphone*	0.464 ± 0.061	110
House finch	*Haemorhous mexicanus*	0.380 ± 0.075	90
Kalij pheasant	*Lophura leucomelanos*	0.236 ± 0.051	56
Spotted dove	*Spilopelia chinensis*	0.219 ± 0.082	52
Northern cardinal	*Cardinalis cardinalis*	0.215 ± 0.032	51
Oʻahu ʻelepaio	*Chasiempis ibidis*	0.173 ± 0.036	41
Erckel's francolin	*Pternistis erckelii*	0.122 ± 0.027	29
Chinese hwamei	*Garrulax canorus*	0.089 ± 0.021	21
Scaly-breasted munia	*Lonchura punctulata*	0.059 ± 0.022	14
Red-crested cardinal	*Paroaria coronata*	0.059 ± 0.018	14
Zebra dove	*Geopelia striata*	0.042 ± 0.018	10
Total		15.43 ± 0.491	3657

* Denotes focal bird species

Table A.2. All fleshy-fruited plant species tested during playback experiment. Fruiting plant species, their respective families, and the total number of frugivory events and number of trials by plant species conducted during social cue experiment from May 2016 to July 2017 on the island of O‘ahu, Hawai‘i, USA.

	Plant species	Family	No. of frugivory events	No. of trials
Native	*Alyxia oliviformis*	Apocynaceae	2	1
	Broussaisia arguta	Hydrangeaceae	0	2
	Cyanea angustifolia	Campanulaceae	3	1
	*Cyanea grimesiana**	Campanulaceae	0	4
	*Cyanea pinnatifida**	Campanulaceae	0	1
	*Cyanea superba**	Campanulaceae	0	6
	*Delissea waianaeensis**	Campanulaceae	1	15
	Dianella sandwicensis	Liliaceae	0	1
	Diospyros hillebrandii	Ebenaceae	0	5
	Kadua affinis	Rubiaceae	0	4
	Leptecophylla tameiameiae	Ericaceae	0	1
	Myrsine lessertiana	Myrsinaceae	30	2
	Pipturus albidus	Urticaceae	61	11
	Psychotria mariniana	Rubiaceae	3	3
	*Schiedea obovata**	Caryophyllaceae	0	2
	Smilax melastomifolia	Smilacaceae	0	1
	*Solanum sandwicense**	Solanaceae	0	1
	Wikstroemia oahuensis	Thymelaeaceae	2	1
Introduced	*Clidemia hirta*	Melastomataceae	0	1
	Passiflora suberosa	Passifloraceae	0	1
	Psidium cattleianum	Myrtaceae	4	4
	Psidium guajava	Myrtaceae	22	4
	Rubus rosifolious	Rosaceae	10	6
	Schinus terebinthifolius	Anacardiaceae	2	1
	Syzygium cumini	Myrtaceae	0	1
	Total		140	80

* State and/or federally listed threatened or endangered species

Table A.3. Outputs of the two models comparing the number of frugivore detections and frugivory events between control and treatments. Outputs of generalized linear mixed effects models of the number of frugivores detected and the number of observed frugivory events by focal bird species during the social cue experiment. The first model's intercept is set as the control period of the experiment. The second model's intercept is set as the control period, Japanese white – eye, and their interaction (JAWE: Control). Red-billed leiothrix (RBLE), red – vented bulbul (RVBU), and red – whiskered bulbul (RWBU) are the focal bird species. Coefficients, standard error of estimates (SE), Z values, and *P*-values are shown. Bold values indicate significance.

Model	Fixed effect	Estimate	SE	Z value	*P* – value
Frugivores detected	(Intercept)*	1.017	0.089	11.46	<0.0001
	Treatment*	1.366	0.069	19.70	<0.0001
Frugivory events	(Intercept)*	-5.566	1.054	-5.280	<0.0001
	Treatment*	2.629	0.391	6.718	<0.0001
	Red – billed leiothrix	-32.791	96.773	-0.339	0.735
	Red – vented bulbul	-30.161	46.267	-0.652	0.514
	Red – whiskered bulbul	-1.253	0.802	-1.563	0.118
	RBLE : Treatment	30.008	96.773	0.310	0.756
	RVBU : Treatment	27.378	46.267	0.592	0.554
	RWBU : Treatment	-0.326	0.839	-0.389	0.697

* Denotes significance

Table A.4. Outputs of four models comparing the minutes of frugivore occupancy between control and treatment periods. Outputs of generalized linear mixed effects models of the total time of occupancy for frugivorous species during the treatment (playback) period of the playback experiment. Intercept for each model is the control period. Coefficients, standard error (SE), Z values, and *P*-values are shown.

Model	Fixed effect	Estimate	SE	Z value	*P* – value
Japanese white-eye	(Intercept)	-0.082	0.139	-0.592	0.554
	Treatment*	1.724	0.107	16.103	<0.0001
Red-billed leiothrix	(Intercept)*	-0.580	0.177	-3.281	0.001
	Treatment*	0.934	0.145	6.432	<0.0001
Red-vented bulbul	(Intercept)*	-2.179	0.311	-7.005	<0.0001
	Treatment*	1.812	0.270	6.722	<0.0001
Red-whiskered bulbul	(Intercept)*	-1.169	0.256	-4.564	<0.0001
	Treatment*	0.967	0.146	6.639	<0.0001

* Denotes significance

Table A.5. Outputs of four generalized linear mixed effects models of the presence of focal bird species during the treatment period with the intercept as the control period of the playback experiment. Coefficients, standard error (SE), Z values, and *P*-values are shown. Asterisks (*) denotes significance.

Model	Fixed effect	Estimate	SE	Z value	*P* – value
Japanese white – eye	(Intercept)*	-1.553	0.224	-6.929	<0.0001
	Japanese white – eye*	3.259	0.460	7.083	<0.0001
	White – eye / leiothrix*	3.477	0.714	4.869	<0.0001
	Red – billed leiothrix*	1.382	0.412	3.354	0.0008
	Red – whiskered bulbul*	1.308	0.354	3.694	0.0002
	Red – vented bulbul	0.271	0.394	0.689	0.491
Red – billed leiothrix	(Intercept)*	-1.930	0.234	-8.252	<0.0001
	Japanese white – eye	0.236	0.435	0.543	0.587
	White – eye / leiothrix*	1.387	0.563	2.463	0.014
	Red – billed leiothrix*	1.464	0.402	3.639	0.0002
	Red – whiskered bulbul	0.475	0.393	1.209	0.227
	Red – vented bulbul	-0.317	0.490	-0.647	0.518
Red – whiskered bulbul	(Intercept)*	-3.214	0.386	-8.324	<0.0001
	Japanese white – eye	0.821	0.544	1.510	0.131
	White – eye / leiothrix	1.433	0.752	1.905	0.057
	Red – billed leiothrix	0.733	0.628	1.167	0.243
	Red – whiskered bulbul*	2.874	0.454	6.330	<0.0001
	Red – vented bulbul	-0.411	0.791	-0.519	0.604
Red – vented bulbul	(Intercept)*	-2.369	0.338	-7.000	<0.0001
	Japanese white – eye	0.403	0.497	0.811	0.418
	White – eye / leiothrix	0.102	0.861	0.118	0.906
	Red – billed leiothrix	-0.211	0.646	-0.327	0.743
	Red – whiskered bulbul	0.406	0.484	0.840	0.401
	Red – vented bulbul*	1.818	0.455	3.992	<0.0001