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Interactions of Avian Frugivores and Invasive Trees in French Polynesia

By

Erica Noelle Spotswood

A dissertation submitted in partial satisfaction of the requirement for the degree of

Doctor of Philosophy

in

Environmental Science, Policy and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor James W. Bartolome, Chair

Professor John Battles

Professor Brent Mishler

Dr. Jean-Yves Meyer

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ABSTRACT

Interactions of Avian Frugivores and Invasive Trees in French Polynesia

by

Erica Noelle Spotswood

Doctor of Philosophy in Environmental Science, Policy and Management

University of California, Berkeley

Professor James W. Bartolome, Chair

Invasive species pose a threat to the persistence of the sensitive endemic biotic communities on oceanic islands. The direct ecological, social and economic effects of invasions have been well documented and can be significant on both islands and continents. The indirect effects on the interactions between species has received less attention despite being of critical importance to the long term stability of ecosystems facing multiple threats from anthropogenic impacts. In this dissertation, I examined how seed dispersal relationships are modified by the presence of multiple introduced species on the islands of Tahiti and Moorea in the Society archipelago of French Polynesia. Additionally, I evaluated the risks associated with one of my research methods; the use of mist nets to capture wild birds.

I first evaluated how the local abundance of the invasive *Miconia calvescens* modifies seed dispersal relationships between birds and plants. The species is an invasive fruit-bearing tree that currently covers much of the island of Tahiti and is present at much lower densities on Moorea. I found that while the overall size of networks was similar across sites, networks on the highly invaded island of Tahiti were less diverse and less even because birds concentrated a greater proportion of their foraging on *Miconia calvescens*. There were fewer links between birds and native plants at highly invaded sites where birds switched their diets away from a broader range of fruit and insects. The endemic Grey-green Fruit Dove (*Ptilinopus purpuratus*) consumed native fruit in larger quantities and more total species than two introduced frugivores. This study demonstrates that the impacts of invasive fruit-bearing plants on seed dispersal networks depends in part on their abundance, and are likely to increase as a species becomes increasingly dominant in a community. Additionally, the dispersal of native plants continues to depend heavily on the single extant native fruit dove on these islands despite the presence of multiple introduced frugivores.

The impact of invasive plants on seed dispersal networks is the result of the cumulative effects of foraging decisions by birds. The available evidence suggests that birds choose which fruit to consume based on the complementarity between fruit traits and their own preferences as well as the relative abundance of fruit in a community. I used fruit choice experiments with captive Red-vented Bulbuls (*Pycnonotus cafer*) to uncouple fruit preferences from the effects of abundance to determine which operates more strongly on foraging decisions in birds. Birds

showed both reliable and consistent preferences for some fruits over others and a strong response to abundance. However, when included simultaneously in the same experiment, the patterns of preference remained intact while the effect of abundance disappeared. Taken together, experimental and field data suggest that foraging decisions are highly context-dependent, and neutral models that consider only the relative abundance of fruit in the community are unlikely to provide reliable predictions about how seed dispersal networks will change in response to invasion.

In the final study of my thesis, I evaluated the risks associated with one of my primary research methods; the use of mist nets to capture birds. Mist nets are used widely for monitoring avian populations. While the method is assumed to be safe, very few studies have addressed how frequently injuries and mortalities occur, and no large-scale comprehensive evaluation has been conducted to determine the associated risks. In collaboration with several banding organizations, I quantified the rates of mortality and injury at 22 banding organizations in the United States and Canada and used capture data from five organizations to determine what kinds of incidents occur most frequently. I compiled a dataset including nearly 350,000 records of capture over a 22 year period and evaluated what makes birds most at risk to incident. I found that the risks varied among species and factors such as body mass and the number of previous captures were related to the probability of an incident. Additionally, I found that birds that were released back into the wild after an injury were recaptured at similar rates compared to birds that were released without an injury, indicating that injured birds survived in similar numbers as those released uninjured. This study fills a gap by providing the first comprehensive evaluation of the risks associated with mist netting and concludes that while overall risks are low, species and traits can predict a bird's susceptibility to incident. These results can be useful for organizations that use mist netting, and should be incorporated into protocols aimed at minimizing injury and mortality. Finally, I emphasize that projects using mist nets should monitor their performance and compare their results to those of other organizations.

I conclude that the indirect effect of species invasions are variable and depend in part on the abundance of the invasive species. Thus, consequences for seed dispersal networks are likely to be most pronounced at the highest levels of invasion. Despite the effects of abundance, birds also showed strong preferences for certain kinds of fruits. Thus, the integration of novel fruit into native seed dispersal networks is likely to depend not only on the relative abundance of fruit but also on the preferences for each fruit relative to others that are available. The Grey-green Fruit Dove is the sole disperser for several native plants, and the maintenance of viable populations of these plants is likely to depend on conservation of this protected and sensitive endemic species. Similarly, it is likely that the Fruit Dove also depends on native plants despite the integration of many exotic fruit into its diet. There is an urgent need for more research evaluating the habitat requirements and population dynamics of this frugivore in order to ensure the long term persistence of the species.

This dissertation is dedicated to the endemic flora and fauna of French Polynesia



I am willing to sacrifice elegance for reality, knowing just how muddy reality can be.

~ David Steadman (2006)

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Chapter 1

Chapter 1

Summary of the Dissertation

BACKGROUND

This dissertation is motivated by a desire to understand the effects of anthropogenic impacts on the ecology of tropical forest ecosystems of oceanic islands so that we might improve our efforts to protect and conserve biodiversity. On oceanic islands, the threat of invasive species to the persistence of endemic species has received a great deal of attention. However, the community level responses to invasive species that emerge as interactions between species are altered by the presence of new highly abundant organisms has received far less attention, and is arguably a key component in understanding the threat to biodiversity. My dissertation tackles these issues by investigating how invasions influence mutualistic species interactions in tropical island systems. I used network theory, seed dispersal ecology, invasion biology, and animal behavior to characterize seed dispersal communities in French Polynesia. Specifically, the objectives of this thesis are to assess 1) the response of seed dispersal patterns to the presence of a highly invasive fruit-bearing tree, 2) the factors that influence fruit choice in frugivores, with an emphasis on how individual foraging decisions will ultimately be reflected in community-wide responses to invasive species, and 3) the risk factors associated with one of my primary research methods: the use of mist netting to capture birds to determine diet. In this opening chapter, I provide some of the context and motivation for this study, including a discussion of the current state of knowledge related to the impacts of invasive species on seed dispersal systems. I provide an overview of issues specific to oceanic islands that influence the ecology and biology of these ecosystems in ways that may be different from continental contexts. This introduction is not intended to be a comprehensive review of the many issues surrounding species invasions on oceanic islands, but is rather a summary of the major themes and background that explain why species invasions may have consequences on islands that are different from those we might expect on continents.

Invasions and the threat to biodiversity

The dramatic increase in the movement of goods and people around the world in the 20th century has allowed plants and animals to colonize new locations at an unprecedented rate. Since Charles Elton published his seminal book on invasion biology in 1958, the study of species invasions has grown, and is now broadly accepted as an important discipline in ecology (Elton 1958, Davis 2011). The introduction of novel organisms coupled with habitat modification and climate change is leading to the development of ecosystems that differ in composition from past systems. These ‘no-analog’ or novel ecosystems is likely to trigger unpredictable changes in ecosystem function (Hobbs *et al.*, 2009). While some authors have cautioned against discounting alien species on the basis of their status as introduced (Davis *et al.*, 2011), many others have highlighted the negative ecological, social and economic consequences of species invasions (Mooney & Cleland, 2001; Allison & Vitousek, 2004; Pimentel *et al.*, 2005; Simberloff, 2005; Richardson, 2011). Despite the often repeated claim that invasive species pose a major threat to biodiversity globally (Wilcove *et al.*, 1998), increasing evidence suggests that invasive species

are not major drivers of extinctions except in a restricted set of cases, the most notable of which are oceanic islands (Davis, 2011).

Mutually beneficial relationships between species such as the dispersal of seeds by animals have played an important role in the maintenance of biodiversity worldwide (Bascompte & Jordano, 2007). The invasion of introduced organisms can alter the connections between native species disrupting these critical relationships (Traveset & Richardson, 2006). The indirect consequences of species invasions are often not immediately obvious, but have the potential to alter community dynamics (Simberloff, 2003; Traveset & Richardson, 2006; Aizen *et al.*, 2008). Resulting communities with many exotic species are often characterized by multiple newly established dispersal relationships between exotic and native frugivores and plants (Holyoak, 1974; Holyoak & Thibault, 1984; Seitre & Seitre, 1992; Richardson *et al.*, 2000; Gosper *et al.*, 2005; Buckley *et al.*, 2006; Gouni & Zysman, 2007). These interactions may simultaneously facilitate alien plants and vertebrates while disrupting native mutualisms (Richardson *et al.*, 2000; Traveset & Riera, 2005; Traveset & Richardson, 2006).

The spatial patterns of seed dispersal have long been recognized as important in determining the structure and dynamics of plant populations (Nathan & Muller-Landau, 2000). Seed dispersal ultimately influences the distribution of adult plants by modifying processes such as predation near and far from the parent plant and the deposition of seeds at favorable micro-sites (Janzen, 1970; Cain *et al.*, 1987; Wenny & Levey, 1998). The kind of dispersal vector is important in determining the seed shadow, or the spatial deposition of seeds away from a source plant. Generally, vertebrate mediated dispersal is assumed to result in a longer mean dispersal distance than seeds dispersed by gravity or wind (Buckley *et al.*, 2006). Birds and other vertebrate frugivores can alter the seed shadow, or the spatial distribution of seeds relative to parent trees. These changes in deposition of seeds can be important in structuring tropical plant communities (Nathan & Muller-Landau, 2000; Levine & Murrell, 2003). Dispersal by birds of the fruit of invasive trees has the potential to influence the dynamics of plant invasions via changes in the speed and spatial distribution of spread from the source of an introduction. Models of the spread of an invading organism predict that successful dispersal of a small number of seeds to distances far from a parent plant can have a disproportionate effect on the dynamics of plant invasions (Neubert, 2000; Hastings *et al.*, 2005). Specifically, long distance transport of seeds can lead to an increase in the speed of spread from an initial population and can result in the establishment of new satellite populations in locations distant from the original site of introduction (Clark *et al.*, 2001b).

The island context

Islands (especially oceanic islands) have a number of characteristics that make them distinct from mainland ecosystems, and some of these factors are likely to influence how interactions between species are modified by invasive species. In particular, islands appear to be more vulnerable to the effects of species invasions than continents, (Vitousek *et al.*, 1997; Fritts & Rodda, 1998; Courchamp *et al.*, 2003; Traveset & Richardson, 2006) and small populations with restricted ranges appear to make island biota more prone to extinction (Steadman, 1995; Frankham, 1998; Blackburn *et al.*, 2004). Many of the characteristics that make islands unique are also those characteristics cited as those responsible for the vulnerability of islands to

extinction and to species invasions. Among others, these characteristics include the disharmonic nature of flora and fauna, low diversity, a steeper slope in the drop-off of the species area relationship (Keir 2009), high rates of endemism (Keir 2009), and large numbers of species with small populations and restricted ranges (Whittaker 1998, among many other references that cover this topic).

The susceptibility of islands to invasions has been the subject of debate since the idea was proposed by Charles Elton (1958). While current evidence suggests that islands are not more susceptible to invasion (Reaser *et al.*, 2007; Blackburn *et al.*, 2008), it is still generally accepted that the effects of invasions are often greater on islands (reviewed in Reaser *et al.*, 2007). Potential reasons for the vulnerability of islands to the impacts of invaders were reviewed by Whittaker (1998) and include the presence of vacant niche space and less competition leading to greater success of invaders, the competitive inferiority of island endemics due to long evolutionary isolation, the release of alien species from their predators and parasites present in their native ranges that keep their populations in check, and the presence of islands along trade routes where stopover of ships and planes might facilitate the spread of propagules. In addition to invasive species, habitat destruction remains a key threat to island ecosystems, and it is likely that the combination of these two factors together is in part responsible for the disproportionate impact of invasive species on islands (Reaser *et al.*, 2007; Whittaker, 2007).

The available evidence suggests that islands are disproportionately affected by extinctions compared to continents. For example, 90% of bird extinctions since 1600 have occurred on islands (Whittaker, 2007) and of 80 documented plant extinction in last 400 years, 50 were island species (Sax & Gaines, 2008). Small islands have higher numbers of endangered and critical status endemic plants (Caujapé-Castells *et al.*, 2010). In Hawaii, 50% of native plants are threatened many of which now have populations numbering between one and 50 individuals (Sakai *et al.*, 2002). On Mauritius, 80 of 680 native plants are already considered extinct, and another 155 critically endangered (Kaiser-Bunbury *et al.*, 2010). However, other authors have pointed out that while 53% of extinctions since 1500 were of birds, the composition of species that are likely to go extinct in the near future is different. Trigger species that are currently highly threatened are disproportionately represented in amphibians (51% of current trigger species) of which only 39% are from islands (Ricketts *et al.*, 2005). Thus, the future patterns of extinction may not follow patterns documented since 1500, and could reverse the trend towards greater extinction on islands. The vulnerability of island species to extinction can be largely attributed to the comparatively small population size and restricted ranges of island species (Whittaker 1998). In a recent study, endemism richness was found to be 9.5 times higher on islands than on continents, and was higher for six groups of organisms (vascular plants, vertebrates, amphibians, birds, mammals, reptiles) (Kier *et al.*, 2009). In another study, isolated island groups had higher numbers of endemics per unit area than islands closer to continents, but isolation did not lead to higher numbers of endangered plants (Caujapé-Castells *et al.*, 2010). The direct causes of species extinctions on islands are numerous (Whittaker 1998) and include habitat modification, species invasions, small population sizes, hunting, trade and human disturbance. The degree to which extinctions are provoked by invasive species is another area of debate in island biology. For example, while introduced mammalian predators have been implicated in the extinction of many birds and reptiles (Whittaker 1998, others), extinctions provoked by other taxa are less common,

and at least one author has pointed out that native and invasive richness on islands are positively correlated in plants (Sax 2008).

There are several ways in which modifications to species interactions might be different on islands compared to continents. For example, many islands have a very low diversity of frugivores, leading to the presence of ‘strong-interactors’ (Cox 1991) or ‘native super-generalists’ (Olesen 2002) upon which many plants depend for their dispersal. In 1991, Cox *et al.* predicted that isolated oceanic islands might contain strong-interactors if relationships between dispersers (or pollinators) and their plant mutualists was highly asymmetric making plants disproportionately dependent on a very small number of vertebrates for dispersal and pollination (Cox *et al.*, 1991). Indeed, many oceanic islands do have reduced communities of dispersers, and the vertebrates that participate in seed dispersal are also of a different composition from those of continents. For example, on continents, frugivorous mammals are diverse and include tapirs, peccaries, monkeys, fruit bats, some ungulates, elephants, and pigs (Herrera, 2002; Donatti *et al.*, 2007; Forget *et al.*, 2007), whereas mammals are often entirely absent from islands, or represented only by fruit bats (Cox *et al.*, 1991; Herrera, 2002; Kaiser-Bunbury *et al.*, 2010). Similarly, avian frugivores on continents include many species across a diverse range of taxa including Toucans, hornbills, mockingbirds, blackbirds, starlings, vireos, broadbills, babblers, bulbuls, waxwings, manakins and barbets. On oceanic islands, avian frugivores are disproportionately represented by pigeons and doves (Columbidae), which are the only native frugivores in much of the remote Pacific (Steadman 1997). Lastly, seed dispersal by reptiles is rare on continents, but common among lizards on islands, possibly as a result of vacant niches and density compensation (Olesen & Valido, 2003). The low diversity and disharmonic nature of the vertebrate disperser community leads to several predictions about seed dispersal networks. First, we might predict smaller and more connected networks with high asymmetry. Strong interactors that are linked to many plant species may lead to ecosystems that are resilient to the extinction of fruit bearing plants but highly vulnerable to the extinction of keystone frugivores that are disproportionately responsible for the dispersal of many native plants.

The French Polynesian context

The remote oceanic islands of the South Pacific are highly simplified systems with low native terrestrial biodiversity and high rates of endemism (Paulay, 1994; Cronk, 1997; Paulay *et al.*, 2002; Wardle, 2002). The Society archipelago consists of six eroded volcanic islands, of which Tahiti is the youngest and largest (Fosberg, 1992; Meyer & Salvat, 2009). Terrestrial biodiversity is very low relative to other tropical ecosystems, but rates of endemism are high (Meyer & Florence, 1996; Meyer, 2007; Meyer & Salvat, 2009). Numerous organisms have been introduced, and in both birds and plants, exotic species now comprise around half of the biodiversity on these islands (Gouni & Zysman, 2007; Fourdrigniez & Meyer, 2008). Tahiti and Moorea (17° 38’S, 149° 30’W and 17° 30’S, 149° 50’W respectively), are small tropical volcanic islands (1045 km² and 142 km² respectively) with high peaks reaching 2241 and 1207 m respectively.

Native plants

Similar to patterns in other taxa, French Polynesia is characterized by an attenuated and disharmonic native flora with relatively low diversity compared to continental ecosystems (Meyer, 2004). The flora is primarily of Malesian and Austro-Melanesian origin with a few New Zealand, Australian, and American elements (Fosberg 1992, Meyer and Salvat 2009). French Polynesia also lies at the eastern most limit of a number of genera that are distributed throughout the Pacific and into South East Asia (*Alyxia*, *Ascarina*, *Cyrtandra*, *Fagraea*, *Metrosideros*, *Meryta*, *Pouteria*, *Pittosporum*) (Meyer 2004). There are also several adaptive radiations represented, including *Bidens* (19 endemics), *Cyrtandra* (27 species), *Glochidion* (22 species), *Myrsine* (27 species), and *Psychotria* (24 species) (Meyer 2004). Overall, endemism is high and 72% of angiosperms are endemic to French Polynesia. Most endemics only occur in upper elevation wet forests where they are probably highly vulnerable to extinction due to small population size and range restrictions (Meyer 2004). An estimated 37% of native species produce fleshy fruit adapted for dispersal by frugivores (Fourdrigniez & Meyer 2008 with data taken from Florence 2003).

Plant introductions

The introduction of alien plant species began with the arrival of Polynesians, who brought with them a number of plants with ethno-botanical value as they moved eastward across the Pacific into remote Polynesia (Kirch, 2002). Some examples of Polynesian-introduced species that became naturalized include the Tahitian Chesnut *Inocarpus fagifer*, the Breadfruit tree *Artocarpus altilis*, the Otahiete apple *Spondias dulcis*, and Polynesian Bamboo *Schizostachyum glaucifolium* (Fosberg 1992). The introduction of alien plants continued into the period following European arrival, and Europeans introduced many other species including including *Tecoma stans*, *Cecropia spp.*, *Spathodea campanulata*, *Albizia spp.*, *Psidium spp.*, *Pinus caribaea*, *Lantana camara* and *Leucaena leucecephala* (Fosberg, 1992; Meyer, 2000, 2004). As a result, the total number of introduced species, estimated at 1,558 is nearly double the 885 described native species across French Polynesia (Fourdrigniez & Meyer, 2008). Of those introduced species, 557 have naturalized populations and 35 are classified as threatening to native biodiversity (Guild, 1938; Bruner, 1972; Holyoak & Thibault, 1984; Thibault & Monnet, 1990; Gouni & Zysman, 2007; Fourdrigniez & Meyer, 2008). Of 579 alien naturalized plant species evaluated by Fourdrigniez and Meyer (2008), 10% fall into the highest two categories of invasive potential while 18% produce fleshy fruit and 20% use animal digestion as a mode of dispersal.

One of the most notable cases of species invasions in French Polynesia is the introduction and subsequent invasion by *Miconia* (*Miconia calvescens*). *Miconia* produces a fleshy fruit that is attractive to frugivores. On Tahiti and Moorea, *Miconia* covers more than 60% and 20% of the land surface respectively (Meyer, 2010). Where present, *Miconia* grows in dense stands where fruit are available year round. Individual trees can produce up to eight million seeds per year, and with three fruiting peaks annually, reproducing individuals are rarely devoid of fruit (Meyer, 1998; Pers. obs.). Evidence from the historic record of *Miconia* invasion on Tahiti and Moorea suggest that both the rapid expansion and the establishment of remote satellite populations predicted by theoretical work have occurred (Meyer, 1998b; Clark *et al.*, 2001b). Though historic records alone cannot point to frugivorous birds as dispersers, it does suggest that long distance transport has been important in the spread of *Miconia* in French Polynesia. On Tahiti

where it was first introduced in 1937, *Miconia* covered ca. 70,000 ha by 1996 while on Moorea where it was introduced in the 1960's, *Miconia* had expanded to cover 1,200 ha by 1999 (Meyer & Florence, 1996; Meyer, 1999). This corresponds to an expansion rate of 3.4 square km/year and 0.64 square km/year respectively. These rates of spread are extremely rapid, corresponding to rates found in human-assisted jump dispersal of Argentine ant invasions in the USA and to spread models incorporating long distance transport of small numbers of seeds over distances greater than 1km (Higgins & Richardson, 1999; Suarez *et al.*, 2001). Additionally, the establishment of numerous remote satellite populations on both Moorea and Tahiti and the presence of plants on cliffs that are not accessible by people on Raiatea (see for details Meyer 2010) suggest that long distance dispersal has been critical in the expansion of *Miconia* since its introduction on Tahiti (Meyer, 1998b; Pasari, 2000; Meyer, 2010).

Avian richness in the pre-human context

The contemporary context of avian richness in Eastern Polynesia is influenced by both extinction and low species diversity (Steadman 2006). The drop-off in diversity moving eastward from South East Asia into the remote Pacific has been termed 'faunal attenuation', and is caused by the isolation of oceanic islands. The variable dispersal abilities of birds acts as a filter, and many groups that are common in New Guinea and Indonesia are entirely absent from Eastern Polynesia (Steadman 2006). Thus, the native avifauna consists of a disharmonic subset of birds from a restricted number of groups including monarchs, kingfishers, lorikeets, swifts, herons, and pigeons and doves (Steadman 2006).

In addition to faunal attenuation, the avifauna of the Eastern Polynesia, and of Oceania in general has been impacted many extinctions provoked by the arrival of humans (Steadman 2006). David Steadman, who has cataloged extinction of birds across the Pacific using paleo-archaeological evidence has estimated that around 2,000 species of birds have already gone extinct from Oceania since human arrival, most of which are flightless rails (Steadman 2006). The factors influencing extinction are diverse, and include hunting, introduced species, habitat modification, forest clearing and agriculture. Upon arrival on formerly uninhabited islands (which occurred from 2500 to 1000 BP in the Society Archipelago), birds were killed by island colonists for fat, protein, bones, and feathers (Steadman, 1997). In most locations, the arrival of Polynesians was accompanied by the commensal animals they brought with them; the chicken (*Gallus gallus*), the dog (*Canis familiaris*), the pig (*Sus scrofa*), and the Polynesian Rat (*Rattus exulans*) (Steadman 2006). These animals preyed directly on native birds, competed with them possibly transmitting diseases, and preyed on their eggs and chicks (especially the rat).

In Eastern Polynesia, including Easter Island, Henderson Island, the Marquesas, the Societies, and the Cook Islands, most extinctions occurred between 1000 and 500 BP (Steadman 2006). The only frugivores present before human arrival were members of the family Columbidae (Columbids) including ground doves from the genera *Gallicolumba* and *Macropygia* and fruit doves, primarily from the genera *Ptilinopus* and *Ducula* (Steadman 2006). Among pigeons and doves in Pacific Oceania including Hawaii and New Zealand there are 61 living species, 18 known extinct, and 36 estimated total extinct species (Steadman 2006). Columbids never colonized Hawaii or Easter Island (Steadman 1997) probably due to extreme isolation. All other islands where Columbids are present are separated from other islands by less

than 1000 km, which may represent the limit of the dispersal ability for this group (Steadman 1997).

The zoo-archeological data from the Societies is limited and comes only from Huahine where five of six species of Columbids have been lost (Steadman 1997). However, Steadman estimated that all six species were probably once distributed across the other islands in the Society Group. While *Ptilinopus* fruit doves are usually not sympatric, it is likely that fruit doves co-occurred with *Ducula* pigeons on many islands (Steadman 1997). The Grey-green Fruit Dove (*Ptilinopus purpuratus*) is the only Columbidae that still lives on multiple islands in the group.

Contemporary avian richness

Contemporary land bird diversity is low all over French Polynesia including the Society Islands, and has been augmented by the presences of introduced species. Currently, there are 20 species of land bird on Tahiti (of which nine are introduced) and 15 on Moorea (of which eight are introduced) (Gouni & Zysman, 2007). Thus, on both islands, the number of introduced species is nearly as large as the number of native species. The diversity of Columbids in French Polynesia is also low, though high relative to other groups of birds. There are currently nine species of dove remaining in French Polynesia of which five are fruit doves from the genus *Ptilinopus*. The ranges of several species are currently highly restricted with populations surviving on only a few islands. Threatened species include the two largest members of the group, both of which are imperial pigeons (Table 1). Only three species of birds on Tahiti and Moorea regularly consume fruit (Table 2); the Grey-green Fruit Dove (*Ptilinopus purpuratus*; (Gmelin 1789) Columbiformes, Columbidae – Fruit Dove hereafter), the Red-vented Bulbul (*Pycnonotus cafer*, (L. 1766), Passeriformes, Pycnonotidae - Bulbul hereafter), and the Silvereye (*Zosterops lateralis* (Hartlaub, 1865) Passeriformes, Zosteropidae).

The Fruit Dove is a native frugivore endemic to the Society Archipelago where it is widespread from sea level up to 800-900m (Gouni & Zysman, 2007). The Fruit dove is a generalist that has incorporated many introduced fruits into its diet (Holyoak & Thibault, 1984), though the extent of its potential to disperse and spread invasive plants including *Miconia* was unknown before this study (Steadman & Freifeld, 1999). Population sizes on Tahiti and Moorea are estimated at a few thousand individuals (Thibault J.C., pers. comm.). Birds are often found in pairs or in small family groups. At all study sites except for two on Moorea, fewer than four individuals were observed per site (pers. obs.).

The Bulbul was introduced to Tahiti in the late 1970s (Bruner, 1979). From its origin in Papeete where it was probably introduced as a cage bird, it spread rapidly across Tahiti. In less than 10 years, it reached all coastal areas on Tahiti and was found inland as high as 1500 meters by 1993 (Monnet *et al.*, 1993). The current distribution covers the island included up to the highest peaks at 2100 m elevation (J.Y. Meyer pers. comm.). From Tahiti, the Bulbul spread to Moorea and to the leeward islands of the Society Archipelago sometime during the 1980s (Thibault *et al.*, 2002). Numbers on Tahiti are now estimated at several tens of thousands (Thibault *et al.*, 2002). Though there is little evidence of the Red-vented Bulbul dispersing invasive plants either in French Polynesia (but see Gaubert, 1992; Meyer *et al.*, 2008) or elsewhere, other species in the genus *Pycnonotus* have been found to be important to the spread

of weeds. For example, the Red-whiskered Bulbul (*Pycnonotus jocosus*) is thought to be partially responsible for the spread of weeds in Florida, Mauritius, and La Reunion (Simberloff & Von Holle, 1999; Mandon-Dalger *et al.*, 2004; Linnebjerg *et al.*, 2010). Some of the plant species consumed by the Red-whiskered Bulbul such as *Lantana camara* and *Schinus terebenthifolius* are also present in French Polynesia, indicating that there is a potential for the Red-vented Bulbul to consume and disperse these plants.

The Silvereye was introduced to Tahiti in 1937 by an American bird fancier (Guild, 1938). Until 1970, the Silvereye remained relatively rare on Tahiti. In the 1970s, the species spread across the entire island, eventually colonizing every habitat type and spreading to all the high islands of the Society archipelago as well as several islands in the Australs (Thibault & Monnet, 1990). First seen on Moorea in 1971 (Holyoak & Thibault, 1984), it is now the most abundant land bird on that island and on Tahiti where it is found up to 2240 m (Thibault & Monnet, 1990). It is a rapid colonizer which expanded its population rapidly on Tahiti and Bora Bora during the 1970s and went from being relatively rare to very abundant in less than 20 years (Thibault & Monnet, 1990). The Silvereye is thought to be responsible for dispersal of weeds elsewhere in the Pacific including Australia, where it has been implicated in the dispersal of the Bridal Creeper (*Asparagus asparagoides*) (Stansbury, 2001).

Mist netting – a low risk tool for monitoring avian populations?

Mist netting and banding of birds is a method that has been used by ornithologists worldwide for over 50 years because it provides a low-risk way to gather information that cannot be obtained using observation alone (Ralph, 1999; Fair *et al.*, 2010). While over a million birds are captured every year in the United States and Canada alone, a detailed assessment of the associated risks has never been carried out in a comprehensive way. Capture is highly stressful to animals and can occasionally be fatal even when precautions are taken to minimize harm. While it is often assumed that the benefits of information gained during wildlife research outweigh the potential harm to animals, the actual risks posed have not been quantified for every research method (Wilson & McMahon, 2006). Procedures which affect the welfare of animals raise ethical considerations and can compromise research objectives by introducing bias into data collection (Wilson & McMahon, 2006).

Though much information can be gained from observation of birds in the wild, there are many questions which can only be answered by direct capture. For example, it is not possible to test competing hypotheses for the causes of avian population declines, or even to determine at what demographic stage mortality is taking place, without information about rates of reproduction and survival (DeSante *et al.*, 2004). The main alternative to mist netting for estimating population sizes is point counting, a method which does not work well for cryptic species which do not call often (DeSante *et al.*, 2004). Furthermore, capture allows for the direct determination of the age and reproductive status of individuals, for the collection of other kinds of data such as DNA, and for the estimation of mark-recapture rates, all of which are not possible using observation alone (DeSante *et al.*, 2004; Dunn & Ralph, 2004; Ralph *et al.*, 2004a; Ralph *et al.*, 2004b).

Mist netting has been used successfully to estimate population sizes, to identify the habitat preferences of birds, to identify sources of population declines, and to assess the demographics of populations (Matlock & Edwards, 2006; Hasui *et al.*, 2007; Stouffer & Vega Rivera, 2007; Vitz *et al.*, 2007; Cruz-Angón *et al.*, 2008). Conservation managers are also using the technique to monitor the long term health of avian populations, to evaluate the impacts of habitat loss, fragmentation and land use change, to quantify recruitment of new individuals into populations and adult survival rates, and to assess the long term impacts of global climate change on avian productivity (Laurance *et al.*, 2002; DeSante *et al.*, 2004; Barlow *et al.*, 2006; Bulluck & Buehler, 2006; Newmark, 2006; Renner *et al.*, 2006; Stouffer *et al.*, 2006; Martensen *et al.*, 2008). Though other methods for estimating populations of birds without capture do exist, they can be problematic, and recent literature advises that accurate population estimates can be more easily obtained with the use of both direct capture and observations using standardized point counts (Blake & Loiselle, 2001). The ability to estimate populations using point counts depends on the behavior of the species in question, and cryptic sedentary behavior coupled with low numbers of individuals can lead to underestimation of population sizes where point counts are used alone (Blake & Loiselle, 2001). Furthermore, point counts require the estimation of the distance between the observer and the bird, which is often difficult in dense tropical forests. In one study in Samoa, population estimates could not be obtained because distance estimations were found to be unreliable for a number of species due to the ventriloquial nature of their calls, including the purple-capped fruit dove and the pacific pigeon (Blake & Loiselle, 2001).

Many studies have used mist nets to determine which habitats are preferred by birds (Blake & Loiselle, 2001; Barlow *et al.*, 2006; Bulluck & Buehler, 2006; Matlock & Edwards, 2006; Stouffer *et al.*, 2006; Stouffer & Vega Rivera, 2007; Vitz *et al.*, 2007; Cruz-Angón *et al.*, 2008). In Madeira, the endemic Madeira laurel pigeon frequently utilized forest edges during foraging. As a result, management recommendations identified these habitats as key resources for the protection of this species, which is on the IUCN Red list for Portugal (Oliveira *et al.*, 2006). In the Amazon basin, a 22-year long mist net monitoring program determined that forest fragments do not support the same avian communities as continuous forests. Management recommendations derived from these results identified the importance of fragments larger than 10 square kilometers for the protection of significant numbers of forest species (Laurance *et al.*, 2002). In Australia, a similar study of two species of fruit dove found a high degree of dependence on large connected patches of intact rainforest (Price *et al.*, 1999).

Information regarding when birds reproduce can also be obtained using mist nets. For example, the proportion of breeding individuals in a population and the ratio of adults to juveniles is key to monitoring bird populations because they are an indicator of overall population stability (Beissinger & Westphal, 1998; Courchamp *et al.*, 1999; Stephens & Sutherland, 1999; Stephens *et al.*, 1999; Sherley & Hay, 2001; Beissinger, 2002; Reed *et al.*, 2002). In one study, reproductive rates gathered from mist netting coupled with other demographic data were used to estimate the long term stability of snail kite populations in the Everglades of Florida. The study identified the occurrence of drought and low hatchling survivorship as critical factors limiting the population and recommended that water levels be maintained at maximum levels in order to alleviate the impact of drought (Beissinger, 1995). Since the publication of this study, the use of demographic models has become widespread in the

management of critically endangered populations of animals (Beissinger & Westphal, 1998; Courchamp *et al.*, 1999; Sandercock *et al.*, 2000; Beissinger, 2002; Cam *et al.*, 2003).

OUTLINE OF THE THESIS

In my dissertation, I used the islands of Tahiti and Moorea as focal sites to investigate how mutualistic relationships between avian frugivores and plants are altered by the presence and abundance of the highly invasive fruit-bearing tree, *Miconia*. I conducted field work at six sites (Figure 2) which were chosen to represent a gradient of increasing abundance of *Miconia*. My goals were to uncover how seed dispersal network properties are altered by the abundance of *Miconia* and to investigate how birds make foraging decisions in order to determine what changes we might predict to seed dispersal networks in response to invasion.

In Chapter 2, I compare seed dispersal network patterns across six sites on Tahiti and Moorea along a gradient of increasing *Miconia* abundance. I used dietary data collected from birds captured using mist nets to determine how bird diets change at sites where *Miconia* is most abundant. While a few recent studies have documented alterations in pollinator networks in response to abundant invasive plants (Aizen *et al.*, 2008; Padrón *et al.*, 2009), similar studies with dispersal networks are lacking (Ings 2009). In addition, I used germination experiments with seeds of native and introduced plants to determine whether germination of seeds is affected by digestion by frugivores. I hypothesized that more highly invaded sites would have altered network patterns, characterized by the loss of links present at less highly invaded sites and by a concentration of links between birds and *Miconia*. I also hypothesized that birds would switch their diets between other things (including other fruits and arthropods) and *Miconia* as *Miconia* abundance increased. Lastly, I hypothesized that dispersal by birds would not be uniform, but that the Fruit Dove would be responsible for dispersing the greatest quantities of native seeds.

In Chapter 3, I investigate how the dual effects of preferences for certain kinds of fruits and relative abundance are guiding the choices birds make in which fruit to consume. Using wild-caught individuals under experimental conditions, I conducted fruit preference trials with one of my study species, the Red-vented Bulbul (*Pycnonotus cafer*). In these experiments, I paired combinations of four species at equal and unequal abundances to test whether birds showed preferences between fruit types and whether these preferences changed when the abundance of one fruit changed relative to the other. In addition, I combined field data using vegetation plots to estimate the relative abundance of focal plant species at my sites on Moorea with bird dietary data to determine if some species are consumed more than expected based on their abundance in the plant community.

In Chapter 4, I investigate the effects of one of my main research methods (mist netting) on birds. While my research has focused primarily on seed dispersal in French Polynesia, during data collection, I came to wonder how mist netting might be affecting captured individuals. In 2008, while applying for a permit to study the locally protected Gray-green Fruit Dove in French Polynesia, I discovered that while mist netting is a commonly used technique for the capture of birds worldwide and over one million birds are banded in the United States alone every year, no study has ever quantified how frequently birds are injured and killed during handling. In 2009, I developed a large collaborative project to investigate this issue. I surveyed organizations to

gather data on overall rates of injury and mortality at bird observatories in the United States and Canada and compiled a dataset of over 350,000 records of bird captures gathered from over 20 years of mist netting across five organizations. With the help of seven co-authors, I quantified rates and types of injury and mortality investigated what factors make some species and individuals at higher risk. This project is the first comprehensive evaluation of the risks associated with mist netting, and we hope it will provide researchers and managers with concrete tools which they can use to assess their own performance and improve their protocols to avoid accidents. Our paper was recently published in the journal *Methods in Ecology and Evolution* and is reproduced with permission here as the final chapter of my dissertation. While I had many co-authors on the project that helped with various aspects of the research, I was responsible for the majority of the work including data gathering and organization, analysis, and writing.

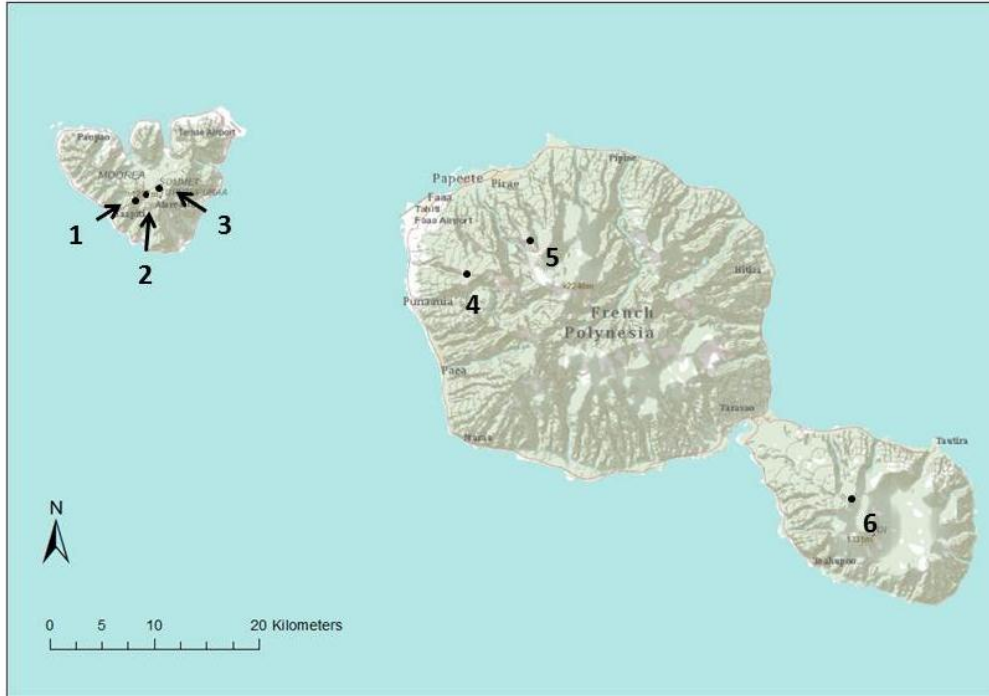
Finally, in Chapter 5, I summarize the key findings and main conclusions of the dissertation and outline several important directions for future research.

TABLES

Table 1. Extant species of pigeons and doves in French Polynesia.

Name	Latin Name	Distribution
Grey-green Fruit Dove	<i>Ptilinopus purpuratus</i>	All high islands in the Society group. Absent from Atolls (Tetiarioa, Tupai, Scilly, Bellinghausen)
Atoll Fruit Dove	<i>Ptilinopus coralensis</i>	Tuamotus where it is present on many atolls
Makatea Fruit Dove	<i>Ptilinopus chalcurus</i>	Makatea (raised limestone island)
Polynesian Imperial Pigeon	<i>Ducula aurorae</i>	Makatea (raised limestone island)
Polynesian Ground-dove	<i>Gallicolumba erythroptera</i>	Eastern Tuamotus on only a few isolated atolls and Rangiroa (only three populations remain)
White-capped Fruit Dove	<i>Ptilinopus dupetithouarsii</i>	Marquesas on most of the high volcanic islands
Marquesan Imperial Pigeon	<i>Ducula galeata</i>	Nuku Hiva in the Marquesas, and was reintroduced in 2000 to Ua Huka
Marquesan Ground-dove	<i>Gallicolumba rubescens</i>	Only remains on two small islands (Hatuta'a and Fatu Huku) in the Marquesas
Rapa Fruit Dove	<i>Ptilinopus huttoni</i>	Rapa (Australis)

FIGURES



#	Site	Latitude	Longitude	Elevation	Habitat	Miconia basal area (cm ² /m ²)
<i>Moorea</i>						
1	Vaianae	17°33'18.76"S	149°50'39.03"W	150	Moderately invaded	2.2
2	Cocotiers	17°32'51.30"S	149°50'27.23"W	350	Mixed native	0.7
3	Belvedere	17°32'27.50"S	149°49'44.05"W	250	Mixed native	0.4
<i>Tahiti</i>						
4	Marau	17°36'33.83"S	149°34'5.21"W	800	Heavily invaded	6.14
5	Aorai	17°34'2.98"S	149°31'37.99"W	600	Mixed native	15.38
6	Taravao	17°46'39.13"S	149°15'21.89"W	600	Heavily invaded	21.92

Figure 1. Locations of six field sites on Tahiti and Moorea

Table 2. Summary of characteristics for three frugivores present on Moorea and Tahiti

	Grey-green Fruit Dove (<i>Ptilinopus purpuratus</i>)	Red-vented Bulbul (<i>Pycnonotus cafer</i>)	Silvereeye (<i>Zosterops lateralis</i>)
Status	Native	Exotic	Exotic
Size (g)	85.67±9.89	36.65±3.39	10.27±0.7
Date of introduction	-	Probably in the late 1970s	1937
Native Range	Society Islands, French Polynesia	India and Pakistan	New Zealand and Australia
Range in French Polynesia	Huahine, Raiatea, Tahiti, Moorea, Maupiti, Bora Bora, Tahaa	Tahiti, Moorea, Huahine, Raiatea, Tahaa	Tahiti, Moorea, Leeward Islands (except coral atolls), Makatea, Raivavae, Tubuai, Rurutu
Elevation range on Tahiti and Moorea	0 – 8 to 900 m	0 - 2100	0 - 2240 m
Habitat preference	Primary and secondary forest, agriculture, gardens. Absent from atolls and montane forest, prefers understory	Very common in farms, residential areas, low elevation valleys and ridge forests, gardens, orchards, less abundant in high elevation forests	Abundant in all habitat types, absent from atolls
Diet	Fruit 2 - 17mm in diameter, occasionally insects	Fruit, flower petals, insects, lizards and geckos	Fruit, nectar, insects

Group size	Most often seen singly or in pairs, but groups up to 12 sometimes gather in fruiting trees, can also be seen in small family groups of 3. Maximum group size ever recorded is 40 (MP Poulsen 1985) on Tahiti	Family groups 2 - 10 individuals	Pairs during breeding season, otherwise gregarious in groups 4 - 50 individuals
Behavior	Shy, skulking, cryptic, not territorial	Vocal, aggressive towards other species and conspecifics, territorial during breeding season	Vocal, maintains contact with group members via contact calls, gregarious, territorial during breeding season
Interactions with other species	Preyed on by Swamp Harriers (<i>Circus approximans</i>) and cats, Competes with and is victim of agonistic interactions with Bubuls and Mynas, Mynas (<i>Acridotheres tristis</i>) and Rats prey on eggs	Preyed on by Swamp Harriers, Aggressive towards most other species and conspecifics, competes with and is aggressive towards Mynas, Fruit Doves, and occasionally silvereyes.	Probably preyed on by Swamp Harriers, victim of occasional aggression from Bulbuls and Mynas
Breeding season	All months except September	November - January in French Polynesia, coincides with monsoon in native range	Records vary, probably year round
Populations on Tahiti and Moorea	Estimated 5 - 6,000 in 1973, 2-3 birds per hectare	Tens of thousands	Extremely abundant. Estimated hundreds of thousands (JC Thibault personal communication)
Population changes during 20th century	Very abundant in 1907. Thought to have declined since 1900, though no systematic surveys have quantified changes	Between 1980s and 1991 high densities only on west coast of Tahiti, in less than 10 years, spread to most coastal areas on Tahiti and up to 1500 m	Rare on Tahiti in 1958s, very abundant by 1970s, First noticed on Moorea in 1971. Colonized several islands Societies and probably the Australs without assistance.

References

(Bruner, 1972; Holyoak, 1974;
Holyoak & Thibault, 1984;
Seitre & Seitre, 1992; Gibbs *et al.*, 2001; Gouni & Zysman, 2007)

(Dhondt, 1977; Roberts, 1991;
Monnet *et al.*, 1993; Kirch, 2002;
Thibault *et al.*, 2002; Blanvillain *et al.*, 2003; Gouni & Zysman, 2007)

(Guild, 1938; Bruner, 1972;
Holyoak & Thibault, 1984; Higgins
et al., 2005; Gouni & Zysman,
2007)

Chapter 2

Chapter 2

Abundance of invasive trees alters the structure of seed dispersal networks in French Polynesia

INTRODUCTION

Mutualisms between species such as the consumption of fruit and associated dispersal of seeds by vertebrates play an important role in the maintenance of biodiversity on Earth (Howe & Smallwood, 1982; Bascompte *et al.*, 2006; Bascompte & Jordano, 2007). In communities, mutualisms can be depicted as networks, with nodes of species connected by the links between them. While some species are highly connected, others form only a few links, and this asymmetry is credited with maintaining communities that are resilient and robust to extinction (Bascompte *et al.*, 2006). The presence of introduced plants and animals in an ecosystem presents an opportunity for novel associations to develop, which may disrupt native relationships if patterns of interaction are altered via the loss in number and strength of links (Traveset & Richardson, 2006; Aizen *et al.*, 2008). Characterizing the structure of seed dispersal networks provides a framework where properties such as the degree of linkage between species and the strength of interactions can be quantified. Because invasive species often establish mutualisms with organisms in their novel environments, an approach that explicitly considers an entire community of interacting partners is required in order to understand the indirect effects of invasive species (Bascompte & Jordano, 2007; Aizen *et al.*, 2008).

Two of the most important factors driving network structure are species traits and abundance. The relative abundance of species in a community can determine the number and strength of interactions between linked pairs (Vázquez *et al.*, 2009). At the same time, species traits including phenology, phylogenetic relationships, and the complementarity between potentially interacting species can also determine which links between species are possible in an ecosystem, irrespective of their abundance (Olesen *et al.*, 2011). In highly invaded communities, the relative strength of these two factors may determine to what extent native networks are influenced by invasive species. For example, if species traits are most important, frugivores may show little or no response to increases in the abundance of a single species (Olesen *et al.*, 2011), and networks might remain unchanged even at a high level of invasion. On the other hand, if abundance strongly determines patterns of interactions, frugivores would be predicted to choose introduced fruit increasingly often as it becomes more abundant in a community leading to larger alterations in network properties at higher levels of invasion. Changes in network properties in invaded ecosystems have been documented in pollination networks including plants and insects in several recent studies (Lopezaraiza-Mikel *et al.*, 2007; Aizen *et al.*, 2008; Padrón *et al.*, 2009). Similar changes in seed dispersal networks due to invasions of fruit bearing plants have received less attention, yet this kind of study is necessary if we are to understand the community-wide consequences of species invasions.

Invasive species frequently achieve levels of abundance that are not matched by co-occurring native species. The extreme population sizes found in areas of high invasion of fruit-bearing plants present an unparalleled fruiting resource to birds and offer a unique opportunity to explore how the local abundance of fruit of a single species changes foraging patterns in birds. The abundance of fruit-bearing plants in a community is known to influence avian foraging (Levey, 1988; Loiselle & Blake, 1991; Herrera, 1998; Ortiz Pulido & Rico Gray, 2000; Blendinger *et al.*, 2008). An increase in the relative abundance of one species may influence others either by facilitation where the attraction of frugivores to an area by the abundance of one species leads to subsequent consumption of other species in the neighborhood (Sargent, 1990; Carlo, 2005; Gleditsch & Carlo, 2010) or via competition whereby the choice to eat the more abundant species leads to decreased consumption of other neighboring species (Saracco *et al.*, 2005; Carlo & Morales, 2008). Competition may occur via diet switching where decisions to consume one food item over another may vary in space and time as a function of the abundance of one resource relative to others (Levey & Karasov, 1989; Carnicer *et al.*, 2009). Diet switching triggered by high abundance of invasive species may lead to a corresponding decline in seed dispersal services to native plants, with consequences for community stability and the regeneration of native plants (Traveset & Richardson, 2006).

On remote oceanic islands, the invasion of introduced species is an important driver of population declines and species extinctions (Vitousek *et al.*, 1997; Reaser *et al.*, 2007). In French Polynesia, multiple fruit bearing plants and frugivorous birds have been introduced within the past 200 years following the arrival of Europeans and current ecosystems are highly modified by the presence of numerous alien species (Monnet *et al.*, 1993; Fourdrigniez & Meyer, 2008). At the same time avian extinction (especially of native pigeons) following the arrival of Polynesians in the past 1000 years has left the islands with only a subset of original avifauna (Steadman, 2006). The existing community of frugivores is extremely small, consisting of one surviving endemic pigeon and three recent passerine introductions. In 1937, the introduction of the fruit bearing tree *Miconia calvescens* D.C. (Melastomataceae, *Miconia* hereafter) resulted in the catastrophic invasion of 60-70% of the land surface on the island of Tahiti (Meyer & Florence, 1996). The nearby island of Moorea remains only 25% invaded (Meyer, 2010), and offers an opportunity to investigate patterns of avian foraging at lower extents of invasion. In this study, we used the variation in abundance of *Miconia* across two islands to test three hypotheses that examine the effects of the abundance of a highly invasive plant on seed dispersal network properties and bird foraging patterns.

The abundance hypothesis states that interactions between species are random (Vázquez *et al.*, 2009), leading to greater numbers and frequency of interaction between abundant species due to probability. If this hypothesis holds, we would expect that as the abundance of an invasive tree increases, we should see changes in seed dispersal networks properties. We predict that links might be lost, leading to smaller networks and fewer total links between birds and plants. We also predict that weighted network metrics that incorporate both the presence and relative frequency of links should reveal a greater concentration of total interactions in a smaller number of species at the most highly invaded sites.

The species traits hypothesis states that the foraging patterns of frugivores are constrained by evolutionary history, phenology, complementarity and behavior (Olesen *et al.*, 2011). This hypothesis predicts that frugivores will not base foraging decisions on the relative abundance of fruit alone, and responses to the availability of fruits should be species-specific. Therefore, we should expect the identity of a frugivore species to be an important predictor its interactions with plants. Because native frugivores are the only species that share evolutionary history with native plants, we expected that frugivore origin would be predictor of the number and frequency of interactions with native plants.

The diet switching hypothesis predicts that consumer species will switch between different dietary items depending on their relative local availability at a site (Carnicer *et al.*, 2009). This hypothesis implies competition between different dietary resources such that the consumption of one item will lead to a corresponding decline in the consumption of others. Under this hypothesis, we expect that the consumption of *Miconia* should be negatively correlated with the consumption of other dietary items.

The objectives of this study were to evaluate whether relative abundance, species traits, and diet switching are important in determining bird foraging patterns and network properties. Specifically, we addressed the following questions: 1) do more highly invaded sites have fewer and more unevenly distributed links between species 2) do native frugivores consume greater numbers and quantities of native plants than alien frugivores, and 3) is *Miconia* consumption negatively correlated with the consumption of other dietary items?

MATERIALS AND METHODS

Study Area

This study was conducted at six sites on Tahiti and Moorea in the Society Archipelago of French Polynesia (17°38'S 149°30'W and 17°32'S 149°50'W, Figure 1). Both islands are eroded extinct volcanoes. Tahiti (0.6-1.1mya) is the largest and highest island in French Polynesia, covering 1,045 km² and reaching 2,241 in elevation at its highest peak. Moorea, located 20 km from Tahiti, is smaller and older (1.3-2 mya), covering only 142 km² with its highest peak reaching 1,207m. The climate is wet tropical with mean annual temperatures ranging from 25.8-27 degrees C and rainfall from 1,690-3,500 mm/year at sea level. The flora of French Polynesia is rich in endemic plant species (520 endemic species of 885 native vascular plant species in French Polynesia) including one of the highest proportions of endangered plants in the Pacific, with a total of 47 endemic species threatened according to the IUCN red lists, 167 species legally declared protected in French Polynesia, and six already extinct (Meyer & Salvat, 2009).

We chose sites in secondary forests comprised of mixed native and alien tree species at elevations between 100 and 800m. We avoided stands of forest dominated by the European introduced *Falcataria moluccana* (Mimosaceae) and the Polynesian introduction *Inocarpus fragifer* (Fabaceae) and placed sites in or near forests with a

diversity of tree species including both native and introduced species. Plant communities on the two islands are not identical, and it was not possible to control for all factors other than the abundance of *Miconia*. In spite of this limitation, we made an effort to locate sites in habitats and with plant communities that were as similar as possible. Sites on Moorea are dominated by the native trees *Rhus taitensis* (Anacardiaceae), *Tarenna sambucina* (Rubiaceae), *Neonauclea forsteri* (Rubiaceae), *Crossostylis biflora* (Rhizophoraceae) and the European introduction *Spathodea campanulata* (Bignoniaceae). Tahitian sites were located in mixed forests with native trees *Rhus taitensis* and *Weinmania parviflora* (Cunoniaceae) as well as the European introductions *Miconia calvescens*, *Spathodea campanulata* and *Cecropia peltata* (Cecropiaceae).

All sites were located adjacent to pre-existing study plots established between 2005 and 2007. In these plots, the diameter at breast height (1.3m) of every stem was measured in 10x10m plots on Tahiti and 20x20m plots on Moorea to estimate the basal area of *Miconia* and other species. Because vegetation plots were small and not well replicated, we used basal area estimates of *Miconia* density only as rough index of the level of invasion at each site.

Study Species

Miconia was introduced to Tahiti from Central America in 1937 where it remained it spread to Moorea in the 1960s (Meyer, 1998a). The tree produces a fleshy fruit 7mm in diameter that is purple-black when ripe (Figure 2a). A single fruit contains between 50 and 250 seeds, each approximately 0.6 mm in diameter (Meyer, 1998b). Where present, *Miconia* grows in dense stands and with three fruiting peaks annually, individual trees can produce up to eight million seeds per year with reproducing trees rarely devoid of fruit (Meyer 1998).

Frugivores on Moorea and Tahiti include the Grey-green Fruit Dove (*Ptilinopus purpuratus* (Gmelin 1789, Columbiformes, Columbidae – Fruit Dove hereafter), the Red-vented Bulbul (*Pycnonotus cafer* L. 1766, Passeriformes, Pycnonotidae - Bulbul hereafter), the Silvereye (*Zosterops lateralis* Hartlaub 1865, Passeriformes, Zosteropidae), and the Common Myna (*Acridotheris tristis*). We chose to exclude the Myna from this study because it consumes relatively little fruit and is not abundant at sites above 200 m (Spotswood, unpublished data). The Fruit Dove is a native frugivore endemic to the Society Archipelago where it is widespread from sea level up to 600m on Moorea and 1000m on Tahiti (Gibbs *et al.*, 2001). The Bulbul was first seen naturalized on Tahiti in the late 1970s (Bruner, 1979). From its introduction in Papeete where it was probably introduced as a cage bird, it spread rapidly across Tahiti. In less than 10 years, it reached all coastal areas on Tahiti and inland as high as 1500m by 1993 (Monnet *et al.*, 1993) and is now found up to 2100 m (J.Y. Meyer pers. obs.). From Tahiti, the Bulbul spread to Moorea and to the Leeward Islands of the Society Archipelago sometime during the 1980s (Thibault *et al.*, 2002). The Silvereye was introduced to Tahiti in 1937 (Guild, 1938) and remained rare on Tahiti until the 1970s when it spread across the entire island followed by colonization of all other high islands of the Society archipelago as well as several in the Austral Islands (Thibault & Monnet, 1990). First seen on Moorea in

1971 (Holyoak & Thibault, 1984), it is now the most abundant land bird on that island and on Tahiti (Thibault & Monnet, 1990) where it is found up to 2240 m (J.Y. Meyer pers. obs).

Estimating Diet

We quantified diets of birds using fecal samples collected from birds captured using mist nets 2.5m wide and 12m long (mesh size 30 and 36 mm) raised to 50 cm off the ground on poles reaching 3m in height. Mist netting was conducted on 2-9 days per month from September 2007 to November 2008 (four nets) and again in 2010 from June to August (12 nets). Total net hours calculated as the number of 12m nets multiplied by the number of hours was 1759 on 64 days of mist netting. Nets were opened between 5:30-6:00 am and closed either after a half day at 11:00 am or after a full day at 5:30 pm. Nets were closed during periods of rain or high wind. All birds were fitted with an aluminum band and standard measurements taken (wing length, weight, fat deposits and reproductive status) (Pyle, 1997).

We obtained fecal samples by placing each bird in a thin breathable paper envelope inside a cloth bag until the bird had produced a sample or until 45 minutes had elapsed. Fecal samples were refrigerated for up to three months until they could be analyzed. We counted and identified all seeds using a dissecting microscope and a reference collection. Our seed reference collection was built during the project with assistance from local botanists. Photographs and measurements of each fruit and seed were taken, and voucher specimens including digital photos will be linked to the reference collection in the Moorea Biocode Project. Seeds from fecal samples that could not be identified are currently being identified using genetic barcoding in collaboration with the Moorea Biocode Project (Check, 2006). The project is collecting specimens and using DNA barcoding to identify every non-microbial species on the island of Moorea. Collection information, location, and availability of voucher specimens for a variety of taxa are available online through the Moorea Biocode database (<http://biocode.berkeley.edu/>).

We quantified the proportion of contents by category using a point sampling method. Each sample was weighed and then spread evenly across a petri dish marked on the bottom with a grid of 50mm points separated by 2mm. To obtain point estimates of contents, we counted the number of points falling on each type of dietary item present in the sample (e.g. insects vs. fruit). Arthropod remains were identified to the highest taxonomic category possible. All samples were stored in 90% ethanol.

Fecal samples were also collected indirectly from Bulbuls by identifying perch trees at each of our study sites and collecting droppings on dense vegetation under the trees (Fig 1b). Dietary contents obtained from fecal samples collected under perch trees did not differ significantly in the quantities of different dietary items from those obtained from birds captured directly. We do not estimate a systematic bias in dietary data obtained from perch sites, however, this type of sample did not allow us to estimate recapture rates or to control for the independence of samples. Bulbuls live in family

groups and are territorial, especially during the breeding season (Kumar, 2004), it is likely that fecal samples collected under the same perch tree are not independent because they represent replicates from a small group of individuals over time. Thus, dietary estimates for Bulbuls may be less generalizable than for the other two species in this study.

We used sample-based rarefaction to examine whether our sampling was sufficient to adequately characterize the diets of birds on Tahiti and Moorea. We removed the Fruit Dove from this analysis because we did not have enough samples from Tahiti for this species to make valid comparisons between islands. We used the incidence based non-parametric Chao coverage estimator which generates rarefaction curves based on the distribution of rare species (Colwell & Coddington, 1994). All rarefaction computations were performed using EstimateS version 8.2 (Colwell, 2005).

Miconia abundance

To assess whether network properties are altered by the relative abundance of *Miconia*, we constructed seed dispersal networks for Moorea and Tahiti by building an interaction matrix for complete networks and networks containing only native plants for each island. We removed the Fruit Dove from this analysis because we did not have enough samples from Tahiti for this species to make valid comparisons across islands. To minimize the impact of unequal sample sizes, we randomly resampled interactions with replacement to generate interaction matrices for each island derived from the same total number of fecal samples. Based on rarefaction curves, we determined that the richness of bird diets reached an asymptote after 50 samples for complete networks and after 100 samples for native-plant only networks. We ran 1,000 bootstrap iterations to calculate standard errors and confidence intervals around estimates of network structural properties. For each iteration, we calculated two unweighted and two weighted network properties. Unweighted properties consider only numbers of links between species whereas weighted properties incorporate both the presence and the frequency of interactions (Blüthgen *et al.*, 2008). The frequency of interaction was defined for our purposes as the number of seeds consumed of a given plant species by a given bird species (Vazquez, 2005). Unweighted network properties included the overall size of each network and the generality of the network. Weighted properties included Shannon Diversity and interaction evenness (Blüthgen *et al.*, 2008). In a network of I consumers (birds) and J resource species (plants), generality is the mean number of resource links per consumer species and network size is the sum total of all interactions between consumer and resource species (Blüthgen *et al.*, 2008). Diversity is based on the Shannon diversity index (Blüthgen *et al.*, 2008). Shannon diversity and the related interaction evenness values vary between zero and one with low values indicating high variations in interaction frequencies and a greater concentration of links between a smaller number of species pairs (Blüthgen, 2010). Interaction evenness, based on the Shannon diversity, follows the form (Blüthgen *et al.*, 2008):

$$E_2 = H_2 / \ln L$$

Where L is the number of all links in the network and H_2 is the Shannon Diversity. All network calculations were performed using the R bipartite package (Dormann *et al.*, 2009). We compared network properties generated via 1000 randomizations to determine whether properties differed on Moorea and Tahiti using a Wilcoxon Rank Sum test.

Species traits

To test the species traits hypothesis, we related the proportion of hits (using point sampling) of native fruit in each fecal sample to the island and period of capture (divided into three seasons, February-May, June-August, and September-November), the frugivore species, the proportion of insects (calculated as % of total hits using point sampling), and the density of *Miconia* at a site. We used the number of hits (corresponding to the total proportion of a given dietary item for each fecal sample) instead of the number of seeds in this analysis because we were comparing dietary contents between three frugivores that are very different in body size. Fruit Doves, because of their greater size, can produce fecal samples with much larger numbers of seeds than Silvereyes. The data set included more zeros than can be accommodated by common error distributions, causing overdispersion. We therefore used a two-part zero-altered hurdle model to first estimate the presence of a dietary item in a fecal sample using a model with a binomial error structure followed by a zero-truncated model with a negative binomial error structure to estimate the conditional abundance of a given dietary item when it was present (Potts & Elith, 2006; Zuur *et al.*, 2009). This approach allows for the possibility that the mechanisms that determine presence and abundance can be different. In our case the quantity of each food item consumed by birds is a product of two separate decisions; the bird first decides what to eat followed by a decision about how many fruit of a given plant to consume. Model selection was carried out using a backwards stepwise procedure. Least important factors were eliminated on the basis of Akaike's Information Criteria (AIC) until no more factors could be eliminated without deterioration in model fit. All models were fit using R version 2.12 with the pscl package (Kock *et al.*, 1987; Jackman *et al.*, 2008; Zeileis *et al.*, 2008; R Development Core Team, 2010).

Diet Switching

To determine whether bird foraging patterns showed evidence of dietary switching, we analyzed Bulbul and Silvereye fecal samples separately. We excluded Fruit Doves from this analysis because we lacked sufficient data from Tahiti for Fruit Doves to make adequate comparisons. We conducted three analyses for each frugivore. For Bulebuls, we modeled the number of *Miconia* seeds, the number of other seeds (all species other than *Miconia*), and the number of native seeds as a function of the variables island, period of capture, *Miconia* density, and the proportion of other dietary contents (calculated as the percent of total hits using point sampling). For Silvereyes, we modeled the number of *Miconia* seeds, the number of other seeds, and the percent insect contents as a function of the island and period of capture, the abundance of *Miconia*, and the proportion of other dietary contents. Each analysis was performed using zero-altered hurdle models as described above.

Germination

We conducted a series of germination experiments to test whether the germinability of seeds was affected by ingestion by frugivores. Specifically, we tested the effects of scarification caused by ingestion on seed germination, but not those of deinhibition, or the removal of the inhibition of germination caused by the presence of fruit pulp (Robertson 2006). *Miconia* germination trials were conducted in 2008 using petri dishes lined with filter paper folded in the middle to separate the petri dish into two sides. Each petri dish contained 100 *Miconia* seeds, 50 ingested and 50 hand cleaned. Hand cleaned seeds were removed from fruit and cleaned using forceps and water from ripe fruit collected at the same location on the same day as the fecal sample. Petri dishes were covered and placed in a laboratory with an even temperature of 20 degrees Celsius and watered as needed. Experiments ran for 100 days, and all seedlings were counted every 3-5 days. We germinated a total of 15,016 of seeds in 330 petri dishes. The effect of scarification on germination has been shown to be greater in experiments using petri dishes than in similar experiments which test germination of seeds in field or glasshouse conditions (Traveset *et al.*, 2007). We chose to use petri dishes in spite of this concern due to the small size of *Miconia* seeds (0.5-0.7mm length). We predicted that a laboratory experiment would be more accurate than an experiment in the field or in a glass house because seeds and seedlings were visible on white filter paper and could be counted using a dissecting microscope when necessary. Thus, our results require a conservative interpretation, and the effects of scarification may be slightly larger for this set of experiments than they would be under field conditions.

Germination trials using three native plants were conducted in 2010 in 10cm diameter round pots outdoors under shade cloth. We compared the germination of ingested *Tarenna sambucina* and *Wikstroemia foetida* seeds passed by the Fruit Dove and *Cyclophyllum barbatum* seeds passed by the Bulbul to hand-cleaned seeds. Two (*Cyclophyllum*), four (*Wikstroemia*) or ten (*Tarenna*) seeds were sown per pot with standard potting soil. The experiment was monitored for 100 days and all seedlings were counted every 3-5 days and watered as needed.

We used generalized linear mixed modeling (GLMM) to determine whether digestion influenced total proportion of seeds germinated after 100 days. Treatment category (hand cleaned vs. digested by Bulbuls, Silvereyes, or Fruit Doves) was a fixed effect and the petri dish or pot was a random effect. This approach allows for the possibility that pot specific or petri-dish specific effects due to differences in watering or spatial position in the experiment could lead to non-independence of seeds germinated in the same pot or petri dish. We used maximum likelihood to estimate parameters and binomial error structure (proportion of seeds germinated in a pot) with a logit link. We compared a single model with treatment group to an intercept-only null model using likelihood ratios. All analyses were performed in R version 2.12 using the package lme4 (Bates & Sarkar, 2007) following guidelines outlined in (Bolker *et al.*, 2008; Zuur *et al.*, 2009).

RESULTS

Diet summary

We collected a total of 1,178 fecal samples from three frugivores during the study period. Sample sizes varied from site to site and from species to species based on ease of capture at different sites (Table 1). Recapture rates also varied by species, with 0% recapture for Bulbuls, 5.8% for Silvereyes and 20.1% for Fruit Doves. Most samples from Bulbuls were collected from under perches (n=427), whereas samples from Silvereyes and Fruit Doves were collected from captured birds, and for a small number of Fruit Doves, retrieved from birds seen defecating in the wild.

The total richness of fruit in Bulbul and Silvereye diets was similar on Moorea and Tahiti. However, the richness of native fruit species in the diets of both species was twice as high on Moorea compared to Tahiti (Figure 3). Confidence intervals for native diet comparisons did not overlap for either species indicating that the difference between native diets was statistically meaningful. Rarefaction curves for both species were approximately asymptotic with the exception of Bulbul native species richness on Moorea (Figure 3).

The total seed dispersal network for both islands and all birds was highly integrated with many links in common between birds and plants (Figure 4a). The Fruit Dove was the most frugivorous of the three species, with fruit parts and seeds found in 99% of fecal samples. Fruit was found in 94.7% of Bulbul fecal samples and only 43.3% of Silvereye samples. Other dietary items included arthropod remains, flower parts and vegetative material. All three species consumed both native and alien fruits, though in varying quantities (Figure 5). *Miconia* was the most common item in the diet of all three frugivores, and was present in 68.1% of all Bulbul samples, 38.3% of Silvereye samples and 44.6% of Fruit Dove samples (Table 2). *Miconia* also vastly outnumbered any other species in terms of the numbers of seeds, accounting for 76.8% of all seeds found in fecal samples (n=215,904).

Miconia abundance

Complete networks were smaller on the less invaded island of Moorea compared to Tahiti (Table 3, Figure 4b). However, native networks were larger on Moorea. Generality was higher on Moorea, indicating a larger mean number of links between birds and plants in less invaded sites. Diversity and interaction evenness were also higher on Moorea for both complete networks and native networks indicating a more uneven distribution of interactions on Tahiti, where a greater number of total links were concentrated among just a few species.

Species traits

The species of frugivore predicted the proportion of native fruit consumed by frugivores and was included in the best fitting model for the consumption of native fruit. Fruit Dove samples contained the greatest percent total hits of native fruit of the three

species (Fruit Dove = 62.94 ± 3.03 SE, Bulbul = 18.83 ± 1.76 SE, Silvereeye = 2.69 ± 0.58 SE, $P < 0.0001$, Figure 2, Appendix A1). Fruit Doves also consumed the largest total number of plant species ($n=29$) and the highest number of native species ($n=12$), including seven species dispersed only by the Fruit Dove. Bulbuls consumed a total of 10 species while Silvereeyes consumed only six (Table 2).

Diet switching

Miconia seeds were present in greater numbers in the diets of Bulbuls and Silvereeyes on Tahiti (Bulbuls mean \pm SD = 150.26 ± 160.13 , Silvereeyes = 48.69 ± 101.89) than on Moorea (Bulbuls = 4.11 ± 29.92 , Silvereeyes = 9.02 ± 32.44 , Figure 6). Best fitting models of Silvereeye consumption of Miconia, other seeds, and insects all included the period and island of capture (Appendix A2). The best model for other seed consumption also included the density of Miconia at a site, and all included the presence of other dietary items. Silvereeyes switched their diets to consume more insects on Tahiti than on Moorea, although insect consumption varied depending on the period of capture and was highest during the months of March, April and May (Figure 6a). Miconia consumption by Silvereeyes was higher on Tahiti than on Moorea, and also showed seasonal changes with highest consumption on Tahiti between March and May and highest consumption on Moorea between June and August (Figure 6b.). Overall, the consumption of other fruit by Silvereeyes was slightly higher on Tahiti than on Moorea, but this pattern varied by season, with higher consumption on Moorea during the months of September through November (Figure 6c).

The best fitting models for Bulbul consumption of Miconia, other seeds, and native seeds included the abundance of insects and the island of capture (Appendix A3). The best model for other fruit consumption also included the period of capture and the abundance of Miconia while the best model for native seed consumption included the period of capture, the density of Miconia at the site, and the abundance of Miconia. Bulbuls switched their diets to consume more Miconia on Tahiti and more other fruit on Moorea (Figure 6d & e).

Germination

Total germination of Miconia after 100 days was moderately affected by treatment category ($P=0.056$ Likelihood Ratio, Figure 4) and slightly lower after digestion by Silvereeyes ($n=3,458$ seeds, mean germination = $89.76\% \pm 22.42$) and Fruit Doves ($n=1,551$ seeds, mean germination = $87.03\% \pm 25.49$ SD) compared to hand cleaned seeds ($n=7,079$ seeds, $94.6\% \pm 9.24$) and those digested by Bulbuls ($n=2,928$ seeds, mean germination = $93.43\% \pm 11.99$). Total germination of native fruit was only affected by digestion in *Tarennia sambucina*. *Tarennia* seeds digested by the Fruit Dove germinated slightly more than germination of hand-cleaned seeds after 100 days (Table 4). Germination speed was similar for both *Tarennia sambucina* and Miconia between ingested and un-ingested seeds (Figure 7).

DISCUSSION

This study demonstrates ways the structural properties of seed dispersal networks can be altered by invasive species, and that the abundance of an invasive species influences the extent of alterations to network properties. Networks were slightly larger on Tahiti on average than on Moorea, but this was a consequence of larger numbers of links between birds and introduced plants. These patterns are similar to those documented for pollinator networks by Aizen *et al.* (2008) where overall connectivity was similar in invaded and native webs, but links were transferred from generalist native species to super-generalist alien species, resulting in a loss of connectivity among native mutualists.

Weighted network properties revealed that at highly invaded sites, more links were concentrated between fewer pairs of species. This result parallels a study of food webs that found lower interaction evenness in more modified agricultural systems compared to coffee plantations and forests, despite few changes in unweighted network properties (Tylianakis *et al.*, 2007). In both studies, more altered systems were more heavily dominated by a single interaction, leading to a decrease in the evenness of interactions within food webs and seed dispersal networks. In our study, the total number of species consumed by birds remained constant from less invaded to highly invaded sites. However, this unweighted metric masked a drop-off in how frequently other fruits are consumed relative to the most abundant invasive plant.

Our study found that interaction patterns are driven by species traits as well as by the relative abundance of different resources in a community. Species identity strongly predicted proportion of native fruit in the diet of frugivores, with the native Fruit Dove consuming more native fruit than either alien frugivore. Shared evolutionary history resulting in the buildup of complementary traits that enable plants and animals to interact have been proposed as a mechanism to explain how species that have evolved in the same environment might interact with each other more frequently than expected by chance (Thompson 2006). Traits such as fruit color and shape can converge among species that are dispersed by similar frugivores (Jordano 2007). In our study, similar color and shape among native fruit may provide cues to Fruit Doves that help maintain links between native species in spite of alterations in relative abundance of native resources triggered by invasive species. While we did not study the effects of color on choice in Fruit Doves, we did notice the prevalence of black fruit in both the native fruiting community and in Fruit Dove dietary items. This is consistent with one study that noted a preference for black fruit in doves in the genus *Ptilonopus* in Australia (Crome, 1975), and could be responsible for the retention of native fruits as well as the integration of *Miconia*, which is also nearly black when ripe, into the diet of the Fruit Dove.

The Fruit Dove diet included seven species that were not found in the diet of either Bulbul or the Silvereye. Missing links can occur in seed dispersal networks when a potential link exists but is not observed due to inadequate sampling. The rarefaction curve of the native richness in the diet of the Bulbul on Moorea did not reach saturation, suggesting that there are probably missing links between Bultuls and native fruit on Moorea that we did not record in this study. On the other hand, among the species consumed only by the Fruit Dove, there are plants that produce fruit that are large and

tough (*Meryta lanceolata*, Araliaceae), fruit that are very dry and black when ripe (*Ixora mooreensis*, Rubiaceae, *Xylosma suaveolens*, Flacouriaceae) and fruit with relatively large seeds (*Macaranga attenuata*, Euphorbiaceae). These fruits may not be particularly attractive to alien frugivores and may be examples of forbidden links that cannot occur due to limitations in gape width, fruit processing ability, and innate preferences (Olesen *et al.*, 2011). Likewise, there is growing evidence that the structure of seed dispersal networks can be influenced by evolutionary history (Rezende 2007 *etc.*). In frugivores and fruit bearing plants, the coevolutionary processes operating on co-occurring species might generate suites of species with shared morphological traits and phenotypic complementarity, or matching of traits between interacting species (Thompson 2005, 2006). Examples for this are the convergence of similarly sized and colored fruits among plants that share dispersers and matching between bird tongue length and flower corolla length in bird-pollinated plants (Bascombe 2007, Stang 2006). While Fruit Doves may have evolved independently of the particular set of species present on Moorea and Tahiti, the genus *Ptilinopus* is widespread in South-east Asia, the Pacific and Australia (Steadman 2006). Several endemic plants in this study are also widespread in the Pacific. Thus, the opportunities for shared coevolutionary history which could generate complementarity in traits are likely to be higher between the Fruit Dove and endemic plants than between the Silvereye or the Bulbul and native plants. Thus, evolutionary history and species origins could in part explain why Fruit Doves consume more native plants than Silvereyes and Bubbles.

Birds responded to the abundance of *Miconia* at a site by increasing the proportion of *Miconia* in their diets. Bubbles ate similar numbers of species and quantities of seeds of fruiting plants on Tahiti compared to Moorea, but switched their diets between *Miconia* on Tahiti and other fruit (including greater quantities of native fruit) on Moorea. The period of capture was not an important predictor of these patterns, indicating that patterns of consumption were more influenced by the island of capture than they were by the seasonality of fruiting resources. This could be a result of the year-round availability of *Miconia* fruit or because the majority of Bulbul fecal samples were collected under perch sites where we could not determine the exact date of consumption.

Silvereyes consumed almost no native fruit, but switched their diets from larger quantities of insects on Moorea to more *Miconia* on Tahiti. Silvereyes ate more *Miconia* on Tahiti, but this pattern was not constant through time. Increases in fruit consumption and corresponding decreases in insect consumption on both islands during the rainy season are probably linked to seasonal patterns in breeding, molting and raising young and spatial and temporal patterns of resource use may reflect patterns of availability of both insects and fruit. This pattern is consistent with findings of Carnicer *et al.* (Carnicer *et al.*, 2009) who documented matching between dietary switching behaviors and the availability of both insects and fruit in the environment. While we did not measure the abundance of insects at our sites, it is likely that Silvereye diet switching is linked not only to fruit availability but also to insect availability and dietary requirements mediated by the seasonality of breeding.

Fruit consumption was lower and arthropod consumption was higher on Moorea than in other similar studies that have characterized the diet of the Silvereye in its native range in New Zealand and Australia where insects have been estimated to comprise only 3-5% of the diet of the Silvereye (Stanley & Lill, 2002). This could be because fruits are a relatively scarce resource in French Polynesia and especially on Moorea. Likewise, insects may be more abundant in native forests than in forests of *Miconia* because *Miconia* in its novel environment may lack many of the arthropod parasites and herbivores present in its native range.

The effects of ingestion on germination did not show a consistent pattern. Ingestion by Silvereyes and Fruit Doves depressed the germination of *Miconia* while ingestion by Bulbuls had no effect. Germination was also variable among plants, and Fruit Dove ingestion depressed germination of *Miconia* seed, but increased germination of *Tarenna sambucina* and had no effect on germination of *Wikstromia foetida* and *Cyclophyllum barbatum*. These results are consistent with the findings of other studies which have also found the effects of ingestion to vary greatly depending on the frugivore and the species of plant (Robertson 2006). The effects of ingestion appear to be quite inconsistent across species and across studies, with some species showing no effect while in others both positive and negative effects have been found (Traveset 1998, Traveset and Verdu 2002, Robertson 2006, Kelly 2010). For example, in one comprehensive study of germination of bird ingested, hand cleaned, and intact fruit for species in the flora of New Zealand, seven species had higher germination in ingested seeds than hand cleaned seeds, one species had equal germination, and 10 had lower germination in ingested seeds. The magnitude of the effect appears to depend on factors related to both the bird and the plant. In birds, the gut retention time, length of digestive tract and the presence of the gizzard can influence the magnitude of scarification effect (Traveset 2006). In the plant, factors such as seed size, endocarp thickness, hardness and texture all appear to make a difference in how much scarification will occur during ingestion by frugivores (Traveset 2006). Seed coat and seed size are both likely to influence scarification in this study. The smallest seeds (*Miconia* and *Tarenna sambucina*) were both influenced by scarification (positive in *Tarenna sambucina*, negative in *Miconia*), while the larger harder seeds in *Cyclophyllum barbatum* and *Wikstroemia foetida* showed no effect. However, we were limited by sample sizes with the latter two species, which occurred relatively rarely in fecal samples, thus limiting the number of seeds we could use in germination experiments.

While *Miconia* germination was negatively affected by ingestion by the Fruit Dove and the Silvereye, it is unclear to what extent this difference is biologically meaningful. In Kelly et al (2010), the authors pointed out that a 10% reduction in germination is unlikely to have large consequences for the regeneration of New Zealand Flora. In a species that produces millions of seeds every year, an 89% germination rate after ingestion is probably sufficient to ensure that dispersed seeds germinate in sufficient numbers. This is probably especially true for ingestion by the Fruit Dove, which can transport thousands of *Miconia* seeds in a single fecal sample.

The germination of *Tarennia sambucina* was 10% higher for ingested seeds compared to hand cleaned seeds. Whether this enhancement is biologically meaningful is likely to depend on the seed shadow context. In other words, the numbers of fruits dispersed compared to those that fall by gravity, the deposition of seeds at favorable microsites, and the strength of negative density dependent Jansen-Connell effects for seeds not dispersed away from the parent tree will all influence how important the dispersal process is for this species (Traveset 1998). Likewise, the environment may impact the extent to which small modifications in germination can influence overall recruitment, with highly unpredictable conditions can increase overall seed mortality, thus augmenting the importance of high seed germination (Traveset 1998).

This study demonstrates that the indirect effects of invasive species are variable and depend on both the abundance of the invasive species in a community and on the complementarity between frugivores and the fruit they consume. We showed that seed dispersal networks can be altered by a single fruit bearing invasive plant, and that these alterations are largest at sites where the species is most abundant. Frugivores in our system responded to the abundance of local fruiting resources by switching their diets between competing resources, and the loss of dispersal of native plants was most pronounced at the highest levels of invasion by *Miconia*.

TABLES

Table 1. Number of fecal samples by island collected using mist netting and collection under perch trees in 2008 and 2010. Totals are shown in rows highlighted in grey.

Site	Bulbul	Fruit Dove	Silvereye
<i>Moorea</i>	136	201	344
Belvedere	24	100	114
Cocotiers	68	101	114
Vaianaë	44	0	116
<i>Tahiti</i>	325	3	175
Aorai	219	0	88
Marau	30	0	43
Taravao	76	3	44

Table 2. Consumption of native and introduced seeds by three frugivores on Moorea and Tahiti. Percent represents the percent of total fecal samples containing seeds. Mean seeds is the average number of seeds per fecal sample. Native species consumed only by the Fruit Dove are highlighted in bold. Rows highlighted in grey represent the total number of species in each category.

Species	Red-vented Bulbul		Fruit Dove		Silvereye				Mean Seeds	
	Moorea	Tahiti	Moorea	Tahiti	Moorea	Tahiti	Moorea	Tahiti		
	%	Mean Seeds	%	Mean Seeds	%	Mean Seeds	%	Mean Seeds	%	
Introduced		5		7		6		3		5
<i>Miconia calvescens</i>	14.29	31.19	90.91	148.92	43.65	485.54	24.59	10.54	66.10	48.24
<i>Rubus rosifolius</i>	5.44	0.41	6.67	2.20	0	0	0.54	0.06	11.86	2.67
<i>Cecropia peltata</i>	2.72	0.09	24.55	3.85	0	0	0	0	0.56	0.01
<i>Schinus terebenthifolius</i>	0	0	1.52	0.02	0	0	0	0	1.69	0.04
<i>Cananga odorata</i>	0	0	0	0	3.05	0.03	0	0	0	0
<i>Psidium guajava</i>	0	0	0.30	0.02	0.51	0.18	0	0	0	0
<i>Passiflora suberosa</i>	0.68	0.01	0.30	0	0.51	0.06	0	0	0	0
<i>Lantana camara</i>	16.33	0.33	7.27	0.12	2.03	0.26	2.43	0.05	1.69	0.02
<i>Pseudelephantoups spicata</i>	0	0	0	0	0.51	0.01	0	0	0	0
<i>Oxalis corniculata</i>	0	0	0.30	0.02	0	0	0	0	0	0
Native		5		3		13		3		1
<i>Tarennia sambucina</i>	38.78	3.53	0	0	56.35	81.08	0	0	0	0
<i>Cyclophyllum barbatum</i>	0.68	0.01	0	0	15.23	0.36	0	0	0	0
<i>Wikstroemia foetida</i>	0	0	0	0	8.12	0.42	0	0	0	0
<i>Rhus taitensis</i>	5.44	0.08	4.55	0.07	0.51	0.04	1.35	0.01	2.82	0.13
<i>Freycinetia impavida</i>	2.04	3.72	0	0	18.27	103.75	0.27	0.05	0	0
<i>Meryta lanceolata</i>	0	0	0	0	3.05	0.42	0	0	0	0
<i>Ficus prolixa</i>	0	0	1.82	1.60	2.54	19.36	0	0	0	0
<i>Ixora moorensis</i>	0	0	0	0	3.05	0.09	0	0	0	0
<i>Xylosma suaveolens</i>	0	0	0	0	1.52	2.07	0	0	0	0
<i>Fagraea berteriana</i>	1.36	0.03	0	0	0.51	0.79	1.08	0.09	0	0
<i>Coprosma taitensis</i>	0	0	0.61	0.02	0	0	0	0	0	0

<i>Premna serratifolia</i>	0	0	0	0	1.02	0.04	0	0	0	0
<i>Melastoma malabathricum</i>	0	0	0	0	0.51	0.01	0	0	0	0
<i>Pittosporum taitense</i>	0	0	0	0	0	0	0.27	0	0	0
<i>Macaranga attenuate</i>	0	0	0	0	0.51	0.01	0	0	0	0
Unknown	2.04	0.04	1.82	0.85	9.64	20.57	1.08	0.01	1.69	0.07

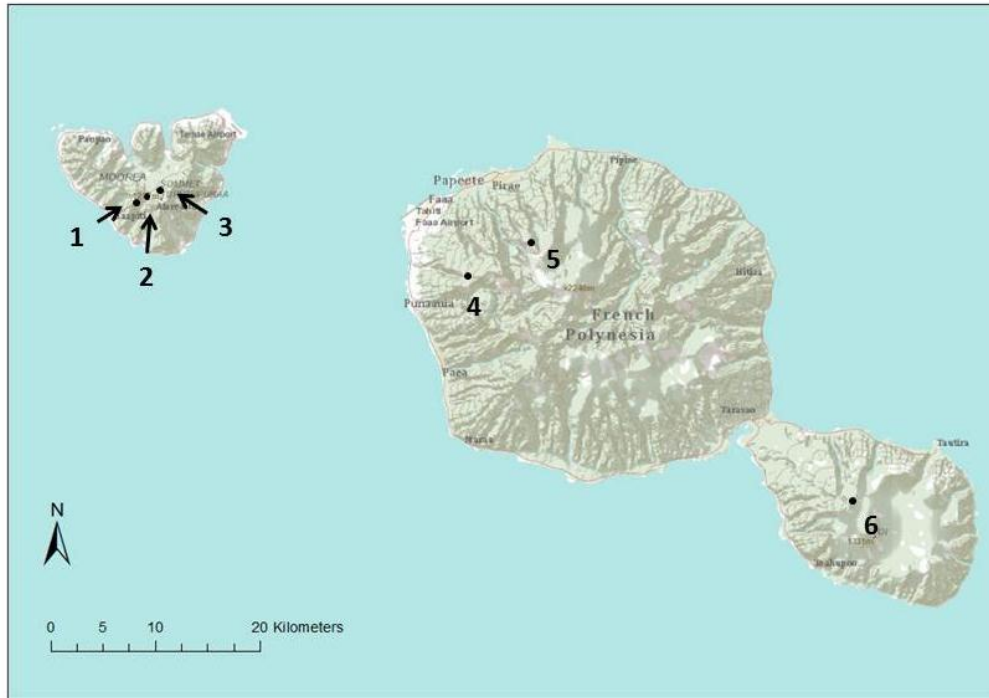
Table 3. Network properties for complete networks and networks containing only native plants on Tahiti and Moorea. Parentheses enclose 95% CI for mean. P values are results of Wilcoxon rank sum test comparing means of properties between Tahiti and Moorea.

Property	Full network			Native plant network		
	Tahiti	Moorea	P	Tahiti	Moorea	P
Size	11.91 (11.82 - 12.057)	10.91 (10.81-11.015)	<0.0001	3.215 (3.17-3.26)	5.77 (5.70-5.83)	<0.0001
Generality	1.278 (1.27-1.284)	2.17 (2.14-2.20)	<0.0001	1.25 (1.23-1.27)	1.85 (1.83-1.87)	<0.0001
Diversity	0.79 (0.78-0.80)	1.28 (1.26-1.29)	<0.0001	0.52 (0.50-0.54)	0.67 (0.66-0.69)	<0.0001
Evenness	0.32 (0.318-0.324)	0.54 (0.53-0.543)	<0.0001	0.47 (0.455-0.49)	0.38 (0.37-0.39)	<0.0001

Table 4. Germination of three native plants after hand cleaning or passage by Fruit Doves (*Tarena* and *Wikstroemia*) or Bulbuls and Fruit Doves (*Cyclophyllum*). P value is for difference in germination percentage between passed and unpassed treatments.

	Passed			Hand-cleaned			P value
	Seeds	Total germinated	% germination	Seeds	Total germinated	% germination	
<i>Tarena sambucina</i>	1,071	898	83.85	1,069	789	73.81	0.052
<i>Cyclophyllum barbatum</i>	95	8	8.42	186	13	6.99	0.62
<i>Wikstroemia foetida</i>	82	10	12.19	82	7	8.5	0.52

FIGURES



#	Site	Latitude	Longitude	Elevation	Habitat	Miconia basal area (m ² /ha)
Moorea						
1	Vaianae	17°33'18.76"S	149°50'39.03"W	150	Moderately invaded	2.2
2	Cocotiers	17°32'51.30"S	149°50'27.23"W	350	Mixed native	0.7
3	Belvedere	17°32'27.50"S	149°49'44.05"W	250	Mixed native	0.4
Tahiti						
4	Marau	17°36'33.83"S	149°34'5.21"W	800	Heavily invaded	6.14
5	Aorai	17°34'2.98"S	149°31'37.99"W	600	Mixed native	15.38
6	Taravao	17°46'39.13"S	149°15'21.89"W	600	Heavily invaded	21.92

Figure 1. Locations of six field sites on Tahiti and Moorea

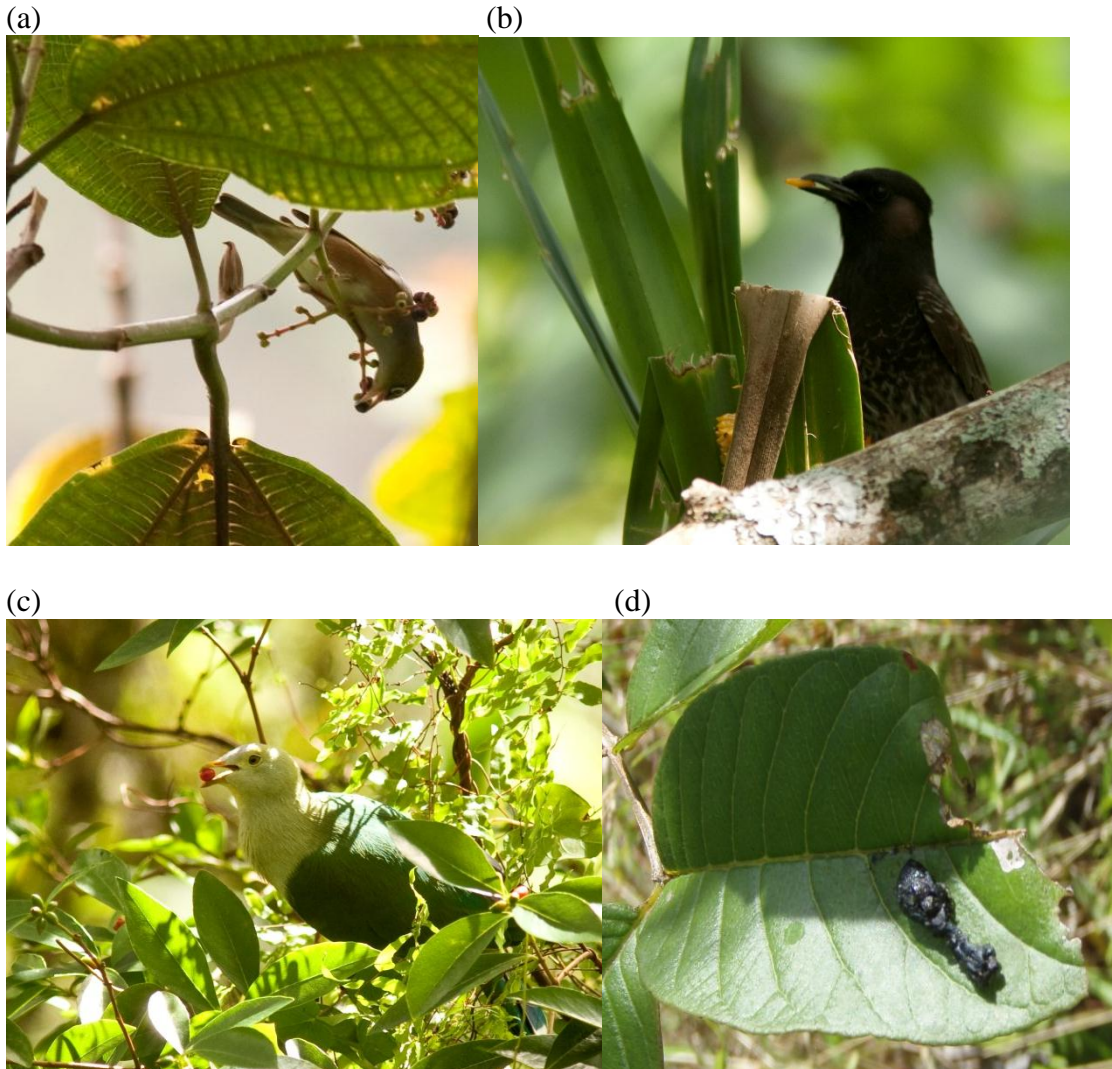


Figure 2. A Silveryeye consuming *Miconia* fruit (a), a Bulbul consuming the fruit of the native vine *Freycinetia impavida* (b), a Fruit Dove consuming fruit of the native *Wikstroemia foetida* (c), and an example of a Bulbul fecal sample collected from dense vegetation under a perch tree (d).

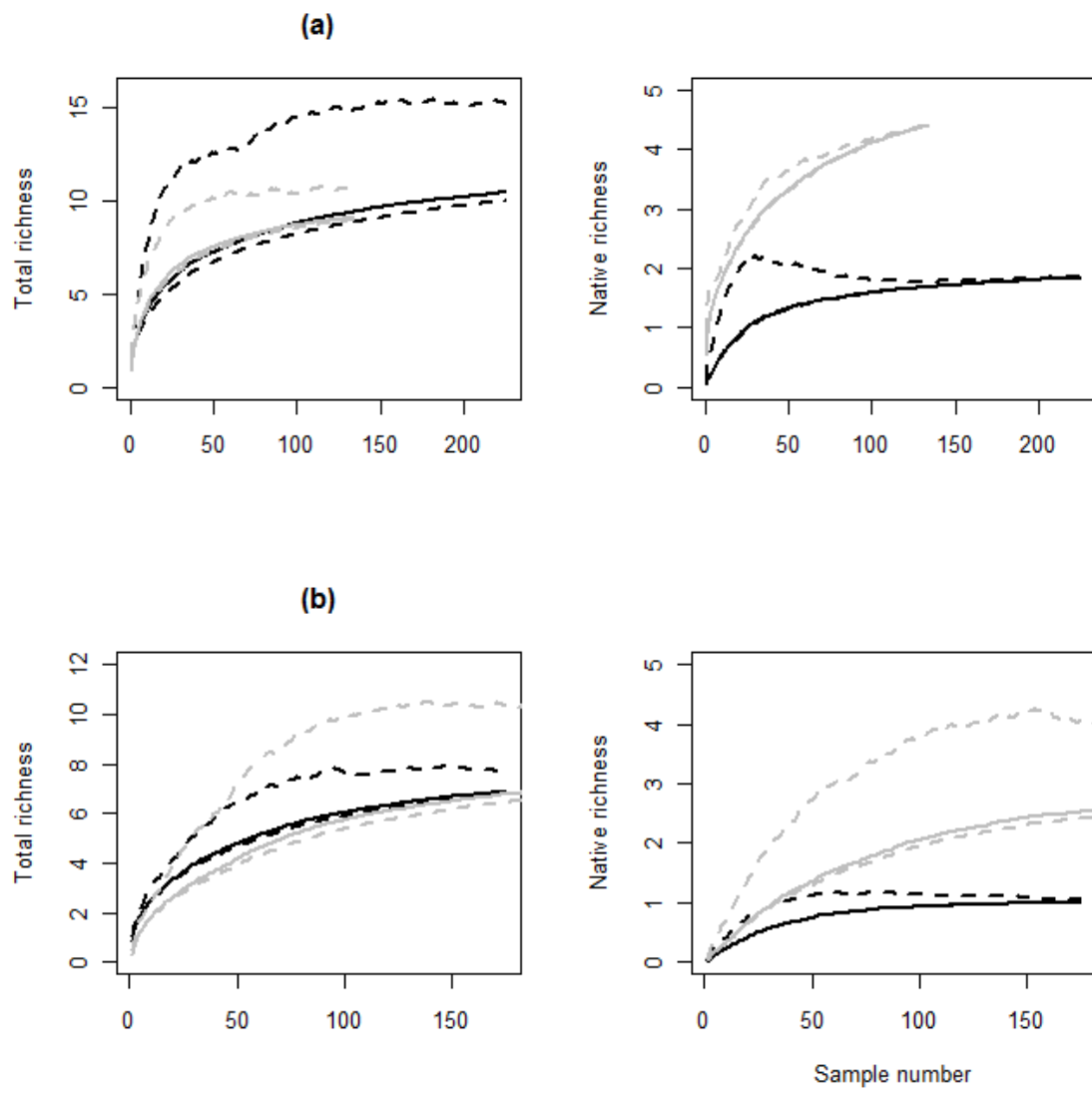
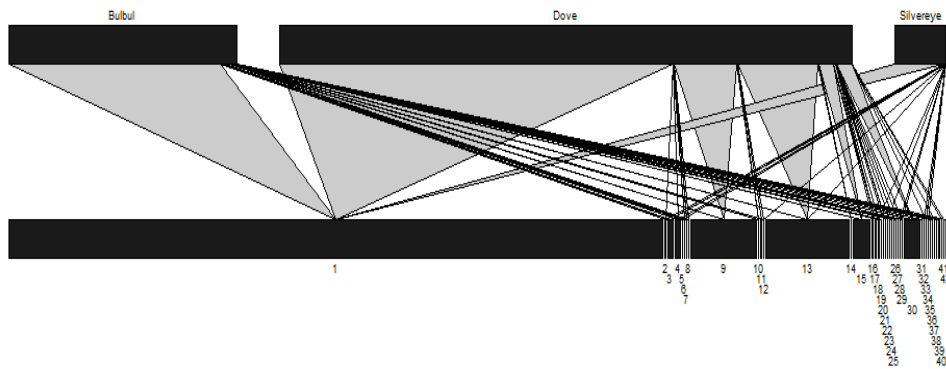


Figure 3. Species richness and richness of native species of diet of (a) Bulbuls and (b) Silvereyes on Tahiti (black) and Moorea (grey). Dashed lines represent 95% confidence intervals.

(a)



(b)

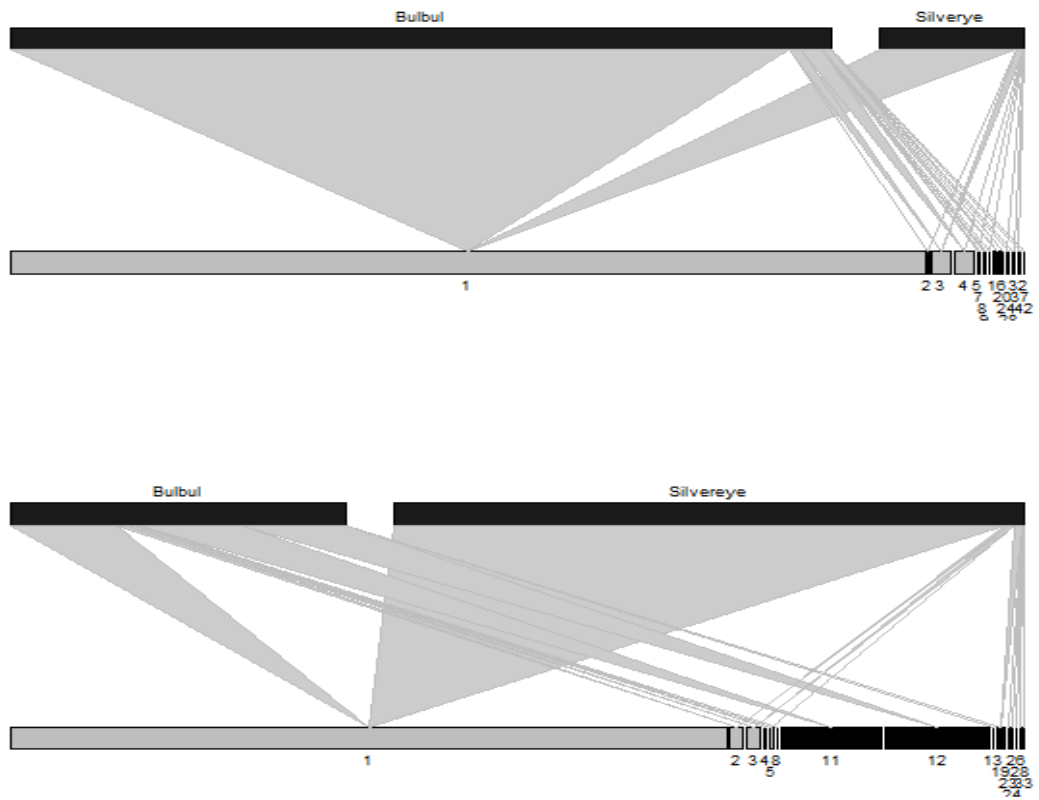


Figure 4. Entire network for all interactions between plants and birds (a) and networks on Tahiti (b, top panel) and Moorea (b, bottom panel). In panel b, introduced plant species are shown in grey and native species in black.

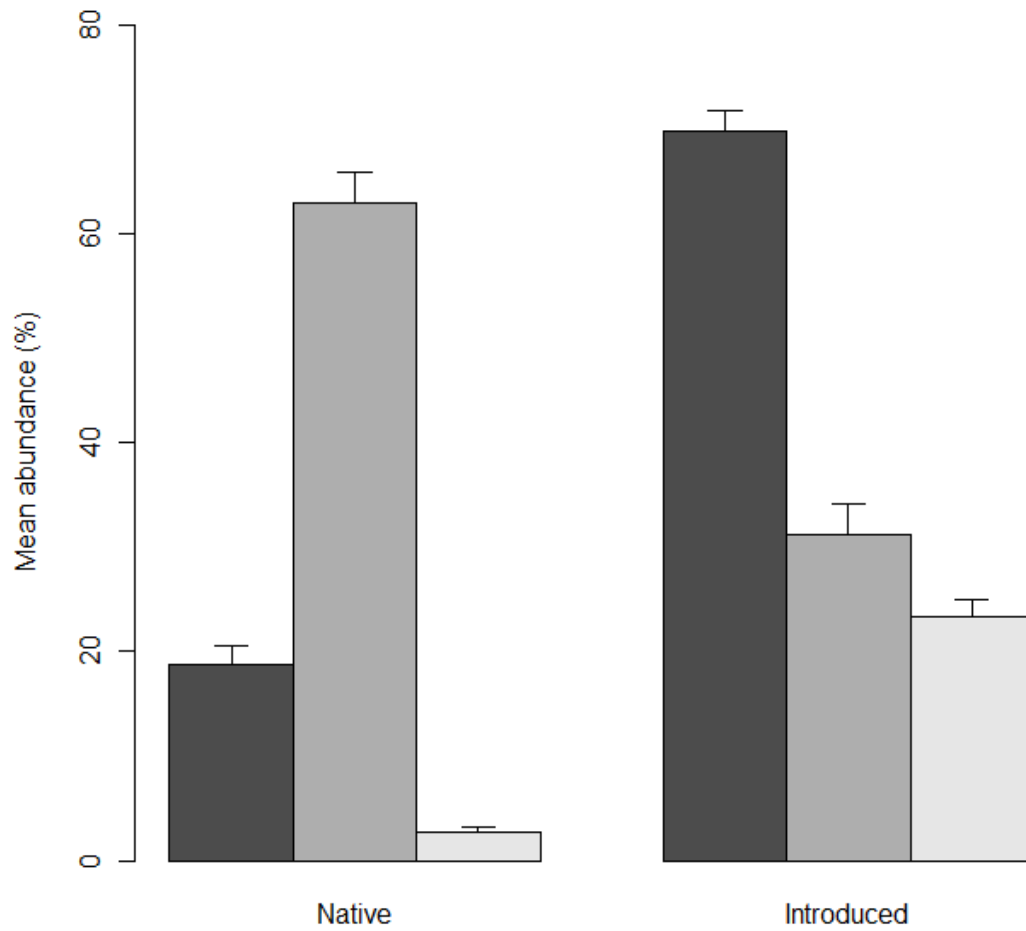


Figure 5. Average abundance (\pm SE) of native and alien fruit in fecal samples from Bulbuls (black), Fruit Doves (dark grey) and Silvereyes (light grey).

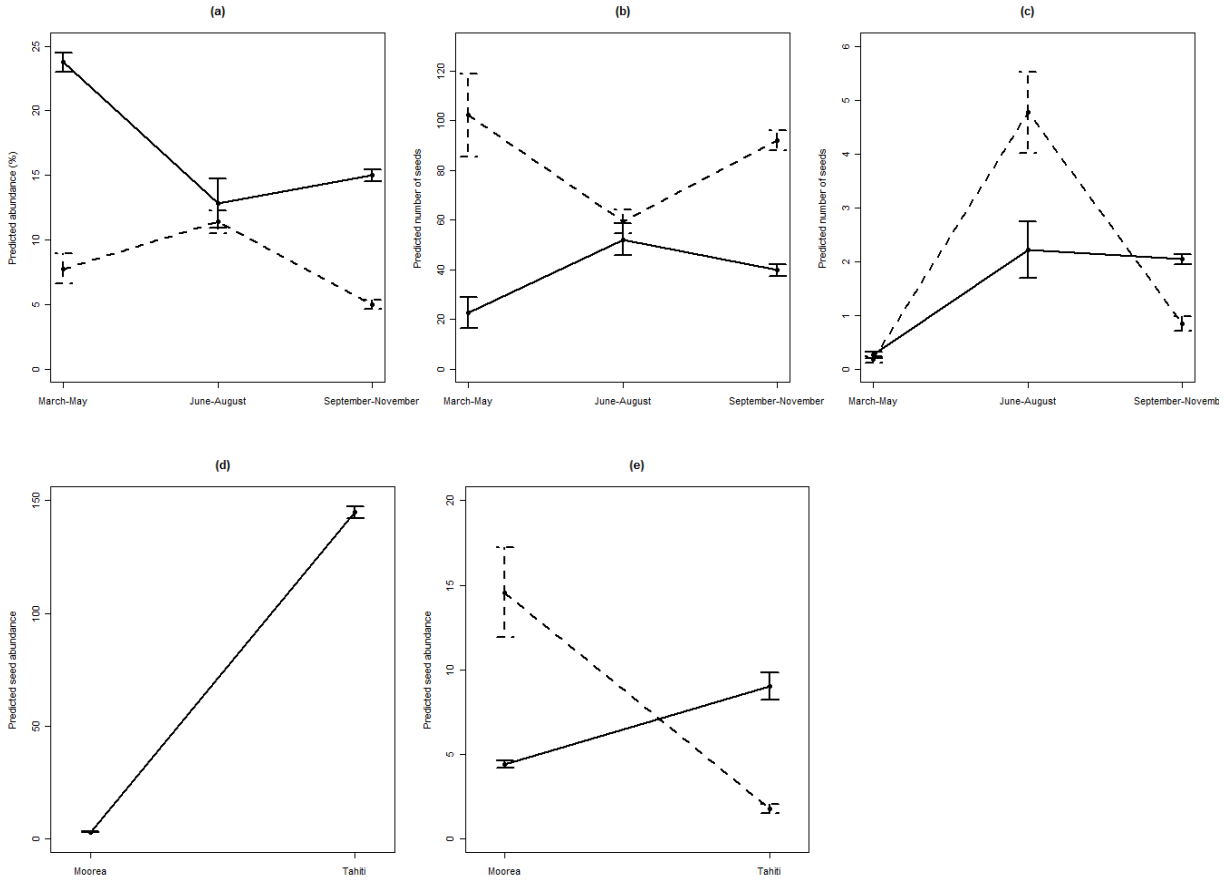


Figure 6. Predicted Silvereys consumption of (a) insects, (b) Miconia, and (c) other fruit on Tahiti (dashed lines), and Moorea (black lines), and Bulbul consumption of (d) Miconia and (e) other fruit (black line) and native fruit (dashed line).

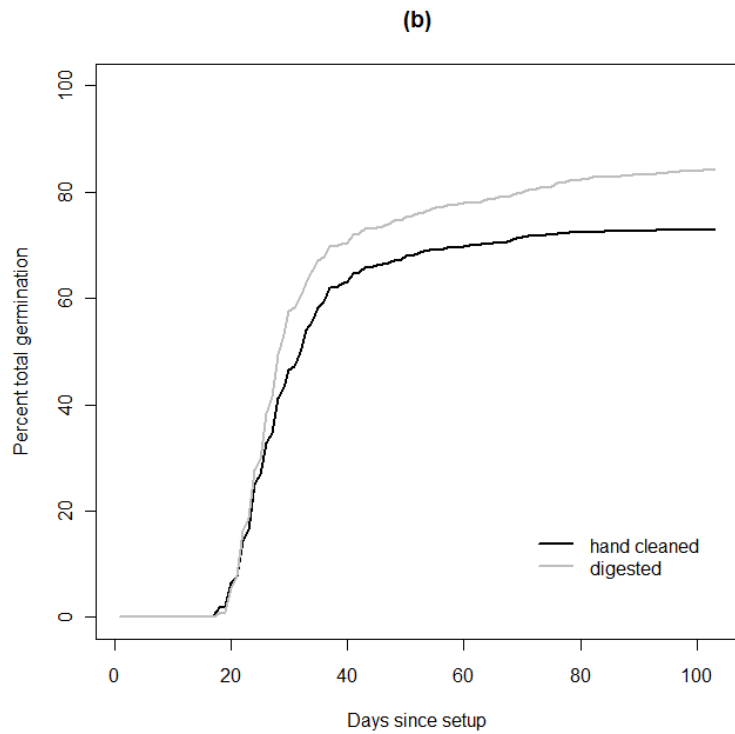
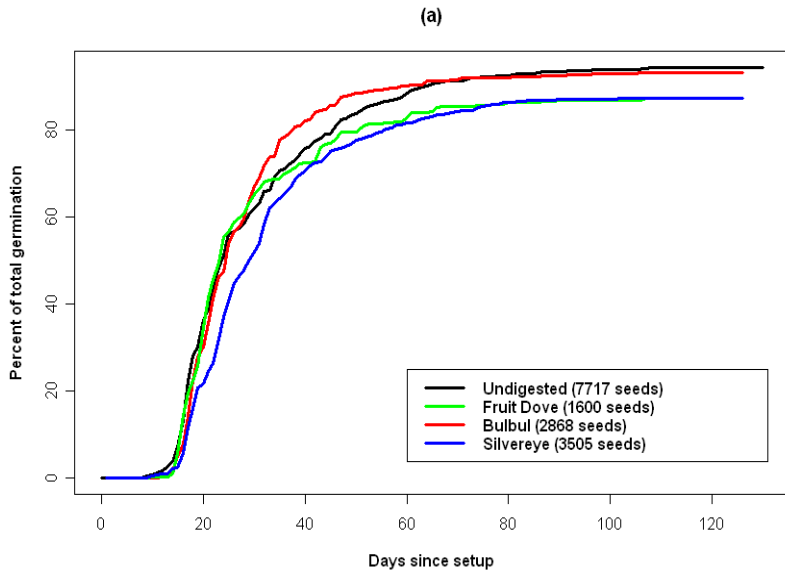


Figure 7. Germination of (a) *Miconia* after digestion by three frugivores and hand-cleaning, and germination of (b) *Tarenna sambucina* after digestion by the Fruit Dove and hand-cleaning over 100 days after planting.

Chapter 3

Chapter 3

Fruit choice in birds is influenced by abundance and fruit type but not invasion status in French Polynesia

INTRODUCTION

Fruit choice by vertebrate dispersers sets the template for which fruits will be dispersed away from parent trees in a community (Schupp, 1993). The ability of a plant to move its seeds away from its crown can permit escape from predation near the parent plant and can increase the probability of deposition on favorable micro-sites (Janzen, 1970; Cain *et al.*, 1987; Wenny & Levey, 1998). Foraging decisions by birds are known to be complex and highly dependent on spatial and temporal context (Levey, 1988; Jordano, 1994; Herrera, 1998). Species invasions can alter patterns of relative availability and quality of fruiting resources. Resulting changes in how birds forage and what they choose to eat may influence the regeneration of native plants if it leads to less reliable dispersal of seeds by birds (Traveset & Riera, 2005). For example, a smaller proportion of an individual's seed crop may be dispersed away from the tree crown, (Wright, 2003) and crops of seedlings can become more highly concentrated around parent trees where they are at higher risk to predation (Traveset & Riera, 2005; Forget & Jansen, 2007; Hansen *et al.*, 2008).

According to optimal foraging theory, birds are expected to adjust their foraging strategies to the abundance and quality of available fruit (Stephens and Krebs 1986), and birds respond to available fruiting resources in the environment at multiple spatial scales (Garcia & Ortiz-Pulido, 2004). At the landscape scale, frugivores can track fruiting resources across different habitats (Levey, 1988; Borgmann *et al.*, 2004; Garcia & Ortiz-Pulido, 2004; Telleria *et al.*, 2008) while within a habitat, birds use crop size to select between fruiting trees (Carlo *et al.*, 2003; Carlo *et al.*, 2004; Saracco *et al.*, 2005; Ortiz-Pulido *et al.*, 2007; Blendinger *et al.*, 2008; Deckers *et al.*, 2008; Hampe, 2008; Blendinger & Villegas, 2011). The quality of a fruiting resource also determines fruit choice, and birds show preferences for some fruits over others in both laboratory and field experiments (Denslow & Moermond, 1982; Moermond & Denslow, 1983; Levey *et al.*, 1984; McPherson, 1988; Carlo *et al.*, 2003). Fruit traits such as color (McPherson, 1988; Gervais *et al.*, 1999; Giles & Lill, 1999), lipid content (Puckey *et al.*, 1996; Herrera, 1998), sugar content (Giles & Lill, 1999), carotenoids (Senar *et al.*, 2010), fruit ripeness (Moermond & Denslow, 1983; Schaefer & Schaefer, 2006), and fruit size (Moermond & Denslow, 1983; McPherson, 1988; Sallabanks, 1993) can all influence foraging decisions. Additionally, frugivore digestive anatomy is highly variable and species specific in birds and can limit which fruits birds are able to consume (Levey & Rio, 2001). Here, I have separated my use of the terms 'choice' and 'preference' in order to clarify these related but not necessarily synonymous ideas. The outcome of fruit choice, or the decision to consume a fruit, may be influenced by a number of factors unrelated to an individual fruit such as the relative abundance and accessibility of fruits in the community. All other factors being equal, birds also have preferences which are defined here as the optimal food-type for a bird. Because the diet of a bird in the wild is the

outcome of choices influenced by both preference and other factors, community-wide consumption patterns may or may not match the relative abundance of fruits (Levey *et al.*, 1984; Herrera, 1998; Carlo *et al.*, 2003; Walker, 2007).

The abundance and quality of fruit can be important at a small scale where birds use crop size to select between fruiting trees (Carlo *et al.*, 2003; Carlo *et al.*, 2004; Saracco *et al.*, 2005; Ortiz-Pulido *et al.*, 2007; Blendinger *et al.*, 2008; Deckers *et al.*, 2008; Hampe, 2008; Blendinger & Villegas, 2011), between infructescences on the same plant which can vary in ease of access (Moermond & Denslow, 1983; Stanley & Lill, 2001), or the size of fruit clusters (Amsberry & Steffen, 2008). When choosing whether to continue feeding in an area, birds are predicted to balance the costs associated with travelling time between patches against the benefits of maximizing energy intake (Stephens & Krebs, 1986). Within-tree or between-tree differences in the relative abundance or quality of fruit clusters may be particularly important if it determines whether a bird decides to travel to a new location (Levey 1984). Differences between adjacent trees are likely to have the most acute consequences for foraging birds in habitats that are dominated by small trees with asynchronous fruiting phenology where frugivores cannot concentrate on a single fruiting tree with a crop large enough to satiate many individuals (Levey 1984).

Novel invasive fruit have been incorporated into the diets of both native and introduced frugivores in numerous locations across the world (reviewed in Richardson *et al.*, 2000; Gosper *et al.*, 2005; Buckley *et al.*, 2006). Invasive fruit can be attractive either because the plants are very abundant, produce larger fruit crops or have longer fruiting periods than native species (Buckley *et al.*, 2006) or because the fruit themselves have traits that make them higher in quality than native congeners (Kueffer *et al.*, 2009). An invasive fruit that is preferred by frugivores may have a number of advantages over fruit that are not preferred. In particular, novel fruit may be adopted more easily by frugivores which could increase the dispersal of seeds in the early stages of invasion when plants are rare. In some communities, plants may compete for dispersers during periods of fruit abundance (Carlo & Morales, 2008), and invasive fruit are likely to be selected more often if they are preferred. Increases in the rate of removal of fruit by birds can translate into greater efficiency and effectiveness of dispersal (Schupp, 1993), which can accelerate the rate of spread of an invasion if dispersal distances are increased (Clark *et al.*, 2001c). Avian preferences for invasive plants could also be costly for native species because birds may abandon the dispersal of native plants more easily than if invasive plants were not preferred. On the other hand, the strength of preferences may be overridden by differences in fruit abundance, and birds may choose invasive plants if their fruit crops are large relative to neighboring native plants regardless of whether they are preferred. Because patterns of relative preference and abundance are context-dependent, the consequences of a single species invasion depend to a large extent on local conditions. Therefore, assessing the strength of frugivore preferences as well as the strength of their response to small-scale variations in abundance provides a key to predicting how frugivores will respond to changes in community-wide fruiting patterns caused by non-native plants.

On remote oceanic islands, the invasion of introduced species is an important driver of population declines and species extinctions (Vitousek *et al.*, 1997; Reaser *et al.*, 2007). In French Polynesia, multiple fruit bearing plants and frugivorous birds have been introduced within the past 200 years following the arrival of Europeans and current ecosystems are highly modified by the presence of numerous alien species (Monnet *et al.*, 1993; Fourdrigniez & Meyer, 2008). At the same time avian extinction (especially of native pigeons) following the arrival of Polynesians in the past 1000 years has left the islands with only a subset of original avifauna (Steadman, 2006). The existing community of frugivores is extremely small, consisting of one surviving endemic pigeon and three recent passerine introductions. In 1937, the introduction of the fruit bearing tree *Miconia calvescens* D.C. (Melastomataceae, *Miconia* hereafter) resulted in the catastrophic invasion of 60-70% of the land surface on the island of Tahiti and 25% on the nearby island of Moorea (Meyer & Florence, 1996; Meyer, 2010). The fruit of *Miconia* is consumed by all three frugivores, and in Chapter 2 of this volume, I found that the consumption of *Miconia* increases at sites where *Miconia* is most abundant. In this chapter, I use choice tests conducted in aviaries to determine whether a common introduced frugivore in French Polynesia prefers *Miconia* relative to three other introduced and native fruit. Specifically, I tested whether 1) birds prefer fruit of the invasive tree, *Miconia* to other fruit of similar size, color and shape when controlling for other factors that influence fruit choice, 2) whether birds respond to variations in the abundance of fruit and 3) whether patterns of preference can be altered by presenting preferred fruit at low abundance. Additionally, I combine aviary experiments with vegetation and dietary data from the field to determine whether birds consume *Miconia* in quantities predicted by its relative abundance on the island of Moorea.

METHODS

Study site

This study was conducted on the island of Moorea in the Society Archipelago of French Polynesia (17°38'S 149°30'W and 17°32'S 149°50'W). Moorea is an eroded extinct volcano covering 142 km² with reaching 1,207m at its highest peak. The climate is wet tropical with mean annual temperatures ranging from 25.8-27 degrees C and rainfall from 1,690-3,500 mm/year at sea level. The flora of French Polynesia is rich in endemic plant species (551 endemic species of 885 native vascular plant species in French Polynesia, Meyer pers. comm.) including one of the highest proportions of endangered plants in the Pacific, with a total of 47 endemic species threatened according to the IUCN Red List, 167 species legally declared protected in French Polynesia, and six already extinct (Meyer & Salvat, 2009). An estimated 30% of native species, 20% of introduced naturalized plants (591 species), and as many as 40-50% of naturalized plants considered invasive contain fleshy fruit adapted for dispersal by vertebrates (Fourdrigniez & Meyer, 2008).

Fruit choice trials

Aviaries

I captured wild Bulbuls on the property of the Richard B. Gump South Pacific field station using a walk-in trap baited with fresh fruit. Birds were held in three aviaries 3x3x2m each located outdoors at the research station. Each aviary held two individuals, and birds were allowed to interact with each other normally for three days to one week before trials began. Aviaries contained perching structures, water and food bowls, potted plants, and partial shade structures on roofs to provide protection from sun and rain. All birds were given a mixture of fresh fruit and whey protein powder as well as fresh water each morning and food was checked periodically during the day. When possible, I also provided maggots in order to augment dietary protein. All birds were weighed on the day of capture and subsequently at least once per week to verify that weight loss was minimal (Levey pers. comm.).

Experimental setup

On the evening before each trial, food was removed from aviaries after dark and birds were not fed again until trials were completed the following morning. Aviaries were equipped with a divider in the middle so that birds could be separated from each other at 5:30 am before trials began. Each aviary contained an experimental perch made of round wooden dowels 45 cm long supported by a pole at a height of 130 cm. Perches held one fruiting structure on either end (Figure 2) constructed with chicken wire and six sharpened plastic cable ties, each of which held a single fruit. A window on the outside of each aviary allowed fruit to be placed on fruiting structures at the beginning of trials without necessitating entry. Trials began when observers raised a plastic box concealing the fruit via a string running from the aviary to a hide ~2-3m away where observers remained seated for the duration of the trial. When experiments began, birds usually flew immediately to land on the experimental perch where they would make a choice between possible combinations of fruit. Trials were ended either when all fruit had been consumed or when 15 minutes had elapsed. To minimize stress to birds, a maximum of four trials was conducted with each bird every morning between 6:00 am and 9:30 am. At 9:30, birds were fed regularly and the divider was opened to allow individuals to interact with each other. Complete sets of 22 trials were conducted with 11 individual birds between August 4th and August 15th, 2010. Data were recorded by hand using a datasheet with a map that allowed observers to easily record the time, position and order of consumption of every fruit as well as the handling of each fruit (consumed, pecked or dropped).

I used four species of fruit in choice trials including two alien species; *Miconia* (*Miconia calvescens*, Melastomataceae) and *Lantana* (*Lantana camara*, Verbenaceae) and two native species; *Rhus* (*Rhus taitensis*, Anacardiaceae) and *Tarenna* (*Tarenna sambucina*, Rubiaceae). All four species are consumed by Bulbuls (Chapter 2), are readily available in the wild during the dry season in French Polynesia, and can be easily collected. Additionally, fruit are all blue to purple-black when ripe and similar in size and shape (Figure 1) which allowed me to control for these important variables (Puckey *et al.*, 1996; Sobral *et al.*, 2010). *Lantana* is a small shrub native to Central and South America that favors disturbed and grassy habitats (Duggin & Gentle, 1998; Fourdrigniez & Meyer, 2008). It produces a fruit that is blue-black when ripe, 5.1 mm in diameter (± 0.94 SD

from 20 fruits) and contains only a single seed, 5 mm in length (Appendix A4). *Miconia* is a small understory tree 10-15m in height that was introduced to Tahiti from Central America in 1937 (Meyer, 1996). Fruits are purple-black when ripe, 4.95 mm in diameter (± 0.59 SD from 20 fruits), and contain many seeds (mean \pm SD= 194.7 \pm 36.7) averaging 0.7 mm in length (Meyer, 1998b). *Tarenna* is a medium-sized tree endemic to the South Pacific from the Mariana and Solomon Islands to French Polynesia (Smith, 1996). It produces a fruit that is black when ripe, 6.95 mm in diameter (± 1.24 SD from 20 fruits), and contains 20-50 seeds, each of which is 1.2-1.5 mm in length. *Rhus* is a large tree 25 m in height native from Southeast Asia eastward to French Polynesia (Smith, 1996). *Rhus* produces a fruit that is black when ripe, 4.7 mm in diameter (± 0.46 SD from 20 fruits), and contains a single seed 4.5 mm in length. In order to maintain the amount of fruit necessary to conduct experiments, I collected large branches from the wild containing many bunches of nearly ripe and fully developed fruit which were then ripened in the lab for several days by placing branches in buckets of water. I picked fruit as it ripened (usually within 24 hours) and stored it in a refrigerator for up to a week until use in trials.

I conducted three types of pairwise trials each of which compared two types of fruit setups for a total of 22 trials per individual bird. The order of trials was randomized and was different for each bird and the position of each fruit species was rotated from trial to trial so that no one species was consistently on either the right or the left fruiting structure for multiple trials in a row.

1. **Equal abundance:** To test whether birds preferred exotic over native fruit, I paired all possible combinations of species together in equal abundance with six fruit on each fruiting structure. Each fruit species was paired once with every other species for a total of six trials per bird.
2. **Single species:** To test the effect of abundance on fruit choice, I paired each species with itself at high (six fruit) and low (two fruit) abundance. Each species was tested only once with itself for a total of four single species trials per bird.
3. **Varied abundance:** To test whether preferences can be overridden by abundance, I paired each species with every other species at high (six fruit) and low abundance (two fruit). Each pair of species was tested twice to include both possible combinations of high and low abundance. Trials were conducted only once with each bird for a total of 12 trials per bird.

I used the results of the equal species trials to determine which species is preferred for each possible pair in order to predict the outcome of trials where abundance and species were varied simultaneously. Specifically, I expected that if abundance can override preference, then the high abundance fruit should be consumed earlier in all cases, no matter which species is preferred for a given species pair. Alternatively, if preferences cannot be overridden by abundance, I expected that more preferred food items should be consumed earlier in both high and low abundance trials. Earlier

consumption of low abundance items by definition will cause later consumption of high abundance food items. Therefore, I expected that less preferred fruit would be consumed later when at high abundance compared to highly preferred food items.

Analysis

I used two variables to quantify preferences. First, I calculated the percent of total fruit consumed in each trial. Second, I used the order of consumption of fruit to determine which fruits were consumed first for each type of trial and species pair. Accessibility has been shown to be an important factor influencing fruit choice in birds (Moermond & Denslow, 1983; Stanley & Lill, 2001), and in these trials, fruit were not equally accessible due to the shape of fruiting structures. Using the shape of the fruiting structures, I generated an expected order of consumption for each fruiting position in which more accessible fruit pointing inward toward the middle of the perch were predicted to be consumed earlier than less accessible fruit pointing outward (Figure 2). I validated expected ranks of consumption by calculating the mean rank for each position across all trials. This method verified that when all other factors were equal, the order of consumption followed predictions.

I then calculated deviations from expectations by subtracting the expected rank from the observed rank for each fruit in each trial (hereafter I will use 'rank' to signify the position of a given fruit in the order of consumption for a trial). Rank shifts for each fruit represented the difference between expected and observed values, and were either zero, negative or positive. Zero represented no shift from expected rank of consumption, indicating that fruit were consumed on basis of accessibility with no preference for one species or abundance over the other. Negative numbers indicated later consumption than expected by accessibility and suggested a less preferred food item. Positive numbers indicated earlier consumption than expected by accessibility, and suggested a preference for a fruit. Rank shifts were normalized by the ratio of fruit consumed to fruit presented for each species in each trial. Normalization was necessary because not all fruit were consumed in each trial, which biased rank shifts towards earlier consumption in trials where all fruit were not consumed. Rank shifts were only comparable for fruiting structures with the same numbers of fruits; therefore equal abundance trials (12 fruit total) were analyzed separately from trials with abundance differences (eight fruit total).

To determine whether the proportion of total fruit consumed depended on the species, I analyzed the equal abundance trials using generalized linear mixed modeling with a binomial error distribution and maximum likelihood estimation. Fixed effects included the species of fruit, the side of the perch (right or left) and time of day (calculated as the number of minutes since sunrise). The individual bird was included as a random effect in order to account for the fact that repeated trials on the same individual are not independent (Larrinaga, 2010). To determine whether rank shifts in consumption order were influenced by the abundance of fruit in the experiment as well as the species pair in the trial, I used linear mixed modeling with maximum likelihood estimation. Fixed factors included the time of day, the side of the perch, the species of fruit consumed, and whether the fruit was at high or low abundance (single species trials only). The individual

bird was included as a random effect in all cases. I tested each species pair separately in the equal and varied abundance trials to determine whether the two species showed different patterns of rank shifts from each other. Additionally, in the analysis of the varied abundance trials, I separated high abundance from low abundance fruit and analyzed each species pair separately (depicted in diagram in Figure 2). When analyzing the single species trials, I included the factors species, side, and whether the fruit was at high or low abundance. For each possible test, I selected between models without species or abundance and models with these factors using a Likelihood Ratio Test (LRT). I chose LRT because while null hypothesis testing has received criticism (see Burnham & Anderson, 2002; Johnson & Omland, 2004 among others), it can be appropriate when a restricted set of experimentally controlled hypotheses are being tested (Stephens *et al.*, 2005). All analyses were conducted in R 2.12.2. Linear mixed modeling was conducted using the nlme package (R Development Core Team, 2010; Pinheiro *et al.*, 2011) whereas generalized linear mixed modeling was conducted using the package lme4 (Bates & Sarkar, 2007). I checked data for violations of assumptions of normality using quantile plots and graphical inspection of residuals plotted against fitted values and explanatory variables following guidelines provided by Zuur *et al.* (2009).

Frugivore diets in the field

I quantified the diet of two frugivores at three sites on Moorea between October, 2007 and November 2008 and again from June to August of 2010. Dietary contents were analyzed for the native Grey-green Fruit Dove (*Ptilinopus purpuratus* (Gmelin 1789, Columbiformes, Columbidae – Fruit Dove hereafter) and the introduced Red-vented Bulbul (*Pycnonotus cafer* L. 1766, Passeriformes, Pycnonotidae - Bulbul hereafter). The Fruit Dove is a small dove (mean mass \pm SD= 85.67 \pm 9.89g) endemic to the Society Archipelago where it is widespread from sea level up to 600 m on Moorea (Gibbs *et al.*, 2001). The Bulbul is a medium sized passerine (mean mass \pm SD= 36.65 \pm 3.49 g) native to India and Pakistan. First seen naturalized on Tahiti in the late 1970s (Bruner, 1979) where it was probably introduced as a cage bird, it spread rapidly across Tahiti and spread to Moorea and to the Leeward Islands of the Society Archipelago sometime during the 1980s where it is now common up to the highest peaks (Thibault *et al.*, 2002).

I quantified diets of birds using fecal samples collected from birds captured using mist nets 2.5m wide and 12m long (mesh size 30 and 36 mm) raised to 50 cm off the ground on poles reaching 3m in height. Mist netting was conducted within 1km of vegetation plots on 2-9 days per month from September 2007 to November 2008 (four nets) and again in 2010 from June to August (12 nets). Total net hours calculated as the number of 12m nets multiplied by the number of hours was 1759 on 64 days of mist netting. Nets were opened between 5:30-6:00 am and closed either after a half day at 11:00 am or after a full day at 5:30 pm. Nets were closed during periods of rain or high wind. All birds were fitted with an aluminum band and standard measurements taken (wing length, weight, fat deposits and reproductive status) (Pyle, 1997).

I obtained fecal samples by placing each bird in a thin breathable paper envelope inside a cloth bag until the bird had produced a sample or until 45 minutes had elapsed.

Fecal samples were refrigerated for up to three months until they could be analyzed. I counted and identified all seeds using a dissecting microscope and a reference collection. I quantified the proportion of contents by category using a point sampling method. Each sample was weighed and then spread evenly across a petri dish marked on the bottom with a grid of 50mm points separated by 2mm. To obtain point estimates of contents, I counted the number of points falling on each type of dietary item present in the sample (e.g. insects vs. fruit). Arthropod remains were identified to the highest taxonomic category possible. All samples were stored in 90% ethanol.

Fecal samples were also collected indirectly from Bulbuls by identifying perch trees at each of our study sites and collecting droppings on dense vegetation under the trees. I do not estimate a systematic bias in dietary data obtained from perch sites, however, this type of sample did not allow for estimation of recapture rates or to control for the independence of samples. Bulbuls live in family groups and are territorial, especially during the breeding season (Kumar, 2004), and it is likely that fecal samples collected under the same perch tree are not independent because they represent replicates from a small group of individuals over time. Therefore, dietary estimates for Bulbuls may be less generalizable than those of the Fruit Dove.

I calculated the abundance of nine fruiting trees using basal area estimates from ten 20x20 m vegetation plots on Moorea. Vegetation plots were located at three sites between 200 and 500 m in altitude in wet forest dominated by the native tree *Neonauclea forsteri* (Rubiaceae), the native understory fern *Angiopteris evecta* (Marattiaceae), and the African Tulip Tree (*Spathodea campanulata*, Bignoniaceae, a European introduction). The diameter at breast height (dbh) was measured at 1.3 m and basal area calculated for each individual as $\text{Basal Area} = (\text{dbh} / 2)^2 \times \pi$. Total basal area for each species is the sum of the basal area for all individuals across all plots. We selected nine species that bear fleshy fruit that are known to be consumed by frugivores (see Chapter 2, this volume) and calculated the proportion total basal area represented by each of the nine trees.

I did not measure fruit quantities directly, and thus it is possible that basal area does not reflect fruit quantity, which could occur if the two variables were not correlated with each other. However, I was most interested in the relative abundance of trees in the community because this measure is least sensitive to temporal fluctuations in fruit quantity, and dietary data did not have enough replication to compare dietary fluctuations among seasons. I calculated the preference from dietary data of each species by each frugivore using a rank preference index similar to that used in Herrera (1998). This measure compares the difference between the ranks of usage and availability, and was chosen because it is robust to the exclusion of rare food categories which occurred in this case because I restricted the dietary dataset to only the nine tree species for which I had vegetation data from forest plots.

RESULTS

Fruit choice trials

Equal abundance

When presented at equal abundance, birds showed strong and consistent preferences, but not for invasive species. The proportion of total fruit consumed depended on the species (Likelihood Ratio Test LRT $P < 0.0001$) and was close to 100% for Miconia and Lantana, over 90% for Tarenna, and between 20 and 40% for Rhus depending on the time of day (Figure 3). Miconia was consumed significantly earlier when paired with Lantana and Rhus, while Lantana was consumed earlier when paired with Rhus (Table 1, Figure 4a). Tarenna was consumed earlier when paired with Rhus, but similarly when paired with both Lantana and Miconia.

Single species

Fruit at high abundance were consumed earlier than fruit at low abundance for all four species (LRT $P < 0.0001$). The effect of abundance depended on the species, and was most pronounced for Lantana and Tarenna (Figure 5).

Varied abundance

I found no evidence that preferences could be overridden by abundance in varied abundance trials (Table 1, Figures 4b and 4c). For all species pairs, patterns of preferences identified in equal abundance trials were retained in varied abundance trials and were remarkably similar for all three types of trials. Preferred fruit were consistently consumed earlier when presented at low abundance relative to less preferred fruit at high abundance.

Frugivore diets in the field

Dietary preferences were similar for Fruit Doves and Bulbuls, and Rank Preference Indices indicated that some fruits were consumed more than expected by availability while others were avoided (Table 2). Tarenna was consumed much more often than predicted by its abundance alone by both Bulbuls and Fruit Doves, whereas several other species such as *Ixora mooreensis* was consumed little or not at all by birds despite being relatively common. *Xylosma suaveolens*, *Psidium guajava* and *Meryta lanceolata* were preferred by Fruit Doves but not by Bulbuls, and Tarenna and *Fagraea berteriana* were preferred by both.

DISCUSSION

Do birds prefer exotic fruit?

Bulbuls showed clear preferences, but they did not consistently prefer invasive fruit. Miconia was consumed earlier when paired with every species except the native Tarenna, which was also a preferred food item. Lantana, which is invasive, was less preferred than both Miconia and Tarenna. Despite suggestions by some authors that invasive species may become invasive in part because they are preferred by frugivores

(Gosper *et al.*, 2005; Buckley *et al.*, 2006), the few studies that have attempted to generalize the trait characteristics of invasive and native plants have not found a coherent pattern (Kueffer *et al.*, 2009). It may therefore not be surprising that I did not find consistent pattern of preference for invasive species in this study. In the Seychelles, the most common frugivorous bird (*Hypsipetes crassirostris*) preferred fruits of the invasive *Cinnimomum verum* which has particularly high protein and lipid content compared to those of all other species except a single endemic (Küffer, 2006). While I did not measure the nutrient contents of *Miconia* fruits, numerous authors have noted the importance of members of this genus to frugivores in other parts of the world (Levey, 1988; Loiselle & Blake, 1999; Carlo *et al.*, 2003; Blendinger *et al.*, 2008), and it is possible that lipids and protein contents make fruit in the genus *Miconia* palatable to a wide range of frugivores. In the Seychelles, native fruits were poor in lipids and higher in water content than those of invasive fruit, though high levels of variation were found among introduced flora (Kueffer *et al.*, 2009). If *Miconia* is higher in lipids than native fruit in French Polynesia, a similar pattern could explain the preference of this fruit by Bulbuls in my study.

Bulbuls showed a clear distaste for *Rhus* in fruit choice experiments. Trials were longer when *Rhus* was involved, and often birds did not consume all fruit presented. Birds also spit out *Rhus* regularly, or pecked at available fruit without consuming them. Other studies have shown pulpiness to be an important factor in dietary choice (Sallabanks, 1993), and the lack of pulp in *Rhus* fruits may explain why it was not preferred by captive birds (Spotswood pers. obs.). It is puzzling to note that *Rhus* appears as the fifth most common food item of ten species recorded in the diet of Bulbuls on Moorea, and is present in 5.4% of fecal samples (Chapter 2, this volume). The tree did not appear in vegetation plots because it is relatively rare, and its appearance in the diet of wild birds suggests that factors other than fruit preference are causing birds to choose the fruit in spite of its low quality as a food item. Levey and Moermond also found that some fruits that were consumed in the wild were consistently rejected by caged birds, and speculated that proximity to less preferred but available fruit might explain why the fruit was sometimes consumed (1984). *Rhus* is a large tree (20-30m) with a wide crown, a large crop, and fruit that remain present for several months out of the year (Spotswood pers. obs.). The size of the fruit crop size and availability of large numbers of fruit for long periods of time are two possible factors that could explain why Bulbuls consume *Rhus* in the wild.

While similar in size, *Tarenna* was the largest of the four fruits in this study, and the difference in size could be responsible for the preference for *Tarenna* by Bulbuls. Fruit size has is a factor determining fruit choice in several studies of avian preference (Moermond & Denslow, 1983; McPherson, 1988; Sallabanks, 1993; but see Gervais *et al.*, 1999; Sobral *et al.*, 2010). Additionally, flesh-to-seed ratios are probably highest in *Tarenna* and *Miconia* because seeds are small, whereas *Rhus* and *Lantana* both contain a very large seed surrounded by a minimal amount of pulp (Spotswood pers. obs.). In tropical ecosystems plants with extended fruiting seasons can be particularly important in the diets of frugivores (Gautier-Hion & Michaloud, 1989; Carlo *et al.*, 2003). In French Polynesia, *Tarenna* begins fruiting in January and does not finish until August or September (Spotswood unpublished data) and *Miconia* fruits three times a year and is

rarely devoid of fruit (Meyer, 1998b). These two species were found consistently in the diets of both Fruit Doves and Bulbuls throughout the period of this study, and the preference for these fruits in aviary experiments could be related to their importance in the diet of Bulbuls in the wild.

Do birds choose abundant fruit first?

In single species trials, high abundance fruit were consumed earlier than low abundance fruit, suggesting that birds are more likely to remove fruit from clusters that are nearly full of fruit than they are to remove fruit on clusters that contain only a few fruit. Optimal foraging theory predicts that travel time between locations incurs a cost which must be weighed against the benefit of energy gained via foraging (Stephens & Krebs, 1986). On a single fruiting bush, the cost of hopping from one fruit cluster to another may be significant, and could deter birds from selecting clusters with very few fruit. Small variations in the abundance of fruit on fruit clusters of the same bush can affect frugivore foraging in the field (Amsberry & Steffen, 2008), and other factors that could impact the amount of time spent flying such as the distance between clusters and the accessibility of clusters have also been shown to be important (Moermond & Denslow, 1983; Levey *et al.*, 1984).

The effect of abundance was significant for all four species, but was most pronounced for Lantana and Tarenna. It is unclear why the impact of abundance would vary by species, and was apparently not related to fruit preference because the two species for which the effect was smallest were Miconia and Rhus which had opposite preference rankings. The apparent abundance of a fruiting resource may also be influenced by fruit size (Sobral *et al.*, 2010), and it is possible that the abundance differences were more obvious to birds in Lantana and Tarenna because these species contain slightly larger fruit than Miconia and Rhus.

Selection for more abundant fruit clusters may also be relevant when birds make choices between trees of different species that vary in the number of fruit produced per infructescence. Preference for plants that produced larger clusters could be particularly important on the oceanic island in the Pacific, where many native fruit-bearing plants produce fruit singly or in small clusters (Spotswood pers. obs). Miconia and Tarenna were preferred by birds both in the field and in the laboratory, and both produce fruit in large clusters with many fruit. Miconia, which produces infructescences with hundreds of fruit (Meyer 1998), may have a competitive advantage over adjacent co-occurring native plants because of the larger number of fruits produced per infructescence.

Can abundance override preference?

I found no evidence that differences in abundance could override fruit preferences, suggesting that the costs incurred by consuming a less abundant food item was not as great as the cost of consuming a less preferred food item. Travelling time and energy expended were greatest when birds were required to hop from one fruiting structure to the other, and captive Bulbuls avoided doing so when possible by reaching as

many fruit as possible while standing on the experimental perch in between the two fruiting structures. More abundant fruit were probably chosen earlier in single species trials because the time spent hopping could be prolonged until after six fruit had been consumed. Given the strong pattern found in the single species trials, it is surprising that birds would choose to consume less abundant fruit earlier when presented with a choice between a preferred fruit at low abundance and a less preferred fruit at high abundance. These results do not support those found by Levey (1988), in which preferences for certain fruits could be overridden by increasing the distance between fruit, and those of Moermod and Denslow (1983), where preferences could be overridden by making fruit less accessible. Instead, this study suggests that abundance is a less important factor in determining dietary choice than either accessibility or distance. However, Levey found that while preferences could be overridden by increasing the distance between fruiting structures, switching only occurred only when fruit clusters were separated by at least three meters (1984). It is possible that abundance differences in my trials were too small to override preferences, in which case larger differences in abundance between fruiting structures may have caused birds to choose less preferred food when it was abundant. In the field, the response to abundance may be stronger when fruits of differing preference and abundance are separated by larger distances, or when differences in abundance are greater than I could present in laboratory conditions. Less preferred food items may also be more readily accepted during periods when fruit are scarce (Schaefer & Schaefer, 2006). While I was not able to get birds to accept less preferred food items when they were at high abundance, there was a slight increase in the total percent of *Rhus* consumed during trials later in the morning, possibly indicating that birds are less selective when they are hungry.

The response to abundance and preferences in this study imply that Bulbuls are capable of rational decision making based on a maximization principle (Moermond & Denslow, 1983). In particular, the shift in response to abundance when fruits presented differed in quality as a food item suggests that Bulbuls balance unlike variables and can make different choices depending on context. This is consistent with the two similar experiments mentioned above in which birds responded to both preferences and to other factors such as accessibility and distance (Moermond & Denslow, 1983; Levey *et al.*, 1984). Taken together, my results support the conclusion that fruit choices depend on small-scale decisions that balance multiple factors simultaneously.

Frugivore diets in the field

Miconia was common in the diets of frugivores, though it was not chosen more than expected based on abundance. This is not consistent the results of the fruit choice trials, in which *Miconia* was among the most preferred food items for Bulbuls. Factors other than preference including the relative abundance of fruit (which may be more important in the field than I found in choice experiments), proximity, accessibility, and phenology may be more important in the field than in laboratory conditions.

In the field, *Tarenna* was found in the diets of two frugivores in proportions not explained by its abundance in the plant community. Herrera (1998) used a similar relative

preference index and concluded that three species were significantly preferred while others were avoided, and that these preferences remained consistent across years. The native tree *Tarenna* was a preferred food item for Bulbuls in both dietary data from the field and fruit choice experiments. In French Polynesia, extinction of native frugivores since the arrival of humans (Steadman, 2006) coupled with the possible decline in population sizes of the native Fruit Dove suggested by some authors (Monnet *et al.*, 1993) makes the future dispersal of native plants uncertain. Bulbuls could act as surrogate dispersers for *Tarenna* in the event that Fruit Doves become extinct or rare (Foster & Robinson, 2007; Kawakami *et al.*, 2009), however, the Bulbul is unlikely to act as an effective disperser of other native plants. In Chapter 2 (this volume), I showed that the Fruit Dove is solely responsible for dispersal of several species of native trees which are not consumed by the Bulbul or the Silvereye. In this study, three of four species that were preferred by the Fruit Dove were native, and the shared evolutionary history between Fruit Doves and the coevolved suite of plants may be key in explaining Fruit Dove preferences for native fruit (Thompson, 2005). If this is the case, it is likely that future dispersal of native plants will depend on maintenance of healthy populations of Fruit Doves.

Implications for the dispersal of native and invasive fruit

My results support other findings that show that patterns of preference are common among frugivores, and that frugivores do not consume fruit indiscriminately (Herrera, 1998; Carlo *et al.*, 2003). Alien species that are preferred by frugivores may be consumed more easily in the early stages of invasion when they are still rare, which could facilitate naturalization and accelerate the rate of spread (Clark *et al.*, 2001c). Furthermore, on oceanic islands dominated by small trees, frugivores may frequently choose between neighboring fruiting plants in close proximity to each other. The cumulative effect of consistent choice for preferred invasive plants could result in increases in the number of invasive seeds dispersed along with a corresponding decline in the number of native fruit dispersed. If invasive fruit are not preferred, larger fruiting clusters or longer fruiting seasons may also lead to more frequent choice of invasive over native fruit.

Bulbuls preferred *Miconia* over other species in choice trials, implying that they could disperse the fruit even when it is rare. Preferences for *Miconia* by frugivores could have influenced the history of invasion of this species on Tahiti, where the fruit was incorporated into the diets of frugivores after its arrival in 1937. *Miconia* spread from its point of introduction to cover much of the island in less than 40 years (Meyer, 2010; Spotswood, 2010). While this lag phase similar to those described in others studies (Crooks & Soulé, 1999), the rate of spread estimated at 400 m per year and the appearance of remote populations distant from the original point of introduction is consistent with frugivore-mediated dispersal (Spotswood, 2010).

The response of frugivores to fruit preferences suggests that the dispersal of native trees is likely to occur more often in species that are preferred by frugivores, and the retention of dispersal services provided by birds (Wenny *et al.*, 2011) may depend on

the continued maintenance of healthy populations of Fruit Doves. I found evidence that birds can respond both to abundance and to preferences for certain food items, and that they can balance decisions about which to prioritize depending on the context. An important conservation implication of this result is that efforts aimed at conserving populations of rare plants or at controlling the spread of alien fruit-bearing plants depend on adequate knowledge of the preferences of the frugivorous community specific to a given location.

TABLES

Table 1. Consumption patterns for each species pair in trials where fruit were presented at equal, high abundance and low abundance. Significance values are derived from likelihood ratio tests between models that included and excluded species as a fixed factor. In each case, the species that ‘won’ the trial for each pair was consumed earlier than expected by accessibility.

Species Pair	Preferred food trials	Equal	High abundance	Low abundance
Lantana - Miconia	Miconia (P<0.0001)		Miconia (P=0.0015)	Miconia (P=0.069)
Lantana - Rhus	Lantana (P<0.0001)		Lantana (P<0.0001)	Lantana (P=0.0012)
Lantana -Tarenna	None (P=0.88)		-	-
Miconia -Rhus	Miconia (P<0.0001)		Miconia (P<0.0001)	Miconia (P<0.0001)
Miconia -Tarenna	None (P=0.15)		-	-
Rhus -Tarenna	Tarenna (P<0.0001)		Tarenna (P<0.0001)	Tarenna (P<0.0001)

Table 2. Basal area, proportional basal area, and selectivity ratios for dietary selection by two frugivores. Total basal area is taken from 10 vegetation plots, and is the sum of basal area across all plots. Proportional basal area is the ratio of basal area of each species to the basal area of all nine fruit bearing trees. Dietary data is calculated as the number of fecal samples containing each of nine species divided by the total number of fecal samples for that species. The Rank Preference Index (RPI) is the difference between ranks of usage (percent of total in diet) and rank of availability (percent total basal area).

Species	Total Basal Area (m ² /ha)	Proportion basal area	Bulbul(n=147)		Fruit Dove (n=197)	
			% Samples containing seeds	RPI	% Samples containing seeds	RPI
<i>Miconia calvescens</i>	23.65	63.96	14.29	0	43.65	0
<i>Ixora moorensis</i>	4.98	13.47	0.00	-4	3.05	-6
<i>Cyclophyllum barbatum</i>	2.03	5.49	0.68	-2	15.23	-3
<i>Xylosma sauveolens</i>	1.51	4.08	0.00	-3	1.52	1
<i>Fagraea berteriana</i>	1.47	3.98	1.36	1	0.51	1
<i>Tarenna sambucina</i>	1.32	3.56	38.78	4	56.35	4
<i>Pittosporum taitense</i>	0.97	2.64	0.00	-1	0.00	-3
<i>Psidium guajava</i>	0.78	2.11	0.00	-1	0.51	1
<i>Meryta lanceolata</i>	0.26	0.71	0.00	0	3.05	5

FIGURES

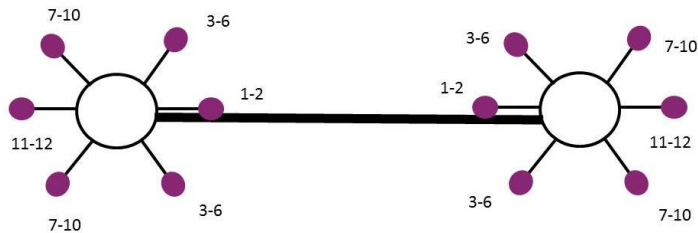
a)



b)



c)



d)

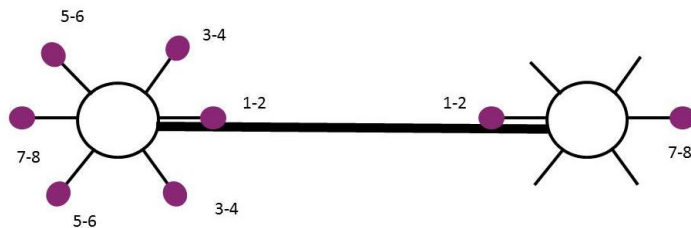


Figure 1. Fruit choice trials with Bulbuls including the four fruit used in a) showing from the left Lantana, Rhus, Miconia and Tarenna, b) fake fruiting structures and perch where Bulbuls make a choice between fruit presentations, c) expected consumption for equal abundance trials if only accessibility were a factor and d) expected consumption for varied abundance trials based only on accessibility.

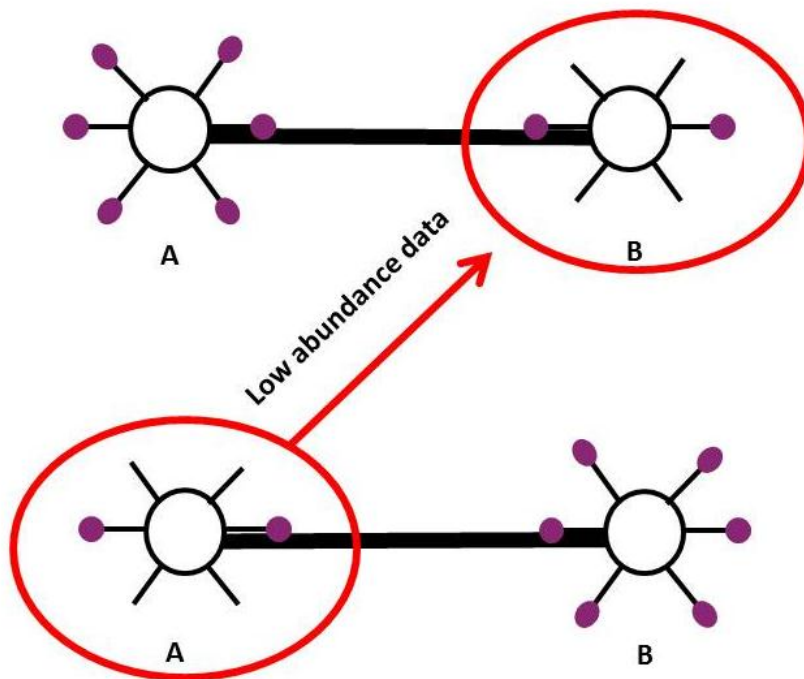


Figure 2. Diagram depicting the varied and single species trial setup. For each species pair (A and B in this case), two trials were conducted to represent both possible combinations of high and low abundance (A at high abundance vs. B at low abundance and the reverse). When data were prepared for analysis, low abundance data were separated from high abundance data and analyzed independently. Therefore, analyses of low abundance data for each species pair represent a comparison between how each species was consumed when at low abundance (For example, A at low abundance in a trial with B at high abundance) compared to the other species at low abundance (For example, B at low abundance in a trial with A at high abundance).

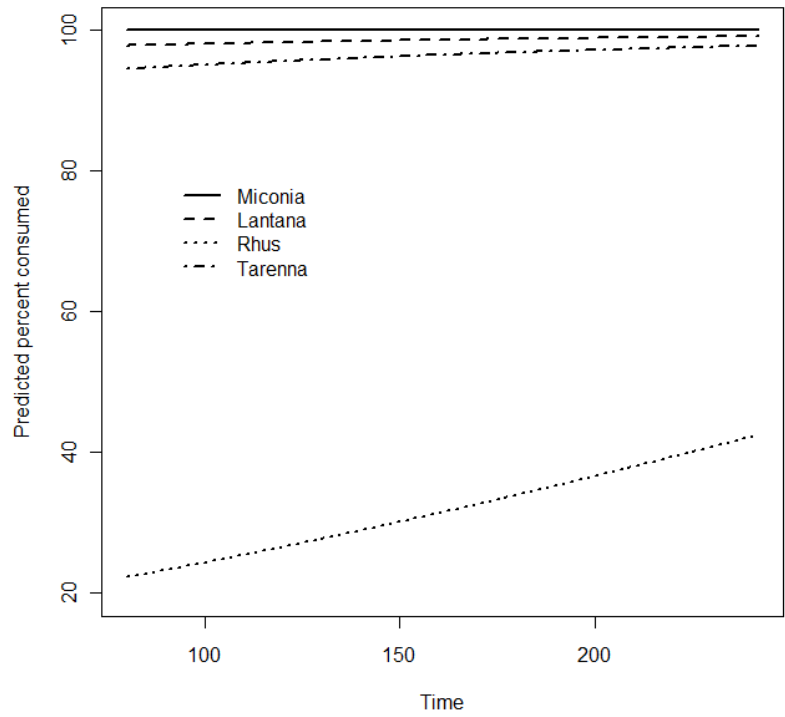
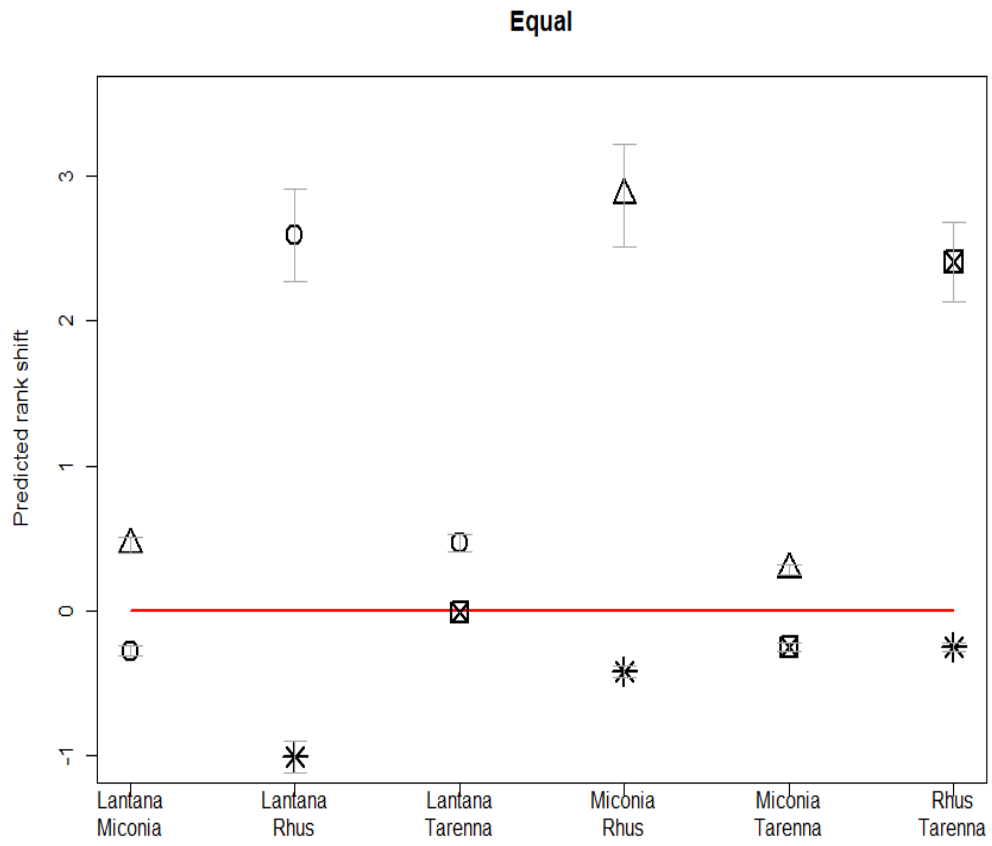
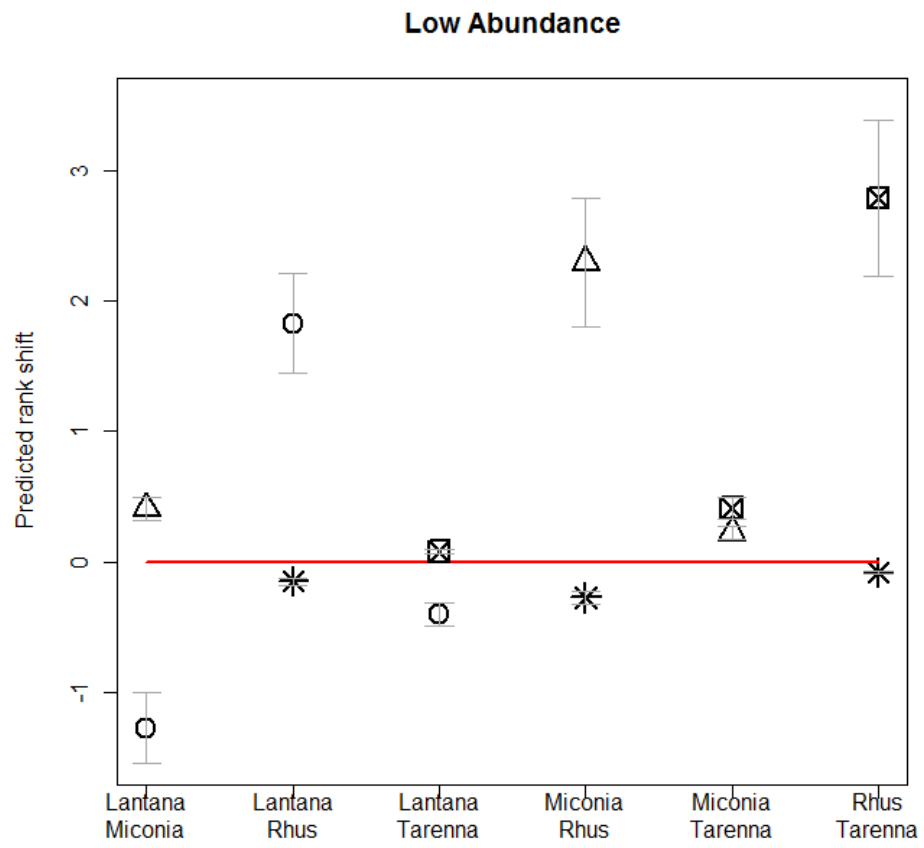


Figure 3. Predicted percent of total fruit consumed in equal abundance trials for each of four species as a function of time of day (calculated as minutes since sunrise at 5:30am). Predicted values are calculated using a generalized linear mixed model including species, side and time as fixed factors and individual bird as a random effect.

a)



b)



c)

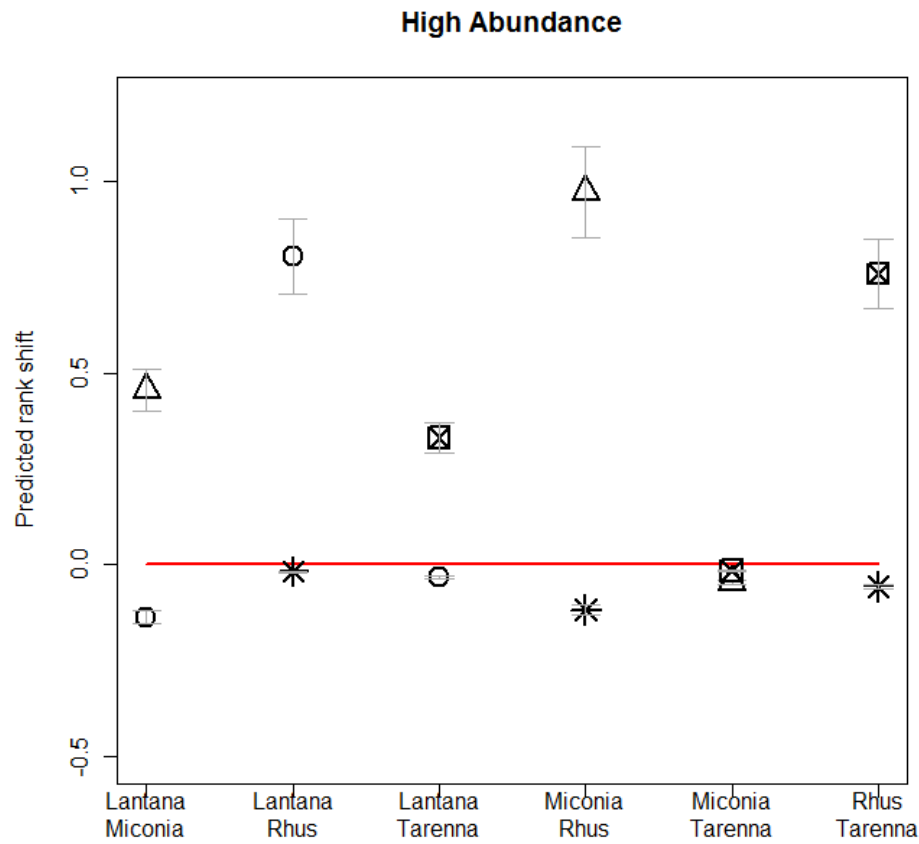


Figure 4. Predicted rank shifts for each species pair including Lantana (\circ), Miconia (Δ), Rhus ($*$) and Tarena (\boxtimes) at a) equal abundance, b) low, and c) high abundance. High and low abundance graphs include each species pair at each abundance compared to the alternative in the pair at the **same** abundance. For an explanation of how data were separated, refer to Figure 2. Error bars (in grey) represent 95% confidence intervals for predicted rank shifts. Predicted values were obtained using generalized linear mixed models of each species pair with fruit species, perch side, and time of day included as fixed effects and bird identity as a random effect. See methods for an additional explanation of modeling approach.

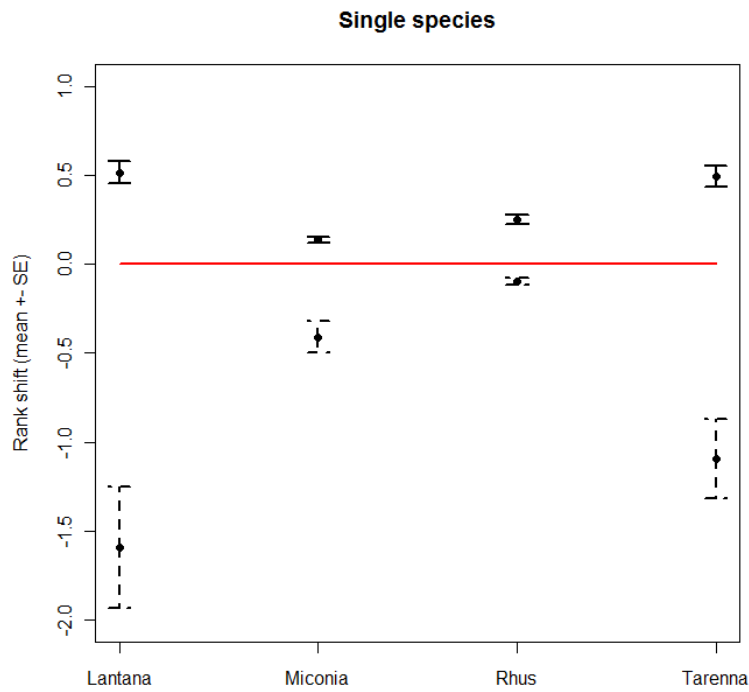


Figure 5. Predicted rank shifts in consumption for single species trials where each species was paired with itself at high (black lines) and low (dashed lines) abundance. Preferences for fruit are represented by positive rank shifts. Predicted values were obtained using linear mixed modeling with abundance, side, time of day and species as fixed effects and bird as a random effect.

Chapter 4

Chapter 4

How safe is mist netting? Evaluating the risk of injury and mortality to birds

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INTRODUCTION

Wildlife research often requires that animals be captured and handled in order to monitor populations, collect morphometric data, attach devices, or record life history characteristics. While researchers often assume that the benefits of information gained outweigh the potential risk to individual animals, the impacts are not always quantified (Wilson & McMahon, 2006). Some methods such as blood and diet sampling in birds (Carlisle & Holberton, 2006; Brown & Brown, 2009; Voss *et al.*, 2010), branding and tagging in seals (McMahon *et al.*, 2005; Baker & Johanos, 2006), and radio telemetry in mammals and birds (Kock *et al.*, 1987; Bailey *et al.*, 1996; Del Giudice *et al.*, 2005; Arnemo *et al.*, 2006; Barron *et al.*, 2010) have been scrutinized carefully to determine potential effects on survival, reproduction, and behavior; whereas other methods such as the use of mist nets to capture wild birds have rarely been evaluated (Wilson & McMahon, 2006; Jennings *et al.*, 2009). Procedures that affect the welfare of animals raise ethical considerations and can compromise research objectives by introducing bias into data collection and should be considered when interpreting results (Dugger *et al.*, 2006; Wilson & McMahon, 2006; Saraux *et al.*, 2011). Furthermore, it is not possible to determine acceptable levels of risk for a research method until a proper evaluation of capture-related injuries and mortalities has been conducted (Wilson & McMahon, 2006).

Mist netting is a commonly used technique for capturing birds to monitor demographic and population parameters. The few existing reports of incidents (hereafter, incident is used to refer either to an injury or to a mortality) associated with mist netting document rates of mortality ranging from 0.6% to 1.4% (Stamm *et al.*, 1960; Recher *et al.*, 1985; Brooks, 2000). However, these reports are all from studies with limited geographic range and sample sizes that are considerably smaller than many long-running projects in the United States and Canada. Although over a million birds are banded in the United States alone every year (Bird Banding Laboratory, 2010), to our knowledge, a systematic analysis of risks has never been conducted. The Handbook of Field Methods for Monitoring Landbirds (Ralph *et al.*, 1993) provides a guideline of a 1% mortality rate, above which mortalities should be considered excessive. However, the recommendation in Ralph *et al.* (1993) is based on expert opinion and it has been unclear whether this rate is achievable in practice. Bird observatories and research programs monitor bird populations using mist netting at hundreds of locations in the United States and Canada,

many of which maintain detailed records of each mortality and injury that occur. These data provide an opportunity to establish a baseline against which all organizations can assess their performance.

When a bird is captured in a mist net, extrinsic factors such as human error during handling, time of year (e.g., breeding, migrating, or molting birds) or time of day of capture (with increasing temperatures throughout the morning), predators, and mist net mesh material and size can all increase likelihood of incident (North American Banding Council, 2001). Mist netting projects typically capture a variety of resident and migratory species (Remsen & Good, 1996) and it is likely that some species are more at risk to incident than others. Factors intrinsic to individual birds may also influence risk, and life stages with reduced survival rates such as post-juvenile dispersal may correspond to increased vulnerability during capture if periods of low survival correspond to poor body condition and increased stress.

In this study, we predicted that species, body size, age, sex and the timing of capture (within a day and year) could influence the likelihood of an incident, and we predicted that birds released after an injury would survive in lower numbers compared to those released uninjured. First, we conducted a survey of bird observatories in order to quantify the rates of incident that are typical for a variety of organizations. Second, we quantified the most common types of injury and mortality, species with highest risk of incident, and whether body size, age, sex, mist net mesh size, number of captures, time of day, or the month of capture influenced the risk or type of incidents commonly sustained. Finally, we evaluated whether recapture rates were different for birds that were released after an injury relative to those that did not sustain injuries. We acknowledge that there are other factors such as daily fluctuations in weather and bander training and experience that could influence the rate of incident that we did not include in this study because we did not have access to these data. Despite these limitations, we have attempted to be as comprehensive as possible. Ultimately, our goal was to provide information that will allow banding organizations to assess their own performance and to improve protocols to reduce the frequency of capture-related incidents.

METHODS

Survey of organizations

To establish baseline rates of injury and mortality, we requested information from 70 bird observatories and banding organizations listed on the BIRDNET (Ornithological Council) and the United States Geological Survey Bird Banding Laboratory (Patuxent Wildlife Research Center) websites. Organizations were contacted twice by e-mail in 2009. Each organization was asked to provide numbers of captured birds in their study, the duration of their activities, and the number of birds that were injured or that died during mist netting operations.

Data collection

All analyses beyond our initial survey are based on data from five organizations that volunteered to also contribute individual records of incidents. The complete dataset contained a total of 345,752 captured birds over the reporting period. Portions of the complete dataset were used for different analyses depending on the data that each organization chose to share. Fourteen species with fewer than 10 captures and no injuries or mortalities were eliminated due to small sample sizes. The remaining dataset contains records from 188 species belonging to 31 families (for a complete species list including capture, injury and mortality data, see Appendix A8).

Contributing organizations included: the San Francisco Bay Bird Observatory (SFBBO, n = 23,995 captures from 2001-2006), the Idaho Bird Observatory (IBO, n = 73,792 captures from 1997-2008), PRBO Conservation Science (formerly Point Reyes Bird Observatory, PRBO hereafter, n = 111,921 captures from 1988-2008 from stations located in Marin County, California), the Alaska Bird Observatory (ABO, n = 69,262 captures from 1992-2008), and the USDA Forest Service Pacific Southwest Research Station, Arcata Laboratory (formerly Redwood Sciences Laboratory, PSW Arcata hereafter) which included captures from collaborators at the Humboldt Bay Bird Observatory (PSW Arcata, n = 66,782 captures from 1999-2008).

All five organizations conduct mist netting for five or six hours beginning within 45 minutes of sunrise. The frequency of operation varies by organization: ABO operates from April to October either daily or every five days, IBO daily from July to October, and PRBO, SFBBO and PSW Arcata operate year round either six days a week, three days a week, once a week or once every 10 days depending on the banding station and season. All five organizations check mist nets for birds every 30 minutes with shorter intervals during periods of heat and cold and close nets during inclement weather and rain. All organizations use protocols for training banders taken from the North American Banding Council training manual (North American Banding Council, 2001). SFBBO uses either nylon or polyester nets, while the remaining four organizations have used only nylon nets during the periods reported in this study. Mesh size also varies by organization; PSW Arcata uses only 36 mm, IBO uses 32 mm, PRBO uses both 30 and 36 mm, and ABO and SFBBO use only 30 mm.

Types of incident

We assessed the frequency of different types of incident by assigning a category and an outcome (injury or mortality) for each record. Assignments were obtained by reading the notes associated with the record which often contained information about the symptoms seen in the bird and any accidents that took place during capture or handling. In cases where two or more incidents were reported, we chose whichever was most likely to have been caused by the mist netting process. Injuries identified as unrelated to capture, such as avian pox or pre-existing deformities, were retained in the dataset but categorized as uninjured birds. Each organization had its own conventions for reporting incidents, and within-organization reporting was not always consistent during the study period due to changes in personnel or protocol revisions. Our identification of the categories of injury is therefore imperfect although we made an effort to standardize by

identifying organization-specific conventions for referring to common injuries and creating categories which could be applied easily to all organizations.

Notes that reported either bleeding from the mouth (excluding tongue injuries) or a ‘burst air sac’ were categorized as internal injuries, and tongue injuries included cases when the bird’s tongue was tangled in the net causing bleeding or obvious muscular strain. Broken bones were nearly always of the leg. Wing strain included birds which had either visibly strained or (rarely) dislocated wings, or were unable to fly upon release. Stress was classified for birds that were panting or lethargic, closed their eyes during handling, raised feathers, or were put in a box with or without heat to recover before release.

Vulnerable species

To determine which species are most vulnerable to incident, we selected the 36 most commonly captured species each of which was represented in the dataset by more than 2,000 captures. We evaluated the relative probability of incident using a Generalized Linear Mixed Model (GLMM) with the logistic (incident=1, no incident= 0) link function and a binomial error distribution fitted using Laplace approximation. We estimated parameters using Maximum Likelihood (ML) and the `glmer` function in the `lme4` package in R 2.10.1 following recommendations in Bolker et al. (2008; R Development Core Team, 2010) and Zuur et al. (2009). GLMM allows the analysis of non-normally distributed data and the inclusion of random effects terms which are useful for datasets with potential temporal and spatial autocorrelation (Crawley, 2007). In our study, sampling locations and when birds were captured could not be controlled, but the spatial and temporal variability is potentially important.

We fitted a single saturated model with species as a fixed effect and year and organization as random effects which we compared to a reduced model without species using a likelihood ratio test (LRT). We included a year by organization interaction term because we anticipated that yearly differences that could affect the probability of incident might vary geographically. While the use of null hypothesis testing in observational studies has been criticized (see Burnham & Anderson, 2002; Johnson & Omland, 2004 among others), it can be appropriate when the primary objective is to determine whether a biologically meaningful difference between groups exists and if only a single hypothesis is being tested (Stephens *et al.*, 2005). In GLMM, using LRT for fixed effects is reliable when sample sizes are large relative to the number of parameters (Bolker *et al.*, 2008). In our case, we considered 305,534 records to be adequate for our saturated model, which contained 39 parameters.

Individual predictors of risk

In order to assess whether risk factors inherent to differences between individuals are related to the probability of incident, we analyzed the data from PRBO alone. We used GLMM with covariates age, individual body mass (measured for each capture record), sex, capture number (the number of times the individual was captured), time of

day, mesh size (30 or 36mm), and month of capture as fixed effects and year, station (PRBO operates several in Marin County separated by up to 32km), species, and species by year and year by station interaction terms as random effects. Capture number and body weight were continuous covariates and mesh size, sex, month and age were categorical variables with two categories for age (hatch year and after hatch year) and mesh size (30mm and 36mm). Whenever possible, age was determined by the degree of skull pneumatization or plumage criteria using the calendar year ageing system and sex was determined by breeding condition, plumage, and rarely by morphometric data (Pyle, 1997). Of the 111,921 captures in the PRBO dataset, 69,414 individuals were captured between one and 44 times. Mist net mesh size is known to influence the size of birds that are captured most frequently (Pardieck & Waide, 1992), and could be related to what types of birds are prone to incident.

We compared models using Akaike's Information Criteria (AIC) after identifying a candidate set of 53 models identified *a priori* following guidelines outlined in Burnham and Anderson (2002). Of the set of candidate models, ten contained all fixed effects terms and varying random effects terms. The remaining 43 models included combinations of extrinsic covariates (month, time of day and mesh size) and intrinsic factors (sex, age, capture number and individual mass) that we thought most likely to be important. We began by comparing all random effects models. Using the best fitting of these models, we then fitted all fixed effects models with the best possible combination of random effects following guidelines in Zuur et al (2009). Model fit was assessed on the basis of low AIC and high AIC weight (w) (Burnham & Anderson, 2002). We calculated importance weights ($w+$) for each covariate using the 95% confidence set of models and we model averaged parameter estimates across top performing models.

Body size

To determine whether larger birds are affected by different kinds of incidents than smaller birds, we selected the eight most common categories in the complete dataset (stress, predation, wing strain, broken bones, tangling, internal bleeding, leg injuries, and cuts), and used GLMM to quantify the relationship between body size and incident type. The saturated model included fixed effect covariates mass (as a measure of body size) and random effects species, organization, year, year by organization and species by organization interaction. Because we did not have the mass for individual birds for all five organizations, we used average species masses (hereafter species mass) taken from Sibley's Guide to Birds (2003) and checked for accuracy against Duning's CRC Handbook of Avian Body Masses (2008). We compared a fully saturated model to a single reduced model without species mass using LRT for each category of incident separately.

Post-injury recaptures

To determine whether recapture rates were similar for injured and uninjured birds, we chose sixteen common species from the PRBO and IBO datasets (PRBO: Western Flycatcher, Chestnut-backed Chickadee, Ruby-crowned Kinglet, Swainson's Thrush,

Hermit Thrush, Varied Thrush, Wrentit, Wilson's Warbler, Spotted Towhee, Song Sparrow, Golden-crowned Sparrow, and Dark-eyed (Oregon) Junco. IBO: Ruby-crowned Kinglet, MacGillivray's Warbler, Spotted Towhee, Chipping Sparrow, (Gambel's) White-crowned Sparrow, Dark-eyed (Oregon Junco), Western Tanager). We chose species with both high numbers of recaptures and at least 30 records of injuries, and we included species with differing migratory habits (year-round resident, winter resident, or summer resident) because recapture rates may not be the same for resident and migratory species. Mortalities were removed from the dataset along with any captures that occurred before an injury. We calculated the number of days between the injury (for injured birds) or the initial capture (for uninjured birds) and each successive recapture at least one day from the first capture or injury to obtain the recapture history for each individual which were pooled into a mean for each species. To determine whether the rates of recapture and recapture histories over time were different for injured and uninjured birds, we used a student's paired, two-tailed t-test.

RESULTS

Survey of organizations

Of 70 organizations contacted, 22 provided numbers of captures, injuries and mortalities (Table 1). An additional 11 organizations reported that they could not provide data because they do not systematically keep track of incidents at their stations, and 10 responded that they do keep track but could not assist us in our inquiries either because of reservations about sharing data or because data were not digitized or otherwise difficult to access.

The 22 contributing organizations reported 4,782 incidents from a total of 620,997 captures. The average rates of mortality and injury were 0.23 ± 0.15 and 0.59 ± 0.68 respectively (percent \pm SD, Table 1). The overall rate of incident that combines injuries with mortalities for all 22 organizations was 0.61 ± 0.66 . Total captures for each organization varied from 717 to over 100,000 birds during study periods from two to 22 years. Seven organizations shared datasets from studies that have been operational for over 10 years, and four of these for more than 20 years. The types of birds banded were predominantly passerines, but we also included organizations which specialize in the capture of raptors, shorebirds, and hummingbirds.

Types of incident

Of the five organizations that provided individual incident records, we identified 15 categories of injury (2,247 records) and mortality (797 records, Figure 1). With the exception of stress, cuts, accidents and incidents of unknown cause (which could occur either during banding or during mist netting) and band related injuries (which occurred only during banding), all other injuries were directly related to the mist net and not to the handling and banding procedures.

Predation attempts were usually fatal, and the types of predators varied geographically. Common predators were reported by many of the 22 contributing organizations and included Sharp-shinned Hawks (*Accipiter striatus*), Cooper's Hawks (*Accipiter cooperii*), Northern Pygmy-owls (*Glaucidium gnoma*), Northern Shrikes (*Lanius excubitor*), Black-billed Magpies (*Pica hudsonia*), Eastern Cottontails (*Sylvilagus floridanus*), squirrels (*Sciurus sp.*), Eastern Chipmunks (*Tamias striatus*), White-tailed deer (*Odocoileus virginianus*), domestic cats (*Felis domesticus*), domestic dogs (*Canis familiaris*), foxes (*Vulpes sp.*), Weasels (*Mustela frenata*), Minks (*Neovision vison*), and Raccoons (*Procyon lotor*).

Vulnerable species

Species was related to incident (LRT $P < 2.2 \times 10^{-16}$, df difference = 35), and of the 36 most commonly captured species, four species had high rates of incident relative to the mean: Spotted Towhee, Allen's Hummingbird, American Robin, and Western Tanager (Appendix A6). These birds differed in the most common categories of injury. For example, Spotted Towhees and Allen's Hummingbirds were more prone to stress whereas Western Tanagers and American Robins were more prone to wing strain (Appendix A6).

Individual predictors of risk

The three top-performing models for individual predictors of risk accounted for 97.6% of Akaike weight (Table 2, Appendix A7) and contained random effects terms year, species, mist net station, species by year and year by station interactions. The probability of incident was most strongly associated with individual body mass (cumulative Akaike weight = 1, Table 3), capture number (cumulative Akaike weight = 1), and time of day (cumulative Akaike weight = 0.996). The predicted probability of incident increased slightly from 5:00 am to noon from three to 3.5 birds per 1000 (Figure 2). The predicted number of incidents more than doubled from three to seven birds per 1000 as individual body mass increased and declined from four to less than one incident per 1000 as the capture number increased. Sex, age, month of capture and mist net mesh size had little effect on the probability of an incident.

Body size

Species mass was negatively related to stress-related incidents, tangling and wing strain, while predation, internal bleeding, leg injuries, broken legs, and cuts were positively related (Figure 3). Likelihood ratios indicated significantly better fits for models including species mass for all eight categories of incident (predation $P = 3.0 \times 10^{-9}$, stress $P = 2.20 \times 10^{-16}$, wing strain $P = 0.027$, break $P = 0.0041$, tangling $P = 9.65 \times 10^{-5}$, internal bleeding $P = 0.0065$, leg injuries $P = 0.00030$, cut $P = 1.92 \times 10^{-9}$).

Post-injury recapture

The overall recapture rate for injured birds was higher than for uninjured birds when all 16 species were pooled (percent recaptured \pm SE (injured, uninjured) = 27.4 \pm 2.9, 19.2 \pm 2.6, $P = 0.0032$ student's t-test). Additionally, we found no evidence for differences in recapture histories over multiple time scales when comparing injured to uninjured birds with all species pooled (Figure 4).

DISCUSSION

For all organizations in this study, reported mortality rates were lower than the 1% target rate specified in Ralph et al. (1993). While the injury rate exceeded the mortality rate, combined rates fell below 1% for 18 of 22 organizations. These rates are lower than many studies published on the risk of capture and handling in other taxa. For example, the mortality rate of shorebirds captured with walk-in traps or mist nets and subsequently blood-sampled varied from 0-3% (Colwell *et al.*, 1988) and was reported at 9% for raptors caught in bal-chatri, noose-harness and bow-net traps (Bedrosian & St. Pierre, 2007). Several mammal studies that require leg traps (Blundell *et al.*, 1999), snares or helicopter darting (Del Giudice *et al.*, 2005) report mortality and injury rates above 1%.

Wing injuries, stress and cuts were the most common categories of incident. There was some ambiguity in how incidents were defined due to differences in classification by personnel among and within organizations. For example, many incidents of bleeding from the mouth assumed that an air sac had burst. However, necropsies of birds that hit windows have found that bleeding from the mouth is often a symptom of internal bleeding in organs and in the brain (Veltri & Klem, 2005). Though it is unlikely that a correct diagnosis can be made for every incident, we are confident that patterns reported in this study identified the most common incidents. The adoption of systematic approaches to defining and reporting injuries across organizations could greatly reduce ambiguity in the categorization of incidents and could make it much easier to interpret patterns of common incidents across organizations.

Species-level differences in risk could be related to physiological and behavioral factors which probably predispose some species to injury. However, despite clear differences in incident risk between species within the same taxonomic group, we did not find obvious patterns in behavior or anatomy that could explain why Spotted Towhees, Allen's Hummingbirds, American Robins, and Western Tanagers were more prone to incident than other birds in the 36 species dataset. Species-specific differences in anti-predator behavior may help to explain how birds respond to capture, which mimics the experience of being caught by a predator (Wilson & McMahon, 2006). Behaviors such as predator mobbing, alarm calls, and freezing are species-specific in birds (Nocera & Ratcliffe, 2009), and could correlate with typical responses in captured birds. Likewise, among larger birds, wing and leg injuries may occur more frequently in some species than in others because of anatomical differences in wing size, leg length or ratio to body size that pertain to life history or foraging strategies, and those birds that use alarm calls may be more prone to predation in the net than those that freeze in the presence of predators.

Heavier birds were more prone to incident both within and among species. In the PRBO dataset, individual body mass was positively correlated with risk of incident within species, while in the analysis of body size and type of incident, species with greater average mass sustained different types of incidents than smaller species. Larger species were more prone to predation, which may be related to greater visibility in the net, or because they make more noise when they are caught. In a study of predation on birds in mist nets in Kenya, predation was most common on the Yellow-whiskered Greenbul (*Andropadus latirostris*), which is larger and noisier than other birds in the study, and predation events tended to happen when nets had the highest numbers of birds in them (Brooks, 2000). Larger birds may also be more prone to internal injuries, breaks, cuts and leg injuries because their size increases their impact with the net.

The stress response in birds is known to vary by species (Matson *et al.*, 2006; Cockrem, 2007), but we found no evidence in the literature of a consistent trend with body mass that could explain why lighter birds were more prone to stress in our study. Smaller birds with faster metabolisms are known to thermoregulate differently than larger birds and thus respond differently to heat stress (Weathers, 1981). In a recent review of stress responses in birds, small birds such as Great Tits (*Parus major*) had lower blood concentrations and a similar magnitude of elevation of corticosterone during capture (a hormone widely used to measure stress response in birds) than the much larger Adélie Penguin, *Pygoscelis adeliae* (Cockrem, 2007). Whether or not the behaviors such as lethargy and eye closing that are used to identify stress by banders are truly correlated directly with stress cannot be determined without further research using blood samples to link corticosterone to indicator behaviors. Despite this limitation, these behaviors still indicate the possibility of a capture related mortality, and thus provide an important cue to banders when it is necessary to respond quickly to prevent a mortality. Lighter birds were also found to be more prone to tangling and wing strain, which may be related to mesh size. In this study, only 30, 32 and 36 mm mesh sizes were used, all of which target small passerines. While we did not find differences in the risk of incident across all species for these mesh sizes, lighter birds will tangle more in small mesh sizes than heavier birds which have wings that are larger than the mesh (North American Banding Council, 2001). More tangled birds may have struggled more in the net resulting in longer extraction times, which could be responsible for increased risk of stress, tangling-injuries and wing strain in smaller birds.

In the PRBO dataset, birds that were captured many times were less vulnerable to incidents. This pattern was persistent when mortalities were removed from the analysis, suggesting that the correlation was not caused by birds that had lower numbers of captures during the study period because they died sooner than those that remained uninjured. Mist net data includes birds captured many times (likely to be resident near the mist net station) and transient individuals because most passerines that hit the nets are captured regardless of territorial or social status (Sillert & Holmes, 2002). The PRBO dataset includes large numbers of birds captured only once in the study period, many of which are likely to be transient individuals (Nur *et al.*, 2004; Chase *et al.*, 2005). Outside the migration season, transients are generally considered to be poor-quality younger birds

that are less likely to possess territories (Newton, 1998) and are likely to have lower capture numbers because they are less site faithful.

There was less support for age and sex as predictors of risk with young birds and females about as likely to sustain an incident as adults and males. While several studies have found lower survival estimates for birds between four and 14 weeks of fledging and breeding females compared to adults and males (Faaborg *et al.*, 2010), in our study, these periods of reduced survival did not translate to increased risk of a mist-net related incident.

Additionally, the month of capture was not strongly associated with the risk of incident. While inclement weather is known to increase the probability of incident (North American Banding Council, 2001), temperatures at the Marin County stations at PRBO on the central coast of California are relatively mild year-round, and weather conditions can be as variable within a season as between seasons (Chase *et al.*, 2005). Thus, any variation in risk of injury related to daily extremes in temperature were likely obscured by considering only the month of capture. Additionally, birds from the same species and those captured in the same year were not independent, indicating the presence of both yearly and species level variation in the risk of incident. The time of day was an important variable in predicting the risk of incident, but there was only a slight increase in the number of predicted incidents throughout the morning, possibly due to increased wind later in the morning.

Injured birds had higher rates of recapture than uninjured birds. This could occur if birds that are injured remain in the area to recover after release more often than uninjured birds. However, among birds that were recaptured, the history of recapture over time was not different for injured and uninjured birds for any of the time periods evaluated, suggesting that birds that are released when injured continue to survive in similar numbers to those that are released uninjured. Because incident rates are consistently low, sample size limitations prevented us from conducting a statistically rigorous survival analysis of injured birds in spite of the large size of our dataset. Such an analysis would provide a more robust assessment of the post-release fate of these individuals and we encourage others to collect incident data so that these kinds of analyses can be conducted in the future.

There are other factors that may influence incident rates at mist-netting stations that we couldn't test with our dataset, including ringer experience. Experienced handlers are generally able to extract and process birds more quickly, decreasing the handling time and possibly decreasing risk of incident. While it is important for continued research and monitoring for new banders to be trained in mist netting techniques, we recommend intensive supervision from a trainer until the trainee can safely extract and process birds captured in mist nets. All banders should follow the Bander's Code of Ethics (North American Banding Council, 2001) or other similar manuals from other countries and should constantly assess their own skill and encourage and offer feedback from fellow banders.

Conclusions

While the level of mortality and injury that should be considered ‘normal’ or ‘acceptable’ has not been defined for wildlife research, it does appear that compared to other techniques, mist netting has low rates of incident when conducted with bird safety precautions in mind and adequate training. Our results indicate that rates of mortality and injury below one percent are achievable for projects utilizing mist nets to capture passerines and near-passerines. We were unable to control which organizations chose to share their data, and due to the potential for bias in our sampling method, we cannot assume that our findings are representative of all organizations. However, the data presented here include numbers that have been achieved by some of the largest and longest-running organizations in the United States and Canada, most of which have highly developed protocols and rigorous training programs to reduce the frequency of incident. We believe that these protocols probably contribute to the very low rates of incident in this study, and we recommend that similar protocols be adopted by all organizations using mist netting. We recommend banders follow guidelines provided in the Guidelines to the Use of Wild Birds in Research and in manuals published by the North American Banding Council, the British Trust for Ornithology, or other similar manuals published in other countries (North American Banding Council, 2001; Redfern & Clark, 2001; Fair *et al.*, 2010).

Incidents were rare events overall. However, our study highlights areas where banding organizations can focus attention. In particular, vulnerable species and individuals captured for the first time should be prioritized, and banders should identify which species are most vulnerable at their own sites. Personnel should pay attention to stress by using cues such as panting, lethargy, raising of feathers and closing eyes and they should be particularly careful in recognizing stress cues for smaller birds. Banders should also watch for signs of wing strain and tangling in smaller birds and internal injuries, leg injuries, cuts and predation in larger birds.

While the tracking of incidents may appear tangential to research goals, these data are essential; without them, it is not possible to detect whether research data are biased by capture methods, or to determine whether survival parameters derived from mark-recapture studies are biased by capture-related mortalities. Therefore, we encourage all banding organizations to consider adopting a consistent approach to the recording of injuries and mortalities which should ideally include an assessment of which species are at highest risk and which injuries occur most frequently. These data will allow organizations to adjust their operations as necessary to minimize incidents.

TABLES

Table 1. Mortality, injury and incident rates from 22 banding organizations in the United States and Canada. Table includes data from 620,997 captures and 4,782 incidents.

Organization	Types of birds banded	Mortality Rate (%)	Injury Rate (%)	Incident Rate (%)
A	Passerines	0.56	0.14	0.7
B	Passerines	0.38	1.51	1.89
C	Passerines	0.36	0.48	0.84
D	Passerines	0.29	2.37	2.66
E	Passerines	0.28	1.04	1.32
F	Passerines	0.28	0.60	0.88
G	Passerines	0.24	0.14	0.39
H	Passerines	0.21	0.42	0.62
I	Passerines	0.18	0.38	0.56
J	Passerines	0.13	0.06	0.19
K	Passerines	0.07	0.15	0.22
L	Raptors	0.07	0.43	0.50
M	Raptors	0.00	0.00	0.00
N	Passerines			1.15
O	Shorebirds			0.38
P	Passerines			0.35
Q	Passerines			0.29
R	hummingbirds			0.24
S	Passerines			0.10
T	Passerines			0.1
U	Passerines			0.1
V	hummingbirds			0.03
Average ± SD		0.23 ± 0.15	0.59 ± 0.68	0.61 ± 0.66

Organizations below black line pooled injuries and mortalities together and are reported here as incidents. Organizations are reported without their names or number of captures in order to protect their anonymity.

Table 2. Fixed effects covariates included in three top performing models out of 53, including 97.6% of cumulative AIC weight for individual predictors that affect the probability of injury or mortality in a mist net. Data are from 111,921 capture records in the PRBO dataset.

Model	k	ΔAIC	w
Individual Mass + Age + Sex + Capture Number + Time	13	0	0.560
Individual Mass + Capture Number + Mesh + Month + Time	23	1.185	0.309
Individual Mass + Age + Sex + Capture Number + Mesh + Month + Time	27	3.312	0.107

Note: All models include random effects terms year, species, mist net station, species by year and year by station interactions. Individual Mass is the mass of each bird recorded for each capture record. K is the number of parameters. ΔAIC is the difference in AIC relative to the best model and w is the Akaike weight.

Table 3. Relative support for fixed effect covariates from models of individual predictors of the risk of injury from the PRBO dataset. N is the number of models in which the covariate occurs w^+ is the cumulative Akaike importance weight for all models sharing a given covariate.

Variable	N	w^+
Individual Mass	29	1
Capture Number	29	1
Time	28	0.996
Age	29	0.689
Sex	29	0.686
Mesh	28	0.436
Month	28	0.436

FIGURES

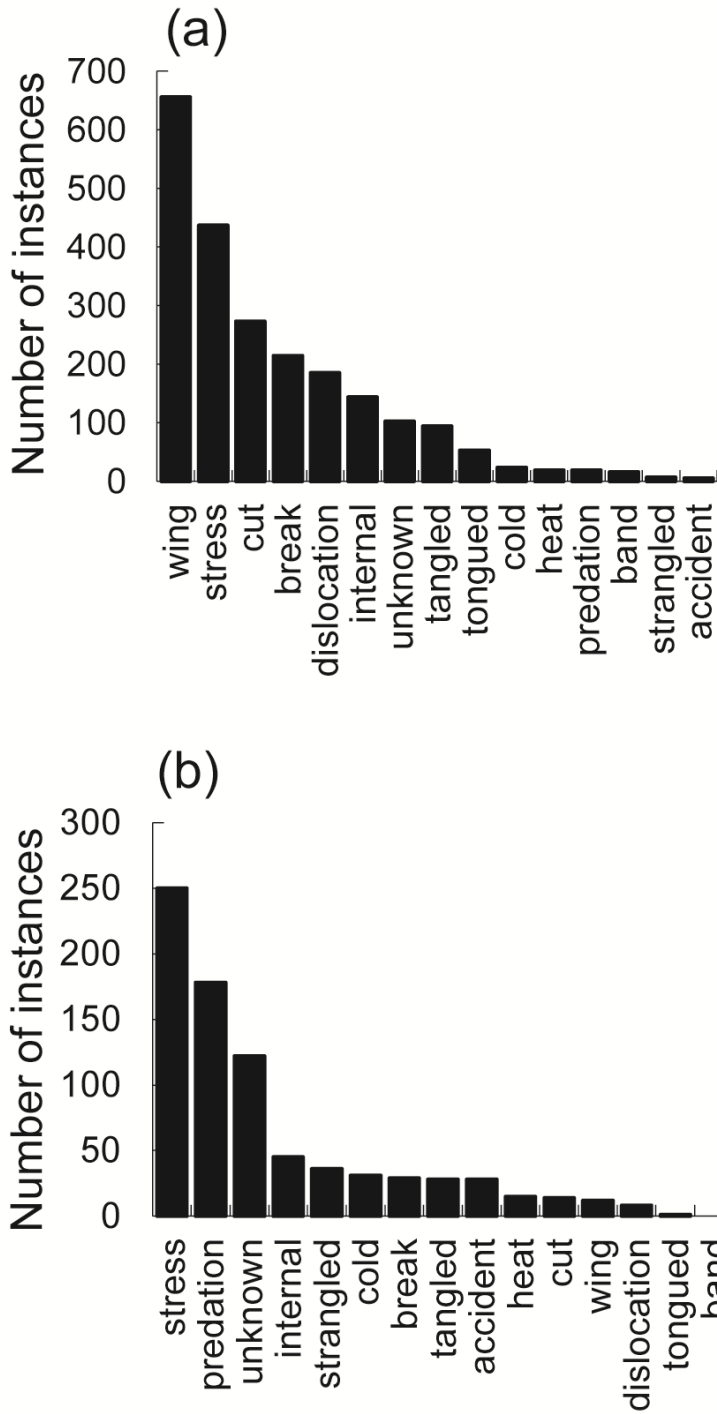


Figure 1. Common categories of (a) injury and (b) mortality associated with mist netting and handling.

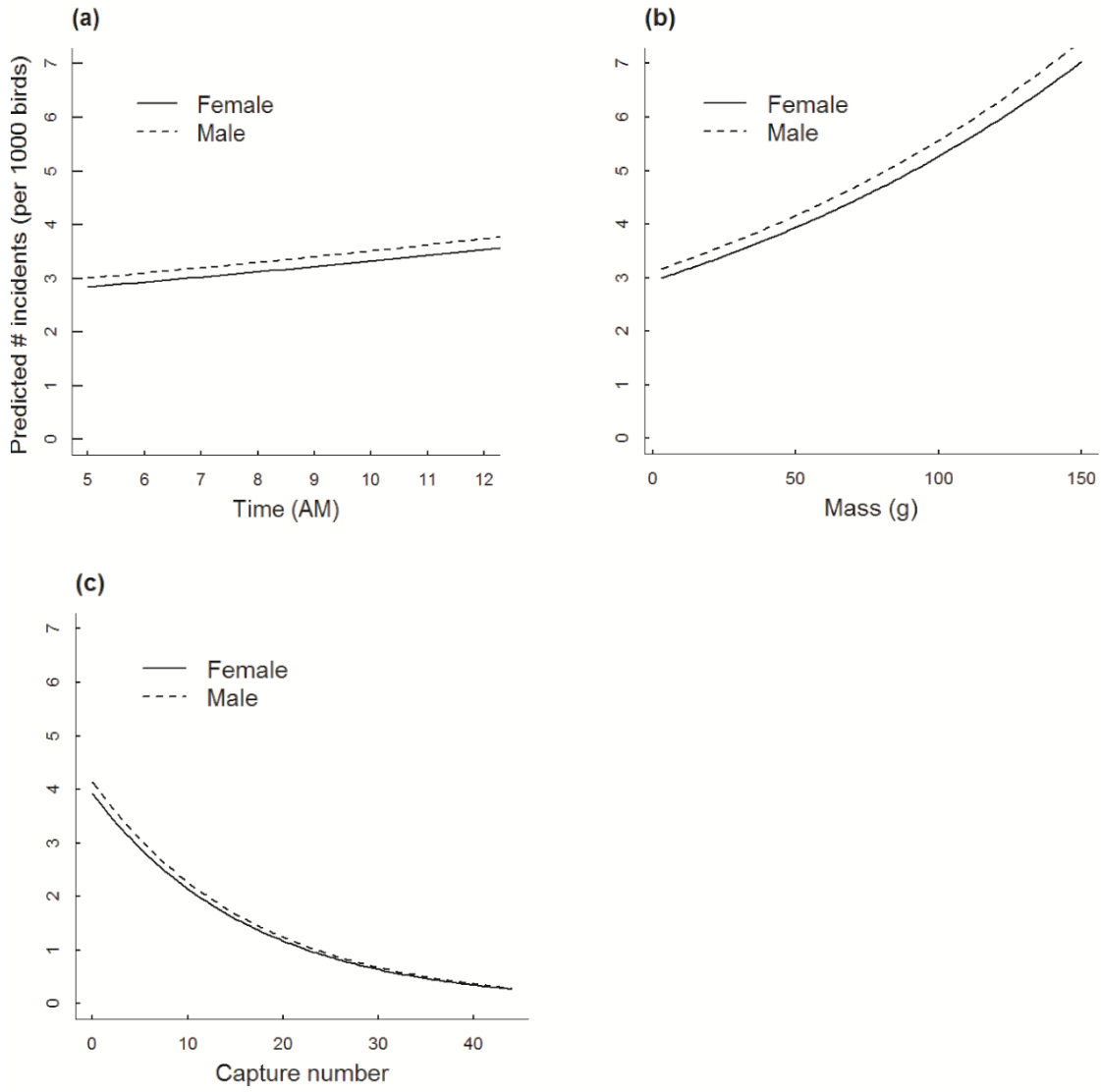


Figure 2. Predicted numbers of incidents per 1000 birds from the PRBO dataset for male and female birds as a function of a) time of day, b) body mass (mass values are individual body measurements for each capture), and c) the capture number (total captures for an individual). Results were model-averaged across three top-performing models in the 95% confidence set (see summary Table 2, and additional details in S2, Supporting Information).

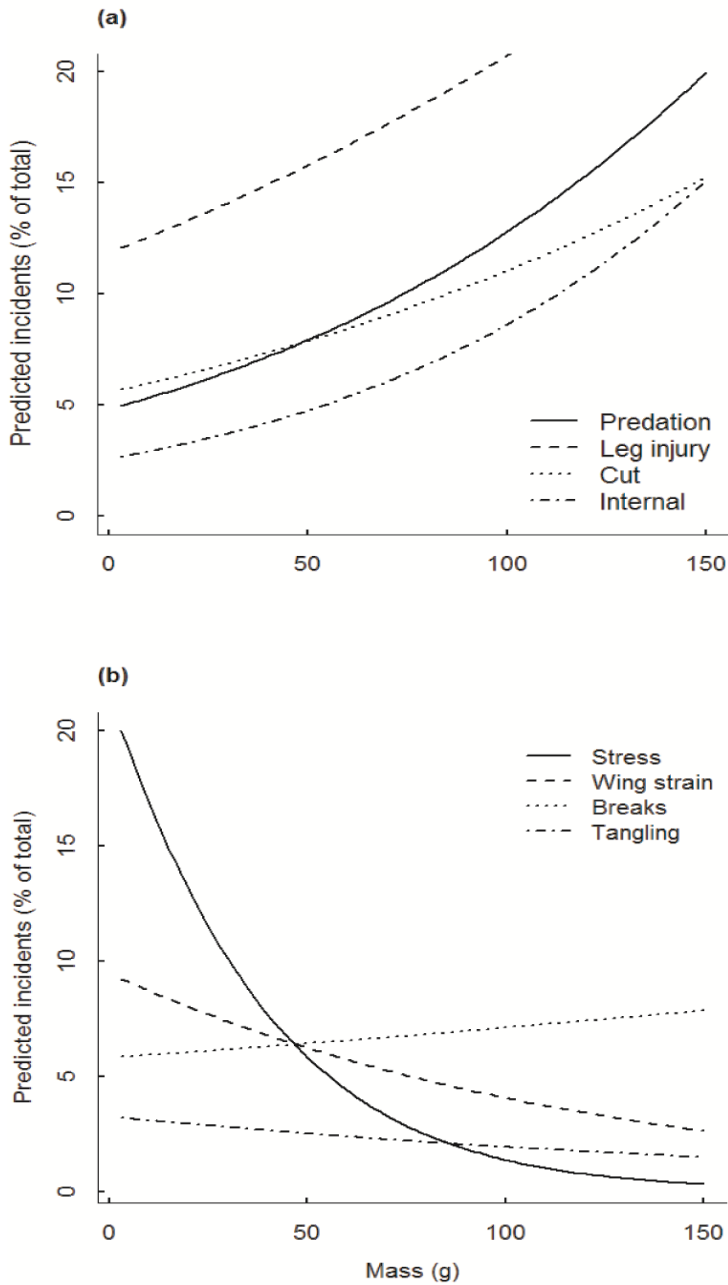


Figure 3. Predicted percent of total incidents for eight types of incident for birds as a function of body size (mass values are species averages). Data are taken from five contributing organizations and include only incident records. Each model included species, organization, year and species X organization and year X organization random effects.

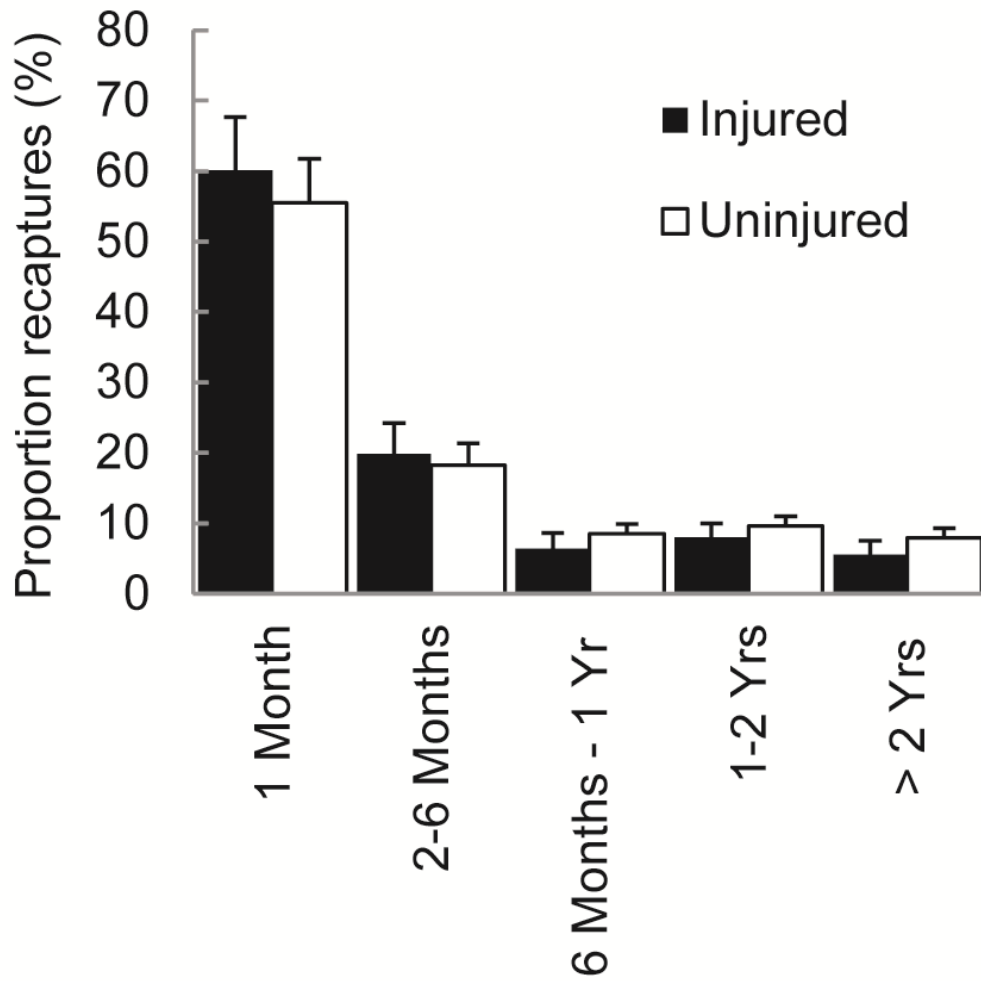


Figure 4. Average recapture history over time for injured and uninjured birds from 12 species captured by PRBO between 1988 and 2008 and seven species captured by IBO between 1997 and 2008. Error bars represent 1 SE.

Chapter 5

Chapter 5

Conclusions & Directions for Future Research

In this dissertation, I investigated aspects of seed dispersal ecology on tropical oceanic islands in the South Pacific. The work was motivated by a desire to understand the effects of anthropogenic impacts on the ecology of tropical forest ecosystems on islands where the threat of invasive species to native biodiversity is magnified by the small population sizes and restricted ranges of many endemic species. My dissertation focused on three key questions: 1) the response of seed dispersal patterns to the presence of a highly invasive fruit-bearing tree, 2) the factors that influence foraging decisions in frugivores, with an emphasis on the community-wide consequences of invasive species, and 3) the risk factors associated with one of my primary research methods: the use of mist netting to capture birds to determine diet.

SUMMARY OF KEY FINDINGS

In my first study (Chapter 2), I investigated how the local abundance of the highly invasive fleshy fruit-bearing tree *Miconia* (*Miconia calvescens* Melastomataceae) influences seed dispersal networks and the foraging patterns of three avian frugivores (two introduced and one native endemic). I conducted the field work for this project on two islands in French Polynesia on two islands (Moorea and Tahiti, Society Islands) that vary in the abundance of *Miconia*. I sampled the diet of three frugivores at six sites and used dietary data to construct seed dispersal networks for each island. I found that exotic species were highly integrated into native seed dispersal networks. While network size was similar between islands, network diversity and evenness were altered at the most highly invaded sites where birds consumed fewer native species and concentrated more heavily on the locally abundant *Miconia*. All three frugivores consumed native fruits, but the quantity of fruit and the number of species was highest in the diet of the endemic Grey-green Fruit Dove (*Ptilinopus purpuratus*) compared to two alien frugivores. Frugivores switched their diets between other resources (insects and other fruiting plants) and *Miconia* at the most highly invaded sites where consumption of native fruit was lowest. My results demonstrate that seed dispersal networks can be altered by a single highly invasive species, and that the local abundance of an invasive species determines the degree of alteration to network properties. The Fruit Dove consumed more native fruit than either alien frugivore highlighting the importance of this endemic frugivore to the dispersal of native fruit-bearing plants.

The structural properties of seed dispersal networks are ultimately governed by the cumulative effects of individual foraging decisions by birds operating in a spatial and temporal context specific to the fruiting environments they encounter. In my second study (chapter 3), I investigated how the dual effects of preferences for certain kinds of fruits and relative abundance are guiding which fruit birds choose to consume. Using wild-caught individuals under experimental conditions, I conducted fruit choice trials with the introduced Red-vented Bulbul (*Pycnonotus cafer*); a highly abundant frugivore

with a diet comprised almost entirely of fruit. In these experiments, I paired combinations of four species at equal and unequal abundances to test whether birds showed preferences between fruit types and whether these preferences changed when the abundance of one fruit changed relative to the other. I found that birds respond strongly to abundance when a single species is paired with itself. Likewise, birds show reliable and consistent preferences for some species over others when paired together at equal abundance. However, when both the type and abundance of fruit are varied simultaneously, the patterns of preference remained intact, while the effect of abundance disappeared. To scale these results up, I combined dietary data with relative abundance estimates taken from vegetation plots to determine whether some species are consumed out of proportion with their abundance in the field. I found that some species were preferred while others were avoided. These results imply that as ecosystems become increasingly invaded by fruit-bearing plants, we should expect that the impact of highly available fruiting resources will depend on both the dietary preferences of frugivores and the relative abundance for fruit in the environment. Thus, it is unlikely that we will be able to use simple neutral models of relative species abundances to predict changes to network patterns in highly invaded systems.

In the final study of my thesis (Chapter 4), I evaluated the risks associated with one of my research methods; the use of mist nets to capture birds live in the wild. The capture of birds using mist nets is a widely utilized technique for monitoring avian populations. While the method is assumed to be safe, very few studies have addressed how frequently injuries and mortalities occur, and the associated risks have not been formally evaluated. I quantified the rates of mortality and injury at 22 banding organizations in the United States and Canada and used capture data from five organizations to determine what kinds of incidents occur most frequently. Analyses focused on passerines and near-passerines, but other groups were included. We evaluated whether body mass, age, sex, mist net mesh size, month of capture, or frequency of capture are related to the risk or type of incident. We also compared the recapture histories over time between birds that were injured and those that were never injured for 16 species. The average rate of injury was 0.59 % while mortality was 0.23%. Birds captured frequently were less at risk to incident. Body mass was positively correlated with incident; larger birds were at greater risk to predation, leg injuries, broken legs, internal bleeding, and cuts while smaller birds were more prone to stress, tangling-related injuries and wing strain. Rates of incident varied among species, with some at greater risk than others. I found no evidence for increased mortality over time of injured birds compared to uninjured birds. This study provides the first comprehensive evaluation of the risks associated with mist netting, and results indicate that (1) injury and mortality rates below one percent can be achieved during mist netting, and (2) injured birds are likely to survive in comparable numbers to uninjured birds after release. While overall risks are low, this study identified vulnerable species and traits that may increase a bird's susceptibility to incident that should be considered in banding protocols aimed at minimizing injury and mortality. I conclude that projects using mist nets should monitor their performance and compare their results to those of other organizations.

Taken together, the studies in this dissertation demonstrate that the indirect effects of invasive species are variable and depend in part on the abundance of alien species in a community. Seed dispersal networks can be altered by a single fruit-bearing invasive plant, with alterations of the largest magnitude occurring at sites where the species is most abundant. Frugivores responded to the abundance of local fruiting resources by switching their diets, and the loss of dispersal of native plants was most pronounced at the highest levels of invasion by *Miconia*. Facilitation between alien species is likely to accelerate at greater degrees of invasion as the abundance of locally available invasive fruit triggers an increase in consumption by frugivores, thus increasing their potential to act as long distance dispersers (Simberloff & Von Holle, 1999). The consequences of these alterations in seed dispersal networks may not be visible if only the total number of species dispersed is considered. Instead, network properties which incorporate the frequency of interactions may reveal shifts in dietary choice at higher levels of invasion.

CONSERVATION IMPLICATIONS

On Tahiti and Moorea, native and introduced frugivores incorporated *Miconia* into their diets in less than 50 years. In this study, the local abundance of *Miconia* influenced the degree to which birds integrate fruit into their diets. Furthermore, Red-vented Bulbuls showed a preference for *Miconia* in aviary conditions. It is therefore likely that other islands with similar frugivorous communities are especially vulnerable to the introduction of *Miconia*. Some evidence of the susceptibility of other islands in French Polynesia already exists. For example, on the island of Raiatea, a 15-year eradication campaign failed to eliminate *Miconia* entirely from the island, and the emergence of remote populations on steep slopes inaccessible by humans and distant from the original site of introduction strongly suggests frugivores could be responsible for the spread of seeds to remote locations (Meyer 2010). Very small *Miconia* populations on the islands of Nuku Hiva and Fatu Hiva in the Marquesas could also become sites of rapid spread in the future (Meyer *et al.*, in press 2011). The islands have surviving populations of two endemic Fruit Doves: the White-capped Fruit Dove (*Ptilinopus dupetithouarsii*) and the Marquesan Imperial-pigeon (*Ducula galeata*), though Silvereyes (*Zosterops lateralis*) and Bulbuls are absent from the Marquesas (Gouni & Zysman, 2007). Elsewhere in the Pacific where *Miconia* is already present such as New Caledonia, Australia and Hawaii are also at risk due to the presence of similar communities of frugivores in all three of those locations (Pizzey *et al.*, 1980; Pratt *et al.*, 1987; Doughty *et al.*, 1999). Three species of endemic fruit dove, four species of white-eye (including the Silvereye), and the introduced Red-Vented Bulbul are all present in New Caledonia (Mayr, 1945; Delacour, 1966). Hawaii has a small frugivorous community that includes two Bulbuls and one White-eye (*Zosterops japonica*) (Pratt *et al.*, 1987). Australia has a diverse population of native and introduced frugivores (though only a few are present in the current location of *Miconia* invasion) including several fruit doves, Silvereyes and Red-vented Bulbuls as well as other groups not represented in the remote Pacific such as starlings, robins and thrushes and bowerbirds (Simpson *et al.*, 2010).

On islands where *Miconia* is already present, the management of *Miconia* in the presence of frugivorous birds should target the reduction in numbers of fruit produced either via manual eradication of reproducing individuals or via the search for bio-control agents that spoil or destroy fruit (Buckley *et al.*, 2006). Additionally, the search for and eradication of satellite populations is likely to be critical to any long term control effort of *Miconia* on islands where the population is still restricted to only a few locations. For example, in a study examining various control methods, efforts were much improved by removing nascent populations while they were still small (Moody & Mack, 1988; but see Meyer *et al.*, in press 2011). Lastly, the presence of frugivorous birds should be considered a risk factor on islands where *Miconia* has not been introduced. Empirical work suggests that though it is often difficult to predict the outcome of a plant introduction, its behavior elsewhere in similar habitat types is often a strong indicator of its behavior in a novel location (Sakai *et al.*, 2001). The presence of similar bird communities is one such factor that could play a role in determining the outcome of the introduction of *Miconia* on Pacific Islands where it is not yet present.

The Fruit Dove consumed more native species than either the Silvereye or the Bulbul on Moorea and native fruit were consumed in higher quantities than predicted by local abundance (Chapter 3). Thus, the dispersal of native plants depends largely on the continued presence of the Fruit Dove, and introduced frugivores are unlikely to act as effective surrogate dispersers if the Fruit Dove were to go extinct or become very rare (Hansen *et al.*, 2008; Kaiser-Bunbury *et al.*, 2010). The preferences showed by the Fruit Dove indicate that this species does not select fruit indiscriminately. The dispersal of preferred native plants is likely to occur even when these plants are rare whereas fruit that are less preferred may be dropped from the diet once they become rare and may be easily substituted for invasive fruit. Good knowledge of frugivore diet is therefore a key first step to understanding their role in maintaining populations of rare plants. Conservation efforts aimed at protecting endemic plants that are known to be dispersed by Fruit Doves should incorporate a clear emphasis on the protection of both the birds and the plants on which they feed.

Abundance data are lacking for the Fruit Dove, though a survey of valleys in Tahiti suggested that populations have remained stable in the 20th century (Monnet *et al.*, 1993). Mist netting data from this study suggest that Fruit Doves are most common at two sites on Moorea located in low elevation native rainforests; a habitat that is rare on most of the Society Islands due to anthropogenic disturbance (Meyer pers. comm.). In Australia, the susceptibility of frugivores to population declines in forest fragments was positively correlated to the proportion of native species in the diets of frugivores (Morales & Aizen, 2005). Additionally, three species of *Ptilonopus* were found to consume high proportions of native species compared to other frugivores. The abundance of Fruit Doves in patches of native forest on Moorea suggests that they could be declining in invaded forests elsewhere, especially if they depend on the suite of fruits available in native forests. Non-native fruit are present in at least half the diet of the Fruit Dove, indicating that these plants are playing an important role in the diet of this sensitive species. However, the low numbers of individuals in forest types not dominated by native species suggests that the species may be dependent on plant communities characterized

by a diversity of native and endemic plants in spite of the apparent generalist nature of its diet. There is an urgent need for more research into the dietary and habitat requirements of the Fruit Dove. In the meantime, conservation efforts should target the protection of remaining low-elevation native forest.

DIRECTIONS FOR FUTURE RESEARCH

One important avenue for future research is a more detailed assessment of the population viability of the Grey-green Fruit Dove. Since the Whitney South Sea Expedition in 1920-1923, several researchers have made anecdotal observations about behavior, diet, and reproduction (Holyoak & Thibault, 1984), but with the exception of one re-survey (Monnet *et al.*, 1993), much remains unknown about the Fruit Dove in the Society Islands (Steadman, 1997; Sherley & Hay, 2001). This information is critical because on many of the islands where fruit doves are still present, they are either the sole frugivores or one of a just a handful of species where they are likely acting as strong interactors, serving as the only dispersers of native plants which depend on them much more than they depend on any individual species of plant (Cox *et al.*, 1991). For a few species of fruit dove such as the Marquesan imperial pigeon, the Polynesian ground dove and the Pink headed pigeon in Indonesia, data collection assessing population size, habitat preference and reproductive ecology of have assisted with the conservation efforts of these species (Blanvillain *et al.*, 2002; Thorsen *et al.*, 2002; Villard *et al.*, 2003; Van Balen & Nijman, 2004). To address the lack of such quantitative estimates for fruit doves in French Polynesia, the South Pacific Regional Environment Program called for the development of monitoring programs to collect basic data on populations and reproduction for the conservation of doves in Polynesia in their report on conservation priorities for South Pacific bird species (Sherley & Hay, 2001). Fruit doves all over the Pacific are similarly at risk due to many contributing factors such as habitat loss, introduced predators, competition with introduced birds, and disturbance (Holyoak, 1974; Seitre & Seitre, 1992). On Tahiti and Moorea, the Bulbul and the Common Myna (*Acridotheres tristis*) compete with the Fruit Dove for resources and display aggressive behavior towards endemic birds (Thibault *et al.*, 2002; Blanvillain *et al.*, 2003). Cats, swamp harriers, and rats prey on fruit dove hatchlings, eggs, and adults (Holyoak & Thibault, 1978; Seitre & Seitre, 1992). Developing a better understanding of the ecology of the species and the threats it faces is critical to its long term persistence.

In addition to conservation priorities for the Fruit Dove, there is also a need to understand more completely the effects of Fruit Dove dispersal on native plant regeneration and forest dynamics. My study focused only on characterizing the diet of frugivores and on determining the effects of gut passage on germination of seeds. However, other components of the seed dispersal pathway remain uninvestigated. For example, information is needed on the movement patterns of frugivores in order to quantify how far from parent plants dispersed seeds are likely to be deposited by each frugivore and in what kinds of habitats. In 1991, Cox suggested that pollinators and seed dispersers may structure the ecosystems of remote oceanic islands much as predators structure communities on continents and intertidal communities (Cox *et al.*, 1991). Twenty years after this study was published, we continue to lack the comprehensive data

that is necessary to demonstrate how birds structure plant communities on oceanic islands.

Several key pieces of information are necessary as part of this effort. For example, information on the rates of survival for seeds and seedlings dispersed by frugivores compared to those that fall close to the crown would help us understand the strength of density-dependent differences in survival of seeds on Oceanic islands. Evidence from Mauritius suggests that these effects can be strong in some locations (Hansen *et al.*, 2008), but too few studies have been conducted to determine whether this is a general pattern. Seed predation rates should also be monitored to determine whether dispersed seeds escaped predation at a greater rate than those that are deposited under crowns. There is evidence from continental ecosystems that seed predation can be more important than dispersal in determining plant distributions, at least in cases where dispersal and microsites are not limiting (Orrock *et al.*, 2006). Evidence from French Polynesia already suggests that the Polynesian Rat is an active seed predator on some native plants with large seeds which has the potential to limit the recruitment of native plants (Meyer & Butaud, 2009). However, an assessment of the role of predator and dispersal limitation on the distribution of native plants has not been conducted, and would greatly advance our understanding of the factors that contribute to the success or failure of these species of conservation concern. Directed dispersal, or the disproportionate dispersal towards a particular type of micro-site can occur in avian dispersal in cases where behavior strongly influences where seeds are deposited (Howe & Smallwood, 1982). For example, deposition under roost sites, or at perch trees can occur if birds more frequently defecate at these locations. The outcome of directed dispersal depends on how favorable micro-sites are to germination and seedling survival (Wenny & Levey, 1998). In French Polynesia, Fruit Doves often fly long distances across valleys to roost sites in the evening at sunset (Spotswood, unpublished data). We do not know what kinds of trees Fruit Doves choose for roosting, and it is possible that these sites are consistent enough to have an impact on the recruitment of seeds deposited under roosts.

A comparative study of the spatial aggregation of native fruit bearing plants on islands with and without fruit doves could yield insight into how avian dispersal affects clumping and aggregation of plants. One such study in Malaysia found that spatial aggregation was highest among species with animal dispersal modes (Seidler & Plotkin, 2006). Spatial clustering can reduce diversity at the local scale, whereas at larger scales, clustering can lead to higher species turnover and greater beta and gamma diversity (Chave *et al.*, 2002). Similarly, the loss of seed dispersers could lead to greater spatial clustering of adults and seedlings, which could limit recruitment if the effects of density-dependent predation and parasitism are important. Such a study in French Polynesia may be possible on atolls with and without fruit doves in some parts of Polynesia where atolls are similar enough to act as replicates for each other.

Finally, additional information is needed in order to more fully understand how seed dispersal networks are altered by highly invasive fruit-bearing plants. For example, while my research used aviary experiments to investigate avian foraging decisions, my work did not couple these trials with an experimental approach in the field. Promising

avenues for this kind of work have been pursued by a few authors who have used fruiting structures attached to bushes, or bushes grown in glass houses and then placed in the wild to manipulate the fruiting neighborhood in a controlled way in order to monitor avian responses (Whelan & Willson, 1994; Gervais *et al.*, 1999; Carlo, 2005; Davis *et al.*, 2010). Such an approach could be very informative in the French Polynesian context, and could provide further insight into how birds respond to abundance and fruit preferences. It would also be useful to examine frugivorous diets on islands that are similar to Tahiti and Moorea but lack *Miconia*, or on Raiatea where *Miconia* populations are still very restricted. Because the Fruit Dove diet has been highly modified by the presence of *Miconia* on Moorea and Tahiti, quantifying the diet of this bird elsewhere could help to uncover whether species have been lost from the Fruit Dove diet where *Miconia* is present. Lastly, some authors have recently called for a move away from observational studies in the field of networks towards an approach that utilizes manipulative experiments (Ings *et al.*, 2009). This kind of study would be costly and difficult for seed dispersal networks where entire communities of fruiting plants would need to be manipulated. The low diversity of oceanic islands makes them simpler systems, and thus more tractable for these kinds of studies, which have the potential to contribute much to our understanding of the responses of communities to the presence of invasive species. Recent authors have called for a need for better monitoring of species interactions in general on oceanic islands as a way to understand biodiversity change and to develop conservation plans (Kaiser-Bunbury *et al.*, 2010). Understanding the effects of invasive species on species interactions is one key component that is required as part of this effort.

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APPENDICES

A1. Best fitting models for the proportion of native fruit in diets of Bulbuls (n=455), Silvereyes (n=519), and Fruit doves (n=204).

	Negative binomial count model				γ	Binomial hurdle model		
	μ	SE	Z	P		SE	Z	P
Native consumption -- All Data								
Intercept	3.609	0.14	26.08	<0.0001	-1.36	0.65	-2.08	0.03754
Fruit Dove	-0	0.02	-0.17	0.8653	1.759	0.32	5.497	<0.0001
Silvereye	0.054	0.05	1.022	0.30667	-0.31	0.35	-0.89	0.37482
Miconia (%)	-0.02	0	-28.6	<0.0001	-0.03	0	-10.4	<0.0001
Sept - Nov	0.365	0.14	2.557	0.01056	1.785	0.68	2.638	0.00833
June - August	0.287	0.14	2.088	0.03679	2.388	0.63	3.788	0.00015
Tahiti	-0.13	0.04	-2.83	0.00466	-1.11	0.28	-3.91	9.22E-05
Insects (%)	-0.02	0	-16.5	<0.0001	-0.04	0	-8.4	<0.0001

A2. Best fitting zero altered hurdle models for Silvereye consumption of Miconia, other fruit and insects.

	μ	Negative binomial count model			Binomial hurdle model			
		SE	Z	P	γ	SE	Z	P
Silvereye								
<i>Miconia seeds</i>								
Intercept	5.735	0.466	12.299	< 0.0001	1.716	0.458	3.747	0.000
Other Fruit (%)	-0.030	0.006	-5.348	< 0.0001	-0.025	0.006	-4.128	< 0.0001
Sept - Nov	-1.090	0.390	-2.790	0.005	1.701	0.459	3.707	0.000
June - August	-0.855	0.395	-2.163	0.031	0.534	0.341	1.566	0.117
Miconia density	-0.060	0.027	-2.259	0.024	0.074	0.043	1.710	0.087
Tahiti	1.076	0.458	2.349	0.019	-0.560	0.715	-0.782	0.434
Insects (%)	-0.036	0.004	-9.198	< 0.0001	-0.044	0.004	-10.023	< 0.0001
<i>Other seeds</i>								
Intercept	1.128	0.798	1.414	0.157	0.965	0.540	1.789	0.074
Miconia seeds	-0.025	0.008	-3.055	0.002	-0.030	0.006	-5.151	0.000
Sept - Nov	1.755	0.795	2.208	0.027	-0.400	0.583	-0.686	0.493
June - August	1.007	0.766	1.314	0.189	-0.876	0.486	-1.803	0.071
Tahiti	2.394	0.682	3.508	0.000	2.586	0.762	3.394	0.001
Miconia density	-0.144	0.056	-2.557	0.011	-0.136	0.046	-2.987	0.003
Insects (%)	-0.033	0.009	-3.565	0.000	-0.041	0.006	-7.354	0.000
<i>Insect abundance</i>								
Intercept	3.538	0.064	55.411	< 0.0001	1.313	0.220	5.958	< 0.0001
Miconia (%)	-0.021	0.001	-15.593	< 0.0001	-0.007	0.004	-1.880	0.060
Sept - Nov	0.402	0.112	3.580	0.000	0.523	0.375	1.393	0.164
June - August	0.081	0.079	1.027	0.304	-0.618	0.248	-2.496	0.013
Other fruit (%)	-0.021	0.002	-9.038	< 0.0001	-0.014	0.005	-2.866	0.004
Tahiti	-0.345	0.087	-3.959	0.000	0.526	0.270	1.947	0.052

A3. Best fitting Zero altered hurdle models for Bulbul consumption of native Miconia, other fruit and native fruit.

	Negative binomial count model				γ	Binomial hurdle model		
	μ	SE	Z	P		SE	Z	P
Bulbul								
<i>Miconia seeds</i>								
Intercept	3.935	0.323	12.183	< 0.0001	1.381	0.322	-4.294	< 0.0001
Other Fruit (%)	-0.015	0.002	-6.519	< 0.0001	0.040	0.007	-6.062	< 0.0001
Tahiti	1.343	0.318	4.218	< 0.0001	5.806	0.568	10.230	< 0.0001
Insects (%)	-0.003	0.004	-0.718	0.473	0.042	0.008	-5.273	< 0.0001
<i>Other seeds</i>								
Intercept	2.489	2.188	1.138	0.255	1.521	0.836	1.820	0.069
Miconia (%)	-0.042	0.006	-6.778	< 0.001	0.051	0.006	-8.259	< 0.001
Sept - Nov	-1.645	1.484	-1.109	0.268	0.812	0.891	-0.911	0.362
June - August	-1.938	1.383	-1.401	0.161	0.180	0.795	0.227	0.821
Tahiti	2.011	0.455	4.424	< 0.001	2.356	0.578	4.076	< 0.001
Insects (%)	-0.026	0.013	-2.108	0.035	0.054	0.008	-7.133	< 0.001
<i>Native fruit</i>								
Intercept	-6.643	59.279	-0.112	0.911	1.160	1.145	1.013	0.311
Miconia (%)	-0.031	0.013	-2.329	0.020	0.022	0.005	-4.235	< 0.001
Tahiti	12.510	3.000	-4.170	< 0.001	1.802	0.995	-1.811	0.070

Sept - Nov	4.356	2.401	1.815	0.070	-	0.672	1.205	-0.558	0.577
June - August	-0.515	2.130	-0.242	0.809	-	0.781	1.117	-0.699	0.485
Miconia density	0.671	0.182	3.694	0.000	-	0.026	0.063	0.415	0.678
Insects (%)	-0.024	0.027	-0.906	0.365	-	0.037	0.010	-3.592	0.000

A4. Fruit sizes (mm) for 20 randomly selected fruit from four species used in fruit choice trials with mean and standard deviations. Fruit sizes were measured using a wing ruler with mm accuracy.

Fruit Number	Lantana	Miconia	Tarena	Rhus
1	6	5	8	5
2	6	5	8	5
3	4	6	6	5
4	5	6	7	5
5	7	5	8	4
6	6	5	7	5
7	7	4	5	5
8	5	5	7	4
9	5	5	9	5
10	5	4	7	5
11	4	5	8	5
12	5	6	5	5
13	5	4	7	5
14	4	5	6	4
15	4	5	7	5
16	5	5	6	5
17	4	5	4	4
18	6	5	8	4
19	5	4	8	4
20	4	5	8	5
Mean	5.1	4.95	6.95	4.7
SD	0.94	0.59	1.24	0.46

A5. Average values (\pm 1SD) for wing length and mass of birds captured during mist netting. N is the total number of captures.

	N	Wing length (mm)	Mass (g)
Fruit Dove	137	142.55 (5.49)	85.67 (9.89)
Bulbul	28	94.76 (3.78)	36.65 (3.49)
Silvereye	551	61.03 (1.54)	10.27 (0.7)

A6. Rates and categories of injury and mortality in the 36 most common species in the regional dataset including 305,534 records from five banding organizations in order of logit estimates of the probability of incident. Injury, mortalities are given as percent of total captures. Common categories are the percent of all incidents for a given species. Estimates and standard errors were obtained from a GLMM predicting the risk of incident as a function of fixed effect species with organization, year and year X organization interactions as random effects.

Species	Total captures	Injury	Mortality	Estimate	SE	Wing	Break	Leg injury	Internal injury	Stress	Tangling	Other
Spotted Towhee	7,389	1.02	0.19	1.18	0.27	7.87	8.99	16.85	11.24	30.34	2.25	22.47
Allen's Hummingbird	4,614	0.89	0.59	0.91	0.28	2.94	0.00	2.94	1.47	48.53	13.24	30.88
American Robin	3,843	1.30	0.29	0.79	0.29	21.31	3.28	6.56	8.20	8.20	4.92	47.54
Western Tanager	3,800	2.95	0.32	0.68	0.28	46.77	4.84	15.32	17.74	4.84	0.00	10.48
Black-Headed Grosbeak	2,168	1.94	0.32	0.59	0.30	38.78	14.29	14.29	22.45	6.12	2.04	2.04
Chipping Sparrow	2,521	2.90	0.32	0.57	0.29	71.60	0.00	2.47	7.41	2.47	4.94	11.11
White-crowned Sparrow	10,416	1.60	0.27	0.48	0.27	27.18	11.28	41.03	7.69	4.62	1.03	7.18
Lincoln's Sparrow	5,854	0.46	0.41	0.43	0.29	1.96	19.61	35.29	0.00	21.57	5.88	15.69
Chesnut-backed Chickadee	5,325	0.60	0.17	0.22	0.30	2.44	26.83	21.95	2.44	21.95	14.63	9.76
Oregon Junco	26,299	0.84	0.41	0.22	0.27	21.04	6.71	17.68	9.76	14.94	6.40	23.48
Purple Finch	4,572	0.39	0.24	0.19	0.30	17.24	3.45	6.90	13.79	34.48	0.00	24.14
MacGillivray's Warbler	5,526	1.41	0.38	0.17	0.28	33.33	4.04	12.12	2.02	26.26	5.05	17.17
Golden-crowned Sparrow	6,730	0.56	0.13	0.15	0.29	12.77	14.89	31.91	2.13	10.64	0.00	27.66
Common Redpoll	3,262	0.06	0.52	0.00	0.36	0.00	5.26	5.26	5.26	21.05	21.05	42.11
Bushtit	4,033	0.45	0.17	0.07	0.32	12.00	4.00	16.00	0.00	36.00	24.00	8.00
Yellow Warbler	6,707	0.72	0.27	-0.03	0.29	25.76	3.03	7.58	6.06	33.33	6.06	18.18
Wilson's Warbler	17,374	0.41	0.17	-0.16	0.28	15.00	12.00	15.00	1.00	40.00	3.00	14.00
Song Sparrow	22,680	1.07	0.31	-0.23	0.28	33.01	7.69	20.83	8.33	11.22	3.21	15.71
Fox Sparrow	10,143	0.39	0.20	-0.22	0.29	5.00	6.67	16.67	5.00	21.67	3.33	41.67
Common Yellowthroat	2,488	0.12	0.04	-0.26	0.37	0.00	25.00	25.00	0.00	25.00	0.00	25.00
Wrentit	9,526	0.37	0.12	-0.24	0.29	0.00	8.70	10.87	0.00	41.30	8.70	30.43
Bewick's wren	3,574	0.31	0.11	-0.24	0.33	0.00	0.00	6.67	6.67	40.00	6.67	40.00

Western Flycatcher	8,380	0.32	0.05	-0.26	0.30	35.48	3.23	3.23	3.23	38.71	6.45	9.68
American tree sparrow	8,603	0.08	0.28	-0.19	0.31	0.00	6.45	16.13	0.00	6.45	3.23	67.74
Swainson's Thrush	14,886	0.40	0.08	-0.33	0.28	7.04	11.27	36.62	5.63	11.27	2.82	25.35
Hermit Thrush	11,589	0.35	0.12	-0.37	0.29	12.96	12.96	22.22	7.41	18.52	3.70	22.22
Golden-crowned Kinglet	4,828	0.23	0.06	-0.39	0.32	7.14	0.00	0.00	0.00	64.29	7.14	21.43
Ruby-crowned Kinglet	28,960	0.47	0.31	-0.45	0.27	20.89	12.44	12.89	3.11	25.33	5.78	19.56
Dusky Flycatcher	4,304	1.00	0.07	-0.46	0.30	63.04	8.70	10.87	6.52	10.87	2.17	0.00
Warbling Vireo	4,540	0.59	0.04	-0.47	0.31	44.83	0.00	0.00	6.90	17.24	13.79	17.24
Pine Siskin	2,018	0.64	0.15	-0.52	0.35	18.75	0.00	0.00	12.50	56.25	6.25	6.25
Townsend's Warbler	2,353	0.38	0.13	-0.58	0.36	50.00	0.00	0.00	0.00	8.33	8.33	33.33
Orange-crowned Warbler	15,572	0.24	0.15	-0.57	0.28	5.00	15.00	13.33	0.00	45.00	10.00	11.67
Yellow-rumped Warbler	25,164	0.15	0.15	-0.95	0.28	17.33	10.67	14.67	4.00	16.00	4.00	33.33
Nashville Warbler	2,822	0.43	0.14	-1.02	0.36	31.25	6.25	0.00	0.00	43.75	12.50	6.25
Hammond's Flycatcher	2,671	0.19	0.22	-1.01	0.39	36.36	18.18	18.18	0.00	18.18	0.00	9.09

A7. Candidate models for the analysis of individual predictors of risk using the PRBO dataset. Fixed and random effects covariates from a candidate set of 53 models, for individual predictors that affect the probability of injury or mortality in a mist net. Data are from 111,921 capture records in the PRBO dataset. Individual Mass is the mass of each bird recorded for each capture record. Δ AIC is the difference in AIC relative to the best model and w is the Akaike weight. The cumulative AIC weight is the cumulative weight of evidence for each successive model included in the total model in order of decreasing model fit.

Model	Fixed Effects	Random Effects	Log Likelihood	AIC	BIC	Deviance	Δ AIC	W	Cumulative W
52	Mass + Age + Sex + Captures + Time	Year + Species + Station + Species*Year + Year*Station	-3806.359	7638.718	7762.620	7612.718	0.000	0.560	0.560
38	Mass + Captures + Mesh + Month + Time	Year + Species + Station + Species*Year + Year*Station	-3798.952	7639.903	7840.052	7597.903	1.185	0.309	0.869
11	Mass + AgeClass + Sex + Captures + Mesh + Month + Time	Year + Species + Station + Species*Year + Year*Station	-3796.015	7642.030	7880.302	7592.030	3.312	0.107	0.976
3	<i>Mass + AgeClass + Sex + Captures + Mesh + Month + Time</i>	<i>Year + Species + Station + Species*Year</i>	-3798.691	7645.381	7874.123	7597.381	6.663	0.020	0.996
48	Mass + Time	Year + Species + Station + Species*Year + Year*Station	-3817.276	7650.552	7726.805	7634.552	11.834	0.002	0.997
16	Mass + Age + Time	Year + Species + Station + Species*Year + Year*Station	-3815.578	7651.156	7746.473	7631.156	12.438	0.001	0.998
53	Mass + Age + Time	Year + Species + Station + Species*Year +	-3815.578	7651.156	7746.473	7631.156	12.438	0.001	1.000

		Year*Station							
34	Mass + Age + Month + Time	Year + Species + Station + Species*Year + Year*Station	-3806.009	7654.018	7854.183	7612.018	15.300	0.000	1.000
36	Mass + Month + Time	Year + Species + Station + Species*Year + Year*Station	-3808.959	7655.917	7837.019	7617.917	17.199	0.000	1.000
31	Mass + Age + Sex + Mesh + Month + Time	Year + Species + Station + Species*Year + Year*Station	-3805.482	7658.964	7887.724	7610.964	20.246	0.000	1.000
6	<i>Mass + AgeClass + Sex + Captures + Mesh + Month + Time</i>	<i>Year + Species</i>	-3811.632	7667.264	7876.944	7623.264	28.546	0.000	1.000
4	<i>Mass + AgeClass + Sex + Captures + Mesh + Month + Time</i>	<i>Year + Species + Station</i>	-3810.761	7667.522	7886.733	7621.522	28.804	0.000	1.000
14	Mass + Age + Sex + Captures	Year + Species + Station + Species*Year + Year*Station	-3828.485	7680.970	7795.366	7656.970	42.252	0.000	1.000
28	Mass + Captures + Mesh	Year + Species + Station + Species*Year + Year*Station	-3831.769	7681.538	7767.334	7663.538	42.820	0.000	1.000
13	Mass + Age + Sex + Captures + Mesh	Year + Species + Station + Species*Year + Year*Station	-3828.472	7682.944	7806.872	7656.944	44.226	0.000	1.000
39	Mass + Captures + Mesh + Month	Year + Species + Station +	-3822.299	7684.597	7875.256	7644.597	45.879	0.000	1.000

		Species*Year + Year*Station							
12	Mass + Age + Sex + Captures + Mesh + Month	Year + Species + Station + Species*Year + Year*Station	-3818.772	7685.543	7914.334	7637.543	46.825	0.000	1.000
40	Mass	Year + Species + Station + Species*Year + Year*Station	-3840.213	7694.425	7761.161	7680.425	55.707	0.000	1.000
15	Mass + Age + Sex	Year + Species + Station + Species*Year + Year*Station	-3837.662	7697.325	7802.195	7675.325	58.607	0.000	1.000
35	Mass + Age + Month	Year + Species + Station + Species*Year + Year*Station	-3829.034	7698.068	7888.743	7658.068	59.350	0.000	1.000
33	Mass + Age + Sex + Mesh	Year + Species + Station + Species*Year + Year*Station	-3837.652	7699.305	7813.709	7675.305	60.587	0.000	1.000
37	Mass + Month	Year + Species + Station + Species*Year + Year*Station	-3832.488	7700.975	7872.582	7664.975	62.257	0.000	1.000
32	Mass + Age + Sex + Mesh + Month	Year + Species + Station + Species*Year + Year*Station	-3828.550	7703.100	7922.376	7657.100	64.382	0.000	1.000
2	<i>Mass + AgeClass + Sex + Captures + Mesh + Month + Time</i>	<i>Year + Station + Year*Station</i>	-3845.182	7736.365	7955.575	7690.365	97.647	0.000	1.000
10	<i>Mass + AgeClass + Sex + Captures +</i>	<i>Year</i>	-3848.732	7739.464	7939.612	7697.464	100.746	0.000	1.000

	<i>Mesh + Month + Time</i>								
7	<i>Mass + AgeClass + Sex + Captures + Mesh + Month + Time</i>	<i>Year + Station</i>	-3848.204	7740.409	7950.088	7696.409	101.691	0.000	1.000
5	<i>Mass + AgeClass + Sex + Captures + Mesh + Month + Time</i>	<i>Species + Station</i>	-3875.978	7795.957	8005.637	7751.957	157.239	0.000	1.000
8	<i>Mass + AgeClass + Sex + Captures + Mesh + Month + Time</i>	<i>Species</i>	-3877.718	7797.435	7997.584	7755.435	158.717	0.000	1.000
9	<i>Mass + AgeClass + Sex + Captures + Mesh + Month + Time</i>	<i>Station</i>	-3915.046	7872.091	8072.240	7830.091	233.373	0.000	1.000
17	<i>Age + Sex + Captures + Mesh + Month + Time</i>	<i>Year + Species + Station + Species*Year + Year*Station</i>	-5886.997	11821.990	12052.870	11773.990	4183.272	0.000	1.000
18	<i>Age + Sex + Captures + Mesh + Month</i>	<i>Year + Species + Station + Species*Year + Year*Station</i>	-5925.232	11896.460	12117.780	11850.460	4257.742	0.000	1.000
20	<i>Age + Sex + Captures</i>	<i>Year + Species + Station + Species*Year + Year*Station</i>	-5939.831	11901.660	12007.510	11879.660	4262.942	0.000	1.000
19	<i>Age + Sex + Captures + Mesh</i>	<i>Year + Species + Station + Species*Year + Year*Station</i>	-5939.539	11903.080	12018.550	11879.080	4264.362	0.000	1.000
50	<i>Age + Time</i>	<i>Year + Species + Station +</i>	-5952.096	11922.190	12008.780	11904.190	4283.472	0.000	1.000

		Species*Year + Year*Station							
22	Sex + Captures + Mesh + Month + Time	Year + Species + Station + Species*Year + Year*Station	-5944.986	11933.970	12145.610	11889.970	4295.252	0.000	1.000
25	Sex + Captures + Time	Year + Species + Station + Species*Year + Year*Station	-5963.262	11946.520	12042.720	11926.520	4307.802	0.000	1.000
26	Captures + Mesh + Month + Time	Year + Species + Station + Species*Year + Year*Station	-5960.659	11961.320	12153.720	11921.320	4322.602	0.000	1.000
49	Captures + Time	Year + Species + Station + Species*Year + Year*Station	-5972.985	11961.970	12038.930	11945.970	4323.252	0.000	1.000
21	Age + Sex	Year + Species + Station + Species*Year + Year*Station	-5980.774	11981.550	12077.780	11961.550	4342.832	0.000	1.000
41	Age	Year + Species + Station + Species*Year + Year*Station	-5991.034	11998.070	12075.060	11982.070	4359.352	0.000	1.000
51	Sex + Time	Year + Species + Station + Species*Year + Year*Station	-5997.998	12014.000	12100.590	11996.000	4375.282	0.000	1.000
23	Sex + Captures + Mesh + Month	Year + Species + Station + Species*Year + Year*Station	-5987.548	12017.100	12219.160	11975.100	4378.382	0.000	1.000
24	Sex + Captures + Mesh	Year + Species + Station +	-6004.050	12028.100	12124.320	12008.100	4389.382	0.000	1.000

		Species*Year + Year*Station							
46	Time	Year + Species + Station + Species*Year + Year*Station	-6011.560	12037.120	12104.470	12023.120	4398.402	0.000	1.000
47	Month + Time	Year + Species + Station + Species*Year + Year*Station	-6002.766	12041.530	12214.720	12005.530	4402.812	0.000	1.000
30	Mesh + Month + Time	Year + Species + Station + Species*Year + Year*Station	-6002.381	12042.760	12225.570	12004.760	4404.042	0.000	1.000
43	Captures	Year + Species + Station + Species*Year + Year*Station	-6014.706	12043.410	12110.770	12029.410	4404.692	0.000	1.000
27	Captures + Mesh + Month	Year + Species + Station + Species*Year + Year*Station	-6003.384	12044.770	12227.590	12006.770	4406.052	0.000	1.000
42	Sex	Year + Species + Station + Species*Year + Year*Station	-6039.599	12095.200	12172.190	12079.200	4456.482	0.000	1.000
44	Mesh	Year + Species + Station + Species*Year + Year*Station	-6053.290	12120.580	12187.950	12106.580	4481.862	0.000	1.000
45	Month	Year + Species + Station + Species*Year + Year*Station	-6045.845	12125.690	12289.290	12091.690	4486.972	0.000	1.000

A8. Complete list of species in dataset from five organizations with total number of captures, injuries and mortalities. Average injury rate, mortality rate, and standard deviations are taken from rates of injury calculated for each species at each location on each year. Family, species and weight information taken from Sibley (2003).

Lainname	Name	Family	Mas s (g)	Total captures	Total injuries	Averag e injury rate (%)	SD injury rate	Total mortalities	Average mortalit y rate (%)	SD mortalit y rate
<i>Accipiter striatus</i>	Sharp-shinnedHawk	Accipitridae	140	721	4	0	0.00	0	0.02	0.00
<i>Actitis macularius</i>	Spotted Sandpiper	Scolopacidae	40	2	0	0.00	0.00	0	0.00	0.00
<i>Aegolius acadicus</i>	Northern Saw-whet Owl	Strigidae	80	25	0	0.00	0.00	0	0.00	0.00
<i>Agelaius phoeniceus</i>	Red-winged Blackbird	Icteridae	52	33	1	8.33	28.87	0	0.00	0.00
<i>Aimophila ruficeps</i>	Rufous-crowned Sparrow	Emberizidae	18.5	43	1	0.98	4.04	0	0.00	0.00
<i>Ammodramus savannarum</i>	Grasshopper Sparrow	Emberizidae	17	4	0	0.00	0.00	0	0.00	0.00
<i>Aphelocoma californica</i>	Western Scrub Jay	Corvidae	85	397	7	2.02	6.17	0	0.00	0.00
<i>Archilochus alexandri</i>	Black-chinned Hummingbird	Trochilidae	3.3	53	0	0.00	0.00	0	0.00	0.00
<i>Baeolophus inornatus</i>	Oak Titmouse	Paridae	17	129	2	0.80	1.85	1	0.15	0.41
<i>Bombycilla cedrorum</i>	Cedar Waxwing	Bombycillidae	32	212	2	0.93	4.81	1	0.25	1.28
<i>Bombycilla garrulus</i>	Bohemian Waxwing	Bombycillidae	56	14	0	0.00	0.00	0	0.00	0.00
<i>Calcarius lapponicus</i>	Lapland Longspur	Emberizidae	27	1	0	0.00	0.00	0	0.00	0.00
<i>Calidris minutilla</i>	LeastFlycatcher	Scolopacidae	20	1	0	0.00	0.00	0	0.00	0.00
<i>Callipepla californica</i>	California Quail	Odontophoridae	180	511	4	0.68	2.37	5	1.02	2.99
<i>Calypte anna</i>	Anna'sHummingbir	Trochilidae	4.3	1958	25	1.74	2.93	8	0.30	0.56

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<i>Carduelis flammea</i>	Common Redpoll	Fringillidae	13	3262	2	0.02	0.07	14	0.22	0.43
<i>Carduelis hornemanni</i>	Hoary Redpoll	Fringillidae	13	93	0	0.00	0.00	0	0.00	0.00
<i>Carduelis lawrencei</i>	Lawrence's Goldfinch	Fringillidae	11.5	6	0	0.00	0.00	0	0.00	0.00
<i>Carduelis pinus</i>	Pine Siskin	Fringillidae	15	2018	18	0.80	2.24	3	2.00	14.00
<i>Carduelis psaltria</i>	Lesser Goldfinch	Fringillidae	9.5	323	4	1.06	3.13	2	0.17	0.93
<i>Carduelis tristis</i>	American Goldfinch	Fringillidae	13	1870	11	1.00	2.41	2	0.13	0.59
<i>Carpodacus cassinii</i>	Cassin's Finch	Fringillidae	26	229	0	0.00	0.00	1	0.17	0.78
<i>Carpodacus mexicanus</i>	House Finch	Fringillidae	21	1056	23	0.71	1.82	2	0.19	0.88
<i>Carpodacus purpureus</i>	Purple Finch	Fringillidae	25	4572	35	0.87	0.95	16	0.38	0.51
<i>Catharus guttatus</i>	Hermit Thrush	Turdidae	31	11589	95	0.73	1.21	18	0.10	0.27
<i>Catharus minimus</i>	Gray-cheeked Thrush	Turdidae	32	653	0	0.00	0.00	0	0.00	0.00
<i>Catharus ustulatus</i>	Swainson's Thrush	Turdidae	31	14886	89	0.83	1.99	19	0.10	0.28
<i>Catherpes mexicanus</i>	Canyon Wren	Troglodytidae	10.5	10	4	50.00	70.71	0	0.00	0.00
<i>Certhia americana</i>	Brown Creeper	Certhiidae	8.4	995	4	0.45	1.79	4	0.25	1.02
<i>Chamaea fasciata</i>	Wrentit	Timaliidae	14	9526	52	0.69	0.95	19	0.18	0.28
<i>Chondestes grammacus</i>	Lark Sparrow	Emberizidae	29	4	0	0.00	0.00	0	0.00	0.00
<i>Cistothorus palustris</i>	Marsh Wren	Troglodytidae	11	59	0	0.00	0.00	0	0.00	0.00
<i>Coccothraustes vespertinus</i>	Evening Grosbeak	Fringillidae	60	23	0	0.00	0.00	0	0.00	0.00
<i>Colaptes auratus</i>	Northern Flicker	Picidae	130	409	7	1.68	6.49	0	0.00	0.00
<i>Contopus cooperi</i>	Olive-sided Flycatcher	Tyrannidae	32	113	0	0.00	0.00	0	0.00	0.00
<i>Contopus sordidulus</i>	Western Wood Pewee	Tyrannidae	13	431	1	0.05	0.32	0	0.00	0.00
<i>Cyanocitta cristata</i>	Blue Jay	Corvidae	85	1	0	0.00	0.00	0	0.00	0.00
<i>Cyanocitta stelleri</i>	Steller's Jay	Corvidae	105	644	9	0.88	1.85	3	0.37	1.33

<i>Dendroica caeruleascens</i>	Black-throated Blue Warbler	Parulidae	10.2	3	0	0.00	0.00	0	0.00	0.00
<i>Dendroica castanea</i>	Bay-breasted Warbler	Parulidae	12.5	2	0	0.00	0.00	0	0.00	0.00
<i>Dendroica chrysoparia</i>	Golden-cheeked Warbler	Parulidae	9.8	1	0	0.00	0.00	0	0.00	0.00
<i>Dendroica coronata</i>	Yellow-rumped Warbler	Parulidae	12.3	25164	43	0.45	1.64	38	0.52	3.52
<i>Dendroica discolor</i>	Prairie Warbler	Parulidae	7.7	1	0	0.00	0.00	0	0.00	0.00
<i>Dendroica magnolia</i>	Magnolia Warbler	Parulidae	8.7	4	0	0.00	0.00	0	0.00	0.00
<i>Dendroica nigrescens</i>	Black-throated Gray Warbler	Parulidae	8.4	267	0	0.00	0.00	1	0.07	0.38
<i>Dendroica occidentalis</i>	Hermit Warbler	Parulidae	9.2	425	2	0.25	1.06	2	0.11	0.44
<i>Dendroica palmarum</i>	Palm Warbler	Parulidae	10.3	11	0	0.00	0.00	0	0.00	0.00
<i>Dendroica pensylvanica</i>	Chestnut-sided Warbler	Parulidae	9.6	10	0	0.00	0.00	0	0.00	0.00
<i>Dendroica petechia</i>	Yellow Warbler	Parulidae	9.5	6707	56	0.69	1.16	19	0.32	1.08
<i>Dendroica striata</i>	Blackpoll Warbler	Parulidae	13	978	0	0.00	0.00	1	0.12	0.64
<i>Dendroica tigrina</i>	Cape May Warbler	Parulidae	11	1	0	0.00	0.00	0	0.00	0.00
<i>Dendroica townsendi</i>	Townsend's Warbler	Parulidae	8.8	2353	13	0.67	2.25	5	0.21	1.02
<i>Dumetella carolinensis</i>	Gray Catbird	Mimidae	37	79	2	1.01	2.47	0	0.00	0.00
<i>Empidonax alnorum</i>	Alder Flycatcher	Tyrannidae	13.5	887	0	0.00	0.00	0	0.00	0.00
<i>Empidonax difficilis</i>	Western Flycatcher	Tyrannidae	11	8380	49	1.42	3.36	4	0.16	1.08
<i>Empidonax flaviventris</i>	Yellow-bellied Flycatcher	Tyrannidae	11.5	6	0	0.00	0.00	0	0.00	0.00
<i>Empidonax hammondi</i>	Hammond's Flycatcher	Tyrannidae	10	2671	6	0.09	0.29	6	0.28	1.14
<i>Empidonax minimus</i>	Least Sandpiper	Tyrannidae	10.3	6	0	0.00	0.00	0	0.00	0.00

<i>Empidonax oberholseri</i>	Dusky Flycatcher	Tyrannidae	10.3	4304	48	0.81	0.93	3	0.04	0.15
<i>Empidonax traillii</i>	Willow Flycatcher	Tyrannidae	13.5	1361	15	0.33	0.82	1	0.03	0.22
<i>Empidonax wrightii</i>	Gray Flycatcher	Tyrannidae	12.5	29	0	0.00	0.00	0	0.00	0.00
<i>Euphagus carolinus</i>	Rusty Blackbird	Icteridae	60	146	0	0.00	0.00	0	0.00	0.00
<i>Euphagus cyanocephalus</i>	Brewer's Blackbird	Icteridae	63	20	0	0.00	0.00	0	0.00	0.00
<i>Gallinago delicata</i>	Wilson's Snipe	Scolopacidae	105	13	1	4.17	10.21	0	0.00	0.00
<i>Gallinago gallinago</i>	Common Snipe	Scolopacidae	105	3	0	0.00	0.00	0	0.00	0.00
	Common									
<i>Geothly pistrichas</i>	Yellowthroat	Parulidae	10	2488	17	1.18	3.22	4	0.29	1.16
	Northern Pygmy-									
<i>Glaucidium gnoma</i>	Owl	Strigidae	70	33	0	0.00	0.00	0	0.00	0.00
<i>Hirundo rustica</i>	Barn Swallow	Hirundinidae	19	700	4	0.28	0.95	0	0.00	0.00
	Yellow-breasted									
<i>Icteria virens</i>	Chat	Parulidae	25	1190	8	5.02	21.77	0	0.00	0.00
<i>Icterus bullockii</i>	Bullock's Oriole	Icteridae	36	510	9	1.33	3.23	0	0.00	0.00
<i>Icterus cucullatus</i>	Hooded Oriole	Icteridae	24	5	0	0.00	0.00	0	0.00	0.00
<i>Icterus galbula</i>	Baltimore Oriole	Icteridae	33	1	0	0.00	0.00	0	0.00	0.00
<i>Ixoreus naevius</i>	Varied Thrush	Turdidae	78	928	44	3.17	5.41	3	0.27	1.23
<i>Junco hyemalis</i>	Oregon Junco	Emberizidae	19	26299	282	9.02	75.85	117	3.83	32.51
<i>Limnodromus scolopaceus</i>	Long-billed Dowitcher	Scolopacidae	115	2	0	0.00	0.00	0	0.00	0.00
<i>Loxia curvirostra</i>	Red Crossbill	Fringillidae	36	115	1	0.09	0.34	0	0.00	0.00
	White-winged									
<i>Loxia leucoptera</i>	Crossbill	Fringillidae	26	3	0	0.00	0.00	0	0.00	0.00
<i>Megasceryle alcyon</i>	Belted Kingfisher	Alcedinidae	150	36	1	5.56	23.57	0	0.00	0.00
	Western Screech-									
<i>Megascops kennicottii</i>	Owl	Strigidae	150	31	0	0.00	0.00	0	0.00	0.00
<i>Melanerpes formicivorus</i>	Acorn Woodpecker	Picidae	80	11	0	0.00	0.00	0	0.00	0.00
<i>Melospiza georgiana</i>	Swamp Sparrow	Emberizidae	17	54	2	3.65	12.53	1	1.56	6.25

<i>Melospiza lincolnii</i>	Lincoln's Sparrow	Emberizidae	17	5854	35	0.61	1.17	24	0.26	0.98
<i>Melospiza melodia</i>	Song Sparrow	Emberizidae	20	22680	140	0.41	0.50	59	0.21	0.22
<i>Mimus polyglottos</i>	Northern Mockingbird	Mimidae	49	133	2	0.92	2.17	0	0.00	0.00
<i>Mniotilt tavoria</i>	Black-and-white Warbler	Parulidae	10.7	16	0	0.00	0.00	0	0.00	0.00
<i>Molothrus ater</i>	Brown-headed Cowbird	Icteridae	44	392	3	0.83	3.27	0	0.00	0.00
<i>Myadestes townsendi</i>	Townsend's Solitaire	Turdidae	34	421	8	2.51	4.52	1	0.10	0.39
<i>Myiarchus cinerascens</i>	Ash-throated Flycatcher	Tyrannidae	27	61	0	0.00	0.00	0	0.00	0.00
<i>Oporornis agilis</i>	Connecticut Warbler	Parulidae	15	3	0	0.00	0.00	0	0.00	0.00
<i>Oporornis philadelphia</i>	Mourning Warbler	Parulidae	12.5	2	0	0.00	0.00	0	0.00	0.00
<i>Oporornis tolmiei</i>	MacGillivray's Warbler	Parulidae	10.5	5526	89	1.23	1.93	21	0.17	0.35
<i>Oreoscoptes montanus</i>	Sage Thrasher	Mimidae	43	2	0	0.00	0.00	0	0.00	0.00
<i>Otus flammeolus</i>	Flammulated Owl	Strigidae	60	3	0	0.00	0.00	0	0.00	0.00
<i>Parula americana</i>	Northern Parula	Parulidae	8.6	2	0	0.00	0.00	0	0.00	0.00
<i>Passer domesticus</i>	House Sparrow	Passeridae	28	31	0	0.00	0.00	0	0.00	0.00
<i>Passerculus sandwichensis</i>	Savannah Sparrow	Emberizidae	20	1859	5	0.11	0.50	6	0.11	0.38
<i>Passerella iliaca</i>	Fox Sparrow	Emberizidae	32	10143	63	0.50	1.11	29	0.45	1.71
<i>Passerina amoena</i>	Lazuli Bunting	Cardinalidae	15.5	896	20	0.99	2.22	1	0.47	3.05
<i>Passerina caerulea</i>	Blue Grosbeak	Cardinalidae	28	2	0	0.00	0.00	0	0.00	0.00
<i>Passerina cyanea</i>	Indigo Bunting	Cardinalidae	14.5	3	0	0.00	0.00	0	0.00	0.00
<i>Perisoreus canadensis</i>	Gray Jay	Corvidae	70	23	0	0.00	0.00	0	0.00	0.00
<i>Petrochelidon pyrrhonota</i>	Cliff Swallow	Hirundinidae	21	75	0	0.00	0.00	0	0.00	0.00

<i>Pheucticus ludovicianus</i>	Rose-breasted Grosbeak	Cardinalidae	45	11	0	0.00	0.00	0	0.00	0.00
<i>Pheucticus melanocephalus</i>	Black-Headed Grosbeak	Cardinalidae	45	2168	46	1.78	3.29	8	0.22	0.74
<i>Phylloscopus borealis</i>	Arctic Warbler	Sylviidae	9	22	1	3.13	8.84	0	0.00	0.00
<i>Phylloscopus fuscatus</i>	Dusky Warbler	Sylviidae	8.8	1	0	0.00	0.00	0	0.00	0.00
<i>Pica hudsonia</i>	Black-Billed Magpie	Corvidae	175	12	1	6.25	8.84	0	0.00	0.00
<i>Picoides albolarvatus</i>	White-headed Woodpecker	Picidae	61	12	0	0.00	0.00	0	0.00	0.00
<i>Picoides arcticus</i>	Black-backed Woodpecker	Picidae	70	2	0	0.00	0.00	0	0.00	0.00
<i>Picoides dorsalis</i>	American Three-toed Woodpecker	Picidae	65	12	0	0.00	0.00	0	0.00	0.00
<i>Picoides nuttallii</i>	Nuttall's Woodpecker	Picidae	38	127	1	0.39	1.56	1	0.37	1.47
<i>Picoides pubescens</i>	Downy Woodpecker	Picidae	27	912	4	0.25	0.96	1	0.05	0.40
<i>Picoides villosus</i>	Hairy Woodpecker	Picidae	66	265	3	0.67	2.66	0	0.00	0.00
<i>Pipilo chlorurus</i>	Green-tailed Towee	Emberizidae	29	25	2	15.00	33.75	0	0.00	0.00
<i>Pipilo crissalis</i>	California Towee	Emberizidae	44	356	10	2.81	5.74	1	0.14	0.83
<i>Pipilo maculatus</i>	Spotted Towhee	Emberizidae	20	7389	259	2.80	3.11	56	0.94	1.85
<i>Piranga ludoviciana</i>	Western Tanager	Thraupidae	28	3800	120	1.53	2.50	12	0.12	0.41
<i>Piranga rubra</i>	Summer Tanager	Thraupidae	29	2	0	0.00	0.00	0	0.00	0.00
<i>Poecile atricapillus</i>	Black-capped Chickadee	Paridae	11	1392	13	0.97	2.65	12	0.68	1.50
<i>Poecile gambeli</i>	Mountain Chickadee	Paridae	11	1146	25	1.69	2.25	8	0.69	1.37
<i>Poecile hudsonica</i>	Boreal Chickadee	Paridae	10	144	0	0.00	0.00	0	0.00	0.00

<i>Poecile rufescens</i>	Chesnut-backed Chickadee	Paridae	9.7	5325	47	0.84	0.95	14	0.22	0.41
<i>Polioptila caerulea</i>	Blue-gray Gnatcatcher	Sylviidae	6	56	0	0.00	0.00	0	0.00	0.00
<i>Poocetes gramineus</i>	Vesper Sparrow	Emberizidae	26	48	2	3.53	9.60	0	0.00	0.00
<i>Protonotaria citrea</i>	Prothonotary Warbler	Parulidae	16	2	0	0.00	0.00	0	0.00	0.00
<i>Psaltriparus minimus</i>	Bushtit	Aegithalidae	5.3	4033	25	0.73	1.02	9	0.21	0.56
<i>Regulus calendula</i>	Ruby Crowned Kinglet	Regulidae	6.5	28960	166	0.66	0.98	99	0.31	0.46
<i>Regulus satrapa</i>	Golden-crowned Kinglet	Regulidae	6	4828	21	0.54	1.26	9	0.14	0.43
<i>Riparia riparia</i>	Bank Swallow	Hirundinidae	13.5	6	0	0.00	0.00	0	0.00	0.00
<i>Salpinctes obsoletus</i>	Rock Wren	Troglodytidae	16.5	4	0	0.00	0.00	0	0.00	0.00
<i>Sayornis nigricans</i>	Black Phoebe	Tyrannidae	19	736	7	1.40	4.03	0	0.00	0.00
<i>Sayornis saya</i>	Say's Phoebe	Tyrannidae	21	3	0	0.00	0.00	0	0.00	0.00
<i>Seiurus aurocapilla</i>	Ovenbird	Parulidae	19.5	6	0	0.00	0.00	1	16.67	40.82
<i>Seiurus noveboracensis</i>	Northern Waterthrush	Parulidae	18	1301	1	0.19	0.96	2	0.08	0.28
<i>Selasphorus platycercus</i>	Broad-tailed Hummingbird	Trochilidae	3.6	3	0	0.00	0.00	0	0.00	0.00
<i>Selasphorus rufus</i>	Rufous Hummingbird	Trochilidae	3.4	979	15	0.86	2.33	8	0.68	1.84
<i>Selasphorus sasin</i>	Allen's Hummingbird	Trochilidae	3	4614	58	1.32	1.68	49	1.00	0.92
<i>Setophaga ruticilla</i>	American Redstart	Parulidae	8.3	33	0	0.00	0.00	1	0.56	2.15
<i>Sialia currucoides</i>	Mountain Bluebird	Turdidae	29	2	0	0.00	0.00	0	0.00	0.00
<i>Sialia mexicana</i>	Western Bluebird	Turdidae	29	32	0	0.00	0.00	0	0.00	0.00

<i>Sitta canadensis</i>	Red-breasted Nuthatch	Sittidae	10	1368	9	0.32	0.96	6	0.59	3.34
<i>Sitta carolinensis</i>	White-breasted Nuthatch	Sittidae	21	44	0	0.00	0.00	0	0.00	0.00
<i>Sitta pygmaea</i>	Pygmy Nuthatch	Sittidae	10.5	10	0	0.00	0.00	0	0.00	0.00
<i>Sphyrapicus nuchalis</i>	Red-naped Sapsucker	Picidae	50	20	0	0.00	0.00	0	0.00	0.00
<i>Sphyrapicus ruber</i>	Red-breasted Sapsucker	Picidae	50	460	2	0.90	3.54	0	0.00	0.00
<i>Sphyrapicus thyroideus</i>	Williamson's Sapsucker	Picidae	50	2	0	0.00	0.00	0	0.00	0.00
<i>Sphyrapicus varius</i>	Yello-bellied Sapsucker	Picidae	50	5	0	0.00	0.00	1	33.33	57.74
<i>Spindalis zena</i>	Western Spindalis	Thraupidae	21	2	0	0.00	0.00	0	0.00	0.00
<i>Spizella arborea</i>	American tree sparrow	Emberizidae	20	8603	13	0.12	0.22	24	0.21	0.40
<i>Spizella breweri</i>	Brewer's Sparrow	Emberizidae	10.5	452	8	1.17	2.34	3	0.34	0.79
<i>Spizella pallida</i>	Clay-colored Sparrow	Emberizidae	12	2	0	0.00	0.00	0	0.00	0.00
<i>Spizella passerina</i>	Chipping Sparrow	Emberizidae	12	2521	78	1.41	1.98	8	0.21	0.64
<i>Stelgidopteryx serripennis</i>	Northern Rough-winged Swallow	Hirundinidae	16	41	0	0.00	0.00	0	0.00	0.00
<i>Stellula calliope</i>	Calliope Hummingbird	Trochilidae	2.7	355	4	3.10	9.56	3	0.89	3.20
<i>Sturnus vulgaris</i>	European Starling	Sturnidae	82	109	2	1.17	3.94	0	0.00	0.00
<i>Tachycineta bicolor</i>	Tree Swallow	Hirundinidae	20	351	1	0.26	1.71	0	0.00	0.00
<i>Tachycineta thalassina</i>	Violet-green Swallow	Hirundinidae	14	208	1	0.30	1.66	0	0.00	0.00
<i>Thryomanes bewickii</i>	Bewick's wren	Troglodytidae	10	3574	15	0.85	2.76	11	0.50	2.03

<i>Toxostoma redivivum</i>	California Thrasher	Mimidae	84	2	0	0.00	0.00	0	0.00	0.00
<i>Toxostoma rufum</i>	Brown Thrasher	Mimidae	69	3	0	0.00	0.00	0	0.00	0.00
<i>Tringa flavipes</i>	Lesser Yellowlegs	Scolopacidae	80	31	0	0.00	0.00	0	0.00	0.00
<i>Tringa solitaria</i>	Solitary Sandpiper	Scolopacidae	50	104	0	0.00	0.00	0	0.00	0.00
<i>Troglodytes aedon</i>	House Wren	Troglodytidae	11	480	10	1.16	3.39	2	0.30	1.31
<i>Troglodytes troglodytes</i>	Winter Wren	Troglodytidae	9	1747	18	2.23	8.29	7	0.27	0.68
<i>Turdus migratorius</i>	American Robin	Turdidae	77	3843	64	1.62	2.63	11	0.24	0.68
<i>Tyrannus tyrannus</i>	Eastern Kingbird	Tyrannidae	40	18	1	3.33	5.77	0	0.00	0.00
<i>Vermivora celata</i>	Orange-crowned Warbler	Parulidae	9	15572	45	0.31	0.55	31	0.23	0.42
<i>Vermivora luciae</i>	Lucy's Warbler	Parulidae	6.6	1	0	0.00	0.00	0	0.00	0.00
<i>Vermivora peregrina</i>	Tennessee Warbler	Parulidae	10	13	0	0.00	0.00	0	0.00	0.00
<i>Vermivora pinus</i>	Blue-winged Warbler	Parulidae	8.5	1	1	100.00	0.00	0	0.00	0.00
<i>Vermivora ruficapilla</i>	Nashville Warbler	Parulidae	8.7	2822	14	2.27	8.82	4	0.04	0.16
<i>Vermivora virginiae</i>	Virginia's Warbler	Parulidae	7.8	2	0	0.00	0.00	0	0.00	0.00
<i>Vireo cassinii</i>	Cassin's Vireo	Vireonidae	16	1377	21	1.15	1.80	5	0.23	0.67
<i>Vireo flavifrons</i>	Yellow-throated Vireo	Vireonidae	18	1	0	0.00	0.00	0	0.00	0.00
<i>Vireo flavoviridis</i>	Yellow-green Vireo	Vireonidae	18	1	0	0.00	0.00	0	0.00	0.00
<i>Vireo gilvus</i>	Warbling Vireo	Vireonidae	12	4540	34	0.77	1.43	5	0.10	0.42
<i>Vireo huttoni</i>	Hutton's Vireo	Vireonidae	11	1375	10	1.16	3.29	6	0.49	1.55
<i>Vireo olivaceus</i>	Red-eyed Vireo	Vireonidae	17	6	0	0.00	0.00	0	0.00	0.00
<i>Vireo solitarius</i>	Blue-headed Vireo	Vireonidae	16	4	0	0.00	0.00	0	0.00	0.00
<i>Wilsonia canadensis</i>	Canada Warbler	Parulidae	10.3	7	0	0.00	0.00	0	0.00	0.00
<i>Wilsonia citrina</i>	Hooded Warbler	Parulidae	10.5	8	0	0.00	0.00	0	0.00	0.00
<i>Wilsonia pusilla</i>	Wilson's Warbler	Parulidae	7.7	17374	100	0.54	0.77	52	0.25	0.48

<i>Xanthocephalus xanthocephalus</i>	Yellow-headed Blackbird	Icteridae	65	6	1	16.67	0.00	0	0.00	0.00
<i>Zenaida macroura</i>	Mourning Dove	Columbidae	120	73	1	1.09	5.21	1	0.36	1.74
<i>Zonotrichia albicollis</i>	White-throated Sparrow	Emberizidae	26	93	0	0.00	0.00	0	0.00	0.00
<i>Zonotrichia atricapilla</i>	Golden-crowned Sparrow	Emberizidae	29	6730	87	1.15	3.33	11	0.08	0.28
<i>Zonotrichia leucophrys</i>	White-crowned Sparrow	Emberizidae	29	10416	221	2.20	4.95	29	0.92	5.68
<i>Zonotrichia querula</i>	Harris's Sparrow	Emberizidae	36	1	0	0.00	0.00	0	0.00	0.00

