

**The Effects of Landscape Structure and Climate
Change on the Movement, Connectivity, and
Population Viability of the Hawaiian gallinule
(*Gallinula galeata sandvicensis*)**

A dissertation

submitted by

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Abstract

This dissertation examines the effects of anthropogenic landscape change on the population structure, functional connectivity, and extinction risk of the Hawaiian gallinule (*Gallinula galeata sandvicensis*), an endangered subspecies of waterbird endemic to Hawai`i. Through a combination of field work, population genetic analysis, geospatial analysis, simulation modeling, and meta-analysis of published and unpublished work, I elucidate the behavioral and ecological mechanisms by which landscape structure impacts Hawaiian gallinule populations persisting on the island of O`ahu, Hawai`i. Hawaiian gallinules exhibited severe population declines throughout the late 19th to mid-20th century, a period coinciding with substantial development and reclamation of wetland habitat throughout Hawai`i. Their population on O`ahu has been slowly increasing since the late 1970's, and remaining populations persist in a fragmented, urbanized landscape. I quantified the extent of wetland loss across the archipelago, and investigated the population genetic impacts of this landscape fragmentation, as well as the recent population bottleneck, on the population structure of O`ahu's gallinule population. O`ahu had the greatest extent of wetland loss (in excess of 65%), concentrated particularly in the coastal lowlands, and sampled gallinule subpopulations across O`ahu showed moderately high genetic differentiation (overall microsatellite $F_{ST} = 0.098$, mtDNA $F_{ST} = 0.248$) across small spatial scales (1-35km). Using these genetic data, I tested a variety of biologically-informed movement hypotheses for how gallinules navigate the island's landscape. Models that treated water features like rivers, streams, and drainage canals as corridors for gallinule movement greatly outperformed other potential

movement models across different molecular markers, simulation methods, and statistical tests. I next combined my own field observations with previous work from government reports, Masters theses and Doctoral dissertations to generate the first comprehensive review and estimation of the vital rates of Hawaiian gallinules. Finally, I used an individually-based, spatially explicit population model to explore the climate and landscape change impacts on the viability of O`ahu's gallinule population. Sensitivity analysis highlighted the importance of juvenile and adult survival for overall population persistence, and the importance of dispersal in mediating source-sink dynamics on the island. I estimated that O`ahu's major gallinule habitats could lose >40% of their carrying capacity under sea level rise conditions predicted for the next century.

Oli Kia`i Manu

*E nā `aumākua
E nā kūpuna
E nā akua ē*

*Eia mai he kanaka holokai
aloha i ka `āina*

*E hō mai ka `ike
E hō mai ke ao
E hō mai nā mea huna
o nā manu ē*

*Eia mai he kia`i
I ka meheu
o nā kia manu ē*

*E hō mai
E ola ai
E manu aku ē*

Oli of the Bird Observer

*To the family guardians
To the ancestors
To the gods*

*Here stands a travelling man
who loves the land*

*Grant me knowledge
Give me enlightenment
Show me the hidden details
of the birds*

*Here stands a protector
in the footsteps
of the ancient feather-gatherers*

*Grant me knowledge
So that the birds may live
on forever*

Hawaiian Waterbird Research Oli (spiritual chant), composed in 2017 and edited for C. van Rees by Kumu Henani Enos and Martha Kawasaki

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“I’ve wandered the earth in search of life:
bird by bird I’ve come to know the earth.”

Pablo Neruda

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**The Effects of Landscape Structure on the Movement,
Connectivity, and Population Viability of the Hawaiian
gallinule (*Gallinula galeata sandvicensis*)**

“The owl and a bird called the *alae* were regarded as gods...”

King David Kālakaua

Legends and Myths of Hawai`i, 1887

Introduction

1.1 The Anthropocene Extinction Crisis

The present rate of species extinction may be 1,000 times higher than the typical (non-mass-extinction) background extinction rate (Lawton and May, 1995; De Vos et al., 2014), which is a normal and expected part of the evolutionary process. This elevated rate of extinction is known to be anthropogenic in origin, resulting from steadily mounting pressures exerted by growing human populations on prevailing geological, atmospheric, hydrological and ecological conditions on our planet (Vitousek et al., 1997; Brook et al., 2003). Notably, current rates of anthropogenic extinction are similar to rates observed in past geological epochs known as mass extinctions (e.g., the end Permian, ~250 million years ago; Wignall et al., 1996). It has been suggested that the present era has precipitated another such mass extinction, this one of human origin (Barnosky et al., 2011). This sixth mass extinction is part of what some researchers call the Anthropocene epoch (Crutzen, 2006) in which the majority of drivers of natural (hydrological, geological, ecological) processes on earth are of human origin (Steffen et al., 2007; Dirzo et al., 2014; Pievani, 2014). The rapidity and ubiquity of declines in populations and distributions of many

species is also referred to as the extinction crisis (Ceballos and Ehrlich, 2002; Thomas et al., 2004).

Though mass extinctions have been a regular part of earth's biological history, Anthropocene extinctions have substantial and unpredictable consequences for ecosystem processes (Ehrlich et al., 1983), many of which are critically valuable to societies, and human wellbeing in general (MEA 2005; Dobson et al., 2006; Turner et al., 2007; Ridder, 2008). The loss of these processes (also known as ecosystem services), is of major concern for future food production (Cumming et al., 2014) and fresh water resource management (Postel and Carpenter, 1997; Jewitt, 2002), among other issues of essential importance for human populations. Direct reliance on ecological processes is more widespread among economically disadvantaged peoples, skewing the negative impacts of biodiversity loss toward less politically and financially powerful groups and adding major concerns of social equity to the extinction crisis (Kumar and Yasahiro, 2014).

Accordingly, research on the mechanisms and drivers of Anthropocene extinctions is of critical importance for two separate and important reasons: 1) to improve theoretical understanding of the extinction process and the impacts of different perturbations on species distributions and abundances, taking advantage of unplanned experiments provided by human impact, and 2) to ensure the social and economic sustainability of modern societies and prevent human suffering on a global scale (MEA 2005; Haines-Young and Potschin, 2010).

1.2 Landscape change as mediator of anthropogenic impacts on biodiversity

Landscape change has been the primary driver in Anthropocene biodiversity loss and alteration of terrestrial habitats (August et al., 2002; Koh et al., 2004), and it is expected to continue in that capacity for the next century (Sala et al., 2000). In fact, landscape change is a primary pathway by which the effects of global climate change is impacting many organisms (McKelvey and Buotte, 2018). The primary mechanisms by which landscape change impacts wild populations is through direct loss of habitat and the fragmentation of remaining habitat, which isolates populations (Ehrlich and Pringle, 2008). While the impacts of habitat loss on population viability are typically related to deterministic drivers of species decline (the declining population paradigm; Caughley, 1994), the impacts of fragmentation are additionally relevant to stochastic processes relating to population extinction (the small population paradigm; Caughley, 1994)

Habitat loss causes declines by reducing the carrying capacity of the landscape through reductions in resource abundance (e.g., food, shelter, breeding sites, territorial space; Fahrig, 1997). At a certain point, populations decline to such a degree that additional, often less predictable factors contribute to extinction risk. Smaller populations are more vulnerable to extinction due to purely stochastic factors like environmental variation and demographic stochasticity (Morris and Doak, 2002). They also become vulnerable to biological pressures like inbreeding depression (Keller and Waller, 2002), and Allee effects (Courchamp et al., 2008). As a result, population reduction due to habitat loss not only brings populations numerically closer to extinction, but it exposes them to a number of new threats that contribute to extinction risk (Figure 1.1).

The persistence of small populations is influenced by the dispersal of individuals between them (Soulé, 1987; Noss, 1991; Hanski and Gaggiotti, 2004), a factor that is affected by a second impact of landscape change, habitat fragmentation. Habitat fragmentation results in a loss of connectivity, the degree to which habitats or populations are connected by the movement of individuals through the landscape (Taylor et al., 1993), and it is another major driver of declines (Wilcove et al., 1986; Wiens, 1995). Note that habitat can be lost without fragmentation, but the reverse is not true. Fragmentation can occur from the splitting of one contiguous habitat patch into two or more smaller, spatially disjunct habitats, with non-habitat matrix in between (Rodewald, 2003; Crooks and Sanjayan, 2006). It can occur with as little as the placement of a road (Keller and Largiadèr, 2003). Alternatively, habitat fragmentation also can be driven by changes in the intervening landscape matrix (Ricketts, 2001; Revilla 2004; Bender and Fahrig, 2005; Eycott et al., 2012), which can make it less permeable to animal movement (or in landscape connectivity terms, increases its *landscape resistance*). The biological mechanisms of fragmentation impacts on movement include reduced resource availability (Graham 2001), increased energetic costs from traversing the matrix (Baker and Rao, 2004; Belisle 2005), physical impediment by the matrix (Stevens et al., 2004), or increased mortality during dispersal (Russell et al., 2003; Driscoll et al., 2013). Habitat fragmentation also creates edge effects, which reduce the effective size of the remaining habitat fragments (Andrén and Anglestam, 1988; Saunders et al., 1991).

Connectivity of populations between habitat patches is primarily viewed through two analytical lenses that operate at different spatial, temporal, and biological scales. These two types of connectivity represent different levels of analysis (population vs.

individual) and they yield different information about animal-landscape interactions (Baguette and Van Dyck, 2007). Structural connectivity pertains more to the first type of fragmentation mentioned above, describing the physical structure of the landscape and the connectivity among populations embedded within it. This population-level viewpoint is useful for describing the impacts of landscape change, and examining threats at a landscape scale. By contrast, functional connectivity is the degree to which the habitat cover on a landscape facilitates movement and dispersal of individuals among habitat patches, and it has greater relevance to the second type of fragmentation. This latter, more mechanistic perspective can be particularly useful for simulation models and predicting the impacts of future conditions on wildlife populations (Knowlton and Graham, 2010).

Connectivity loss contributes to extinction risk by reducing the exchange of individuals between habitat patches, thereby affecting stochastic processes that threaten small populations (Crooks and Sanjayan, 2006). For example, reduction in movement reduces gene flow between populations, thus decreasing genetic diversity over time (Hill et al., 2006; André, 2008). This reduced genetic diversity can lead to inbreeding depression (i.e., negative changes in vital rates due to the accumulation of deleterious alleles, Frankham et al., 2002) or a loss of the evolutionary or adaptive potential of a population (Frankham, 2002). Connectivity loss also decreases the probability of population rescue (Pulliam, 1988) or recolonization (Hanski, et al., 2001), thus reducing the chances of species persistence at a larger, landscape scale. Where dispersal is uncommon and multiple populations are characterized by frequent extinction and

recolonization, populations are said to be part of a metapopulation (Hanski, 2001; Reed and Levine, 2005; Smith and Green, 2005).

Landscape changes can thus increase extinction risk through two related and complex mechanisms (Fahrig, 2002; Stevens et al., 2004), both of which are strongly dependent on animal behavior (Harris and Reed, 2002; Reed and Levine, 2005; Fordham et al., 2014). A quantitative understanding of such landscape-organism relationships (i.e., movement behavior; Johnson et al., 1992; Schick et al., 2008) is essential to predicting the effects of continued landscape and climate change on wildlife populations (Knowlton and Graham, 2010; Fordham et al., 2014).

1.3 Animal movement, population viability, and the importance of single-species studies

Research on animal movements explores the mechanisms behind many important phenomena in evolution and ecology (Baker, 1978; Tilman and Kareiva, 1997), and more recently it is helping to make conservation biology a more rigorous, predictive science (Lima and Zollner, 1996; Wiens, 1997; Haig, 1998). Indeed, interest in the ability of behavioral ecology to contribute to conservation theory has grown substantially in the 21st century (Reed, 1999, Gosling and Sutherland, 2000; Caro, 2007), with movement ecology and connectivity playing an especially substantial role (Berger-Tal et al., 2016).

Population viability analysis (PVA) is a key process by which conservation biologists integrate information on a species' natural history and behavior to generate quantitative and predictive measures of extinction risk (Morris and Doak, 2002). Such analyses are a powerful tool for assessing the impact of anthropogenic landscape change on wildlife

populations, and, depending on their design, can include deterministic and stochastic mechanisms related to both habitat loss and fragmentation (Morris and Doak, 2002; Reed et al., 2002). Although PVAs come in many forms, spatially explicit, individual-based analyses that simulate the stochastic and behavioral elements of individuals within a population are of special interest for measures the effects of landscape change on extinction risk (Dunning et al., 1995; Haig et al., 1998). Individual-based models (IBMs) are effective at modeling populations where spatial heterogeneity and demographic stochasticity are important components of extinction risk, as with small and fragmented populations (DeAngelis and Mooij, 2005). IBMs also capture the potential variation between individual life histories, taking a mechanistic approach that can yield probability estimates across stochastic replicates, rather than describing the average behavior of a population, as is done with matrix-based models (DeAngelis and Rose, 1992; Uchmanski and Grimm, 1996; Letcher et al., 1998).

With the advent of remote sensing, geographic information systems (GIS), high-resolution genetic data, and more powerful computing capacity, data on animal movements have become a growing resource for conservation research (Macdonald and Johnson, 2001; Thurfjell et al., 2014). For example, geolocators have been used to help identify important overwintering sites for migrating birds (McKinnon et al., 2013), and landscape genetic analyses have highlighted previously unknown routes in dispersing salamanders (Wang et al., 2009). Although simulation-based PVAs and research on animal movement behavior are powerful tools to understand important drivers of extinction risk, they have key shortcomings that can limit their widespread application.

Movement behavior is difficult to study in many, especially highly mobile, organisms, due to the expense of tracking equipment or effort involved with tagging and resighting or recovering individuals (Ims and Yoccoz, 1997; Wiens, 1997). Among other challenges are the difficulties of achieving a meaningful sample size, and analyzing large volumes of spatial data (Bauer and Klaassen, 2013). At the same time, PVAs require detailed information across most of an organism's life cycle, and stochastic, simulation-based models also call for information on the variation in these parameters (Beissinger and Westphal, 1998; Morris and Doak, 2002). Large sample sizes are needed to account for the potential variation in vital rates possible in the populations being modeled, and studies of between 8-20 years are recommended to account for temporal variability that may bias extinction predictions (Pimm and Redfearn 1988; Pimm 1991; Arino and Pimm, 1995). Integrating movement data into PVAs of multiple populations requires accurate data on movement between multiple sites and further increases data requirements (Fahrig and Merriam 1985; King and With 2002; Reed et al., 2002). In addition to large data demands (Radchuk et al., 2016), both PVA and movement studies typically also lack generalizability, being based on types of data that vary widely between species and even between populations of the same species (Clobert et al., 2004; Baguette and Van Dyck 2007). For example, PVAs are highly context-specific (Traill et al., 2007) with little forthcoming evidence that specific population viability estimates can be predicted by ecological correlates (Reed et al., 2002; Traill et al., 2007).

The substantial data needs for examining the interactions between landscape change and population dynamics from animal movement to population connectivity and even to extinction risk make studies on these topics amenable to a single-species approach, which

requires concentration on one study organism to seek out specific mechanisms behind their decline (Haig et al., 1998; Lindenmayer et al., 2007). Because they often lack generality (van Kleunen et al., 2014), single-species studies merit careful attention to the selection of study system. Selection should focus on two key aspects: The selected study species should 1) have ecological characteristics and threats that are widely relevant to other threatened taxa, and 2) should have sufficient existing data on its habitats and natural history to allow sufficiently detailed and useful research.

1.4 Hawaiian wetlands and the Hawaiian gallinule (ʻAlae ʻula)

In this dissertation I investigate the life history of the Hawaiian gallinule (ʻAlae ʻula, also known as the Hawaiian moorhen; *Gallinula galeata sandvicensis*), an endangered waterbird subspecies endemic to the Hawaiian Islands, with particular focus on the consequences and mechanisms of landscape change on population persistence. Hawaiian gallinules are a useful taxon for a single-species approach to landscape effects on extinction risk for several reasons. First, they have a number of characteristics associated with a disproportionate number of endangered species, including habitat specialization (Brown, 1971; Brown and Maurer, 1989), reliance on freshwater habitats (Ricciardi and Rasmussen, 1999; Poff et al., 2012), and a narrow distribution (McKinney, 1997; Owens and Bennett, 2000) – in this case on islands (Diamond 1984; Vitousek, 1988; Blackburn et al., 2004). These aspects collectively make detailed studies of the Hawaiian gallinule potentially informative for the conservation of a variety of other taxa.

Over the last century, the Hawaiian gallinule has had its range reduced to only two islands, Oʻahu and Kauaʻi, and all of my research was on the Oʻahu population. The

spatial context of Hawaiian gallinules on the island of O`ahu is also relevant to their value as a focal species. On this island the birds persist in fragmented populations within an increasingly urbanizing, tropical landscape undergoing rapid human population growth (van Rees and Reed, 2014). This type of setting and suite of threats is shared by many declining and threatened taxa found in developing countries (Myers et al., 2000). In addition to the similarity of their situation to many other threatened taxa, Hawaiian gallinules are also an analytically tractable study species, because they are discretely distributed (within discrete, isolated wetland patches, and within islands, a closed system), enabling simple analysis based on discrete subpopulations. Unlike many endangered taxa in developing, tropical regions, the Hawaiian gallinule is in a part of the world that should have sufficient funding (though Hawaii receives a disproportionately small amount of endangered species spending in the U.S.; Leonard, 2008; Luther et al., 2016), there are extensive existing spatial and ecological databases, and the infrastructure to support continued, in-depth study. Accordingly, some of the life-history data needed for the analyses discussed in section 1.3 is available from published and unpublished reports (e.g., Nagata, 1983; Banko, 1987; Chang, 1990), spatial data are available, and remaining data can be collected.

My overall goals of this thesis are to **1)** quantify the extent and effect of habitat loss and fragmentation on Hawaiian gallinule populations on O`ahu, **2)** gain insights into the movement ecology of Hawaiian gallinules on a changing landscape, and **3)** determine the relative impacts of habitat loss, fragmentation, and climate change on extinction risk for Hawaiian gallinules. Although an exhaustive investigation of the movement ecology of the Hawaiian gallinule and its impacts on population viability is beyond the time frame of

this thesis, this work should serve to synthesize information on the taxon, fill in key knowledge gaps from both an applied and theoretical perspective, and highlight research priorities for the future.

In Chapter, 2, I synthesize geospatial analysis and simple hydrological models with historical reports to estimate the extent of natural wetlands in the main Hawaiian Islands prior to human settlement, and from this assess the degree of loss of this imperiled habitat on each of the main Hawaiian Islands. This study reveals the extent of habitat fragmentation due to wetland loss in Hawaii, especially on O`ahu.

In Chapter 3, I examine the degree to which this habitat loss and fragmentation has affected current populations of Hawaiian gallinules, by examining genetic evidence of past population decline, and of current structure (patterns of gene exchange) between remaining subpopulations. Genetic distance data collected in this study also provide information on dispersal rates between spatially-isolated subpopulations, although these estimates are limited to dispersal events which led to breeding (gene flow).

I examine the potential mechanisms that might have caused observed patterns of genetic structure in Chapter 4. To do this, I use a landscape genetics framework to study the movement behavior of Hawaiian gallinules, using gene flow as a proxy for individual dispersal. I test a suite of biologically-informed hypotheses about gallinule movement to determine which hypothesis is most consistent with the observed genetic differentiation.

In Chapter 5, I combine four years of my own field observations and mark-resight data with unpublished studies to estimate the vital rates—survival rate and reproductive success—of Hawaiian gallinules on O`ahu. These synthesized data form the foundation for population projection models in this taxon.

Combining information from the previous four chapters, in Chapter 6 I conduct a spatially explicit PVA of the Hawaiian gallinule population of O`ahu. This study makes use of vital rate estimates synthesized and generated in previous chapters, including survival, reproduction, and movement rates, and assesses the relative contribution of these parameters to extinction risk in gallinules. Part of my focus in this chapter is to determine the potential effects of climate change—specifically, sea-level rise—on population viability, and the degree to which current and potential management actions affect the viability of gallinule populations.

Finally, Chapter 7 provides a summary of the findings from this thesis, with a specific section on management recommendations based on this single-species analysis. Additionally, I discuss what insights this study has provided that might apply to other threatened taxa, and make recommendations for further study in this system and on related topics.

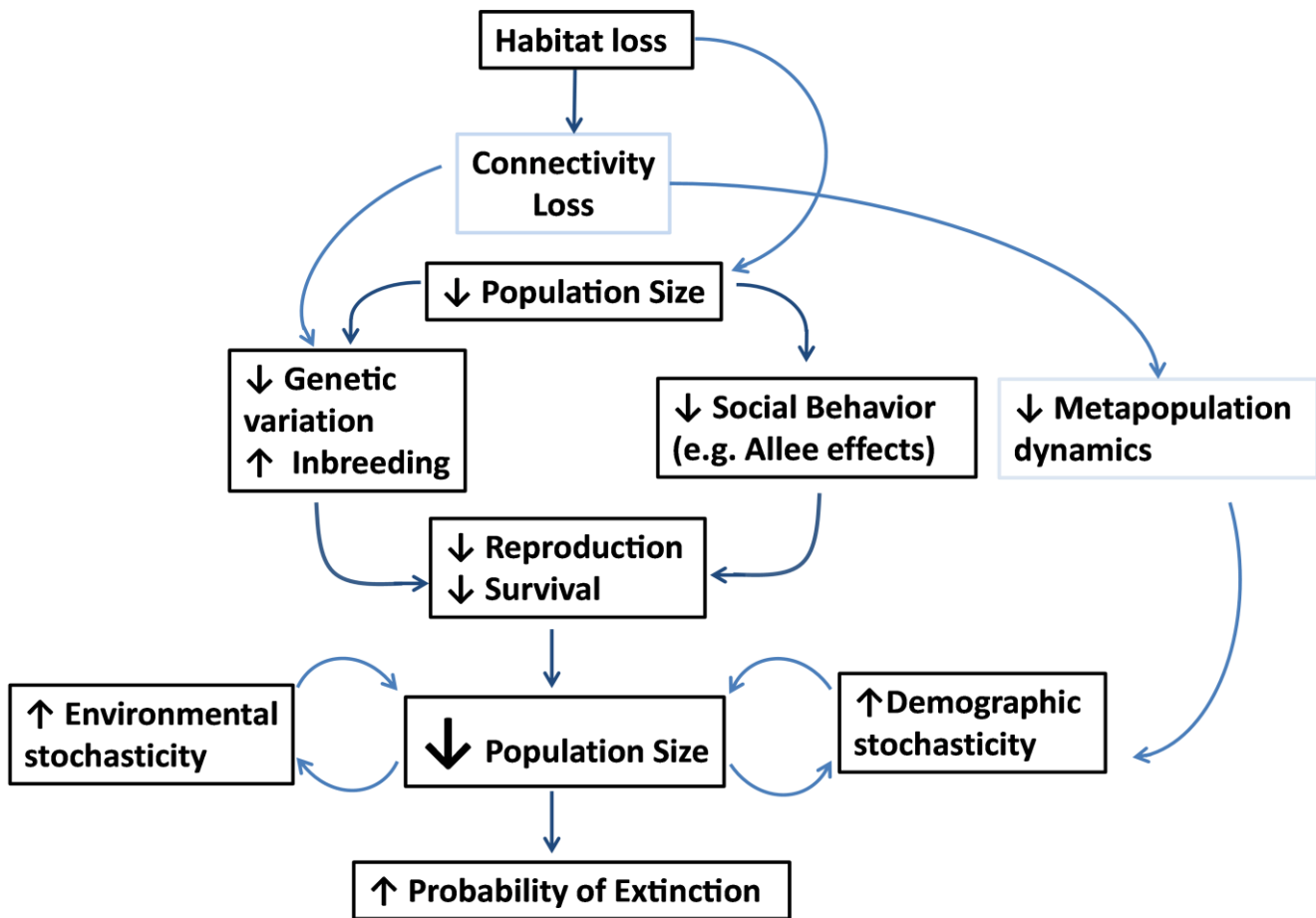


Figure 1.1: Loss of connectivity exacerbates the genetic consequences of small population size, and increases effects of demographic stochasticity by reducing the buffering effect of metapopulation dynamics. Figure modified from Mills, 2007.

Chapter 2

Wetland Loss in Hawai`i since human settlement

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Abstract

Wetland inventories are essential to understanding human effects on wetland distributions, estimating rates of wetland loss and setting recovery goals for endangered species. Wetlands in the Hawaiian archipelago (U.S.A.) support human water demands for agriculture, a rapidly expanding urban population, and 222 federally listed threatened or endangered plants and animals. The only published assessment of wetland loss for Hawaii was done in 1990, before significant advances in Geographic Information Systems (GIS) and computing technology. We estimated wetland loss on the 5 main Hawaiian Islands since human settlement using the National Wetlands Inventory, hydric soil maps, rainfall, and topographic data. We used the Topographic Wetness Index (TWI) to estimate pre-settlement wetlands in sites where hydric soil evidence was unavailable or unreliable. We found that TWI makes a useful complement to hydric soil evidence in estimating wetland loss in highly developed areas. We estimate statewide wetland loss at 22%, compared to 12% from the 1990 estimate, ranging from 6-8% loss on Maui, Moloka`i, and Kaua`i to 65% loss on Oahu, the most developed of the islands. The majority of wetland losses occurred in coastal areas where 61% of wetlands have been lost, while only 8% were lost at higher elevations.

2.1. Introduction

The first widely publicized assessment of the ecological services that wetlands provide placed their global value at approximately US\$4.8 trillion per year (Costanza et al., 1997). Although the exact value of wetlands is uncertain and context dependent (Turner, 2000; Woodward and Wui, 2001), it is well established that wetlands provide a wide variety of valuable ecological services (Barbier et al., 1997; Zedler and Kercher, 2005; Ghermandi et al., 2010; Blackwell and Pilgrim, 2011; de la Hera et al., 2011; Horowitz and Finlayson, 2011). This makes wetland losses particularly significant. It is estimated that during the 20th century, more than 50% of wetlands in parts of North America, Europe, and Australia were lost to anthropogenic landscape change (OECD/IUCN, 1996; Millennium Ecosystem Assessment, 2005). Information regarding the extent and rate of loss of wetlands is lacking throughout much of the world and warrants further efforts (Finlayson et al., 1999; Scott, 1993). Wetland inventories are important in landscape and water planning, and they can play an important role in documenting and anticipating conflicts over water resources (Ellison, 2009; Griffin, 2012), as well as the losses of wetland-dependent ecosystems and their associated species and ecological services (Jones and Hughes, 1993).

Consequently, our goal was to estimate wetland loss from the main islands of the Hawaiian archipelago, a biodiversity hotspot with high rates of extinction due to human activities, introduced diseases, and non-native invasive species (e.g., Ziegler, 2002; Reed et al., 2012). The Hawaiian Islands are a volcanic archipelago in the central Pacific Ocean, stretching across 2450 km. The Hawaiian Islands are the most isolated land mass on the planet, situated 3800 km from North America and nearly twice that distance from

East Asia and Australia. The islands have a wide variety of wetlands, ranging from small, anchialine pools along the coast to large, high-elevation bogs (Stone, 1989a). The most extensive types of wetlands on the main Hawaiian Islands (Kaua`i, O`ahu, Moloka`i, Maui, Hawai`i) are freshwater lowland marshes and montane wet forests and bogs (U.S. Army Corps of Engineers, 2012; U.S. Fish and Wildlife Service, National Wetlands Inventory data, 2010). Despite abundant orographic rainfall, precipitation is unevenly distributed between the windward and leeward sides of the younger, higher elevation islands. Average rainfall on the windward sides of these islands ranges from 2.5–7.6 m annually, while the leeward sides of Hawai`i and Maui average only 0.25 m (Meier et al., 1993). This uneven distribution, coupled with intense population growth and water supply uncertainty over the last century, has given rise to competition and conflict over water resources (Gopalakrishnan et al., 1996, 2007; Ridgley and Lumpkin, 2000; Liu, 2007; Miike, 2004; Shield et al., 2009; Lasky, 2010). Contemporary water conflicts on Hawai`i are the product of not only climatic factors but also the area's unique historical context.

Prior to European arrival, Polynesian colonists managed water extensively through stream diversions and wetland alteration for traditional taro (*Colocasia esculenta*) agriculture (Kirch, 2000; Müller et al., 2010). Water diversion and groundwater use increased exponentially with the arrival of Europeans and the advent of plantation agriculture in the 18th and 19th centuries and much of the landscape was converted to sugar cane, pineapple, and rice agriculture (Coulter, 1933; Handy et al., 1972, Meier et al., 1993; Wilcox, 1996). The decline in the relative economic importance of plantation agriculture after World War II coincided with rapid human population

growth and urban development, which had the cumulative effect of extensive wetland loss in Hawai`i, especially on O`ahu (Giambelluca, 1986; Meier et al, 1993). For example, the largest wetland in Hawaii was in the Mana region (central west coast) of Kaua`i, which was lost to water diversions for sugar cane (Swedberg, 1967; Shallenberger, 1977). Currently, basal aquifers are the primary source of freshwater in Hawai`i (Liu, 2007), and continued human population growth increases ground-water withdrawals (e.g., Ridgley and Giambelluca, 1991; USGS, 2007) while changes in land use patterns may be reducing groundwater recharge (Giambelluca, 1986). The uncertainty of Hawai`i's water security may give rise to conflicts between societal and ecological needs for fresh water; further threatening Hawai`i's remaining wetlands. Water security might be further compromised by global climate change; Hawaiian wetlands and groundwater resources will be affected by shifts in precipitation and temperature regimes and accelerating sea level rise (Nicholls et al., 1999; Chu et al. 2010, Keener et al. 2012). In contrast, the collapse of the sugarcane and pineapple industries in Hawai`i in the early 1990s has created an unprecedented opportunity for reallocating water and land resources, addressing water scarcity, and for wetland restoration (Ridgley et al., 1997; Ridgley and Lumpkin, 2000; Derrickson et al., 2002; Shield et al. 2009). Accurate information on wetland distributions before human settlement would help inform allocation decision-making and resolution of water conflicts.

Included in future water allocations will be considerations for Hawaiian wildlife (including plants) conservation, particularly for endangered species. Wetlands on Hawai`i support 222 taxa (species, subspecies, varieties, island populations) of plants and animals that are listed under the U.S. Endangered Species Act (ESA), most of which are

endemic to the islands (list available from authors). To put this number in perspective, ESA-listed taxa native to Hawai'i account for 28.5% of the 1476 listed, and of these 53% occupy wetlands in at least part of their range. Human activities began affecting wetland wildlife soon after the arrival of Polynesian settlers, who arrived as early as 500 C.E. (Graves and Addison, 1995). These early settlers converted and drained wetlands for agriculture, especially the cultivation of taro (Kirch et al., 2004). Subsequent to both Polynesian and European settlement of Hawaii were impacts to native wildlife from introduced, invasive competitors, predators, and diseases (e.g., Stone, 1989b; U. S. Fish and Wildlife Service, 2011; Reed et al., 2012). For example, despite containing approximately 280 ha of wetlands, Kawainui Marsh, a wetland on `Oahu that is designated as a Ramsar site, provides less than 8 ha of habitat for native waterbirds because the rest is overgrown with non-native, invasive vegetation (Ramsar Sites Information Service; <http://www.wetlands.org/RSDB/default.htm>). The U.S. Army Corps of Engineers has begun efforts to change this trend; for example in restoring 16 ha of habitat in the Kawainui marsh which makes available an additional 9.7 ha of wetland habitat. Wetlands like the Kawainui will require regular removal of non-native invasive plants to remain suitable (U.S. Army Corps of Engineers, 2008). Climate change will exacerbate threats to wetland specialists (Loope and Giambelluca 1998, Benning et al. 2002, Baker et al. 2006, Atkinson and LaPointe 2009, Reynolds et al. 2012), making wetland protection and mitigation even more important.

The only published estimate of wetland loss in Hawai'i is found in Dahl (1990), which cited an assessment by the United States Fish and Wildlife service (by A. Yuen, unpubl. data) estimating that Hawai'i had lost 12% of its wetlands since 1780. Although

the analysis by Yuen no longer exists (A. Yuen, and numerous others, pers. comm.), the results were summarized by Kosaka (1990 *in litt.*; available from the authors). This summary notes that all of the estimated wetland loss was from coastal and low-elevation areas (<~300 m), where 31% of the wetlands were lost; no wetland loss was reported from higher elevations. The summary results from the 1990 study do not provide information specific to particular Hawaiian Islands, nor is information provided on data sources or methods used to analyze data. Island-specific data would be an important addition to any estimate of wetland loss for the Hawaiian Islands, because it is likely that loss varies greatly between islands due to differences in human population size and levels of urbanization. The 1990 study was completed before significant advances in computing and geographic information systems (GIS) technology, which have significantly improved the accuracy and rigor of studies of landscape change. In this paper we present an estimate of anthropogenic wetland loss for the five largest islands of the state of Hawai`i using newly available data and spatial analysis software to improve upon the estimates currently used for wetland management in Hawai`i. We used surveys by government agencies, remotely sensed images, a simple hydrological model, and GIS to estimate the extent of wetlands in Hawai`i in the absence of human activities, and compared this to a current estimate of wetland area to estimate wetland losses since human colonization.

2.2 Materials and methods

2.2.1 Study area

We estimated wetland losses for the islands of Hawai`i, O`ahu, Maui, Kaua`i, and Moloka`i; these are the main islands of Hawaii, comprising 95.6% of the land area and 97.5% of the population of the state. The smaller islands of Lana`i and Ni`ihau were excluded because of insufficient or low-quality data. We estimated wetland cover before Polynesian colonization using inventories of existing wetlands, soil survey data and hydrological models to simulate the distribution of wetlands prior to anthropogenic disturbance. We followed the wetland definition used by the U.S. Environmental Protection Agency and U.S. Fish and Wildlife Service (Federal Interagency Committee on Wetland Delineation, 1989), but excluded deepwater marine habitats included in National Wetland Inventory maps. This definition includes wetlands that are typical for volcanic Pacific islands, including depressional wetlands, sloped marshlands, hanging bogs, high elevation montane bogs, forested wetlands, riverine wetlands, and salt- and mud-flats (U.S. Army Corps of Engineers, 2012). To simplify analysis, we excluded small offshore islands, whose contribution to wetland extent was considered negligible, and where human alterations that would affect hydrology have been minimal.

2.2.2 Data sources

We downloaded National Wetlands Inventory (NWI) data (U.S. Fish and Wildlife Service, 2010) using the U.S. Fish and Wildlife Service's wetland mapper tool (<http://www.fws.gov/wetlands/Data/Mapper.html>) for all of Hawai`i's main islands. NWI maps were used as the primary data source in estimating current wetland extent, and as a reference for estimating the distribution of pre-settlement wetlands. We acquired data layers on hydric soils from the National Resources Conservation Service (NRCS) Soil

Data Mart (<http://soildatamart.nrcs.usda.gov/>) which included tabular data updated in 2012 and survey data collected in the early 1970s. We used hydric soils as evidence of pre-settlement wetlands, as in Tiner (2005) (see also Dahl, 1990; Moorhead and Cook, 1992; Tiner and Bergquist, 2003). Hydric soils, soil types which show physical and chemical signs of periods of anoxia and inundation with water, can persist in the environment after alteration of the landscape and hydrological regime, and hence are often used as indicators of lost wetlands (Moorhead, 1991). We also used hydric soil data to detect portions of current wetlands not mapped in NWI surveys.

In certain cases, (for example in heavily developed, altered landscapes, or in areas with impervious cover), hydric soil data can be missing (e.g., landcover impedes sampling, as with parking lots) or misleading (e.g., where soil has been altered, removed, or replaced). These instances are most common in urban areas, in which case, hydric soils may not accurately indicate the presence of pre-settlement wetlands (Moorhead and Cook, 1992). To account for this uncertainty, we applied the Topographic Wetness Index (TWI, Beven and Kirkby, 1979), a hydrological model which uses elevation maps to predict where water accumulates on a landscape, to gauge whether intensely developed areas were likely to have supported wetlands prior to development. TWI has been shown to accurately predict hydrogeological processes affecting soil morphology (Gessler, 1995), and more recently to predict wetland bird assemblages in floodplains (Besnard et al, 2013). We calculated TWI using 10 m digital elevation models created in 2007 (Department of Commerce et al., 2007).

We used three additional data sources for visual analysis of land cover and truthing of wetland estimates. These included Landsat 7 ETM+ images (U.S. Geological

Survey, 2002), false-color Digital Orthophoto Quarter Quadrangle (DOQQ) images (U. S. Geological Survey, provided by the Hawai'i Geospatial Consortium and the State of Hawaii GIS Program), and land-cover maps from NOAA's coastal change analysis program (NOAA Coastal Services Center, 2000).

2.2.3 Pre-settlement wetland cover estimation

We processed hydric soil data using SoilDataViewer 6.0 (National Resources Conservation Service, 2011) in ArcGIS 10.1 (ESRI 2012). Map units were classified as “All Hydric” (all soils in the map unit received a hydric rating), “Partial Hydric” (one or more components of the map unit received a hydric rating), “Unknown Hydric” (at least one component in the map unit received no rating, and at least one received a hydric rating) or “Not Hydric” (no components of a map unit received a hydric rating).

All map units classified as “All Hydric” were classified as pre-settlement wetlands. All map units classified as “Partial Hydric” or “Unknown Hydric” were assumed not to be wetlands unless visual analysis, landcover datasets, or NWI maps showed evidence of a past wetland or that a wetland had been altered (e.g. water diversion channels, drainage canals, etc.). Hydric map units located on currently developed land were considered pre-settlement wetlands lost to development. All hydric map units associated with artificial wetlands (e.g. golf course water hazards, irrigation ponds) that were not surrounded by hydric soils or other evidence of natural wetlands were excluded and assumed to be generated by artificial wetlands. In all ambiguous cases map units were assumed not to represent pre-settlement wetlands.

We used NWI data to detect extant wetlands that were not recognized by hydric soil surveys. Wetland map features representing artificial wetlands were excluded for

pre-settlement estimates. Artificial wetlands were identified by context (surrounding structures), shape, or local map information (e.g. area labeled as “sewage treatment plant”). Map features in undeveloped areas, or with no sign of human alteration to local hydrology, were included as pre-settlement wetlands under the assumption that natural wetlands existing in 2010 existed before human colonization and development.

TWI was calculated using 10 m Digital elevation models and the Geomorphology and Topology toolbox (Evans and Oakleaf 2011) in ArcGIS 10.1. To avoid overestimation of pre-settlement wetlands, TWI was run only on regions identified to have undergone high-intensity development that would preclude soil sampling or would give misleading soil results. These areas were identified using Landsat 7 ETM+ and DOQQ images in conjunction with NOAA landcover analyses, and were chosen based on criteria of housing density, amount of impervious cover, and evidence of water management like ditches and canals. These areas accounted for 5% or less of the total land area of the islands analyzed, with the exception of Oahu, of which 18% was considered highly developed. TWI values, which are unitless and can run from 0 (no water accumulation potential) to higher values with increasing accumulation potential, were calculated for 10 m x 10 m pixels within each developed zone. There is no set TWI value associated with the presence of a wetland, so a cutoff value had to be determined for our study area. We did this by running TWI for each of our study islands to determine what values were associated with extant wetlands. We found that pixel values within an island were generally bimodally distributed, with one large peak in the lower end of the range (3-9), and a smaller, right-tailed peak at around 10-12. Pixels falling within the range of the second peak tended to fall within existing wetlands or areas with

hydric soils. We therefore set threshold TWI values for the developed portions of each island at the peak of the higher mode of that island's TWI distribution, classifying all pixels with TWI beyond the threshold as pre-settlement wetlands. The island of Hawai'i was an exception, in that the distribution of TWI values did not create a clear bimodal distribution, but rather a positively skewed unimodal distribution with a tail toward higher TWI values. For this island we chose a threshold value representing the 75th percentile of TWI values on the island, which contained values found in known runoff-fed wetlands. Because of the small proportion of developed land on the island of Hawai'i, our results were fairly insensitive to this threshold value.

Pre-settlement wetland coverage maps were then created by converting modified hydric soil and NWI maps to 10 m x 10 m raster images, and combining these with TWI data using the raster calculator in ArcGIS. These maps were then reclassified so that all pixels indicated to be pre-settlement wetland by any of the three datasets were given a value of "1" and all other pixels given a value of "0". Calculations were done independently for each island.

2.2.4 Current wetland inventories

NWI maps were used as the main data source for current wetland estimates. Deepwater marine habitats were excluded for the analysis, but artificial wetlands were included to recognize where human development contributed to the total extent of current wetlands. For many existing wetlands, the spatial extent of associated hydric soils was beyond the limits of the wetland identified by the National Wetland Inventory. In such cases, pre-settlement wetlands would appear larger than current wetlands simply because different evidence was used. To avoid this potential bias toward wetland loss, we

augmented NWI surveys with hydric soil data. All hydric soil map units corresponding to natural wetlands were identified as current wetlands. Natural wetlands were identified by shape, presence on undeveloped landscape, and distance from nearest development, as well as through maps of protected areas. On developed lands, hydric soil map units were counted as current wetlands if (a) they were adjacent to or apparently resultant from an existing wetland feature or (b) visual analysis indicated an extant wetland was possible in the region (water sources evident without diversion canals, houses, impervious cover, etc.). In ambiguous cases, hydric soil units were included as current wetlands to maintain a conservative estimate of wetland loss. NWI and hydric soil layers were converted to raster files and reclassified using the same processing steps as for pre-settlement data, then added to create a complete map of current wetlands.

2.2.5 Wetland loss

Overall wetland loss statistics were calculated by subtracting pixel counts of current estimates from pre-settlement estimates. Maps of wetland loss distribution were calculated by subtracting pre-settlement estimate images from current estimate images in the raster calculator. Inventories were subdivided by elevation category (coastal plains, elevation < 304.8m, vs. mid to high elevations, elevation > 304.8m), and values for loss in each elevation category calculated. These elevation categories were selected to allow direct comparison to the 1990 estimate of wetland loss in Hawaii (Kosaka, *in litt.*)

2.3. Results

2.3.1 *TWI model performance*

TWI values for each pixel in our island-wide assessment for all islands ranged from 0 to ~35. Threshold TWI values for designating a developed area as having supported a pre-settlement wetland were: 9.85 for Hawai`i, 11.2 for O`ahu, Maui 11.0, Kaua`i 12.6, and 11.12 for Moloka`i. Thresholded TWI images accurately predicted the location of extant wetlands that are supported by accumulation of surface or groundwater (e.g., inland estuarine marshes, lowland depressional wetlands), but were not used in calibration. The model was generally unable to predict the presence of wetlands created and sustained by water sources independent of natural surface water flow, such as tidal inundation, irrigation, and extremely high rainfall. This last category was important in high-elevation forested areas on the islands of Hawai`i and Kauai, which sustain hydric soil conditions despite steep slopes. The thresholded TWI model successfully identified several developed areas that were known *a priori* to have supported wetlands prior to development, e.g. the area in and around Kailua, which was formerly part of the larger wetland now restricted to Kawainui marsh (Figure 2.1).

2.3.2 *Wetland loss*

We estimated that the state of Hawai`i has lost 526 km², or 22% of its pre-settlement area of wetlands, and that these losses were spread unevenly across the islands. The islands of Maui, Moloka`i, and Kaua`i experienced losses on the order of 6-8% of their estimated pre-settlement total, and each lost <30 km² of wetland (Fig 2). The island of Hawai`i had the highest gross wetland loss, about 375 km², or 23% of the island's estimated pre-settlement wetlands, accounting for 71% of loss for the state (Fig

2). The second highest observed loss was on Oahu, where 106 km² were lost, accounting for 65% of its pre-settlement total (Figure 2.2).

Wetland losses on all islands were greater at lower elevations than at higher elevations (Table 1). Losses in lower elevations accounted for 62% of total wetland losses in the state. The islands of Molokai and Kauai show almost no loss of higher elevation wetlands and about 15% wetland loss in coastal regions. Mid-to-high elevation losses are negligible on Maui, but low elevation losses are estimated at 35%. Wetland losses at all elevations were highest on Hawai'i, although Oahu lost the largest fraction of its pre-settlement wetlands. Hawai'i and Oahu lost 64% and 71% of their low elevation wetlands, respectively (Table 1).

Wetland losses on Molokai were minimal and sustained mainly in southeastern coastal regions, where most development has taken place. Based on proximity to NWI-identified current wetlands, most lost wetland was likely freshwater emergent and freshwater forested/shrub wetland. The majority of estimated loss was generated by the threshold TWI model, which indicated the likelihood of pre-settlement wetlands on patches of developed land; this assessment was often supported by some hydric soil evidence. Extensive areas of cultivated land in the center of the island showed little evidence of developed wetlands. Highly developed areas in this agricultural region that were recorded as lost wetlands were supported only by TWI evidence.

Based on our analyses, Kauai retains 100% of its extensive mid-to-high elevation wetlands, and has sustained only small losses in coastal areas. The majority of loss was in low-density development and agricultural areas, and was therefore not assessed using TWI, but rather was supported by hydric soil evidence. Hydric soil and some TWI

evidence indicate that river-fed freshwater emergent wetlands were lost around suburban developments along the southwest and east coasts, including Kekaha, Waimea, Hanapepe, `Ele`ele, Lihue and Kapa`a (locations of sites named in the results are shown in Figure 2.2c, wetland loss maps). Substantial conversions of riparian wetlands to irrigated agriculture are notable along the island's north side, near Princeville, but account for minimal losses because abundant artificial wetlands were created in the region. Similar changes are evident in the Mana plain on the island's west side, where evidence suggests the presence of a large pre-settlement wetland now replaced with artificial wetlands, a reservoir sewage treatment plant and agricultural fields. If these artificial wetlands were not included in our analysis of Kaua`i's wetland loss, the island's low elevation losses would be considerably higher.

Wetland loss on Maui (24 km^2) was only slightly higher than on Kaua`i, but accounted for a larger fraction of the island's wetlands. The vast majority of losses were sustained around urban and suburban coastal developments like Kihei on the south side of the island, Kahului in the north and Lahaina in the west. The evidence for most of these losses was generated by the thresholded TWI model, though on the west side of the island it was also supported by the presence of hydric soils in the Mana plain.

The island of Hawai`i suffered the largest loss of wetlands overall, and these losses were distributed almost evenly between high and low elevations. Virtually all of the loss is indicated by huge tracts of hydric soils underlying Hilo (east, coastal) and the surrounding agricultural and rural areas, which span a wide elevational gradient. NWI surveys show large mid-elevation freshwater forested scrub/shrub wetlands contained within the undeveloped portions of those hydric soil units, implying that the lost wetlands

may have been primarily of this type. The TWI model also indicated smaller areas of loss around Waiakeia pond in Hilo.

Coastal wetland losses on Oahu are extensive and generally supported by multiple sources of evidence. Based on our analyses, Honolulu, Pearl Harbor, and Kapolei regions formerly supported large tracts of estuarine and marine wetland along the coast, with areas of freshwater emergent and freshwater scrub wetlands farther inland along streams. Wetland losses in the less developed part of the region are indicated by hydric soil evidence, while in the most heavily developed parts, the thresholded TWI model shows dense areas with a high likelihood of having supported wetlands. Large losses of freshwater emergent wetland are also evident in Kailua and Kaneohe, the former indicated by TWI model evidence and the latter by hydric soils. On the northern side of the island, hydric soil evidence suggests large wetland losses from Waialua bay to Mokuleia.

2.4. Discussion

2.4.1 Use of TWI in pre-settlement wetland assessment

As a simple steady-state wetness index, the topographic wetness index (TWI, also referred to as the Compound Topographic Index) determines where water is likely to accumulate on a landscape given hypothetical conditions of uniform rainfall (Beven and Kirkby, 1979; Besnard et al. 2013). Our study indicates that TWI can be very successful at identifying current wetlands sustained by surface runoff or areas where wetlands of that type were supported prior to human settlement. However, the TWI model does not account for precipitation patterns and soil types, which are important factors in

determining whether water will actually accumulate in an area, even if local topology indicates it is possible. Even if an area is flat, low, and has a large catchment, if there is no precipitation a wetland will not form. Similarly, if soils are unable to hold water, it will infiltrate into groundwater and not be sustained near the surface. Consequently, relying solely on TWI to identify pre-settlement wetland locations could lead to overestimates of wetland distributions. Conversely, TWI could underestimate pre-settlement wetland cover where soil and precipitation conditions support wetlands despite topological traits that do not indicate they would accumulate water. The latter is evident on the northern side of the island of Hawai`i, where steep slopes give relatively low TWI values, but wetlands persist because of annual rainfall in excess of 6 m (Giambelluca et al., 2013). Given the high rainfall rates on even the dry sides of the Hawaiian Islands, the former bias for overestimation is unlikely when TWI is applied to the Hawaiian Islands. We conclude that hydrological models like TWI are practical and convenient tools for assessing the likelihood of an area supporting a pre-settlement wetland, could be improved by the inclusion of information such as rainfall and soil type. Where hydric soil data are available, it might be best to restrict the use of TWI as we did in this study to areas so heavily developed that soil data cannot be relied upon.

2.4.2 Loss of wetlands in the state of Hawai`i

Our estimate of 22% wetland loss on Hawai`i since human settlement is nearly twice the previous estimate for the state, which was 12% (Kosaka *in litt.*, 1990). There are a number of differences between the studies that might have contributed to the difference, but since the original documentation of the earlier analysis is lost, some of the differences are speculation. The first difference manifests in the observation that our

estimates for pre-settlement wetland area, current wetland area, and gross wetland loss for the state were each about an order of magnitude higher than the earlier estimates, indicating that we included or identified substantially more pre-settlement and current wetlands in the state. Specifically, the NWI data used in this study recognized more than three times as much current wetland area for the state than the Kosaka study (652 km² vs. 210 km², respectively). If there was a bias in the types of wetlands included in the two studies, it could explain some of the differences in results. If this is the case, our study was the more comprehensive. The definition of wetlands used in our study and by the U.S. Fish and Wildlife Service in 1990, however, should not have differed. We and the National Wetlands Inventory used Cowardin et al. (1979) for wetland definitions, which is the standard for U.S. government agencies. Despite this, the earlier assessment might still have used a subset of wetland types. Another potential difference between the studies is that we estimated wetland loss since first human settlement, which occurred around 500 C.E. (Graves and Addison, 1995), while the previous study attempted to estimate wetland loss since 1780 (Kosaka *in litt.*, 1990). However, we think that the large differences in results between the two studies are more likely due to our study having available more numerous and accurate data sources (e.g., soil layers) as well as more sophisticated analytical tools that were unavailable to the authors of the previous study. This resulted in a more comprehensive survey of wetlands and evidence of wetlands in the state of Hawai`i.

Our estimates of wetland loss in Hawai`i since human settlement may be conservative. In particular, by restricting the use of the TWI model to areas of heavily developed land, we failed to detect pre-settlement wetlands in less-developed areas that

were not indicated by hydric soil data. Our estimate of wetland loss was conservative in some respects because we included all types of artificial wetlands in the current wetland inventories. The potential for underestimating loss due to artificial wetlands is especially evident on the Mana plain (west side of Kauai), where what is known to have been a large pre-settlement wetland near Kaanapali and Lahaina has been replaced by many artificial wetlands not useful to wildlife. If one considers merely water storage, this might not be an underestimation, but if one values ecological services and wetland value to native wildlife, artificial wetlands tend to not functionally replace natural wetlands (e.g., Elphick, 2000; Ma et al., 2004; Bellio et al., 2009). Even natural wetlands within urban landscapes can have reduced function for wetland specialists (e.g., Ehrenfeld, 2000; Tavernia and Reed, 2010). Wetlands in non-urban sites might also have reduced value for native wildlife (including plants) due to the presence of exotic invasive plants and predators (U.S. Fish and Wildlife Service, 2011).

The results of this study are especially important for the long-term management of wetlands in the state of Hawai'i because of the large number of wetland-dependent threatened and endemic species and the multitude of threats to wetland habitats on these and other small pacific islands, particularly for coastal wetlands (SPREP, 2011). This will be particularly true for adaptive planning for climate change and its effects (e.g., Hartig et al., 1997; Nicholls, 2004). Of concern from an ecological standpoint is that, like Kosaka *in litt.* (1990), we found that the vast majority of wetland losses in Hawai'i were sustained along the coastal plains. Unfortunately, these low-elevation wetlands are also the most important for wetland species of conservation concern (Griffin et al., 1990; U.S. Fish and Wildlife Service, 2011; Reed et al., 2012). Climate change and sea level

rise are likely to pose a significant future threat to coastal wetlands (Nicholls, 2004; Nicholls et al., 1999), especially on geologically younger islands such as Hawai`i and Maui, which are still undergoing high rates of subsidence (Moore, 1970; Ludwig et al., 1991). Wetland restoration or creation will be especially important in areas like Oahu where the vast majority of coastal wetlands have been lost.

Our estimates of wetland loss correspond well with the intensity of development on individual islands in the state. For example, the two most populous islands, Oahu and Hawai`i, have lost the highest proportion of their pre-settlement wetlands. Urban and rural development appears to be the largest cause of wetland loss on the Hawaiian Islands, especially in the Honolulu and Pearl Harbor area, where extensive natural and artificial wetlands are known to have existed (Summers, 1964; Shallenberger, 1977). This is generally consistent with current and historical trends in wetland loss elsewhere in the United States, as summarized by Dahl (1990, 2006). Making general comparisons to other tropical islands, however, is more difficult because of the dearth of inventory data in even current wetlands, let alone pre-settlement wetland cover for such islands (Scott, 1993). It is recognized, however, that wetland specialist species and ecosystem services from wetlands are at risk in Oceania and that at least some of that risk is due to wetland loss (Millennium Ecosystem Assessment, 2005). From the available limited data for other islands in Oceania (e.g. Guam, American Samoa), reviews by Scott (1993) and Ellison (2009) imply that, as indicated by our study, urbanization is the primary threat to coastal wetlands on these islands, and is threatening endemic flora and fauna dependent upon wetland habitats. Wetland losses in the Hawaiian Islands are also similar to loss

patterns in Caribbean Islands, which were caused by the expansion of coastal settlements, agriculture, and finally development for the tourist industry (reviewed by Bacon, 1987).

2.5. Conclusion

We have identified extensive wetland losses in Hawai'i, particularly on Oahu. The lower estimated losses on the other islands are deceptive in that significant gains in artificial wetlands in those regions mask more substantial losses of natural wetlands. From an ecosystem services and wildlife perspective, many benefits provided by natural wetlands have still been lost, although the area of what may generally be called wetlands has changed little. Consequently, the loss of wetland ecosystem services would be underestimated by our assessment. The collapse of the sugar cane and pineapple industries starting in the mid-1990s created a state of transition whereby opportunities for wetland restoration arose (Ridgley et al., 1997). To provide some idea of the amount of water that might be reallocated, as of 1996 the sugar industry applied 1.05 million cubic meters per day to cane fields; roughly 19% of water use in the state of Hawaii (Gopalakrishnan et al., 1996). This was already considerably less than agricultural water use during the peak of the sugar industry over the previous several decades. In 1985, agricultural fresh water use was 64% of Hawaii's use, which declined to 55% in 1990 (Department of Business Economic Development and Tourism (Hawai'i), 1993 and 1994). Agricultural water use has declined to 5% in recent years (CH2M Hill, 2013). Despite this freeing of agricultural water, however, water demand is rising in Hawai'i due to urban development and rapid population growth (Gopalakrishnan et al., 2007), leading to increased conflicts over water resources. For example the Waiahole ditch, which

formerly transferred water through the Ko`olau mountain range to the sugar plantations on the center of the island, has become the center of a fierce dispute over the water resources it transports (Gopalakrishnan et al., 2007). Urban development is greatest on Oahu, the island with the greatest wetland losses to date (this study), and it is predicted that groundwater use on Oahu will exceed recharge rates by 2018 (Hawaii Water Resources Act of 2005, <http://www.gpo.gov/fdsys/granule/CREC-2005-09-13/CREC-2005-09-13-pt1-PgH7830/content-detail.html>). Consequently, the potential to take advantage of alternative or additional uses of this water, such as restoring or creating wetlands for endangered species protection or other wetland services, is disappearing rapidly. Fortunately, unlike many natural resources, water is a flexible resource; that is, the same water can be used sequentially for many objectives (e.g., Hawaii Division of Land and Natural Resources, 2005; Islam and Susskind 2013). Consequently, it is important to convene stakeholders and determine common goals in order to protect multiple wetland and water-use values in the state while allowing efficient and equitable use of this valuable resource (Rahaman and Varis, 2005; Field et al. 2007; Gopalakrishnan et al., 2007; Sheild et al. 2009).

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Table 2.1: Estimated pre-settlement and current wetland areas, gross wetland losses, and percentage losses for each island subdivided by elevation category: ‘coastal’ is elevation <304 m. Elevation categories chosen to match the 1990 Hawai`i wetland loss assessment (last rows).

Island	Elevation	Pre-settlement	Current	Gross Wetland Loss (km ²)	% Wetland Area Lost
		Wetland Area (km ²)	Wetland Area (km ²)		
Molokai	Mid & High	30	29.8	0.21	0.69%
	Coastal	45.7	39.9	5.84	13%
Kauai	Mid & High	76.8	76.8	0	0%
	Coastal	101	86.2	15	15%
Maui	Mid & High	298	293	4.86	1.6%
	Coastal	56	36.4	19.6	35%
Hawai`i	Mid & High	1320	1124	196	15%
	Coastal	279	101	178	64%
Oahu	Mid & High	6.13	5.58	0.55	9%
	Coastal	152	43.8	108	71%
Total	Mid & High	1731	1529	202	12%
	Coastal	634	307	327	51%
Total, Kosaka (<i>in litt.</i> , 1990)	Mid & High	147	147	0	0%
	Coastal	91	63	28	31%

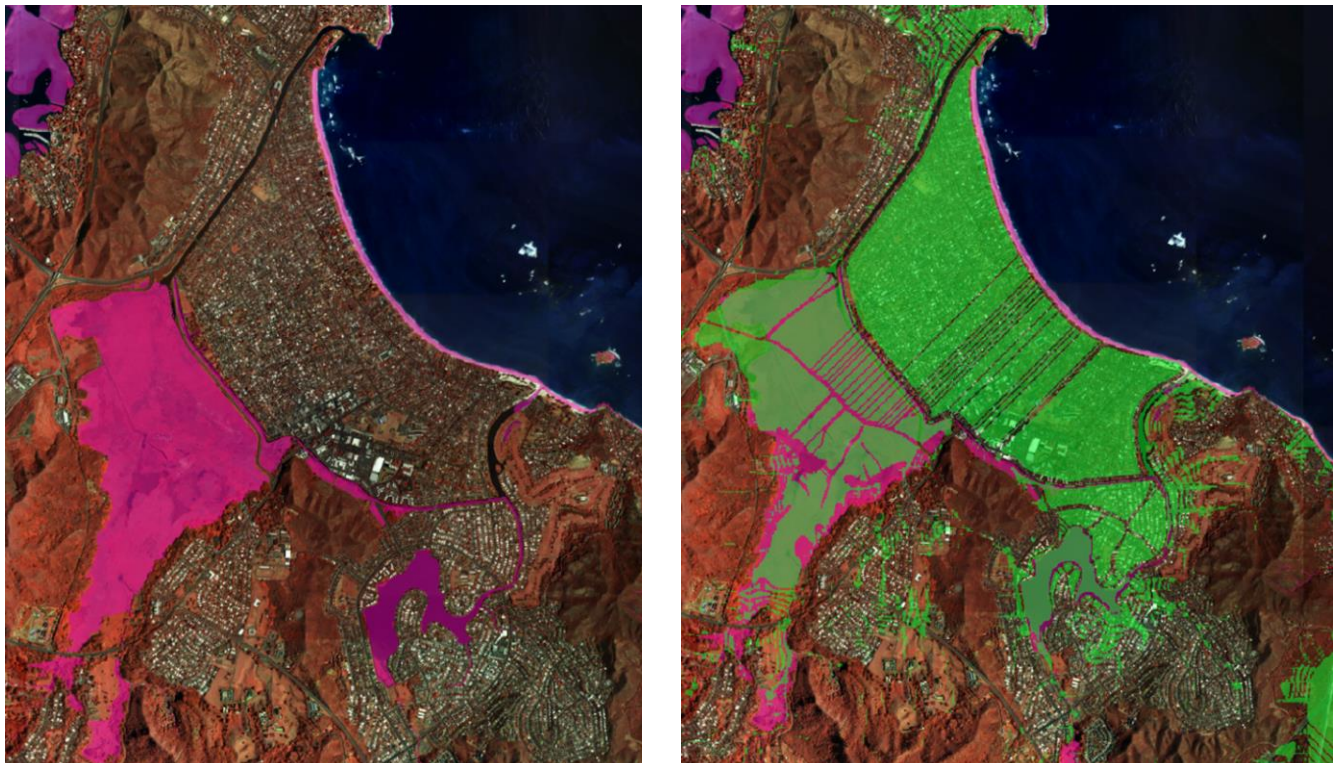


Figure 2.1: False-color Digital Orthophoto Quarter Quadrangle (DOQQ) image of the Kailua town area of eastern Oahu (see Figure 2.2 for location) showing National Wetlands Inventory (NWI) surveyed wetlands (in pink, left) and NWI wetlands overlaid by the Topographic Wetness Index (TWI) threshold model (in green, right). The Kawainui marsh is the large wetland feature on the left side of both images.

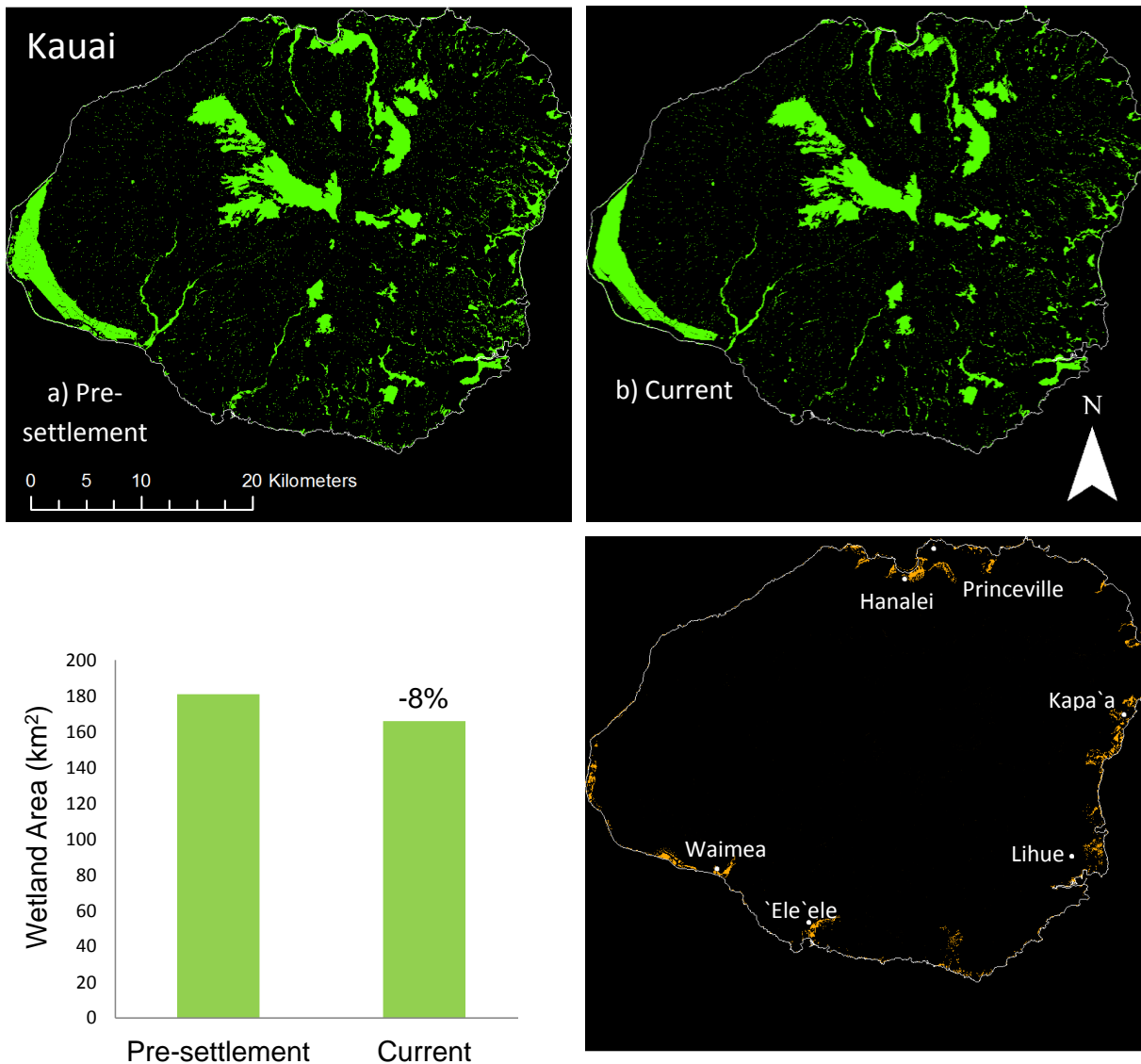
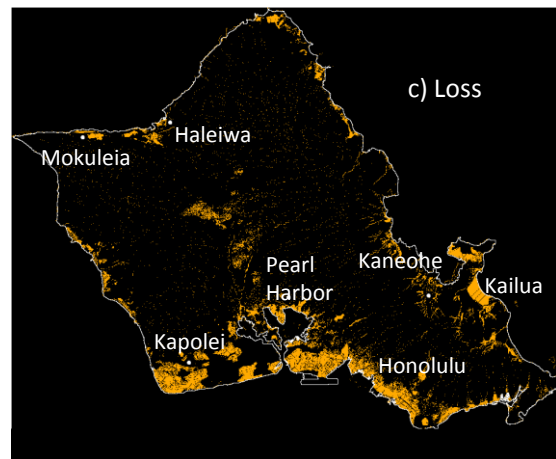
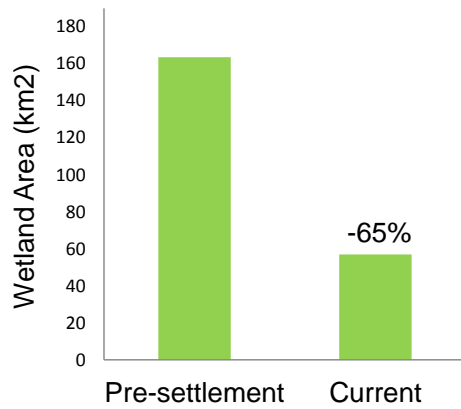
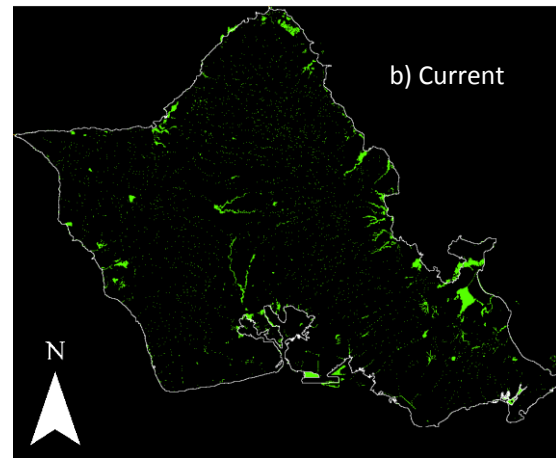
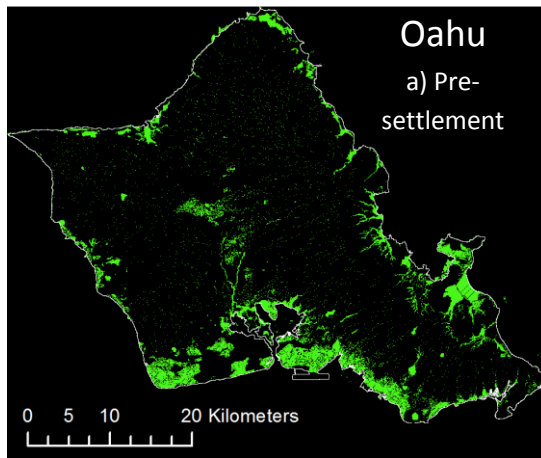
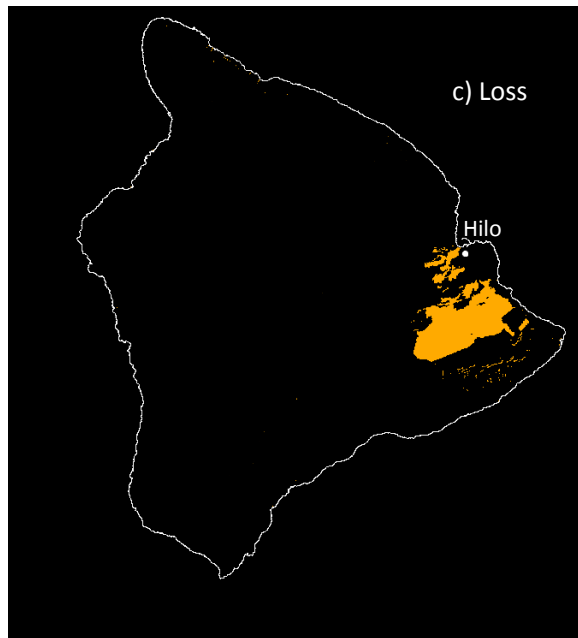
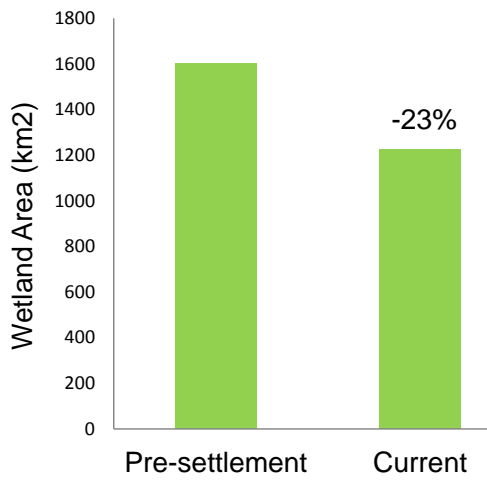
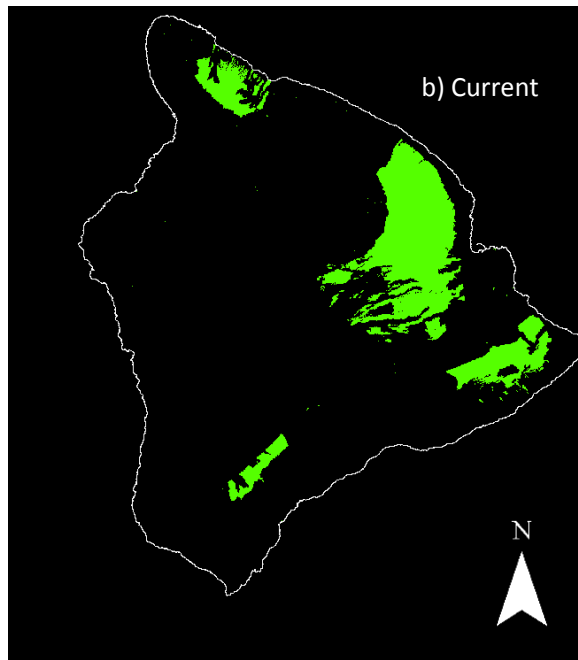
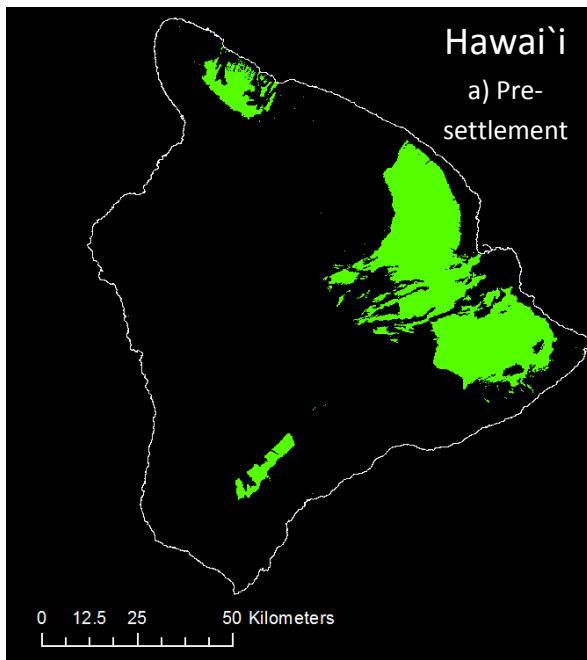
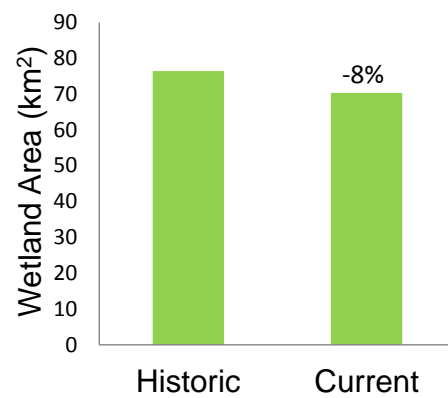
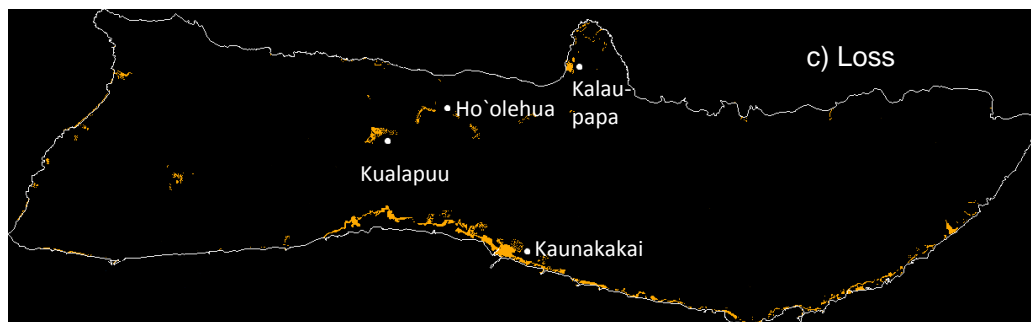
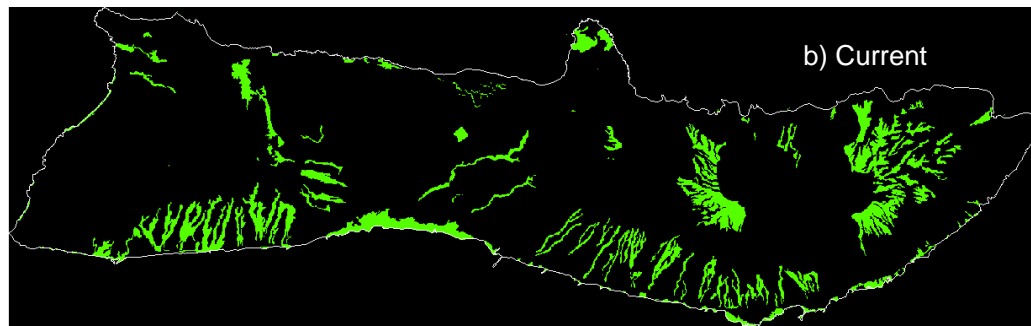
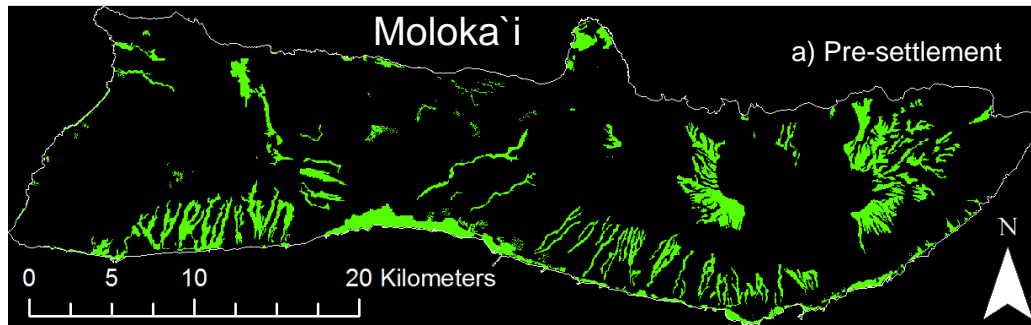
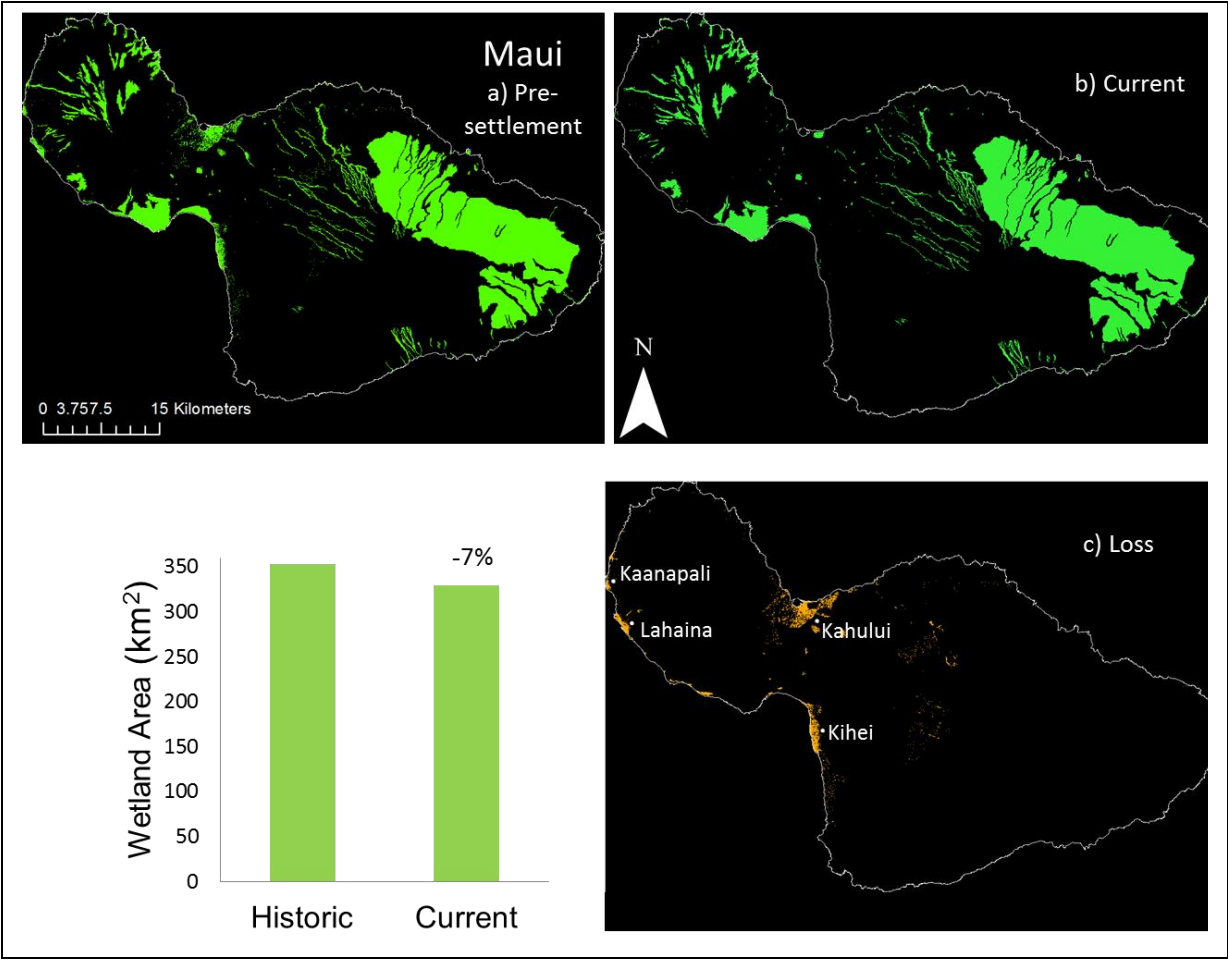


Figure 2.2 (and below): Maps of **a** pre-settlement wetland cover, **b** current wetland cover, and **c** wetland loss on the five largest islands of Hawai‘I; these islands represent just over 95% of the state’s land cover. For each island, we also include a bar graph showing original vs. current wetland cover. Sites mentioned in the results are labeled by name on the loss (c) maps; cities and towns are indicated with a white dot where possible without distracting from results.









Chapter 3

Small-scale genetic structure in an endangered wetland specialist: possible effects of landscape change and population recovery

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Abstract

The effects of anthropogenic landscape change on genetic population structure are well studied, but the temporal and spatial scales at which genetic structure can develop, especially in taxa with high dispersal capabilities like birds, are less well understood. We investigated population structure in the Hawaiian gallinule (*Gallinula galeata sandvicensis*), an endangered wetland specialist bird on the island of O`ahu (Hawai`i, USA). Hawaiian gallinules have experienced a gradual population recovery from near extinction in the 1950s, and have recolonized wetlands on O`ahu in the context of a rapidly urbanizing landscape. We genotyped 152 Hawaiian gallinules at 12 microsatellite loci and sequenced a 520 base-pair fragment of the ND2 region of mitochondrial DNA (mtDNA) from individuals captured at 13 wetland locations on O`ahu in 2014-2016. We observed moderate to high genetic structuring (overall microsatellite $F_{ST} = 0.098$, mtDNA $F_{ST} = 0.248$) among populations of Hawaiian gallinules occupying wetlands at

very close geographic proximity (e.g., 1.5-55 km). Asymmetry in gene flow estimates suggests that Hawaiian gallinules may have persisted in two to three strongholds which served as source populations that recolonized more recently restored habitats currently supporting large numbers of birds. Our results highlight that genetic structure can develop in taxa that are expanding their range after severe population decline, and that biologically significant structuring can occur over small geographic distances, even in avian taxa.

3.1 Introduction

Research on anthropogenic impacts on population connectivity (Ricketts 2001; Baguette and Van Dyck 2007), and growing attention to connectivity's effects on population persistence (Fahrig and Merriam 1985; Hanski and Gaggiotti 2004), have made the study of fragmented populations highly germane to biodiversity conservation (Opdam 1991; Hawkes 2009, Goldberg and Waits 2010; Murphy et al. 2010).

Fragmented populations suffer increased extirpation risk because these populations are often relatively isolated, and smaller, making them more strongly influenced by stochastic processes, all of which may result in increased likelihood of inbreeding depression, and low evolutionary potential due to decreased genetic diversity (Keller and Weller 2002; Mills 2007; Frankham et al. 2009). As connectivity among habitat patches is reduced, genetic drift can promote divergence in allelic and haplotypic frequencies among populations, resulting in genetic structuring when there is little or no emigration or immigration to counteract it (Selkoe and Toonen 2006; Broquet and Petit 2009).

Conversely, habitat connectivity (Taylor et al. 1993) can ameliorate many risk factors and allow physically disjunct populations to persist as part of a network (Macdonald and Johnson 2001; Crooks and Sanjayan 2006) or, under particular circumstances, as a metapopulation of interconnected habitats (Hanski 1999; Smith and Green 2005; Doleman 2012). Thus, genetic structure can be a useful indicator of the interactions between spatially isolated populations, that provides potentially valuable information for their conservation (Gibbs and Reed 2007; Mills 2007).

Though many studies have investigated population connectivity in stable populations, the development of genetic structure in growing populations (e.g.,

recovering or following colonization) is less well-understood. Specifically, it is unclear at which temporal and spatial scales fragmentation (and consequently population differentiation) will occur in dynamic, human-altered landscapes. Research on the population structure of fragmented, recovering populations at small spatial scales may yield valuable insights into the demographic and genetic effects of recovery and landscape change of populations at larger scales (Greenbaum and Fefferman 2017; Moreno-Mateos et al. 2017).

Islands are particularly vulnerable to landscape changes because anthropogenic pressures can more readily affect a significant portion of the available habitat (Fordham and Brook 2010). Here we investigate the population structure of an endangered bird, the Hawaiian gallinule (ʻAlae ʻula, *Gallinula galeata sandvicensis*), whose populations have been recovering from near-extinction in a highly modified landscape. The island of Oʻahu, a moderately sized (1500 km²) volcanic island in the central Pacific Ocean once supported a diversity of terrestrial habitats, including extensive lowland forests and coastal freshwater wetlands (Ziegler 2002). Throughout the 20th century, urban land cover has increased markedly with growing tourist visitation and resident population size while agricultural land use on the island decreased (Giambelluca 1986; Klasner and Mikami 2003; NOAA Coastal Services Center 2014). Oʻahu is now heavily urbanized, supporting more than 60% of the population of the state of Hawaiʻi (953,000 of 1.4 million people) in ~10% of its land area. More than 65% of Oʻahu’s freshwater lowland wetlands have been lost to land conversion, primarily because they occupied ideal locations for agricultural residential areas (van Rees and Reed 2014). Due to the island’s topography, wetland habitats have always been spatially separated on the landscape, but

habitat loss and anthropogenic landscape change may have introduced new barriers to dispersal among animal populations persisting in remaining wetland patches on the island. Accordingly, information on the population structure of wetland-specialist taxa on the island would be valuable for their conservation and management.

The Hawaiian gallinule is an endangered waterbird subspecies endemic to the Hawaiian Islands that lives only in shallow, coastal, freshwater wetlands. Hawaiian gallinules are hypothesized to be recent colonizers of the Hawaiian Islands (Fleischer and McIntosh 2001), with archaeological evidence of gallinules only found in deposits post-dating human colonization of the islands (~1,500 years before present, James 1987). Hawaiian gallinules were formerly distributed among most of the main Hawaiian Islands (Hawai`i, Maui, Moloka`i, O`ahu, and Kaua`i), but were extirpated from all islands except Kaua`i and O`ahu during a period of severe population decline throughout the 19th and early 20th centuries (Schwartz and Schwartz 1949; Munro 1960; Banko 1987). This decline was driven by the introduction of invasive mammalian predators (esp. small Indian mongoose *Herpestes javanicus*, domestic dogs *Canis lupis familiaris*, and cats *Felis catus*), habitat loss and degradation by agriculture and later urbanization, and habitat modification by exotic invasive plants (e.g., *Urochloa mutica*) (Griffin et al., 1990; Reed et al. 2012). The population reached a minimum estimated total population size of 57 individuals in the 1950s (Engilis and Pratt 1993). The establishment of National Wildlife Refuges on O`ahu and Kaua`i, and associated predator control and habitat restoration have helped Hawaiian gallinules make a steady recovery over the last 50 years, with current statewide population estimates from 400-1000 total individuals (Reed et al. 2011; Underwood et al. 2013; USFWS pers. comm.). Currently, between

200-300 Hawaiian gallinules persist on O`ahu (Reed et al. 2011; USFWS 2011) in a number of spatially isolated, relict or artificially maintained wetland habitats. These habitat patches occur within state, county, and federal protected areas, private farms, golf courses, and waterways. Wetland habitats are separated by a highly heterogeneous landscape of highways, agriculture, dense urban and suburban areas, and active military bases. To date, no formal studies have been undertaken to understand the genetic structure of gallinule populations among these physically isolated patches.

Hawaiian gallinules are a member of the family Rallidae (rails), which are known for their remarkable propensity to colonize islands and disperse long distances over open water despite many species being reluctant fliers (Ripley 1977). Rails are often freshwater wetland specialists, and can exhibit limited dispersal and subsequent genetic structuring under conditions of habitat loss and landscape change (e.g. California Ridgway's rail, *Rallus obsoletus obsoletus*, Wood et al. 2017). Several rail species in North America are migratory (e.g. yellow rail *Coturnicops noveboracensis*, Sora *Porzana carolina*, common gallinule) with vagrant sightings well outside of their breeding range, indicating substantial dispersal abilities (Ripley 1977; Taylor, 2010). In contrast to the migratory behaviors of other *G. galeata* subspecies, Hawaiian gallinules do not migrate, and are thought to be highly sedentary. For example, they have not colonized restored or unoccupied habitats on other islands in their historical range despite gradual population recovery (USFWS 2011). Hawaiian gallinules are weakly seasonal breeders, and can have multiple broods per year (average clutch size is three to six eggs; Byrd and Zeillemaker 1981) with an estimated generation time of 5.9 years (BirdLife International 2016), though individuals are observed breeding at age 2 (van Rees, pers. obs.). For

species with known limited dispersal propensities and relatively rapid generation times, understanding the level of connectivity (effective dispersal) among local wetlands is important when assessing the spatial ecology and likely persistence of small endemic populations (Van Strien 2014). O`ahu's small size, rapid landscape change, and the discrete distribution of wetland habitats provide an excellent study system for examining the spatial scales at which population structure may be influenced by changing landscapes, including habitat loss and matrix alteration, as well as by population recovery.

The structure and connectivity of O`ahu's Hawaiian gallinule population is also pertinent to the long-term conservation prognosis of the subspecies. The majority of habitat patches on O`ahu support fewer than 30 individuals (CVR pers. obs.), and therefore each population may have a high extinction risk without genetic and demographic rescue. As has been demonstrated in other habitat specialist birds (e.g., Florida scrub-jay, *Aphelocoma coerulescens*, Chen et al. 2016), habitat fragmentation and reduced dispersal lead to increased inbreeding coefficients, affecting vital rates important to population persistence (e.g., increased hatch failure). Consequently, we investigated the spatial patterns of genetic diversity within Hawaiian gallinules on O`ahu to evaluate the effects of population decline and recovery in an urbanized, fragmented landscape.

3.2 Methods

3.2.1. Sample Collection

We captured Hawaiian gallinules using walk-in Tomahawk live-traps baited with cracked corn, cat food, or other attractive food items (e.g. mango fruit *Mangifera sp.*).

We captured Hawaiian gallinules at 13 coastal wetlands on O`ahu in summer (May – July) from 2014 to 2016 (Figure 3.1). Wetland names and their corresponding four-letter codes are given by region in Table 3.1: North Shore (includes TURT, JCNR, SHRI, WAIM, LOTU), Windward (KLIP, HAMA, ENCH, KAWA, OLOM), Maunalua (KEAW), and Pearl Harbor (POUH, HONO). Our sampled wetland sites represent all known major habitats for the species on O`ahu. James Campbell National Wildlife Refuge was sampled only in 2014. Marine Corps Base Hawai`i, Kahuku, Kawainui marsh, and Pouhala marsh were sampled only in 2016. All other wetlands were sampled in 2015 and 2016. Inter-site Euclidean distances ranged from 1.5 to 54 km, with a mean of around 30 km. Notably, sample sizes for some wetlands (POUH, HONO, KEAW, KAWA, and SHRI) are small; however, sample sizes represent between 20 and 100% of birds occupying individual wetlands. Due to small sample size and close geographic proximity, samples from Pouhala and Hono`uli`uli wetlands were pooled into a regional population, Pearl Harbor (PEHA). We collected 3-6 body feathers from post-fledging Hawaiian gallinules and stored feather samples in plastic bags at room temperature. We extracted DNA using DNeasy Blood and Tissue Kits (QIAGEN; Valencia, CA).

3.2.2. Laboratory techniques

We genotyped individuals at 12 autosomal microsatellite loci: Fal08, Fal10, Fal12, Fal14, Fal 17, Fal19, Gch06, Gch12, Gch13, Gch17, Gch19 (Sonsthagen et al. 2014), and KiRa9 (Brackett et al. 2013). The forward primer for locus KiRa9 was modified for this study (KiRa9.1F: 5'-GCGAGACTTGAAGTAGTGG-3'). We amplified microsatellites using polymerase chain reaction (PCR), and electrophoresed

with fluorescent-tailed primers following the protocols described in Sonsthagen et al. (2004). We also sequenced 520 base pairs (bp) of the NADH dehydrogenase 2 (ND2) region of mitochondrial DNA (mtDNA) using primer pair ND2_224L (5'–CTMCTACTATTCTCCAGCAC–3') and ND2_720H (5'–GCCTGCTAGGGAKAG–3'), following Sonsthagen et al. (2007) for PCR amplifications, cycle-sequencing protocols, and post-sequence processing. Lastly, 10% of samples were randomly selected, reamplified, and genotyped in duplicate for quality control. No inconsistencies in genotype scores were observed between replicates. Sequences are accessioned in GenBank (MF673902-MF673904).

3.2.3. Analysis of genetic diversity

We calculated allelic richness (AR), inbreeding coefficient (F_{IS}), observed and expected heterozygosity (H_O and H_E , respectively) and tested for Hardy-Weinberg equilibrium and linkage disequilibrium among microsatellite loci in FSTAT version 2.9.3.2 (Goudet 1995). We estimated haplotype (h) and nucleotide (π) diversity of the ND2 region of mtDNA using Arlequin 3.1 (Schneider et al. 2000). We tested for selective neutrality for sequence data from the mtDNA ND2 region using Fu's F_S (Fu 1997) and Tajima's D (Tajima 1989) in Arlequin. We constructed an unrooted haplotype network for mtDNA ND2 using the reduced median method (Bandelt et al. 1995) in NETWORK 5.0.0.0 (Fluxus Technology Ltd.).

Because we collected samples from both adult and hatch-year individuals, we used Queller and Goodnight's (1989) index of relatedness (r_{xy}) to calculate levels of familial relationship between pairs of individuals within wetlands using IDENTIX 1.1

(Belkhir et al. 2002). Relatedness values of < 0.5 represent first order (i.e. full-sibling, parent-offspring) relationships, 0.25 for second order (i.e. half-sibling) relationships, and 0 for unrelated individuals.

3.2.4. Estimation of genetic structure

We calculated estimates of inter-population variance in allelic and haplotypic frequencies (F_{ST}) in Arlequin; P-values were adjusted for multiple comparisons using the B-Y method (Benjamini and Yekutieli 2001; Narum 2006) with a starting α of 0.05. We used RecodeData version 1.0 (Meirmans 2006) to calculate the maximum possible F_{ST} values for the sampled suite of microsatellite loci. Hierarchical analysis of molecular variance (AMOVA) was performed using Arlequin to determine the magnitude of spatial variance in haplotypic and allelic frequencies among wetland regions on the island. Because the Pearl Harbor and Maunalua regions were both represented by only a single wetland (Pearl Harbor made up of the combined wetland PEHA and Maunalua by KEAW), and groups must be represented by more than one population to avoid violating assumptions of the AMOVA analysis, we made comparisons only between the Windward side and North Shore regions. The Pearl Harbor region could not be considered a group based on the original populations HONO and POUH because of the small sample sizes of these sites. We tested for isolation by distance by comparing a matrix of Euclidean geographic distances and genetic distances (F_{ST}) between all wetland pairs using a Mantel test implemented in the Isolation By Distance Web Service (Jensen et al. 2005).

Finally we used STRUCTURE 2.3.2.1 (Pritchard et al. 2000; Hubisz et al. 2009) to infer the occurrence of population structure among sampled individuals without using

prior knowledge of sample collection locations based on our genotypic microsatellite data. STRUCTURE was conducted using an admixture model assuming correlated frequencies and with sample group information as a prior, with the possible number of populations (K) ranging from 1–11 (search strategy; burn-in of 50,000 iterations followed by 500,000 Markov chain Monte Carlo iterations); the analysis was repeated 10 times. We followed the method of Evanno et al. (2005) and maximum likelihood (Pritchard et al. 2000) to determine the most likely number of clusters (K) given the data. The results were summarized in STRUCTURE HARVESTER Web v0.6.94 (Earl and von Holdt 2012).

3.2.5. Estimation of gene flow

We estimated gene flow between wetlands in MIGRATE v3.6.11 (Beerli and Felsenstein 1999, 2001) based on the 12 microsatellite loci. We ran MIGRATE with a full gene flow model, θ ($4N\mu$ or $Nf\mu$, composite measure of effective population size and mutation rate), and all pairwise gene flow parameters (M) were estimated individually from the data and were compared to a restricted island model for which θ was averaged and pairwise gene flow parameters were symmetrical between populations. We estimated gene flow using a maximum likelihood search parameter; ten short chains (5000 trees used out of 1,000,000 sampled), five long chains (15,000 trees used out of 3,000,000 sampled), five static chains (start temperatures: 1, 1.5, 3, 6, and 12; swapping interval = 1) with a 5M burn-in per chain. Models were run three times to ensure the convergence of parameter estimates. The alternative model was evaluated for goodness-of-fit given the data using a log-likelihood ratio test. The resulting statistic from the log-

likelihood ratio test is equivalent to a χ^2 distribution with the degrees of freedom equal to the difference in the number of parameters estimated in the two models (Beerli and Felsenstein 2001).

We aggregated several wetlands that were adjacent and shared low genetic structure to reduce the number of estimated model parameters. JCNr and SHRI were pooled into JCSF (James Campbell-Shrimp Farms), and HAMA, OLOM, KAWA, and ENCH were combined into WIND (Windward side), resulting in a total of eight unique wetland patches in our gene flow analysis.

3.3 Results

3.3.1 Genetic diversity

We obtained multi-locus genotypes for 152 Hawaiian gallinules at 13 wetland sites on O`ahu (sample distribution shown in Figure 3.1). Each individual had a unique multi-locus genotype. Four hatch-year birds had pairwise r_{xy} values > 0.5 with adults sampled from the same wetland (HAMA $n = 2$, KEAW $n = 1$, WAIM $n = 1$), suggestive of a parent-offspring relationship. The four hatch-year birds were omitted from subsequent analysis; our final data set comprised 148 individuals (Table 2). Number of alleles per microsatellite locus ranged from 1 to 4, with a mean of 2.2 and standard deviation of 0.5 alleles per locus. The average number of alleles per locus was similar across sampled wetlands with values ranging from 2.1 to 2.3 (Table 2). Within wetlands, observed heterozygosity ranged from 33.9 to 52.0% (Table 2). All loci and populations conformed to the assumptions of Hardy-Weinberg equilibrium, and all loci were in linkage equilibrium.

We observed three unique haplotypes at the ND2 region of the mtDNA ($n = 148$) characterized by two variable sites (Figure 3.2). Number of ND2 haplotypes observed per wetland ranged from 1 to 3. Individuals from KLIP and KEAW were represented by a single haplotype (1), while all other wetlands were represented by at least two haplotypes. In wetlands with more than one ND2 haplotype observed, moderate levels of haplotype ($h = 0.516\text{--}0.726$) and nucleotide ($\pi = 0.0026\text{--}0.0043$) diversity were detected (Table 3.2).

3.3.2 Genetic structure

Moderate to high genetic structure was detected based on the 12 microsatellite loci ($F_{ST} = 0.098$, $p < 0.001$, Table 3) and mtDNA ($F_{ST} = 0.248$, $p < 0.001$, Table 3). The upper limit of F_{ST} for our microsatellite data set is 0.584; therefore the F_{ST} of 0.098 accounts for 16.8% of the maximum possible level of genetic structure. KLIP and KEAW were differentiated from most wetlands with the highest number of significant comparisons, followed by LOTU, HAMA, and TURT based on microsatellite data and WAIM and LOTU based on mtDNA variance. The regional analysis uncovered within-population structure (microsatellites $F_{ST} = 0.096$, $p < 0.001$; mtDNA $F_{ST} = 0.248$, $p < 0.001$); however, region (North Shore vs. Windward side) did not explain a significant portion the variance at either marker type (microsatellites $F_{CT} = 0.007$, $p = 0.301$; mtDNA $F_{CT} = 0.112$, $p = 0.086$). We observed no evidence of isolation by distance among wetlands based on microsatellite data or mtDNA (Mantel test, microsatellites: $r = 0.107$, $p = 0.131$; mtDNA: $r = -0.134$, $p = 0.926$).

STRUCTURE uncovered genetic partitioning of Hawaiian gallinules on O`ahu;

two clusters were identified based on Evanno et al.'s (2005) method ($\Delta K = 53.3$; $\text{LnPr}|\text{K} = -2417.6$, Figure 3.3A) and four clusters were identified based on the maximum likelihood given the data ($\Delta K = 2.0$, $\text{LnPr}|\text{K} = -2374.3$, Figure 3.3B). Based on Evanno's method, individuals from KLIP had high membership coefficient to group 1 (white), and individuals from WAIM had moderate coefficients (Figure 3.3A). The individuals representing the remaining wetlands clustered into group 2 (black). Based on Pritchard et al.'s (2000) method, individuals from KEAW (group 2; light gray) and KLIP (group 1; white) formed wetland specific clusters (Figure 3.3B). Individuals from KAWA, HAMA, ENCH, OLOM, and PEHA clustered together into group 3 (dark gray). Individuals from TURT and half of the LOTU individuals clustered into group 4 (black). Individuals from WAIM, SHRI, JCNR, and KAWA, had intermediate membership coefficients. The four-population model detected one known dispersal event (ENCH87856); that individual hatched in KEAW and dispersed to ENCH; this individual's assignment profile more closely resembles those of birds from KEAW than ENCH. The sample group information was informative ($r < 1.0$) for both models. The average proportion of cluster membership across all individuals within each wetland are shown over their respective sampling location in Figure 3.4.

3.3.3 *Gene flow*

Asymmetrical gene flow was detected based on the microsatellite data; the full model (all parameters allowed to vary independently) had significantly higher likelihoods than did the restricted model (symmetric interpopulation M and θ) indicating asymmetric gene flow among wetlands [$\text{LnL}(\text{full}) = -4436$, $\text{LnL}(\text{test}) = -4789$, $p < 0.001$]. Gene flow

(Nem) maximum-likelihood estimates and 95% confidence intervals are provided in Table 3.4, and gene flow between populations is displayed schematically in Figure 3.5. We observed asymmetrical gene flow (as indicated by non-overlapping 95% confidence intervals) between 17 of 66 pairwise wetland combinations. Overall, most gene flow occurred from other wetlands into JCSF and WIND, with JCSF receiving the highest magnitude of asymmetrical gene flow from the greatest number of wetlands. Highly asymmetrical gene flow was detected from KLIP outward to almost every other wetland, and limited dispersal into KLIP. PEHA and TURT both had moderate levels of dispersal outward, with gene flow into both wetlands only from KLIP. It is important to note that gene flow estimates for KEAW are based on few individuals ($n < 10$); though sampling represents all birds occupying the wetland.

3.4 Discussion

Hawaiian gallinules on O`ahu exhibit moderate to high genetic structure (*sensu* Wright 1978) among small and geographically close wetlands surrounded by a diverse and increasingly urbanized landscape matrix. These results are particularly noteworthy considering the small distances by which wetland habitats on the island are separated (1.5–55 km) coupled with moderate to high levels of genetic structure observed at two marker types (pairwise msat $F_{ST} \leq 0.261$; pairwise mtDNA $F_{ST} \leq 0.919$; Table 3). Genetic drift had limited variation upon which to act in this population, ($AR \leq 2.2$; Table 2), so dispersal among remnant patches was likely markedly reduced in order to promote the levels of genetic partitioning observed. Hawaiian gallinules experienced a severe and recent population bottleneck (Engilis and Pratt 1993) and are relatively recent colonizers

of Hawai'i (James 1987; Fleischer and McIntosh 2001). We thus hypothesize that the population bottleneck and subsequent isolation of some habitat patches throughout population recovery promoted the rapid development of genetic structure among wetlands through the process of genetic drift.

The magnitude of genetic differentiation observed among wetlands in this study is higher than that observed for highly vagile bird species (e.g., Swainson's warbler *Limnothlypis swainsonii*, microsatellite $F_{ST} = 0.023\text{--}0.049$, Winker et al., 2000), and more closely resembles values for other wetland specialist birds in habitat fragmented by urbanization (e.g. white-fronted chats *Epthianura albifrons*, microsatellite $F_{ST} = 0.035\text{--}0.183$, Major et al. 2014), highly sedentary tropical birds (e.g. bicolor antbirds *Gymnopythis bicolor*, microsatellite $F_{ST} = 0.012\text{--}0.278$, Brown et al. 2004), and other rail species (Girard et al. 2010; Miller et al. 2012; Miller et al. 2015). Yellow rails, a migratory species, exhibit moderate genetic structure (microsatellite $F_{ST} = 0.083\text{--}0.113$) between an isolated population in Oregon, with the rest of the breeding population distributed over much of Eastern North America; no genetic structure was detected within the contiguous distribution (Miller et al. 2012). High genetic structuring (microsatellite $F_{ST} = 0.19\text{--}0.63$; distance 100–850km) was found among nonmigratory Californian populations of black rail (*Laterallus jamaicensis coturniculus*; Girard et al. 2010). Similarly, the closely related Marianas common moorhen (*Gallinula chloropus guami*) is also highly structured, with interisland estimates (F_{ST}) of 0.152 for microsatellites and 0.390 for the ND2 region of mitochondrial DNA (distance ~200 km), between Saipan and Guam (Miller et al. 2015). Unfortunately no studies of within-island structure for

Marianas moorhen or between-island structure for Hawaiian gallinules have been conducted for comparison.

Although inter-population estimates of genetic structure observed here are similar across a range of avian taxa, assessments described above were conducted at a much larger geographic scale relative to our study (distances 100–10,000 km vs 1.5–55 km, respectively). Indeed, the spatial scale of our study is smaller than most reports of notable avian population differentiation (e.g., Nicholls et al. 2006; Roberts et al. 2011; Nogueira et al. 2014; Vidal et al. 2015; Greenberg et al. 2016; Levy et al. 2016), even for sedentary tropical species (Brown et al. 2004; Abalaka et al. 2015). Genetic structure observed in our study is similar in magnitude and spatial scale to that observed by Delaney et al. (2010) in what was described as the highest amount of genetic structure observed over small distances in avian taxa. The small spatial scale at which genetic structure is observed within Hawaiian gallinule of O`ahu highlights two important drivers of genetic structure: low dispersal propensity and the influence of genetic drift as a result of a severe bottleneck event. We hypothesize that the alteration of O`ahu's landscape and the reduction of habitat for waterbirds (Griffin et al., 1990; van Rees and Reed 2014) has likely played a role in the creation of a mosaic of spatially isolated wetlands enabling genetic drift to quickly act and promote genetic structure among populations in close geographic proximity.

Landscape and behavioral ecologists have challenged the notion that inter-patch Euclidean distances alone are an effective measure of potential population isolation or connectivity, suggesting instead that the type of landscape cover making up that distance (i.e., the landscape matrix) plays a larger role in many terrestrial systems (Ricketts 2001;

Rodewald 2003; Revilla and Wiegand 2008; Aben et al. 2012). We observed a small number of populations (in particular KLIP, KEAW, WAIM, and TURT) that show strong and consistent structure that is not correlated with physical distance. The patterns of genetic structure we observed may be explained, at least in part, by the influence of the physical structure of the landscape matrix on Hawaiian gallinule dispersal among wetlands (i.e., functional connectivity; Taylor et al. 1993; Baguette and Van Dyck 2007), the history of O`ahu's Hawaiian gallinule population, and source-sink dynamics among persisting populations (Pulliam 1988).

The severity of the population decline experienced by Hawaiian gallinule populations in the late 1800s to mid-1900s (gallinules reduced to ~60 individuals across the state of Hawai`i) and subsequent recovery (Shallenberger 1977; Reed et al. 2011), likely erased signatures of genetic structure prior to the decline. Genetic drift acting on remnant populations during the bottleneck and subsequent recolonization likely played a large role in current patterns of genetic structure observed. Hawaiian gallinules on O`ahu likely survived the population bottleneck in a few (2–3) isolated strongholds (as indicated by high pairwise F_{ST} estimates) and subsequently colonized unoccupied or newly available habitats (created through restoration or active management) as numbers increased. Wetland size and quality differ widely between contemporary habitats, and may have influenced dispersal rates and population connectivity via habitat effects and source-sink dynamics (Pulliam 1988; Pfluger and Balkenhol 2014). JCNr and HAMA, two wetlands that currently support larger populations of Hawaiian gallinules, are weakly differentiated from most other populations on the island, and are known to have supported few if any birds prior to recovery (Shallenberger 1977). Limited genetic

structure coupled with larger census sizes suggests that these now presumably high-quality habitats received a high number of immigrants from other wetland populations during the recovery period (Figure 3.5). Spatially isolated wetlands (e.g. KEAW, a wetland located in an urban development surrounded by mountains, and KLIP, located on a fenced military base) exhibited asymmetrical gene flow to most other wetlands on the island, notably those in the WIND and JCSF regions. Prior to the decline, these wetlands (KEAW, KLIP, and TURT) may have been strongholds for Hawaiian gallinules as they are located on restricted military and private properties, and potentially experienced reduced persecution from hunting, which was legal until 1939 (Shallenberger 1977). Wetland habitats in WIND and JCSF supported few Hawaiian gallinules prior to the 1970s and 1980s (Shallenberger 1977; Banko 1987; M. Silbernagle, USFWS, pers. comm.), after which significant habitat management and predator control efforts began. Once management was enacted and protected habitat became available, WIND and JCSF wetlands apparently received immigrants from throughout the island (see Figure 3.6), as large populations developed quickly where birds had not been observed for some time (Shallenberger 1977; Banko 1987).

Hawaiian gallinules suffer mortality near roads (K. Doyle, Hawai'i State Department of Fisheries and Wildlife, pers. comm.), are typically shy of humans, and are rarely seen flying >2m off the ground. These factors suggest mechanisms by which anthropogenic landscape change could limit dispersal success through psychological, mortality-based, and physical barriers (Zeller et al. 2012). Population structure in other wetland birds (e.g. white-fronted chat, Major et al. 2014) is driven in part by urbanization around remaining habitats, regardless of the level of protection within these habitats; it

may be that observed structure in Hawaiian gallinules follows similar patterns. Though the low connectivity of urban wetlands like KEAW and KLIP to nearby wetlands supports this hypothesis, observed structure between TURT and two adjacent wetlands (WAIM and JCNR) might be a notable exception, given that O`ahu's North shore is among the island's least-developed regions and that these wetlands are embedded in a largely rural matrix. However, there are other possible barriers to dispersal that might apply within O`ahu's North shore, such as fence lines and dense scrub-forest. Linear features like roads can increase mortality and act as barriers to movement in many taxa (Andrews 1990; Vanak et al. 2010), including cursorial birds occupying open habitats (e.g. *Tympanuchus pallidicinctus*, Wolfe et al. 2007). In contrast, connectivity between spatially distant populations can be increased by corridors, or other landscape features that encourage or facilitate movement (Baum et al. 2004; Tewksbury et al. 2002). In the case of Hawaiian gallinules, birds use streams as breeding and foraging habitat (Banko 1987), and it is suspected that they may disperse more readily along stream margins and drainage canals (M. Silbernagle, USFWS, pers. comm). Finally, steep topography and mountain ranges may physically or psychologically (e.g. behavioral inhibition; *sensu* Harris and Reed 2002) impede dispersal. The Ko`olau mountain range, for example, separates the windward wetlands from PEHA, KEAW, and wetlands on the leeward side of the North shore (Figure 3.1). These additional possible matrix effects on dispersal rates may also play a role in the observed structure among wetlands that are not located in urbanized areas. Though perhaps not of direct conservation concern, the influence of natural barriers on gene flow may be exaggerated by more recent modifications to the landscape. Given the diversity of potential landscape-relevant drivers of genetic structure

in Hawaiian gallinules, formal analysis of patterns observed in this study using a landscape genetic framework (Manel et al. 2003; Storfer et al. 2010) should be considered an important next step in research on this threatened population.

3.4.1 Conservation implications

Our results illustrate the development of genetic structure in a taxon that is expanding its range after severe population decline, showing that biologically significant structuring can occur over small geographic distances. This raises an important, management relevant possibility—that populations recovering in altered landscapes may experience isolation or poor connectivity after recruitment. Given the relationship between fragmentation and extinction risk (Saunders et al. 1991; Fahrig 2003), this genetic structuring could be of conservation concern. For example, the recovery plan for the Great Lakes population of the Piping plover *Charadrius melodus* in the U.S. has as one of its delisting criteria the maintenance of genetic diversity sufficient for population persistence (USFWS 2003). If genetic structuring of this kind can be attributed to landscape characteristics, methods that increase connectivity in the context of altered landscapes (e.g. translocations, Wright et al. 2014; corridors, Tewskbury et al. 2002; stepping stone habitats, Saura et al. 2014) may be useful in ameliorating the potential demographic and genetic effects of fragmentation. The influx of gene flow we observed for James Campbell National Wildlife Refuge and Hamakua Marsh wildlife sanctuary suggests that restored and managed wetlands can be rapidly recolonized by Hawaiian gallinules. This suggests that wetland restoration and management may be effective tools for the management of this subspecies.

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Table 3.1: Code names and regions of sampled wetlands on O`ahu that are depicted in Figure 3.1, listed in clockwise order starting at the western side of the island.

Code	Region	Wetland
LOTU	North Shore	Private lotus farm, Hale`iwa
WAIM	North Shore	Waimea Valley Park
TURT	North Shore	Arnold Palmer Golf Course at Turtle Bay Resorts
SHRI	North Shore	Shrimp farms leased from USFWS, Kahuku
JCNR	North Shore	James Campbell National Wildlife Refuge – Ki`i unit
JCSF	North Shore	Combination of SHRI and JCNR
KLIP	Windward	Klipper Golf Course at Marine Corps Base Hawaii
KAWA	Windward	Kawainui Marsh State Wildlife Sanctuary
HAMA	Windward	Hamakua Marsh State Wildlife Sanctuary
ENCH	Windward	Ka`elepulu wetland and Kuilima Estates at Enchanted Lakes
OLOM	Windward	Olomana Golf Links
KEAW	Maunalua	Keawawa Wetland and Hawea Heiau, Hawaii Kai
POUH	Pearl Harbor	Pouhala Marsh State Wildlife Sanctuary
HONO	Pearl Harbor	Pearl Harbor National Wildlife Refuge – Hono`uli`uli Unit
PEHA	Pearl Harbor	Pearl Harbor region (combination of HONO and POUH)

Table 3.2: Estimates of genetic diversity of Hawaiian gallinule on O`ahu, Hawai`i, including; average number of alleles, allelic richness (AR), observed and expected heterozygosity (H_o , H_e , respectively), inbreeding coefficient (F_{IS}), and sample size calculated from 12 microsatellite loci, as well as, number of haplotypes (no. hapl.), haplotype diversity (h), and nucleotide diversity (π), Fu's F_s , and Tajima's D calculated from 295 bp of mtDNA ND2. Standard deviations are in parentheses.

	LOTU	WAIM	TURT	SHRI	JCNR	KLIP	KAWA	HAMA	ENCH	OLOM	KEAW	PEHA
Microsatellites												
No. Alleles	2.3 (0.5)	2.3 (0.5)	2.3 (0.5)	2.2 (0.7)	2.3 (0.5)	2.0 (0.4)	2.3 (0.5)	2.1 (0.3)	2.3 (0.5)	2.3 (0.7)	2.2 (0.4)	2.3 (0.5)
AR	2.1 (0.4)	2.1 (0.3)	2.2 (0.5)	2.2 (0.7)	2.2 (0.4)	1.8 (0.3)	2.2 (0.4)	2.0 (0.3)	2.1 (0.4)	2.1 (0.4)	2.1 (0.4)	2.1 (0.3)
H_e (%)	43.3 (4.1)	45.2 (3.4)	42.9 (5.5)	42.6 (6.5)	45.3 (3.3)	33.5 (4.8)	45.1 (4.0)	39.0 (4.9)	41.5 (4.7)	43.9 (3.9)	38.1 (4.6)	40.7 (4.4)
H_o (%)	42.6 (3.5)	52.1 (4.2)	34.0 (3.8)	50.0 (6.5)	43.9 (3.7)	40.0 (3.7)	42.8 (5.9)	35.3 (3.4)	44.1 (3.5)	41.1 (3.8)	39.7 (5.8)	45.9 (4.4)
F_{IS}	0.015	-0.160	0.215	-0.200	0.032	-0.204	0.057	0.098	-0.066	0.067	-0.048	-0.137
n	17	12	13	5	15	15	6	17	16	14	7	11

mtDNA

No. Hapl.	2	2	2	2	3	1	2	3	3	3	1	2
<i>h</i>	0.458	0.167	0.539	0.600	0.676	0.000	0.600	0.662	0.575	0.582	0.000	0.533
	(0.090)	(0.130)	(0.060)	(0.180)	(0.070)	(0.000)	(0.180)	(0.070)	(0.080)	(0.090)	(0.000)	(0.090)
π	0.001	0.000	0.001	0.001	0.001	0.000	0.001	0.001	0.001	0.001	0.000	0.001
	(0.001)	(0.000)	(0.001)	(0.001)	(0.001)	(0.000)	(0.001)	(0.001)	(0.001)	(0.001)	(0.000)	(0.001)
Fu's Fs	2.5	-0.5	1.5	0.6	0.6	-	0.6	0.5	0.1	0.0	-	1.0
Tajima's D	1.3	-1.1	1.2	1.2	1.1	0.0	1.2	0.9	0.2	0.0	0.0	1.3
<i>n</i>	17	12	13	5	15	15	6	17	16	14	7	11

Table 3.3: Pairwise F_{ST} values for all sampled wetlands, separated by region. Microsatellite data are above the diagonal, and mitochondrial ND2 region data below. Values in bold text are statistically significant (P values for comparisons based on microsatellite data were corrected for multiple comparisons using the B-Y method; $\alpha=0.05$, $P=0.0009$). Sample sizes for each wetland are shown in parentheses.

	North Shore					Windward Side					Maunaloa	Pearl H.
	LOTU (17)	WAIM (12)	TURT (13)	SHRI (5)	JCNR (15)	KLIP (15)	KAWA (6)	HAMA (17)	ENCH (16)	OLOM (14)	KEAW (7)	PEHA (11)
LOTU	-	0.099	0.066	0.090	0.116	0.205	0.017	0.101	0.068	0.049	0.236	0.060
WAIM	0.139	-	0.077	0.071	0.035	0.090	0.005	0.066	0.037	0.052	0.139	0.075
TURT	0.211	0.240	-	0.080	0.113	0.233	0.037	0.169	0.110	0.092	0.252	0.105
SHRI	0.297	0.446	-0.116	-	0.012	0.261	0.044	0.102	0.033	0.068	0.142	0.022
JCNR	0.081	0.208	-0.022	-0.048	-	0.209	0.039	0.040	0.024	0.036	0.101	0.051
KLIP	0.765	0.919	0.523	0.516	0.493	-	0.135	0.232	0.180	0.143	0.266	0.213
KAWA	0.123	0.176	-0.152	-0.154	-0.094	0.720	-	0.032	0.004	-0.003	0.119	0.032
HAMA	0.201	0.320	-0.014	-0.100	-0.040	0.357	-0.058	-	0.035	0.044	0.159	0.070
ENCH	0.130	0.162	-0.063	-0.066	-0.042	0.531	-0.144	-0.007	-	-0.004	0.142	-0.008
OLOM	0.292	0.387	-0.030	-0.148	-0.002	0.331	0.059	-0.051	0.003	-	0.153	0.006
KEAW	0.697	0.885	0.411	0.331	0.389	0.000	0.571	0.260	0.433	0.225	-	0.215
PEHA	0.161	0.174	-0.089	-0.084	-0.034	0.621	-0.176	0.000	-0.082	-0.003	0.501	-

Table 3.4: Gene flow estimated among Hawaiian gallinules sampled on eight wetlands in O`ahu, based on 12 microsatellite loci. Effective number of migrants per generation ($N_e m$) and 95% confidence intervals are listed for each population pair, where the columns are the wetland of origin and the rows are the wetland destination. Comparisons in bold text indicate the dominant direction of asymmetrical gene flow between wetland pairs and values in gray text represent comparisons with overlapping 95% confidence intervals. Total immigration for each wetland is shown in the right-most column, and emigration in the bottom row. Total immigration and emigration rates were calculated by totaling mean gene flow values to and from each individual wetland.

Origin									
Destination	LOTU	WAIM	TURT	JCSF	KLIP	WIND	KEAW	PEHA	Total Immigration
LOTU	-	2.9	5.2	1.7	3.1	1.8	2.6	1.3	18.7
		(2.0-3.8)	(3.8-6.5)	(1.1-2.4)	(2.1-4.0)	(1.2-2.5)	(1.7-3.4)	(0.8-1.9)	
WAIM	1.6	-	1.0	1.6	5.1	1.0	1.8	1.8	12.3
	(1.1-2.2)		(0.7-1.5)	(1.2-2.2)	(4.0-6.4)	(0.4-1.5)	(1.3-2.5)	(1.3-2.5)	
TURT	2.0	1.2	-	1.2	2.9	0.6	3.0	4.3	13.2
	(1.5-2.6)	(0.8-1.7)		(0.8-1.6)	(2.3-3.8)	(0.4-1.0)	(2.3-3.8)	(3.5-5.4)	
JCSF	4.2	5.5	10.3	-	5.9	2.7	9.6	4.2	38.2
	(2.9-6.0)	(4.0-7.6)	(7.8-13.6)		(4.3-8.2)	(1.9-3.7)	(7.2-12.8)	(2.9-6.0)	
KLIP	2.2	2.5	1.6	1.3	-	0.4	0.6	1.3	7.8
	(1.8-2.8)	(2.0-3.1)	(1.2-2.0)	(1.0-1.7)		(0.3-0.6)	(0.4-0.9)	(1.0-1.7)	
WIND	4.4	2.0	2.1	2.3	2.6	-	2.0	3.5	14.5
	(2.7-5.8)	(1.4-3.7)	(1.4-3.0)	(1.7-3.2)	(1.9-3.6)		(1.4-2.8)	(2.5-4.7)	
KEAW	1.9	2.1	2.0	2.2	4.8	2.2	-	2.9	16.1
	(1.0-2.8)	(1.4-2.9)	(1.4-2.9)	(1.5-3.1)	(3.1-6.3)	(1.6-3.2)		(2.1-4.0)	
PEHA	2.1	0.7	2.6	1.2	2.4	0.9	1.1	-	8.8
	(1.6-3.0)	(0.5-1.2)	(2.0-3.7)	(0.8-1.8)	(1.8-3.4)	(0.6-1.4)	(0.8-1.6)		
Total	18.4	16.9	24.8	11.4	26.7	9.6	20.7	19.4	-
Emigration									

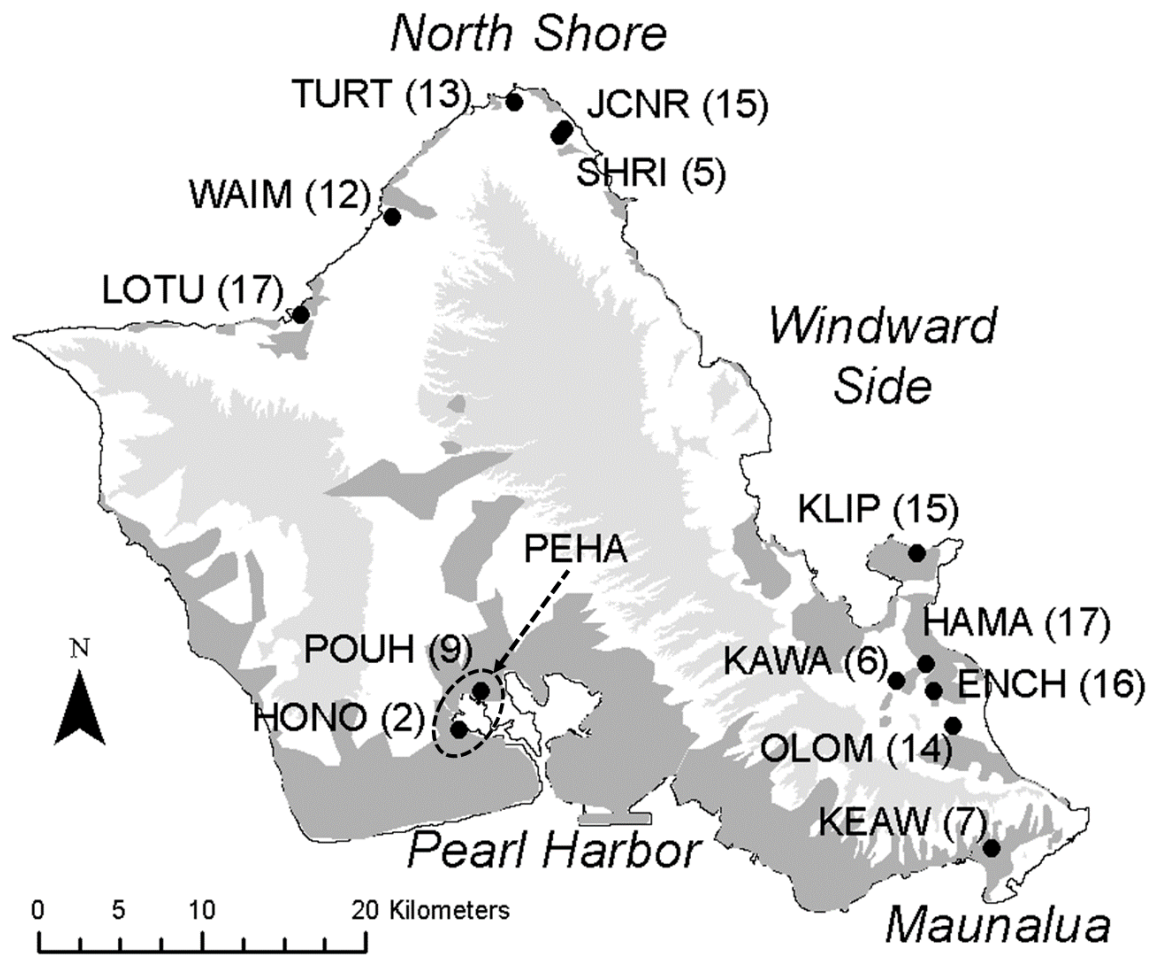


Figure 3.1: Locations of sampled wetlands on O`ahu; four-letter codes are defined in Table 1. Note that PEHA (Pearl Harbor) represents the combination of two adjacent wetlands with smaller sample size, POUH (Pouhala Marsh) and HONO (Pearl Harbor National Wildlife Refuge, Honouliuli Unit). Light gray regions indicate mountain ranges (elevation > 300 m) and darker gray represents developed and urban areas. Parenthetic values indicate the number of birds sampled at each site.

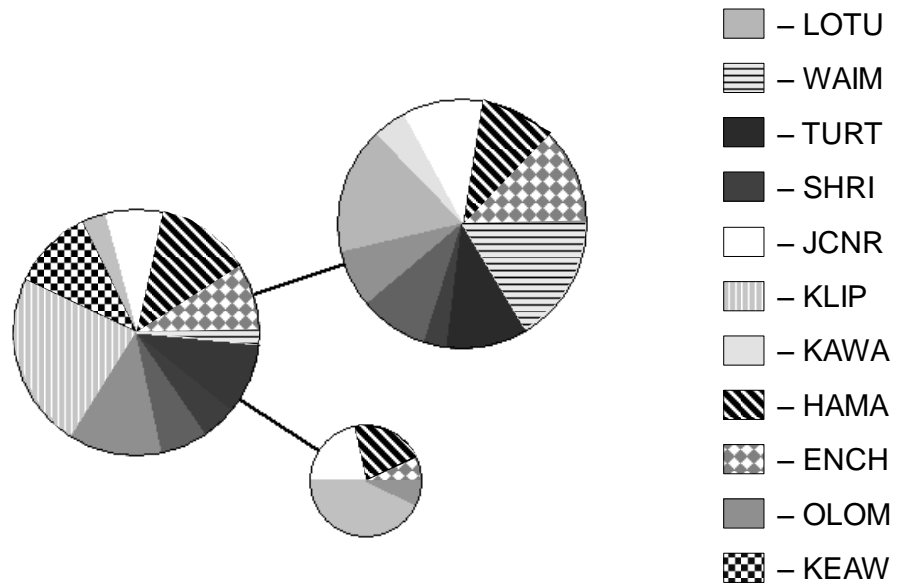


Figure 3.2: Network diagram illustrating relationships of mtDNA haplotypes among sampled wetlands of Hawaiian gallinules on O`ahu. The size of the circle corresponds to the frequency of each haplotype, and connecting lines represent a change in a single nucleotide. Each sampled wetland has a unique shading pattern.

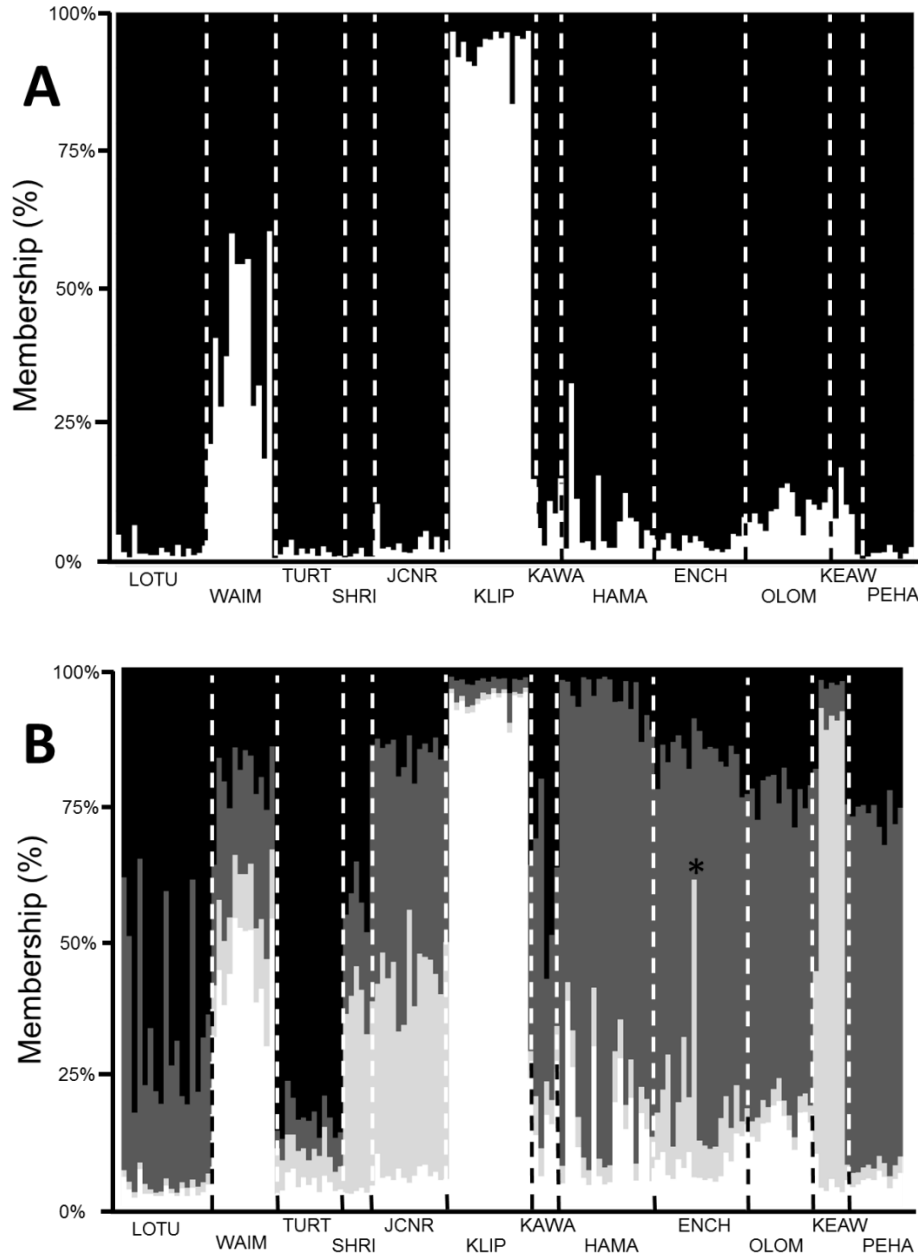


Figure 3.3: Average membership coefficient of genotyped Hawaiian gallinules that were sampled at 12 wetlands on O`ahu, Hawaii; A shows assigned membership among two clusters (the most likely number according to the Evanno method), and B shows membership among four clusters (the most likely number according to the maximum-likelihood method) inferred with data from 12 microsatellite loci in STRUCTURE.

Dashed lines separate individuals from different wetlands. Asterisk denotes an individual banded at KEAW (Keawawa wetland, Maunaloa region) that was later resighted and captured at ENCH (Enchanted Lakes, Windward side).

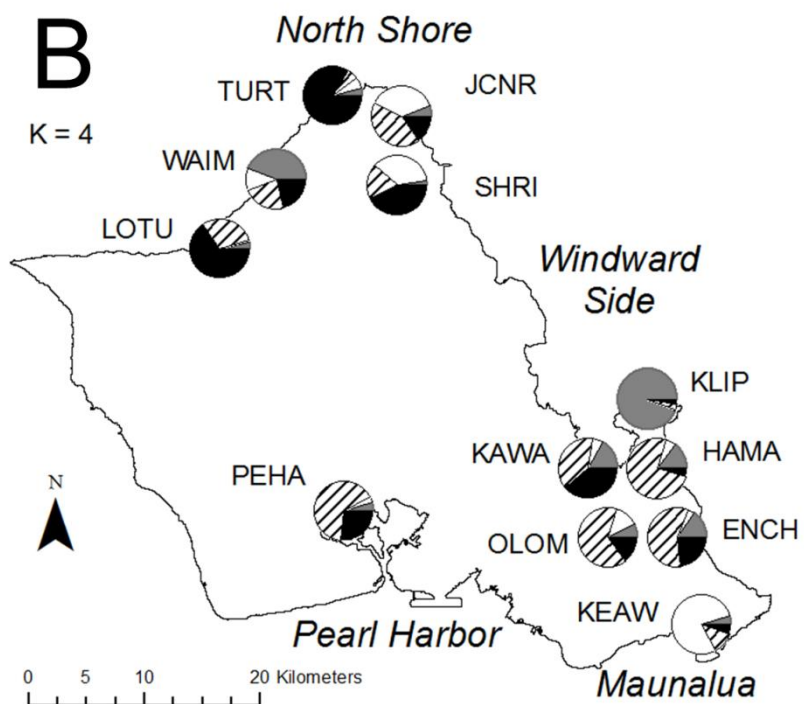
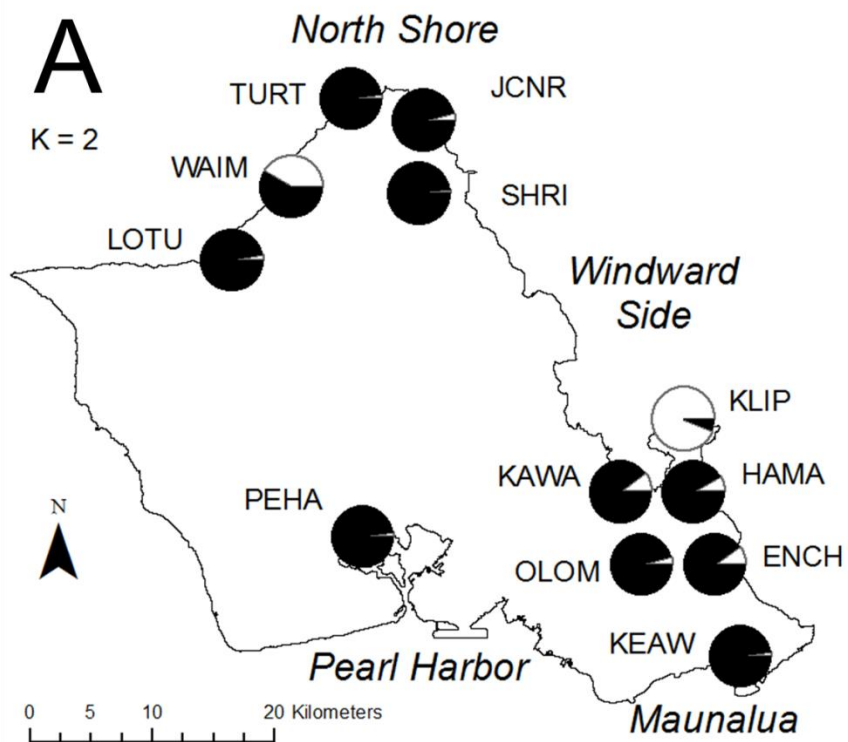


Figure 3.4: Within-wetland average membership coefficients of genotyped Hawaiian gallinules sampled at 12 sites on O`ahu, Hawai`i, USA. Image A shows assigned membership among two clusters (the most likely number according to the Evanno method), and B shows membership among four clusters (the most likely number according to the maximum-likelihood method) based on data from 12 microsatellite loci analyzed in STRUCTURE.

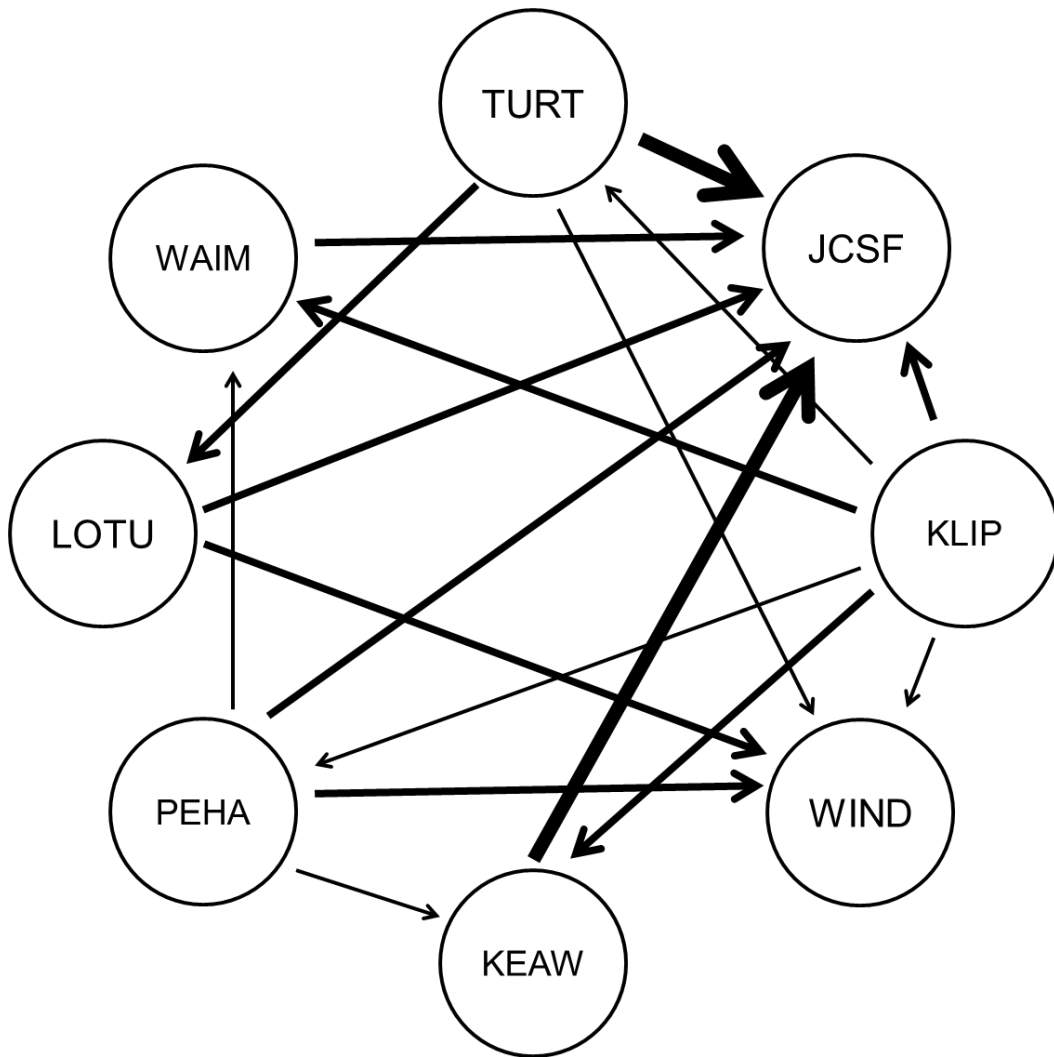


Figure 3.5: Diagram showing direction of prevailing gene flow between wetland sites where Hawaiian gallinules were sampled on O`ahu, Hawai`i, USA. Gene flow estimates with non-overlapping 95% confidence intervals between wetland pairs are shown. Arrow thickness represents the magnitude of gene flow (N_m): small arrows 1.0 – 2.4, medium arrows, 2.5 – 5.0, and large arrows >5.0 .

Chapter 4

Landscape genetics identifies streams and drainage infrastructure as dispersal corridors for an endangered wetland bird

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Abstract

Anthropogenic alterations to landscape structure and composition can have significant impacts on biodiversity, potentially leading to species extinctions. These population-level impacts of landscape change are mediated by animal behaviors, in particular dispersal behavior. Little is known about the dispersal habits of rails (Rallidae) due to their cryptic behavior and tendency to occupy densely vegetated habitats. The effects of landscape structure on the movement behavior of waterbirds in general are poorly studied due to their reputation for having high dispersal abilities. We used a landscape genetic approach to test hypotheses of landscape effects on dispersal behavior of the Hawaiian gallinule (*Gallinula galeata sandvicensis*), an endangered subspecies endemic to the Hawaiian Islands. We created a suite of alternative resistance surfaces representing biologically plausible a-priori hypotheses of how gallinules might navigate the landscape matrix, and ranked these surfaces by their ability to explain observed patterns in genetic distance among 12 populations on the island of O`ahu. We modeled effective distance among wetland locations on all surfaces using both cumulative least-cost-path and resistance-distance approaches, and evaluated relative model performance

using Mantel tests, a causal modeling approach, and the mixed-model maximum-likelihood population-effects framework. Across all genetic markers, simulation methods, and model comparison metrics, surfaces that treated linear water features like streams, ditches, and canals as corridors for gallinule movement outperformed all other models. This is the first landscape-genetics study on the movement behavior of any waterbird species to our knowledge. Our results indicate that lotic water features, including drainage infrastructure previously thought to be of minimal habitat value, contribute to habitat connectivity in this listed subspecies.

4.1 Introduction

Research on animal movement behavior, in particular how landscape features affect dispersal, is essential for predicting, understanding, and managing the impacts of ongoing changes in climate and landscape structure on animal populations (Hanski, 2001; Knowlton and Graham, 2010; van Strien et al., 2014; Holyoak and Heath, 2016). Although direct data on animal movement can be time consuming and expensive to collect, and often limited by constraints on sample size, the development of methods using indirect information like genetic markers as a surrogate of movement has greatly increased understanding of population connectivity; informing management plans (Epps et al., 2007; Lowe and Allendorf, 2010; Anderson et al., 2015). These indices can be especially important for studying the movement of behaviorally cryptic species that are difficult to study otherwise, such as through mark-resighting (Finnegan et al., 2012). By comparing the frequency of alleles among selectively neutral genetic markers, it is possible to estimate genetic distances between individuals or populations; these distances are assumed to correlate with the dispersal and subsequent breeding of individuals across space and time (i.e. gene flow; Waser and Strobeck, 1998; Sexton et al., 2014).

The field of landscape genetics provides an analytical framework to assess the potential effects of spatial features on genetic differentiation of wildlife populations, and to explain observed population genetic patterns within the context of landscape structure and composition (Manel et al., 2003; Manel and Holderegger, 2013). The most basic landscape genetic model, isolation by distance, is based on the assumption that net movement across a landscape follows Brownian motion. As a result, genetic similarity

among populations (or individuals) is correlated with geographic or Euclidean distance (Wright, 1943). The concept of effective distance extends this model by incorporating information on the movement behavior of an organism, and by considering distances between points or populations, and the type of matrix vis-à-vis its relative permeability to movement (Adriaensen et al., 2003; McRae, 2006). Accordingly, populations or individuals can have a high effective distance between them if dispersal barriers (e.g., difficult terrain) are located between them, even if the actual geographic or Euclidean distance between them is not large (e.g., Ferreras, 2001; Scriven et al., 2016; Lecompte et al., 2017).

Effective distances can be quantified using spatially explicit models that reflect hypotheses about the effects that landscape features have on the movement of the focal organism (Storfer et al., 2007). Estimates of effective distance for a given organism are generated by simulating animal movement according to these spatially explicit models. These models, known as resistance surfaces, are represented by a raster image in which pixels on a landscape have values that describe their relative permeability or resistance to movement (Spear et al., 2010). Among a suite of surfaces, which are treated as hypotheses, those that best explain observed movement data are assumed to represent the most likely representation of how a given set of landscape features affects movement in an organism (Cushman and Landguth, 2010; Zeller et al., 2012). Typically, measures of genetic distance (e.g., F_{ST}) or effective migration rate are used to compare the explanatory power of resistance surfaces (Zeller et al., 2012). These metrics do not require recaptures or resightings of individuals, but are limited in that they only capture dispersal events that lead to breeding. The landscape genetics approach can thus provide

an important first look into the movement ecology of organisms that may be difficult to track or recapture across time.

Current work using this framework is generally biased toward temperate climates and forest ecosystems on large continents (Balkenhol et al., 2015; Waits et al., 2016). However, avian taxa are under-represented in these studies (Haig et al., 2011; Zeller et al., 2012; Kozakiewicz et al., 2017). Behavioral research on birds in human-altered landscapes has demonstrated that the effects of landscape change on movement rates are typically species specific (Fahrig, 2007). Thus, landscape genetic analyses of threatened and endangered bird taxa are urgently needed for a better understanding of the impacts of continued anthropogenic landscape change on wild bird populations. Among avian taxa, rails (family Rallidae) are among the most poorly understood with regard to their movement ecology, due to their cryptic behavior and tendency to inhabit densely vegetated habitats (Ripley et al., 1977; Taylor, 2010). Rails also exhibit the interesting behavioral-evolutionary tendency to colonize widespread and isolated islands or habitat patches, while appearing to have a natural antipathy to disperse after colonization, often becoming flightless (Livezey, 2003; Steadman, 2006). Coupling these behaviors with the discrete and naturally fragmented nature of many wetland ecosystems, and further isolation by anthropogenic landscape change, wetland-specialist birds like rails are a convenient study system for landscape genetics research. The sensitivity of wetland ecosystems to a diversity of anthropogenic threats (Strayer and Dudgeon, 2010; Green et al., 2017) makes wetland birds a group for which landscape genetics research is likely of substantial importance to conservation.

Our interest is in one member of the Raillidae, the Hawaiian gallinule (*Gallinula galeata sandvicensis*), which is an endangered subspecies of the common gallinule endemic to freshwater wetlands of the Hawaiian Islands (United States; Bannor and Kiviat, 2002). These birds persist in small, spatially isolated populations restricted to coastal freshwater wetlands, and connectivity among these populations is considered an important factor in their conservation and management (USFWS, 2011; Reed et al., 2012; Underwood et al., 2013). However, little is known about the movement behavior of Hawaiian gallinules, and their cryptic behavior leads to poor detection rates, limiting the efficacy of mark-resight studies (DesRochers et al., 2008). Anecdotal observations of Hawaiian gallinules, as well as work on other habitat specialist birds, have yielded a number of hypotheses about the effects of landscape features on gallinule movement that can be tested using a landscape genetics framework. .

For example, urban landcover has been implicated as a dispersal barrier in several taxa (e.g., stream insects, including Plecoptera and Ephemeroptera, Smith et al., 2009; Alpine Newts, *Mesotriton alpestris*, Emaresi et al., 2011; Yellow-faced bumble bees *Bombus vosnesenkii*, Jha and Kremen, 2013), because of increased mortality in urban areas, the physical difficulty of traversing them, or psychological inhibitions that prohibit dispersal across densely developed areas or roads (Harris and Reed, 2002; Shepard et al., 2008). An analytical example of the role of urbanization in connectivity is seen in landscape integrity models, which correlate landscape resistance with human modification, and are thought to be a general approach to connectivity modeling widely applicable across taxa (Baldwin et al., 2012). Repeated accounts of road mortality of Hawaiian gallinules (K. Doyle, Hawaii Division of Forestry and Wildlife, pers. comm.)

imply that these birds are highly susceptible to being struck and killed by automobiles and even bicycles (L. Pool, Waimea Valley, pers. comm.). Gallinule movement may be impeded by high-traffic roads, which could prevent movement through direct mortality. Furthermore, Major et al. (2014) found that urbanization acted as a barrier to dispersal and gene flow for the White-fronted chat (*Epthianura albifrons*), a coastal wetland-specialist bird. We hypothesized that urban developments would similarly act as barriers to movement for Hawaiian gallinules.

Another potential barrier to dispersal and gene flow by Hawaiian gallinules could be natural landscape features like ridges and mountains. van Rees et al. (*in review*) marked over 200 gallinules with unique color bands on the island of O`ahu, and the few resightings of dispersed individuals were been parallel to, rather than across mountain ranges. This, coupled with observations by Perkins (1903) and Banko (1987) that gallinules and moorhen are rarely seen at high elevations, may suggest that either high elevation or steep slopes are prohibitive to movement.

An alternative hypothesis about how gallinules move across a landscape comes from the species' habitat affiliations – they nest and feed exclusively in and near emergent vegetation (Bannor and Kiviat, 2002), and they typically make use of open water and emergent hydrophytic vegetation for escaping potential predators (Lima, 1993; Dear et al., 2015). Areas with wetter conditions that are associated with wetland habitat may thus be more permeable to movement by gallinules, by decreasing both actual predation risk and behavioral barriers (*sensu* Harris and Reed, 2002) as opposed to moving through areas without water and emergent vegetation. The openness of wetland habitats typically occupied by gallinules may also be a feature influencing movement.

Keyel et al. (2012) identified openness (an unobstructed view) as an influential habitat characteristic on patch selection of grassland specialist birds. In this context, openness was related to perceived predation risk by individuals. Because Hawaiian gallinules also tend to occupy open areas with little tree cover, we could hypothesize that the degree of openness associated with a type of land use (agricultural fields, shrubland, forest) would vary negatively with landscape resistance.

The dispersal behavior of rails in general, and gallinules in particular, is poorly understood (Taylor, 2010). Although there has been little speculation on the role of barriers in gallinule movement, Nagata (1983) suggested that Hawaiian gallinules may use rivers or other linear water features as corridors for dispersal, and are more prone to movement during floods, when those features are enlarged. The assertion that movement by Hawaiian gallinules is triggered by floods is also supported by anecdotal evidence of major population turnovers within a small population of banded individuals during two large flooding events in 2005 and 2017 (L. Pool, Hi`ipaka LLC, Waimea Valley, pers. comm.). Similarly, on Guam, radio-tracked Marianas common moorhen (*Gallinula chloropus guamii*) frequently moved from marshes into rivers, and did so more often during the wet season (Takano and Haig, 2004). If Hawaiian gallinules use water features on the landscape, then wetland habitats that are connected by riparian areas or other linear water features (e.g., drainage canals, roadside swales) should have increased inter-habitat dispersal relative to wetlands that do not.

There are a great many alternative explanations for how Hawaiian gallinules might perceive landscape features during dispersal between wetlands. Consequently, we generated a suite of models of the O`ahu landscape matching our proposed hypotheses

about the relative resistance of both natural and anthropogenic landscape features to gallinule movement across the landscape. The models are based on observations and biologically informed speculation about distributions and movements across the landscape. Once these models were created, we determined the expected patterns of movement and compared their fits to recently published data on micro-geographic genetic differentiation of Hawaiian gallinules on O`ahu (van Rees et al. 2017). Our goal was to determine the relationships among landscape features and observed genetic differentiation. Results from this study will provide important information for the subspecies' recovery, and to predicting the potential vulnerability of Hawaiian gallinules to future modifications to the landscape as attributable to land-use and climate change.

4.2 Methods

4.2.1 Study Species

We studied Hawaiian gallinules on the island of O`ahu (Hawaii, USA, 21.3156 N, -157.858 W), one of two islands that make up the subspecies' entire range. These birds were once found on the five main Hawaiian Islands, but they were extirpated from all islands but O`ahu and Kauai from the late 19th to mid-20th century (Banko, 1987). During this time, habitat loss from land alteration and exotic, invasive wetland plants, as well as predation from introduced mammalian predators drove a severe decline and retraction in population size and range (USFWS, 1977; Griffin et al., 1990). This precipitous decline was eventually halted with legal protection, the establishment of National Wildlife Refuges and state protected areas on these two islands, and the advent of habitat management (predator control and vegetation restoration), which are associated with a

slow but consistent recovery of Hawaii's endangered waterbirds over the last 50 years (Schwartz and Schwartz, 1949; Reed et al., 2007, 2011; Underwood et al., 2013). O`ahu's current gallinule population consists of between 200-300 individuals scattered among relict and fragmented wetlands, isolated by severe wetland loss on the island (USFWS, 2011; van Rees and Reed, 2014). Wetland habitats are distributed with varying degrees of geographic isolation and in a variety of landscape contexts, within landscape matrix consisting of mountain ranges, active military bases, urban and suburban areas, highways, agriculture, and recreational areas (e.g., golf courses and resorts).

4.2.2 Genetic Data

We obtained multi-locus genotypes for 152 Hawaiian gallinules from 12 different wetlands on O`ahu from a previous study (van Rees et al., 2017) (Figure 4.1). We defined wetlands as complexes of spatially proximate and hydrologically linked water bodies. The sampled wetlands included all major breeding areas for the Hawaiian gallinule on the island, and our sample accounts for at minimum 30% of the known population of the island, covering all known major subpopulations (Reed et al., 2011; USFWS, 2011). We obtained estimates of inter-population genetic variance (F_{ST}) among the 12 wetland sites from van Rees et al. (2017); estimates are based on microsatellite genotype data collected from 12 autosomal loci and 520 base pairs (bp) of the NADH dehydrogenase 2 (ND2) region of mitochondrial DNA (mtDNA). All microsatellite loci were tested for Hardy-Weinberg equilibrium and linkage disequilibrium prior to analysis. Information on genetic diversity, population structure and analysis of genetic data can be found in van Rees et al. (2017).

4.2.3 Landscape Variables

We represented landscape variables and movement capacities using resistance surfaces, which treat landscapes as a raster grid, with different features (landscape types) given a value of resistance related to the difficulty of passing through that point (Spear et al., 2010; Figure 4.2). We analyzed 20 resistance surfaces that addressed 10 hypotheses pertaining to the movement ecology of Hawaiian gallinules (Table 1). These hypotheses were derived from expert opinion and literature on this and related taxa (see introduction). We named these surfaces according to the datasets from which they were derived; the named groups are Elevation, Topographic Wetness Index (TWI), Land Use (LU), Roads, and Proximity to Water. All surfaces were resampled to 30m resolution and degree of resistance was scaled from 1 to 100, with 100 being the maximum resistance. We assigned values to different landscape features based on expert opinion and available field evidence, with the objective of defining relative resistance values (e.g., roads have higher resistance than agricultural fields), rather than specific numerical relationships (e.g., roads have a resistance value of 70, rather than 40) (Figure 4.2 a-d) (see Spear et al., 2010; Zeller et al., 2012).

Elevation datasets were derived from 30m resolution digital elevation models from the Hawaii Department of Commerce et al. (2007). Three types of surfaces were created using digital elevation models, with two versions each, for a total of six resistance surfaces (Table 1). The first of the elevation-based hypotheses are binary models, in which we assigned a low resistance to all pixels below an empirically derived elevation threshold (resistance value = 10), and assigned a high value (80) to all pixels above that

value (Hypothesis 1). Birds could move through high elevations, but would move more readily (by a factor of 8) through low elevations. The threshold (100m) was based on the observation that most recorded occurrences and habitats of Hawaiian gallinules on O`ahu were at elevations below 100m (USFWS 1977; van Rees and Reed, unpubl. data). For linear resistance surfaces, we assumed a direct linear relationship between elevation and landscape resistance, with minimal resistance (resistance value = 1) at coastal elevations and maximum resistance (resistance value = 100) at maximum elevation for the island (Hypothesis 2). Finally, for sloped surfaces, we assumed a linear relationship between degree of slope and resistance, where the maximum slope was given a value of 100, and flat ground was given a resistance value of 1 (Hypothesis 3). Each hypothesis we propose could have multiple scenarios, referred to as resistance surfaces. The scenarios are summarized in Table 1.

Two additional hypotheses, with a total of four resistance surfaces, were based on the TWI (Beven and Kirkby, 1979). The TWI is a simple hydrological model that uses a digital elevation model (a spatial representation of elevation across a landscape) to approximate the likelihood that water would accumulate at any single point under uniform rainfall conditions. The TWI highlights areas that are likely to support standing water or mesic conditions, which are strongly associated with the occurrence of common gallinules and gallinule habitats (Bannor and Kiviat, 2002). We calculated TWI using the Geomorphology and Topology Toolbox (Evans and Oakleaf, 2011) in ArcGIS 10.2. In binary TWI models, we divided the landscape between low-resistance pixels (resistance value = 1) at or above a threshold TWI value, and high-resistance pixels (100) below that value (Hypothesis 4). We used a threshold value (TWI value = 11) for binary TWI

surfaces based on van Rees and Reed (2014), who used TWI to infer the likely locations of historical wetlands on the Hawaiian Islands. We took high TWI values to infer the presence of wet conditions and a high likelihood of wetland cover. Linear TWI models assumed an inverse linear relationship between TWI and landscape resistance, scaled from 0 to 100m, where higher TWI values had lower resistance, and vice-versa (Hypothesis 5).

Some inter-wetland pathways (the intervening space between two wetland habitats) included open ocean, but the landscape resistance of open ocean to Hawaiian gallinules is unknown. Rallidae species have colonized oceanic islands all over the world, but are reluctant fliers when not dispersing (Ripley, 1977). Although genetic (Miller et al., 2015) and observational (Worthington, 1998; Takano and Haig, 2004) evidence of long-distance (~77km) movements over open ocean water exist for the Marianas common moorhen, no movements of Hawaiian gallinules have been observed between the two islands they inhabit (Kaua`i and O`ahu, approximately 138km apart), despite extensive mark-recapture efforts (Dibben-Young, 2010; van Rees et al., *in review*). There is accordingly some uncertainty with regard to the willingness of Hawaiian gallinules to disperse over open ocean. Consequently, we developed two scenarios each for the Elevation and Topographic Wetland Index hypotheses; version A, in which we assign high resistance (100) to open ocean water, and version B, where we assign lower resistance (20) to open ocean water.

Land use surfaces were created using the 2011 C-CAP Land Cover dataset for O`ahu, Hawaii (NOAA Ocean Service 2014), and used to model three hypotheses with regard to potential landscape effects on gallinule movement. In the binary land use model

we assigned low resistance (resistance value = 1) to all land cover types except for urban cover, and high resistance (resistance value = 100) to urban land (Hypothesis 6). This binary urban resistance surface specifically pertains to the hypothesis that urban areas act as dispersal barriers to Hawaiian gallinules. In the land use three-class surface, we assigned the same high value to urban areas, and low resistance value to wetland land cover, with a moderate resistance (resistance value = 50) to all other pixels. The three-class land use surface thus integrates the hypotheses that wetland habitat may facilitate dispersal in Hawaiian gallinules with that of urban cover impeding dispersal. The structural land use model groups land use types into three categories along a gradient of habitat openness (cf. Keyel et al., 2012), open (grassland, wetland, agricultural land, resistance value = 1), intermediate (shrubland, resistance value = 50), and closed (forest and urban, resistance value = 100). This structural land use surface reflects the hypothesis that gallinule movement may be affected by the physical structure of the landscape, either by physical or psychological mechanisms (e.g., Harris and Reed, 2002; Trizio et al., 2005; Tremblay and St. Clair, 2009; Zeller et al. 2012) (Hypothesis 7). Finally, the full land use model combines all previous land use models, and assigns different landscape resistance values for five habitat types: wetland, open, shrubland, forest, urban, in order of increasing landscape resistance (resistance values = 1, 10, 30, 50, 80, 100, respectively; Hypothesis 8).

The roads resistance surface was derived from the O`ahu Street Centerlines dataset (HOLIS 2015), and assigns high landscape resistance values to highways and major roads, moderate values to all other roads, and low resistance to all other pixels. Our road-based resistance surface addresses the hypothesis that roads impede dispersal of

Hawaiian gallinules through either direct mortality or psychological inhibition (e.g., Benitez-Lopez et al., 2010; Thinh et al., 2012; Zeller et al., 2012) (Hypothesis 9).

Finally, we derived resistance surfaces based on Proximity to Water from the National Wetlands Inventory dataset for Hawaii (USFWS, 2010) downloaded using the U.S. Fish and Wildlife Service's wetland mapper tool (<http://www.fws.gov/wetlands/Data/Mapper.html>). We excluded all large lacustrine (open water) wetlands, ocean shoreline wetlands, and estuarine marshes from this dataset because they are not used by Hawaiian gallinules (Banko, 1987), and we retained rivers, streams, freshwater low-elevation wetlands, other water features (drainage ditches, irrigation infrastructure). We then used the Euclidean distance tool to generate a raster dataset where each pixel was assigned a value based on its proximity to the nearest water feature; all Proximity to Water resistance surfaces were generated using the National Wetlands Inventory dataset. All resistance surfaces in the Proximity to Water category are based on anecdotal accounts that Hawaiian gallinules tend to travel along river margins, observations by the authors that the birds appear behaviorally inhibited from moving far from water, and evidence from related taxa that movement occurs along riparian corridors (Nagata, 1983; Takano and Haig, 2004; Hypothesis 10). In the binary Proximity to Water surface, we assigned a low resistance value (resistance value = 1) to all pixels within a distance of 30m of a water feature and a high value (resistance value = 100) to all pixels outside of that radius. The threshold distance of 30m was derived from observations by the authors of the distances at which Hawaiian gallinules are rarely seen away from water features. For the three Water Linear surfaces, we assumed a linear increase in landscape resistance with distance from a water feature, which reaches its

maximum at 30, 100, or 200m from the water feature, respectively. Finally, for the Water Negative Binomial surface we assumed a nonlinear relationship according to the negative binomial equation ($Y = 100 - 4e^{-(x-8)}$), based on a function used by Trainor et al. (2013) to describe potential effects of distance from habitat features affecting dispersal in habitat specialists. The equation was parameterized using expert opinion to identify the minimum distances from a landscape feature at which landscape resistance would increase and at which increasing distance would cease to affect landscape resistance.

4.2.4 Effective and Euclidean Distances

Because little is known about the movement behavior of Hawaiian gallinules, we calculated effective distances among all pairwise combinations of occupied (and sampled) habitat patches using both cumulative least cost paths and resistance distances (McRae, 2006). All distances were calculated between approximate centroids of each habitat patch, rather than between closest patch edges, because wetlands on O`ahu are small, isolated patches surrounded by large amounts of non-wetland matrix (van Rees and Reed, 2014). Consequently, the amount of within-patch distance from centroid to patch edge is a negligible amount of total distance between centroids. These two approaches to modeling effective distance have different assumptions about movement behavior, with cumulative least-cost paths assuming complete knowledge of the landscape, and while resistance distances use a random walk model. We calculated least-cost path distances using the `costdistance` function from the package `gdistance` in R (van Etten, 2017) and resistance distances using `Circuitscape 4.0` (McRae et al., 2016). We also calculated topographically-adjusted Euclidean distances between population pairs

using the near-to-table tool in ArcGIS.

4.2.5 Landscape Genetic Analyses

There is disagreement in the recent literature on which statistical methods are most appropriate for assessing the relationships between landscape features and genetic differentiation (Zeller et al., 2016; Shirk et al., 2017). Consequently, following Balkenhol et al. (2009), we used three methods of analysis to reduce the potential for method-dependent biases in our results. Datasets were analyzed in the form of distance matrices, with pairwise genetic distance (F_{ST}) of microsatellite and mtDNA markers as the response variable and pairwise effective distance for a given model as the predictor variable. F_{ST} values were taken from van Rees et al. (2017), changing non-significant and negative values to zero. We used F_{ST} values from both microsatellites and mtDNA in all analyses. As in Phillipsen et al. (2015), we chose to compare only univariate models for our analysis, due to the high likelihood of collinearity between some of our resistance surfaces (e.g., TWI-based vs. Proximity to Water).

We used simple Mantel tests (Mantel 1967; Legendre and Fortin, 2010) to analyze landscape genetic relationships while accounting for the non-independence of data points, because it is the most widely used method for this type of analysis. Mantel tests have been criticized, however, for having high Type I error rates (Balkenhol et al., 2009; Guillot and Rousset, 2013; Graves et al., 2013). Accordingly, we followed the causal modeling framework using partial Mantel tests (Cushman et al., 2006; Cushman and Landguth, 2010) and evaluated mean relative support (\overline{RS}) for all models as in Zeller et al. (2016). We performed all Mantel tests using the package *vegan* (Oksanen et al.,

2016) in R.

We also analyzed landscape genetic relationships using the Mixed-model Maximum-likelihood Population-Effects framework (MLPE; Clarke et al., 2002; van Strien et al., 2012), following the methods described in van Strien et al. (2012). This method accounts for the pairwise dependency of genetic and effective distance data by incorporating it into the covariance structure of the linear model, and accounting for it using a random effect, allowing differentiation from the fixed effects associated with predictor variables. We assessed these effects by calculating the R^2_{β} statistic (Edwards et al., 2008), which measures the proportion of observed variation explained by the fixed effects of the model, based on van Strien et al. (2014). We used this method, rather than AIC, due to assertions that AIC was not an appropriate method of model comparison for MLPE models (Verbeke, 1997; Orellien and Edwards, 2008; van Strien et al., 2012). We fitted mixed effects models with REML estimation using the lmer function in the package lme4 (Bates et al., 2011) in R.

4.3 Results

4.3.1 Landscape Genetics Analysis

Models of the Proximity to Water group generally explained a higher amount of observed variation in pairwise population differentiation than any other group of models (Table 2). These models had consistently lower p-values and higher r values in simple Mantel tests across both methods of estimating effective distance, and had much higher \overline{RS} scores than all other models. The observed patterns of model support were consistent between genetic distances calculated using microsatellite and mitochondrial DNA

(microsatellite results in Table 2, mitochondrial DNA in Supplemental Materials, Table 4.S1). All observed statistically significant p-values from simple Mantel tests were restricted to models from the Proximity to Water group. R^2_β values were also highest for Proximity to Water models, although the difference was less pronounced, and R^2_β were generally low. The Euclidean distance model performed poorly across all methods of comparison, and models from all groups except for distance to water varied widely in performance across methods of estimating effective distance, but always performed more poorly than Proximity to Water models. We observed no clear pattern of model support between models with high resistance assigned to ocean water (A models; see Table 1) and models with low resistance assigned to ocean water (B models).

Among Proximity to Water models, r values, \overline{RS} values, and R^2_β values were consistently higher using effective distances calculated with cumulative least-cost paths than those calculated in Circuitscape. While all Proximity to Water models using least-cost-path had statistically significant p-values, only one, the binary model, had a significant p-value among those with effective distances measured in Circuitscape. The best overall models differed according to both measure of effective distance and method of statistical analysis, with the two-class, linear to 100m distance, linear to 200m distance, and negative binomial distance functions scoring highest for at least one statistic and effective distance measure.

4.4 Discussion

To our knowledge, this is the first landscape genetics analysis for a waterbird species. As such, it represents a step toward overcoming one bias in the growing

literature of landscape genetics (Zeller et al., 2012; Kozakiewicz et al., 2017). We found consistent support for resistance surfaces that were based on Proximity to Water, while all other resistance surfaces showed low explanatory value and statistical significance. The higher explanatory power and statistical significance of Proximity to Water surfaces was robust across three model selection metrics (Mantel's r and p -value, \overline{RS} , and R^2_β), two simulation frameworks (least-cost paths and resistance distance), and two genetic markers, suggests that the presence of water features explains 10.7-63.7% of variation in observed genetic structure among Hawaiian gallinule populations inhabiting wetlands on O`ahu (Table 2). Although the results of simple Mantel tests should be interpreted cautiously (Balkenhol et al., 2009; Zeller et al., 2016), we see parallel patterns in more robust metrics. Zeller et al. (2016) found that simple Mantel's r and \overline{RS} performed best when comparing resistance surfaces where landscapes were highly fragmented, and we believe our study system fits this condition well. We also analyzed our results using linear mixed effects models fit with MLPE, which is currently considered the best performing method for performing regressions on matrix data (Shirk et al., 2017), and had similar, though less distinct results (see Supplemental materials, Table 4.S1). The consistency across model-selection metrics and sharp contrast in support compared to all other models of landscape resistance provide evidence that the presence of small wetlands, drainage canals, and streams enhances genetic connectivity in this endangered subspecies, supporting suggestions by other authors that *G. g. sandvicensis* tend to move along river systems or other linear water features. This finding coincides with observations in the Marianas common moorhen, which, as mentioned above, has been documented using streams during dispersal (Takano and Haig, 2004).

Visual inspection of least-cost paths developed using our 100m corridors, distance-to-water surface, and the least-cost-path function in ArcGIS 10.0 (Figure 4.3 and 4.4), shows that our leading resistance surfaces result in pathways that are in line with expert opinion on gallinule behavior. For example, a pathway between James Campbell National Wildlife Refuge and Keawawa wetland (Figure 4.3) involves traveling along the coastline and parallel to the Koʻolau mountains, rather than over the mountains, and the least-cost-path between Kawainui marsh and the Olomana golf links makes use of extensive drainage infrastructure and nearby streams, avoiding urban areas (Figure 4.4).

To further evaluate our model choice, we used a post-hoc analysis to test three additional models (see Supplementary materials, Table 4.S2) designed to account for three potential confounding factors that might have led to the high performance of distance-to-water models. These were 1) that any resistance surface consisting of low-resistance, linear features (corridors) outperforms all others, 2) that surrounding wetland habitat at source and destination nodes was driving patterns of simulated effective distance, and 3) that the spatial arrangement of features in the distance-to-water resistance surfaces, and not their resistance values, was driving their ability to describe observed genetic structure. Factor 1 was a special concern, considering that the distance-to-water resistance surfaces were the only ones that contained linear features that could act as corridors. To test scenario 1, we repeated our methods using an inverse version of the roads map, in which Oʻahu’s roads had low resistance, acting as corridors. For factor 2, we created a resistance surface identical to the distance-to-water 100m buffer layer, but using a new dataset that only featured streams and drainage infrastructure, and from which all wetland areas had been removed. Finally, for scenario 3, we tested the

explanatory value of an inverse version of the distance-to-water 100m buffer resistance surface. These extra resistance surfaces were tested against our microsatellite genetic dataset.

The roads-as-corridors resistance surface performed very poorly overall, with a low \overline{RS} and R^2_β value, although the mantel p-value for effective distances created in Circuitscape were near significance (Mantel $r = 0.182$, $p=0.07$). The poor performance of this resistance surface using our least-cost-path algorithm implied that linear features alone cannot explain the high performance of distance-to-water models using least-cost-path effective distances. The streams and drainage surface with wetlands removed performed comparably to other distance-to-water models, with a high Mantel r value (0.474 for LCP, 0.327 for CS), and lower Mantel p (0.021 for LCP, 0.058 for CS), and high \overline{RS} . Though this model did perform more poorly than other distance-to-water resistance surfaces, its sustained high performance compared to other resistance surfaces supports our initial interpretation that distance-to-water surfaces are explaining gene flow on a landscape context, and not simply because they include local habitat features at population nodes. Finally, our inverse “water as barrier” resistance surface performed extremely poorly, indicating that the resistance values assigned to the original distance-to-water surfaces are indeed responsible for high model performance. Having addressed these potential concerns, we are more confident in the statistical support shown for our hypothesis that Hawaiian gallinule movement is facilitated by water features in a varied landscape.

Recent research on the antipredator behavior of three other rail species, including one congener of the Hawaiian gallinule (Eurasian coot *Fulica atra*, purple swampphen

Porphyrio porphyrio, and dusky moorhen, *Gallinula tenebrosa*) provides some insights on the possible behavioral mechanisms of this tendency for dispersal to trace water features. These three other rail species showed greater alertness when farther from water features, indicating a higher degree of perceived predation risk with distance from water (Dear et al., 2015). The tendency of many rail species to flee toward water features as part of their normal predator escape behavior (Lima, 1993), and observations of increased alertness at greater distances from water, indicate that perceived predation risk may drive patterns of landscape resistance (i.e. movement) with respect to Proximity to Water. If this is the case, then gene flow and dispersal in Hawaiian gallinules may be governed in part by the so-called “landscape of fear” (Laundré et al., 2010). Field studies of the behavior of dispersing and foraging Hawaiian gallinules would be needed to evaluate whether this was indeed the mechanism driving observed gene flow patterns.

The potential use of linear water features as dispersal corridors by Hawaiian gallinules is similar to other tropical avian species that use riparian areas for dispersal (e.g., Gillies and St. Clair, 2008; Sekercioglu, 2009), though likely driven by a different mechanism. The prevailing understanding of most river-dispersing birds is that they are forest specialists that rely on riparian areas because they retain forest cover in otherwise deforested landscapes. Interestingly, rivers and other linear water features are often dispersal barriers for landbirds (Hayes and Sewlal, 2004; Weir et al., 2015). Data on the effects of landscape features on fine-scale movements of waterbirds are generally scarce, possibly because most waterbirds have great dispersal abilities and readily move great distances (Weller, 1999)

Because the ranking of correlation coefficients are mixed between different proximity-to-water models, we cautiously refrain from selecting one of those models as being the best supported. Given the limited genetic variation exhibited by the species (van Rees et al., 2017), and impacts of a recent population bottleneck on genetic diversity within Hawaiian gallinules (Sonsthagen et al., 2017), it could be that our current sample is insufficient to distinguish between functions relating proximity-to-water to resistance values. It could also be that there are additional constraints or facilitations (e.g., conspecific attraction) associated with dispersal behavior. While genetic structure was detected at small spatial scales, addition of whole genomic or reduced representation genomic data may provide greater spatial resolution and increase our ability to detect landscape features that are influencing gallinule movement patterns (Szulkin et al., 2016; Kozakiewicz et al., 2017). Finally, Zeller et al. (2016) note that model selection criteria for resistance surfaces perform very well at selecting the best among competing models, but not necessarily in estimating precise parameter values. Consequently, we do not attempt to quantify the relationship between Proximity to Water and landscape resistance, but value the acquired results as among the first empirical evidence describing the movement behavior of gallinules (but see Takano and Haig, 2004).

Consistently higher correlation coefficients and greater statistical significance among models that were applied using least-cost-path effective distances implies that the random walk model (upon which Circuitscape resistance distances are based) performs poorly in simulating movements of Hawaiian gallinules on O`ahu, and that birds may navigate the island with some degree of knowledge of their landscape context. Use of prior landscape knowledge may be typical of waterbirds, which often conduct long-

distance dispersal by means of higher-altitude flights, which can provide a view of a larger portion of the landscape. Furthermore, the finding that models based on road mortality, slope, and difficulty of traversing urban areas performed poorly may provide additional support for the hypothesis that Hawaiian gallinules are not dispersing on foot, despite being highly cursorial and rarely seen in flight. The hypothesis of flying dispersal in gallinules is supported by observations from Taylor and Anderson (1973), who reported 11 common gallinules (*G. g. cachinnans*) that were killed after striking a television transmission tower (~430m above ground level) in central Florida during nocturnal flights. It is worth noting that the tower was near “a small lake drained by a 20-foot wide canal; both contained water during the kills”. Also of interest is that kills occurred at night, supporting other observations that common gallinules and common moorhen (*G. chloropus*) perform higher-altitude flights at night (Roselaar, 1980; Taylor, 2010), which may explain why long flights are rarely observed on O`ahu.

Although our analysis yielded a strong and consistent signal that water features decrease landscape resistance to movement for Hawaiian gallinules on O`ahu, several important limitations to our study are worth noting. First, although genetic data are a useful descriptor of overall gene flow as a result of dispersal, they ultimately represent only a portion of animal movements (Spear et al., 2010), specifically movements that lead to inter-wetland dispersal and successful breeding (Cushman et al., 2014). Accordingly, although they match limited observations in related taxa (Takano and Haig, 2004), and anecdotal observations in this subspecies (Nagata, 1983), results from this study do not necessarily reflect the actual behavioral decisions made by individual Hawaiian gallinules as they traverse the island landscape. Additionally, the reliance of

this study on the testing of expert-designed models against empirical data and the subsequent process of model selection limits results to the best model among those chosen, and not necessarily the best possible model for describing gene flow in Hawaiian gallinules (cf. Beissinger and Snyder, 2002).

Empirical studies on the movement behavior of Hawaiian gallinules will be important to validate the results of our landscape genetic analysis and investigate the fine-scale behavioral decisions that lead to the observed population-level patterns of gene flow. Long-term banding and resighting programs over the subspecies' entire range (both O`ahu and Kaua`i) would need to continue with consistent effort. Banding and monitoring of gallinules and other Hawaiian waterbirds have been sporadic (Dibben-Young 2010). Study methods with higher spatiotemporal resolution may overcome the difficulty of detecting Hawaiian gallinules (Desrochers et al., 2008) and will be important for future movement studies. For example, GPS dataloggers and transmitters have been used to great effect in tracking a number of bird species (Gagliardo et al., 2007; Rodriguez et al., 2012), although the small spatial scale of our study area (wetlands 5-55km apart) would require high accuracy of locational fixes, and the tendency of gallinules to spend most of their time concealed in dense vegetation, reducing signal strength (C. van Rees, pers. obs.) reduces the efficacy of such methods. Another possibility is to gather data from translocation studies. Gillies and St. Clair (2008) translocated Neotropical forest birds varying distances from their home territories in Costa Rican dry forest and used radio telemetry to track the steps taken on their return. This approach allowed them to experimentally manipulate distances traveled and the types of landscape features that were navigated during travel. Although translocations of

endangered taxa like Hawaiian gallinules are not likely permissible solely for research purposes, in the past translocations have been undertaken to remove problematic individuals from areas where they were unwanted, and birds returned to their original territories within two weeks (Dibben-Young, 2010). Such management translocations provide excellent and as of yet untapped opportunities for exploring movement behavior in gallinules.

An important implication of this study is that habitats formerly hypothesized to have little value to Hawaiian gallinules (e.g., drainage ditches and canals, forested and vegetated streams, roadside swales) may actually affect their population persistence by increasing population connectivity. Hawaiian gallinules are a management dependent taxon (Reed et al., 2012) that typically persists only where wetland conditions can be maintained by artificial means (management for waterbirds, e.g., wildlife refuges, or else for aesthetic or agricultural purposes, e.g., golf course water hazards and taro farms). Exotic invasive plants and mammalian predators strongly reduce abundance and occurrence of Hawaiian gallinules in otherwise suitable wetland habitats (USFWS, 2011), which has led to the assumption that unmanaged wetlands and riparian systems have little conservation value. To the contrary, this study suggests that such unmanaged water features, even if small and linear or of limited to no value as breeding habitat, may have value in facilitating movement between relict wetlands and managed habitats for the subspecies. Such features may be acting as corridors, which may increase population persistence in fragmented landscapes by alleviating problematic consequences of isolation (Gilbert-Norton et al., 2010). As van Rees and Reed (2015) speculated, shifts in water management towards a greater emphasis on green stormwater infrastructure might

simultaneously provide conservation benefits by creating such corridors for waterbirds like the Hawaiian gallinule. Such landscape changes would represent a gain for both the management of imperiled (Giambelluca, 1986; Ridgley and Giambelluca, 1991) water resources and threatened wildlife on O`ahu.

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Table 4.1: Hypotheses of landscape effects on movement in Hawaiian gallinules and associated resistance surfaces, sources, and datasets for surface creation. TWI stands for Topographic Wetness Index, and LU for Land Use.

Hypothesis	Resistance Surface	Citation	Dataset
(1) Movement through low elevation	<ul style="list-style-type: none"> – <i>Elevation Two-Class A</i>: Areas below a threshold elevation have low resistance, areas below that value have low resistance; open ocean has high resistance – <i>Elevation Two-Class B</i>: Areas below 100m have low resistance, higher elevation has high resistance; open ocean has low resistance 	Perkins, 1903; Banko, 1987; Svensson, 2008; M. Silbernagle (USFWS, ret.), pers. comm.	O'ahu Digital Elevation Model (DEM)
(2) Movement through low elevation, no sharp threshold	<p>(3) <i>Elevation Linear A</i>: Landscape resistance has linear relationship with elevation; open ocean has high resistance</p> <p>(4) <i>Elevation Linear B</i>: Landscape resistance has linear relationship with elevation; open ocean has low resistance</p>	Same as above	Same as above
(3) Avoidance or higher cost to traversing steep terrain	<p>(5) <i>Elevation Slope A</i>: Landscape resistance has linear relationship with steepness of slope; open ocean has high resistance</p> <p>(6) <i>Elevation Slope B</i>: Landscape resistance has linear relationship with steepness of slope; open ocean has low resistance</p>	M. Silbernagle (USFWS, ret.), pers. comm.	Same as above
(4) Movement through wet or mesic habitat, with a sharp threshold	<p>(7) <i>Topographic Wetness Index (TWI) ^a Two-Class A</i>: Areas below threshold wetness value have high resistance, areas above that have low resistance; open ocean has high resistance</p> <p>(8) <i>TWI Two-Class B</i>: Areas below threshold wetness value have high resistance, areas above that have low resistance; open ocean has low resistance</p>	Van Rees and Reed, 2014; van Rees and Reed, unpubl. data	Same as above
(5) Movement through wetter areas but no sharp threshold	<p>(9) <i>TWI Linear A</i>: Landscape resistance has a linear, inverse relationship to wetness; open ocean has high resistance</p> <p>(10) <i>TWI Linear B</i>: Landscape resistance has a linear, inverse relationship to wetness; open ocean has low resistance</p>	Same as above	Same as above
(6) Avoidance or high cost to traversing urban areas (Landscape Integrity)	(11) <i>Land Use (LU) ^b Two-Class</i> : Urban land use areas have high resistance and all other land use types have low resistance	M. Silbernagle (USFWS, ret.), pers. comm.; Baldwin et al., 2012; Major et al., 2014	NOAA LULC Dataset

	(12) <i>LU Three-Class</i> : Urban land use areas have high resistance, wetland areas have low resistance, and all other land use types have moderate resistance		
(7) Movement through open areas, avoid closed areas	(13) <i>LU Structural</i> : Structurally open areas (agricultural fields, grassland, wetland) have low resistance, intermediate areas (shrubland) have moderate resistance, covered areas (urban, forest) have high resistance	Keyel et al., 2012	Same as above
(8) Graded ease of use	(14) <i>LU Full</i> : Wetlands have low resistance; other land types have increasing resistance in the following order: open land (grassland, agriculture), shrubland, forest, urban	M. Silbernagle (USFWS, ret.), pers. comm.; Keyel et al., 2012; Major et al., 2014	Same as above
(9) Roads as barriers	(15) <i>Roads</i> : Large roads (highways) have maximum resistance, other roads have high resistance, all other areas have low resistance	K. Doyle (Hawaii DOFAW) pers. comm.	O`ahu Street Centerlines
(10) Proximity to Water (Movement through riparian, drainage, and wetland corridors)	(16) <i>Water Binary</i> : Areas within a threshold distance value of water features have low resistance, all other areas have high resistance	Nagata, 1983; Takano and Haig, 2004	National Wetlands Inventory
	(17) <i>Water Linear 30m corridor</i> : Landscape resistance has a linear relationship with distance from water features, reaches maximum at 30m		
	(18) <i>Water Linear 100m corridor</i> : Landscape resistance has a linear relationship with distance from water features, reaches maximum at 100m		
	(19) <i>Water Linear 200m corridor</i> : Landscape resistance has a linear relationship with distance from water features, reaches maximum at 200m		
	(20) <i>Water Negative Binomial</i> : Landscape resistance has a non-linear relationship with distance from water features, whereby resistance increases rapidly and then levels off		

Table 4.2: Test statistics from Mantel (r) and partial Mantel tests, as well as mean relative support (\overline{RS}) and R^2_β values for all landscape resistance models evaluated using data on genetic differentiation (F_{ST} among 12 microsatellite loci) among 12 populations of Hawaiian gallinules on O`ahu. For each model, statistics are given separately for effective distances calculated using Cumulative Least-cost Path (LCP) and resistance distances in Circuitscape (CS). The Euclidean distance model did not include effective distance, so only one value is presented for each statistic, with the exception of partial mantel \overline{RS} , where mantel r values were compared to those from models run with effective distances calculated using both methods. Asterisks (*) indicate statistically significant p-values at the $\alpha = 0.05$ level. TWI and LU stand for Topographic Wetness Index and Landscape Use, respectively.

Model Name (Resistance Surface)	Mantel r		Mantel p		\overline{RS}		R^2_β	
	LCP	CS	LCP	CS	LCP	CS	LCP	CS
Elevation Two-Class A	0.055	0.048	0.231	0.263	0.183	-0.075	0.082	0.075
Elevation Two-Class B	0.014	0.075	0.386	0.255	-0.211	-0.054	0.065	0.085
Elevation Linear A	0.053	0.032	0.243	0.271	0.150	-0.243	0.082	0.064
Elevation Linear B	0.038	0.038	0.280	0.285	-0.240	-0.204	0.074	0.068
Elevation Slope A	0.054	0.128	0.233	0.096	0.132	0.129	0.081	0.083
Elevation Slope B	0.037	0.128	0.277	0.095	-0.251	0.139	0.073	0.083
TWI Two-Class A	0.055	0.021	0.233	0.332	0.150	-0.353	0.083	0.053
TWI Two-Class B	0.047	0.088	0.344	0.227	-0.254	-0.140	0.048	0.066
TWI Linear A	0.050	0.053	0.240	0.294	-0.094	-0.131	0.076	0.079
TWI Linear B	0.037	0.045	0.315	0.350	-0.205	-0.245	0.076,	0.077
LU Two-Class	0.032	0.012	0.298	0.404	-0.402	-0.150	0.072	0.074
LU Three-Class	0.040	0.190	0.284	0.126	-0.196	0.224	0.076	0.099
LU Structural	0.031	-0.066	0.302	0.596	-0.266	-0.443	0.075	0.056
LU Full	0.084	0.015	0.144	0.436	0.305	-0.158	0.102	0.074
Roads	0.036	0.100	0.275	0.198	-0.348	0.061	0.072	0.085
Water Binary	0.368	0.375	0.009*	0.046*	0.522	0.470	0.131	0.132
Water Linear 30m Corridor	0.530	0.281	0.011*	0.069	0.596	0.396	0.181	0.115
Water Linear 100m Corridor	0.637	0.273	0.024*	0.092	0.545	0.341	0.343	0.114
Water Linear 200m Corridor	0.313	0.219	0.009*	0.102	0.445	0.287	0.122	0.107
Water Negative Binomial	0.562	0.251	0.015*	0.074	0.650	0.355	0.206	0.111

Euclidean Distance ^a	0.026	0.317	-0.458	-0.302	0.069
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^a Because Euclidean distance cannot be simulated

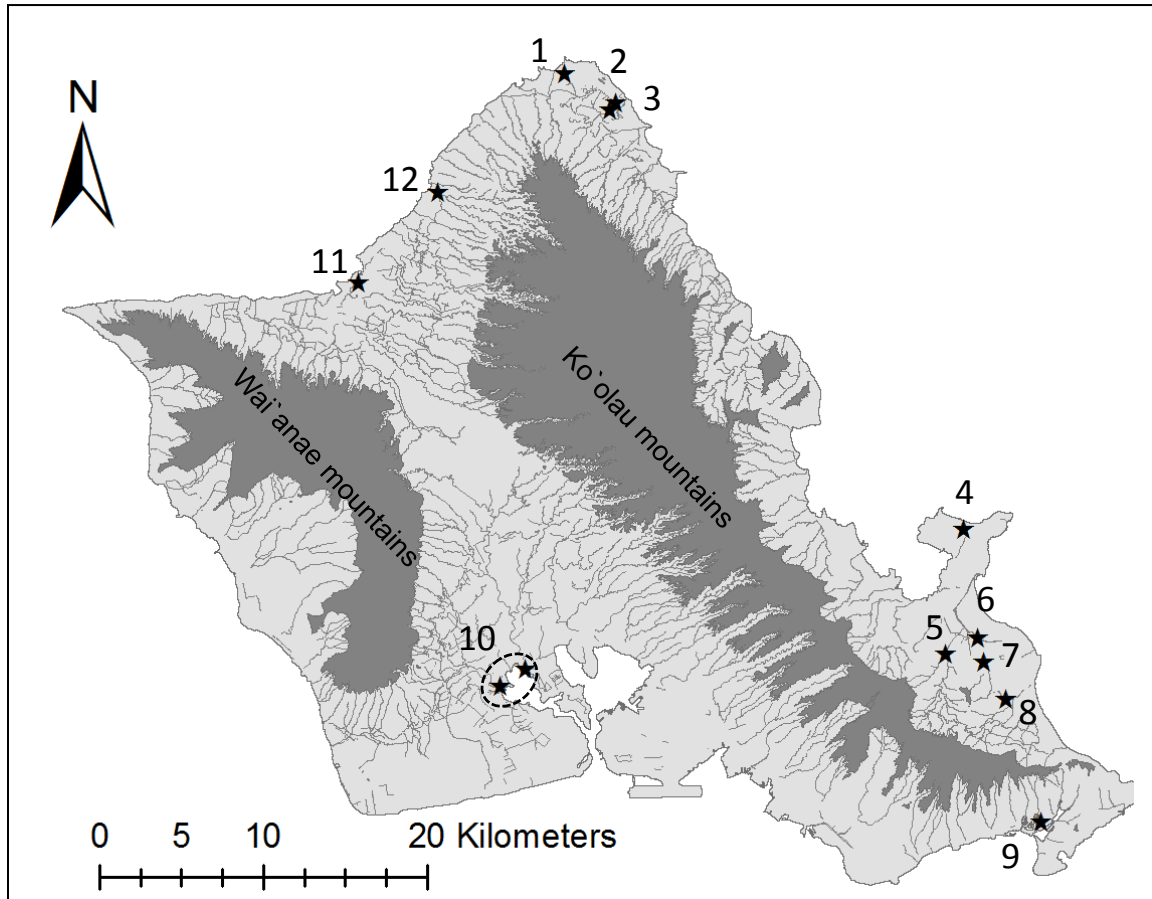


Figure 4.1: Map of the island of O`ahu, showing locations of the 12 populations sampled for genotyping by van Rees et al. (2017). Mountain ranges and waterways are pictured in dark gray. Population names are as follows: 1) Turtle Bay resorts, 2) James Campbell National Wildlife Refuge, 3) Kahuku Shrimp Farms, 4) Marine Corps Base Kaneohe, 5) Kawainui Marsh, 6) Hamakua Marsh, 7) Enchanted Lakes, 8) Olomana Golf Links, 9) Keawawa wetland, 10) Pearl harbor (composed of Pouhala marsh and Pearl Harbor National Wildlife Refuge, Hono`uli`uli unit), 11) Private lotus farm, and 12) Waimea Valley.

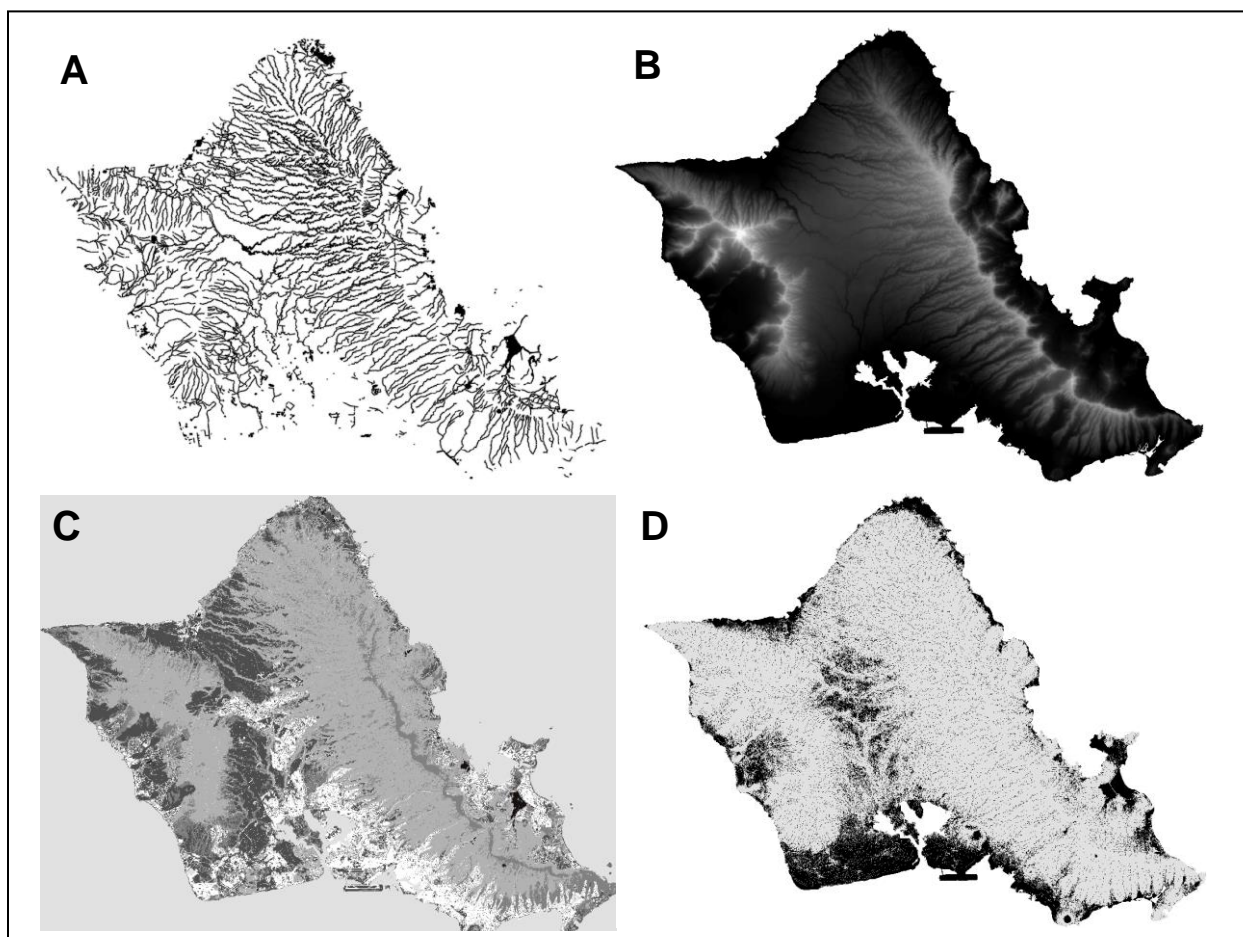


Figure 4.2: Four example resistance surfaces derived from different spatial datasets. Darker pixels have lower resistance, and lighter pixels have higher resistance. A) Distance to water, 100m corridor. B) Linear elevation, version A. C) Land use with all land use classes. D) TWI two-class threshold model, version A.

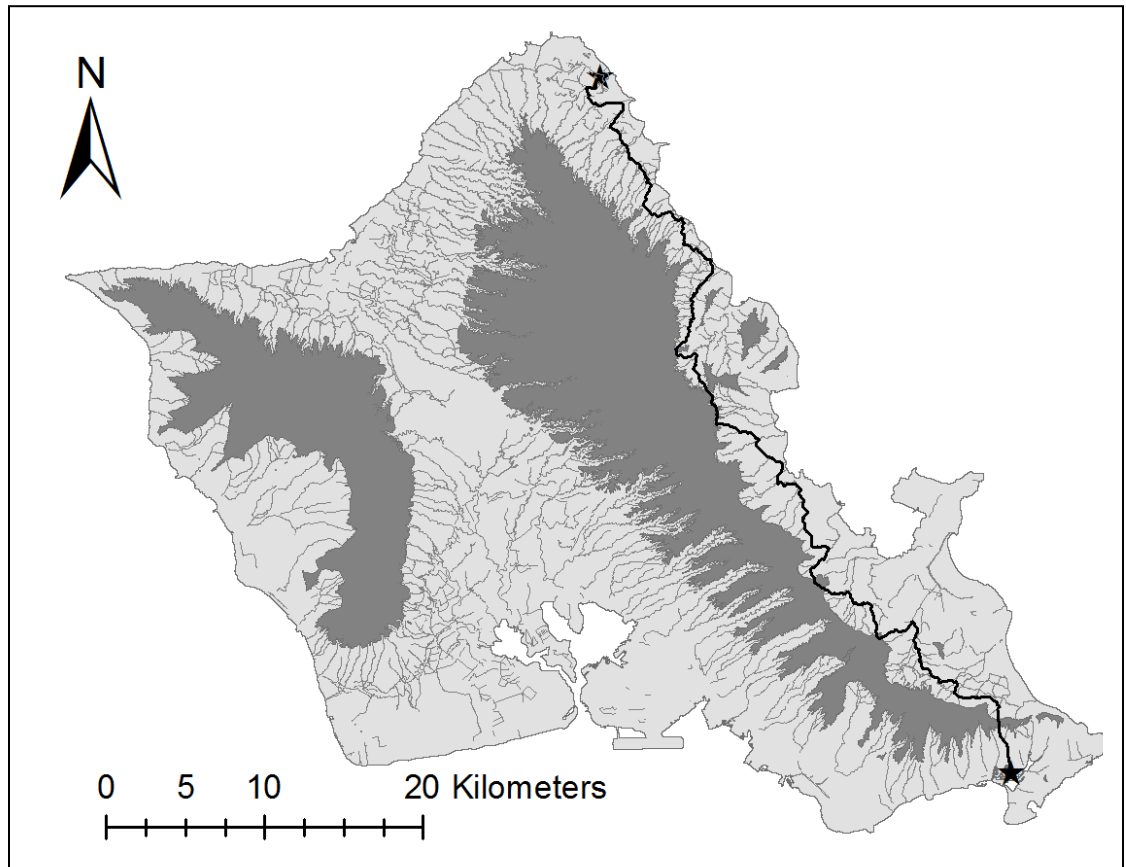


Figure 4.3: Approximation of least-cost pathway between James Campbell National Wildlife Refuge and Keawawa Wetland, calculated using the 100m corridor distance-to-water resistance surface and the least-cost path tool in ArcGIS.

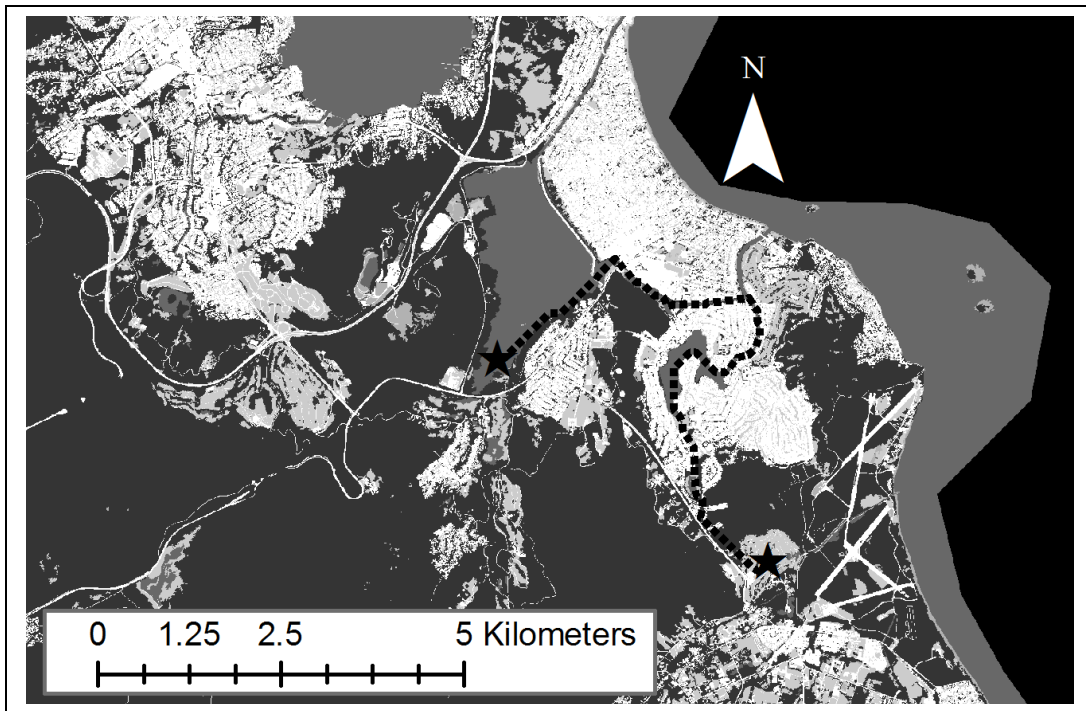


Figure 4.4: Approximation of least-cost pathway between Kawainui Marsh and Olomana Golf Links, calculated using the 100m corridor distance-to-water resistance surface and the least-cost path tool in ArcGIS. For illustrative purposes, the path has been projected over a modified version of the NOAA CCAP 2011 map of O`ahu, showing urban areas in white and undeveloped areas in dark and light gray, with water features in medium gray.

Supplemental Materials (Chapter 4)

Table 4.S1: Test statistics from mantel and partial mantel tests, as well as R^2_β values for all landscape resistance models evaluated using data on genetic differentiation (F_{ST} among 520bp sequences of ND2 region of mtDNA) among 12 populations of Hawaiian gallinules on Oahu. For each model, statistics are given separately for effective distances calculated using Cumulative Least-cost Path (LCP) and resistance distances in Circuitscape (CS). The Euclidean distance model did not include effective distance, so only one value is presented for each statistic, with the exception of partial mantel \overline{RS} , where mantel r values were compared to those from models run with effective distances calculated using both methods. Asterisks (*) indicate statistically significant p-values at the $\alpha = 0.05$ level.

Model Name	Mantel r		Mantel p		\overline{RS}		R^2_β	
	LCP	CS	LCP	CS	LCP	CS	LCP	CS
Elevation Binary A	0.033	0.026	0.279	0.309	0.157	-0.160	0.077	0.0698
Elevation Binary B	-0.029	0.030	0.540	0.34	-0.219	-0.126	0.059	0.076
Elevation Linear A	0.027	0.017	0.301	0.308	0.073	-0.326	0.076	0.062
Elevation Linear B	0.010	0.012	0.362	0.350	-0.278	-0.286	0.068	0.064
Elevation Slope A	0.038	0.132	0.273	0.097	0.162	0.185	0.077	0.085
Elevation Slope B	0.021	0.132	0.3275	0.0959	-0.181	0.159	0.069	0.085

TWI Binary A	0.038	0.032	0.268	0.291	0.178	-0.278	0.078	0.057
TWI Binary B	0.012	0.095	0.444	0.213	-0.117	-0.052	0.052	0.069
TWI Linear A	0.027	0.046	0.287	0.315	-0.058	-0.184	0.073	0.072
TWI Linear B	-0.017	0.031	0.500	0.389	-0.222	-0.289	0.067	0.067
LU Binary	0.018	0.036	0.343	0.379	-0.338	-0.161	0.066	0.067
LU Three- Class	0.022	0.21	0.332	0.097	-0.173	0.302	0.069	0.100
LU Structural	0.020	-0.051	0.335	0.582	-0.197	-0.273	0.070	0.066
LU Full	0.072	0.043	0.184	0.372	0.358	-0.008	0.096	0.080
Roads	0.019	0.081	0.338	0.252	-0.287	0.018	0.067	0.076
Water Binary	0.323	0.347	0.013*	0.051	0.518	0.509	0.122	0.137
Water Linear 30m Corridor	0.454	0.265	0.016*	0.072	0.555	0.426	0.158	0.116

Water Linear 100m Corridor	0.535	0.248	0.025*	0.096	0.458	0.326	0.247	0.112
Water Linear 200m Corridor	0.277	0.216	0.013*	0.101	0.459	0.337	0.115	0.108
Water Negative Binomial	0.476	0.240	0.018*	0.080	0.565	0.383	0.170	0.111
Euclidean Distance	0.008		0.378		-0.395	-0.407		0.063

Table 4.S2: Test statistics from mantel and partial mantel tests, as well as R^2_{β} values for validation landscape resistance models evaluated using data on genetic differentiation (F_{ST} among 12 microsatellite loci) among 12 populations of Hawaiian gallinules on Oahu. For each model, statistics are given separately for effective distances calculated using Cumulative Least-cost Path (LCP) and resistance distances in Circuitscape (CS). The Euclidean distance model did not include effective distance, so only one value is presented for each statistic, with the exception of partial mantel \overline{RS} , where mantel r values were compared to those from models run with effective distances calculated using both methods. Asterisks (*) indicate statistically significant p-values at the $\alpha = 0.05$ level.

Model Name	Mantel r		Mantel p		\overline{RS}		R^2_{β}	
	LCP	CS	LCP	CS	LCP	CS	LCP	CS
Facilitation by Roads	-0.073	0.1816	0.641	0.07	-0.7992	-0.148	0.04	0.06
Water as barrier	0.074	-0.3906	0.253	0.932	-0.338	-0.531	0.06	<0.001
Water 100m corridor – all wetlands removed	0.474	0.327	0.003*	0.058	0.507	0.260	0.14	0.09
Distance to Water (Best of original models)	0.552	0.430	0.004*	0.021*	0.6305	0.42	0.17	0.1108

Chapter 5

Estimation of vital rates for the Hawaiian gallinule, a cryptic, endangered waterbird

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Abstract

Vital rates describe the demographic traits of organisms and are an essential resource for wildlife managers to assess local resource conditions and to set objectives for and evaluate management actions. Endangered waterbirds on the Hawaiian Islands have been managed intensively at state and federal refuges since the 1970s, but with little quantitative research on their life history. Information on the vital rates of these taxa is needed to assess the efficacy of different management strategies and to target parts of the life cycle that may be limiting their recovery. Here we present the most comprehensive data to date on the vital rates (reproduction and survival) of the Hawaiian gallinule (*Gallinula galeata sandvicensis*), a behaviorally cryptic, endangered subspecies of wetland bird endemic to the Hawaiian Islands that is now found only on Kaua'i and O'ahu. We review unpublished reproduction data for 252 nests observed between 1979 and 2014, and assess a database of 1620 sightings of 423 individually color-banded birds between 2004 and 2017. From the resighting data, we estimated annual apparent survival

at two managed wetlands on O'ahu using Cormack-Jolly-Seber models in program MARK. We found that Hawaiian gallinules have smaller mean clutch sizes than do other species in the genus *Gallinula*, and that clutch sizes on Kaua'i are larger than those on O'ahu. The longest-lived bird in our dataset was recovered dead at age 7 years, 8 months, and the youngest confirmed age at first breeding was 1 year 11 months. In four years of monitoring 14 wetland sites, we confirmed three inter-wetland movements on O'ahu. In our pooled dataset, we found no statistically significant differences between managed and unmanaged wetlands in clutch size or reproductive success, but acknowledge that there were limited data from unmanaged wetlands. Our best supported survival models estimated an overall annual apparent survival of 0.663 (95% CI 0.572-0.759); detection varied across wetlands and study years. First-year survival is a key missing component in our understanding of the demography of Hawaiian gallinules. These data provide the foundation for quantitative management and assessment of extinction risk of this endangered subspecies.

5.1 Introduction

Vital rates, which include reproduction and survival rates, are the basic components of life tables and population models (Caughley 1977; Morris and Doak 2002). Quantifying vital rates is a priority for increasing the efficacy of species conservation and management (Tuljapurkar and Caswell 1997; Taylor et al. 2012). Specifically, vital rates are central to endangered species recovery planning because they are used for population viability analysis (Beissinger and Westphal 1998; Reed et al. 2002), they guide harvest rate assessments for sustainable resource management (Taylor et al. 1987), and vital rate sensitivity analysis is used to guide some management activities (Wisdom et al. 2000; Akçakaya et al. 2003; Reed et al. 2009). Reduction in vital rates can contribute to critical slowing down, which is an increase in recovery time to equilibrium after perturbation for populations in some nonlinear systems that are near a tipping point (Wissel 1984; Ghandi et al. 1998; also referred to as resilience; Holling 1973). It has been suggested that population growth rate, particularly within the context of recovery following a perturbation, might be an excellent metric for evaluating population health, and might act as an early warning signal of impending collapse (Wissel 1984; Sibly and Hone 2002; van Nes and Scheffer 2007). Vital rates are also commonly used as indices of habitat quality (e.g., Todd and Rothermel 2006), particularly where the abundance of a species might otherwise be misleading (e.g., Hagan et al., 1996; Purcell and Verner 1998), but this should be done with caution because values for a population near carrying capacity that exhibits density-dependent growth might be difficult to interpret (Watkinson and Sutherland 1995). As such, vital rates are a major resource for a wildlife manager's toolbox, at once acting as a barometer for a

population's overall condition, and enabling quantitative analysis for evidence-based conservation and management.

The Hawaiian gallinule (*Gallinula galeata sandvicensis*), an endangered subspecies of the common gallinule (Figure 1), is currently endemic to shallow, coastal freshwater wetlands on O'ahu and Kaua'i (Hawai'i, USA). Hawaiian gallinules were reported as being common on all of the five main Hawaiian Islands during the 1890s (reviewed by Shallenberger 1977; Banko 1987), but they began exhibiting dramatic population declines and range retractions during the early 20th century. By 1947, the species was reported as extirpated from the island of Hawai'i and as 'precarious' on Maui, Moloka'i, and O'ahu (Schwartz and Schwartz 1949; Shallenberger 1977). Declines were driven by habitat loss and predation by introduced mammals (Griffin et al., 1990; Chang 1990). Hawaiian gallinules reached their lowest numbers in the early 1960s with an estimated 57 individuals (Engilis and Pratt 1993), although visual survey methods are recognized as being underestimates because of the species' secretive nature, and early surveys did not incorporate their entire possible range (Shallenberger 1977; DesRochers et al. 2008). With legal protection as endangered (United States Department of the Interior, 1967) under the U.S. Endangered Species Act (ESA 1973, as amended) and active habitat and predator management, Hawaiian gallinules have since increased to an estimated 600 individuals, but the subspecies is still limited to two islands (Reed et al. 2011).

Hawaiian gallinules are considered to be conservation-reliant because their wetland habitats require continual management to exclude exotic, invasive plants and predators (Reed et al. 2012; Underwood et al. 2013). In addition to constant vegetation

management, trapping predators (e.g., small Indian mongoose, *Herpestes javanicus*) and careful management of water levels to prevent flooding and create breeding and feeding habitat are common activities in Hawaiian waterbird conservation (Vanderwerf, 2012). Although Hawaiian gallinules persist in small numbers in relict and artificial wetland habitats (e.g., golf course water hazards, lotus (*Nelumbo nucifera*) farms, water features in gardens) on both islands, managed and protected wetlands at James Campbell National Wildlife Refuge (JCNWR) and Hamakua Marsh on O'ahu, and Hanalei National Wildlife Refuge on Kaua'i are current strongholds for the subspecies (USFWS 2011). Threats to the subspecies are similar on the two islands, but with some notable differences (Reed et al. 2012). For example, gallinule populations on both islands are threatened by introduced predators and wetland loss. However, wetland loss has been substantially higher on O'ahu (>65%) compared to Kaua'i (8%; van Rees and Reed 2014), and the introduced small Indian mongoose is numerous on O'ahu but not established on Kaua'i (Hays and Conant, 2007; U.S. Fish and Wildlife Service 2011). Avian botulism (*Clostridium botulinum*) is an additional risk factor for Hawaiian waterbirds (Brock and Breese 1953; Morin 1996; Work et al. 2010), and is more common on Kaua'i than O'ahu (K. Uyehara and J. Underwood, pers. obs.). However, any significant effect on the vital rates of Hawaiian gallinules is unknown, and baseline information on vital rates are necessary to understand the impacts of this and other potential threats to the subspecies.

Despite being federally protected, with substantial resources allocated to studying their ecology, status, and management (DesRochers et al. 2009; DesRochers et al. 2010; Gutscher-Chutz 2011; Reed et al. 2011, 2012; USFWS 2011; Underwood et al. 2013), published data on vital rates for this subspecies are limited or absent. A single published

paper (Byrd and Zeillemaker 1981) and three unpublished theses (Nagata 1983; Chang 1990; Gee 2007) are the only reports of Hawaiian gallinule reproduction, and to date there have been no studies of survival rates. This is likely due in part to the cryptic behavior of the subspecies. Species-specific call-response surveys are required to effectively detect Hawaiian gallinules in the field, where birds are often concealed from view by dense vegetation (DesRochers et al. 2008). Furthermore, visual observations of nests and young are difficult because they are obstructed by dense emergent vegetation (Byrd and Zeillemaker 1981; Gee 2007). Estimation of vital rates is an important part of long-term conservation planning for Hawaiian gallinules, which calls for quantification of extinction risk through population viability analysis (Mitchell et al. 2005; USFWS 2011; VanderWerf 2012). Vital rate estimates are also important for improving recovery plans for this subspecies, and will allow for comparisons among islands and sites to ascertain under what conditions gallinules do best, and to distinguish source and sink populations (e.g., Dias 1996). Until recently, nothing was known about the movement behavior and population structure of Hawaiian gallinules in their apparently relict, fragmented wetland habitats, but recent work by van Rees et al. (2017) showed evidence of low geneflow between many wetlands on O'ahu, indicating that movement rates may currently be very limited on that island. Field study on the movement rates of this taxon is also needed to inform their management and conservation.

Our objectives are to: (1) summarize unpublished data on reproduction (clutch size, hatching rate, nest fate, senescence, annual number of clutches) for Hawaiian gallinules across the subspecies' current range; and (2) estimate annual survival rate, age at first breeding, and longevity based on sightings of individually banded birds, and (3)

assess available evidence of the occurrence and frequency of inter-wetland movement. Our hope is that by synthesizing these data we can give managers accurate and reliable estimates of critical life-history information on the Hawaiian gallinules that will allow population modeling and demographic management assessment, thus facilitating evidence-based conservation and management on this endangered subspecies.

5.2 Methods

5.2.1 Reproduction

All known, unpublished data on reproduction for the Hawaiian gallinule were collected from studies conducted during 1979-present on the islands of Kaua'i (22.065143° N -159.517492° W) and O'ahu (21.455580° N -158.038709° W; Hawaii, USA). We were unable to obtain the raw data from the single published study (Byrd and Zeillemaker 1981) after contacting the authors, so we compare our results with theirs. Due to the potential for differences among nest-monitoring protocols between the studies included in our synthesis, we analyzed data first by study, and then for all studies as a meta-analysis. Because a larger, synthesized (though possibly less precise) dataset might be useful to managers in certain contexts (e.g., population viability analysis; Morris and Doak 2002), we also pooled the raw data from these studies and conducted overall comparisons between islands and management and non-management settings. This pooled dataset excludes data for reproductive vital rates where monitoring methods indicated that they might yield biased estimates (see below and supplemental material). For the pooled dataset, we compared reproduction metrics of Hawaiian gallinules

between managed and unmanaged habitats, between islands (O'ahu vs. Kaua'i), and with conspecific data found in our literature search.

Reproductive data documented in this study included clutch size, brood size, and nest fate. For nest success in both our pooled dataset and meta-analysis, we excluded observations where nest fate could not be unambiguously confirmed (e.g., chicks sighted nearby after termination of nesting activity, but unclear if those chicks indeed hatched from that nest), and where insufficient or inconsistent information in raw data gave ambiguity to the observations at a single nest. For this reason, our summary statistics may differ from those presented in the written accounts of some of these studies (e.g., Master's theses).

All studies of reproductive success used behavioral observations taken during prolonged periods in the field to locate nests, and defined a nest as successful if at least one egg hatched. All researchers noted when egg counts may not have been completed clutches (due to premature failure, or discovery of the nest late in the nesting cycle). Where possible, all researchers associated broods with nests based on visual inspection of the nest (evidence of hatching, no evidence of nest depredation), or chick activity around nest. We excluded all data that had no confirmation of nest success, hatch rate, or clutch completion when calculating relevant vital rates. Nagata (1983) and Gutscher-Chutz (this study) encountered nests incidently to other work in wetland habitats, so their sampling was haphazard. Once found, Nagata (1983) monitored nests through weekly visits, while Gutscher-Chutz only recorded data from incidental nest encounters. Chang (1990) located nests using exhaustive surveys (walking through the entirety of a pond and searching emergent vegetation) of study sites every 2-3 weeks, and visited nests twice per

week once they had been located to monitor clutch completion. He monitored broods twice weekly for 30 min periods. Gee (2007) also used exhaustive surveys to locate nests, and also employed playback surveys to locate nesting birds. He marked individual eggs to monitor egg loss throughout the nesting cycle, and visited nests three times per week until clutch completion was evident, and monitored broods during weekly waterbird surveys of study sites. Cosgrove (this study) and Silbernagle (this study) visited nests once per week from nest discovery to hatching. Post-hatch, all researchers except Gutscher-Chutz checked nests for signs of unhatched eggs. Because Gutscher-Chutz's (this study) data did not involve repeated visits to nests to confirm clutch size or post-hatch brood size, they were excluded from our pooled dataset. All other studies were retained in the analysis, because their methods were deemed sufficiently similar to have not strongly bias separate estimates. We also opportunistically collected data for additional vital rates that are necessary for population viability analysis, but for which only limited or anecdotal accounts are available, and synthesized these for publication. In particular, we sought information on the prevalence and degree of multiple-brooding (i.e., successfully breeding multiple times per year), the maximum number of broods produced in a year, and evidence of reproductive senescence.

5.2.2 Survival and Movement

Survival estimates were derived from recaptures and sightings (including banding as the first encounter) of uniquely marked (color banded) gallinules on O'ahu. Banding of Hawaiian gallinules on O'ahu started in 1979 at private lotus farms and the Hamakua Marsh wildlife sanctuary (Dibben-Young 2010). Extensive marking and resighting efforts

on Hawaiian Gallinules did not begin until 2004 (Dibben-Young 2010), and occurred on an irregular, ad-hoc basis for the next decade, primarily at James Campbell National Wildlife Refuge (O'ahu), where the most banding occurred. Starting in 2014, annual surveys from May to August were conducted island-wide, and we expanded banding efforts to include wetlands across the entire island of O'ahu (Figure 2). May-August survey periods were chosen due to the availability of personnel, but are not considered a source of bias given the absence of a strong annual cycle in Hawaiian gallinule life history (DesRochers et al. 2009; USFWS 2011). Birds were identified by a unique combination of colored plastic (Darvic) leg-bands and an aluminum U.S. Geological Survey leg band. Resightings were acquired during biannual surveys, recaptures and recovery, through our ongoing citizen-science monitoring program started in 2014 (<http://sites.tufts.edu/Hawaiianmoorhen>), and as ad hoc observations. For ambiguous resightings (partial combinations seen) or birds with missing color bands, we checked all possible bird identities for a given resighting; where only one individual was possible (i.e., other candidates seen elsewhere at the same time, or known dead), we recorded the sighting as that individual. Where no single possible candidate was available, we excluded the record. Hawaiian gallinules cannot be sexed visually in the field (Bannor and Kiviat 2002), so we were unable to analyze data separately by sex. We used this database to estimate mean annual apparent survival of adults, and we reviewed written, unpublished reports from the surveyed studies to find accounts of post-hatching and post-fledging (chick and juvenile) survival. We were unable to conduct mark-resight studies on chicks because they could not be safely banded at that stage. We also used our resighting database to document movements between islands and between wetland

habitats on the island of O'ahu.

We estimated yearly apparent survival (the estimated survival parameter used in mark-recapture frameworks, wherein mortality is indistinguishable from repeated failure of detection or permanent emigration) using standard Cormack-Jolly-Seber (CJS) models in program MARK 8.2 (White and Burnham 1999) and R (R Core Team 2015). Years were determined based on calendar date (Years start January 1, end on December 31), which was chosen for computational convenience. As with banding field seasons, the year was not considered to be a source of bias because of the weak seasonal breeding phenology of Hawaiian gallinules (DesRochers et al. 2009; USFWS, 2011), and because the majority (>70%) of marking and sighting events occurred during May-August.

Resighting data were converted to yearly encounter histories and MARK input files using an R script written by the authors. To prevent violation of the CJS model assumption of relatively small survey periods compared to between-encounter intervals, we restricted our analysis to resightings in the months of May and June, when most sightings occurred. We compared the likelihood of a suite of potential survival models in MARK using AICc (Sugiura 1978; Hurvich and Tsai 1989; Burnham and Anderson, 1998). These were a null model (constant ϕ [survival] and p [detection]), a time model for detection (constant ϕ , and p varies by study year), a wetland model for survival (ϕ varies by wetland, constant p), a time model for survival and detection (ϕ and p vary by study year), three by-wetland survival models (ϕ varies by wetland, and p is either constant, varies by study year, or varies by wetland), and four models where p varied by wetland, year, and their interaction (ϕ was either constant, or varied by year, wetland, or their interaction).

We implemented four tests of goodness of fit (TEST.SR, TEST.SM, TEST.CT,

TEST.CL) in program U-CARE (Choquet et al., 2009) to evaluate the fit of a CJS model with and without wetland groupings. We also evaluated goodness of fit of our general model (ϕ and p vary by wetland, year, and their interaction) using the bootstrapping goodness-of-fit test in MARK. Following Cooch and White (2015), we checked for overdispersion by comparing the observed deviance of the full model to the range of deviances from 1000 bootstrap simulations of the model and calculated a p-value based on the rank of the observed deviance. We also estimated \hat{c} (a measure of overdispersion) by dividing the observed deviance by the average deviance of 1000 bootstrap simulations. Because this process showed interspersions and some lack of fit for our full dataset when observations from all sampled wetlands were included, we reduced our dataset to the two wetland sites with the most extensive histories of mark-resights (James Campbell NWR and Waimea Valley) and carried out all analyses with birds from these wetlands only. We observed no evidence of overdispersion or poor model fit using this reduced dataset. We also examined individual life histories to find the oldest Hawaiian gallinules among all banded birds.

5.3 Results

5.3.1 Reproduction

Our data on reproduction came from 252 individual nests monitored on Kaua'i and O'ahu from 1979-2014. Reproductive data were collected at eight different locations including National Wildlife Refuges with active predator control and wetland management (Table 5.1). All studies except for Gutscher-Chutz and Gee (2007) had lower clutch sizes, and all except for Chang (1990) had lower nest success, than those

reported by Byrd and Zeillemaker (1981; mean nest success = 0.75, mean clutch size = 5.6) from 64 clutches on the same island from 1975 – 1980 (Table 5.2). Gee (2007), Gutscher-Chutz, and Chang (1990) had higher mean numbers of chicks per successful nest than Byrd and Zeillemaker (1981). Notably, hatch rates (the proportion of eggs per nest that hatched) were much smaller than those reported by Byrd and Zeillemaker (1981); in the case of our meta-analysis average, they were 50% smaller. Data from Gutscher-Chutz (this study) showed extremely low nest success, number of chicks per nest, and overall hatch rate, but high number of chicks per successful nest. Generally, studies from O’ahu (Chang, Silbernagle, and Nagata) showed somewhat smaller clutch sizes than those on Kaua’i (Gee, Gutscher-Chutz, and Cosgrove). Silbernagle (this study) and Chang (1990), working on wildlife refuges on O’ahu, saw higher hatch rates than any of the studies on Kaua’i.

Our pooled dataset included clutch size data from 125 nests on Kaua’i, and 127 nests on O’ahu (Table 5.S1). Pooled clutch sizes on Kaua’i were very similar to Byrd and Zeillemaker (1981). Nest success, number of chicks per successful nest, and hatch rate, in contrast, were all lower for our pooled dataset than the values reported by Byrd and Zeillemaker (1981), and hatch rates for Kaua’i were much lower. Hawaiian gallinule clutch sizes in this study ranged from two to 11 eggs (Table 5.S1). Comparing between islands in our pooled dataset, nests on Kaua’i had significantly larger clutch sizes than did nests on O’ahu (Welch’s t-test, $t = 4.40$, $df = 169.68$, $P < 0.001$), although nest success (the proportion of nests that hatched at least one chick) did not differ significantly between the islands (Welch’s t-test, $t = -0.46$, $df = 212.09$, $P = 0.65$; Table 5.S1). Clutch sizes on O’ahu ranged from two to eight eggs, while those on Kaua’i ranged from two to

11. Nests on O'ahu produced a similar number of chicks per nest (Welch's two sample t-test, $t = -1.73$, $df = 219.99$, $P = 0.08$) but a higher number of chicks per successful nest (Welch's two sample t-test, $t = -2.64$, $df = 135.19$, $P < 0.01$; Table 5.S1). Using our pooled dataset, we saw no statistically significant differences between managed and unmanaged wetlands in nest success ($df = 24.78$, $P = 0.56$; managed $n = 230$, unmanaged $n = 22$; Table 5.S3), number of chicks per nest ($df = 25.33$, $P = 0.5$; managed $n = 202$, unmanaged $n = 22$), or number of chicks per successful nest ($df = 13.65$, $P = 0.7$; managed $n = 132$, unmanaged $n = 13$). The sample size of confirmed clutch sizes and brood sizes in unmanaged habitats were insufficient for comparing clutch size or hatch rate between managed and unmanaged habitats. Nagata (1983)'s dataset was the only one with data gathered on unmanaged habitats. Among breeders of known age ($n = 7$), the youngest bred at an approximate age of 23 months.

Information on causes of nest failure was not available for most (74%) nests in our study, which precluded analyses based on nest fate. The most frequent cause of nest failure in our review among 51 failed nests of known fate (50 in managed wetlands and one in an unmanaged wetland) was predation ($n = 30$), followed by abandonment ($n = 17$), and flooding ($n = 4$).

Nagata (1983) documented Hawaiian gallinules successfully producing two and even three broods in a year at Hamakua marsh and private lotus farms on O'ahu. Two monitored, banded pairs of gallinules (one at Waimea Valley, the other at Keawawa wetland) had a maximum of four successful broods per year in 4 years of monitoring. We saw no evidence of reproductive senescence (reduction in brood or clutch size) for the pair at Waimea Valley over 6 years of monitoring (see longevity data in next section).

5.3.2 *Survival and Movement*

We documented 1620 sightings of 423 individually marked birds over 14 years. Resighting data were collected at 14 locations on O’ahu (Figure 2). At least some monitoring for banded birds occurred in all years 2004-2017, yielding 13 annual survival intervals. Hanalei National Wildlife Refuge on Kauai (the only other island in the subspecies’ known range) was surveyed biannually throughout the study period for banded birds from O’ahu but none were ever encountered. Number of marked individuals, as well as timing, frequency, extent, and methods of surveys varied substantially between wetlands (see Table 5.S2 for summary information on resighting records). Our reduced dataset, which was limited to sightings in May and June at wetlands with the longest mark-resight records (James Campbell National Wildlife Refuge and Waimea Valley), consisted of 637 resightings of 209 individually marked birds. All other wetlands had short (2 – 4 year) encounter histories, which appeared to be driving model overdispersion; 95% confidence intervals of yearly apparent survival for these wetlands were also uninformative when all wetlands were included in analyses (~ 0.1 – 0.99).

All candidate survival models are presented in Table 5.3. Our suite of yearly survival models overwhelmingly supported a model with detection varying by study year, wetland and their interaction (Table 5.3). The ΔAIC_C value of the second-best supported model (survival varying by wetland, and detection by year, wetland, and their interaction) was below 2, indicating limited evidence for a statistical difference in model support between the first two models (Burnham and Anderson, 1998), and these two top models account for virtually all of the AIC weight assigned to our suite of models (Table 5.3).

The third-ranked model has a $\Delta AIC_C > 10$, indicating substantial difference in model support. In general, models with detection varying by wetland, year, and their interaction performed best (4 of the top 5 models). The annual apparent survival estimate for the top model was 0.663 (95% CI 0.553 – 0.759), while wetland-specific annual apparent survival estimates for the second-ranked model were 0.565 (95% CI 0.356-0.753) for James Campbell NWR, and 0.696 (95% CI 0.572 – 0.797) for Waimea Valley. Notably, the confidence intervals of estimated annual apparent survival in these two subpopulations overlap. The null model (constant ϕ and p) had the lowest ranking. Estimated detection rates varied across wetland-years from near 0 (0.5×10^{-15}) to 1, with detection rates at Waimea Valley typically much higher than those at James Campbell. Our null model for detection estimated an overall detection rate of 0.496.

Neither global tests nor individual component tests of the assumptions of CJS models yielded significant p-values in U-CARE for either reduced dataset. The estimated \hat{c} for our general model using the reduced dataset was 1.317, while the p-value of its deviance rank was 0.092. Generally, \hat{c} values close to 1 and non-significant deviance rank p-values indicate that the model is a good fit for the data. These values indicate that our yearly model had acceptable goodness of fit with respect to our dataset. The oldest individual gallinule in our dataset was found dead in 2013 and had been banded in 2005 at the age of 28-35 days. Its estimated age was thus seven years, eight months.

No birds banded on O'ahu have ever been detected on Kaua'i since the start of mark-recapture studies in 1979. Our own monitoring, combined with citizen-science resighting data, detected only three confirmed movements between wetlands (treating a wetland complex as a single wetland) on O'ahu. One adult bird (USGS #107639253,

YA:WL) banded on September 23, 2005 at James Campbell National Wildlife Refuge was seen on January 29, 2008 at Pearl Harbor National Wildlife Refuge (~36km straight-line distance; Figure 3). A first-year bird (USGS #119687856, HA:PO) banded at Keawawa wetland on July 2, 2014, was seen on January 22, 2015 at Enchanted Lakes (10km straight-line distance). A third bird, banded as an adult on June 10, 2015 at Turtle Bay Resorts' Arnold Palmer Golf course (USGS #119687902, WA:RB) was recovered dead on July 13, 2016 at Olomana golf links (~47km straight-line distance). Unconfirmed reports (for which reported bands were incomplete, or for which no photographic evidence could be provided) include a bird moving from James Campbell National Wildlife Refuge to a drainage ditch in Haleiwa in 2015 (20km straight-line distance), a bird banded at Keawawa wetland seen in Kamilonui valley in 2015 (~2km straight-line distance), and a bird banded at Waimea Valley seen at Olomana golf links in 2016 (45km straight-line distance; Figure 3).

We found no information on post-fledging (juvenile) survival rates in unpublished studies. Two studies in our meta-analysis (Chang 1990 and Gee 2007) included repeated observations of broods across time, from which rough estimates of survival can be derived. Chang (1990) observed that 28 out of 67 (41.7%) chicks observed from a blind throughout the fledging period (50-60 days, Bannor and Kiviat 2002) at James Campbell National Wildlife Refuge survived from hatch to fledging. Gee (2007) observed much lower survival (37% of 162 chicks) across the same time frame at Hanalei National Wildlife Refuge on Kaua'i.

5.4 Discussion

This study presents the first survival rate data of which we are aware for the Hawaiian gallinule, and a large expansion on what is known about their reproductive success. Data from this study will enable quantification of extinction risk via population viability analysis for this subspecies across its current range, a management priority according to the U.S. Fish and Wildlife Service's recovery plan for Hawaiian waterbirds (USFWS, 2011). Our meta-analysis illustrates the range and central tendency in several vital rates for Hawaiian gallinules, synthesizing unpublished information from several studies from 1979 to 2014. In our analysis of pooled data, we found clear differences in several reproductive parameters between Hawaiian gallinules on O'ahu and Kaua'i, with smaller clutches but greater hatching rates on O'ahu. We also generated an overall estimate of annual apparent survival for the subspecies on O'ahu using over 600 resightings of 209 individuals at two wetland sites.

We found that Hawaiian gallinules have relatively small mean and range of clutch sizes compared to the North American subspecies (*G. g. cachinnans*, e.g., $\bar{x} = 7.9\%$, $n = 2685$; Greij, 1994) showing greater similarity to gallinules at tropical latitudes (e.g., *G. angulata*, $\bar{x} = 5.0$, $n = 55$, Taylor & van Perlo, 1998). This is consistent with the general observation that clutch sizes are directly related to latitude, where higher clutch sizes are observed in temperate regions at high latitudes, and smaller clutch sizes are observed in tropical regions at low latitudes (Cody 1966; Rose and Lyon 2013), especially in low-elevation habitats (Balasubramaniam and Rotenberry 2016). Small clutch sizes of Hawaiian gallinules may also be due to a suite of evolutionary or ecological island effects (Cody 1966; Klomp 1970; Lack 1947, 1970; Frankham 1998). Higher clutch sizes on

Kaua'i may be the result of brood parasitism, a prominent behavior in common moorhen (*Gallinula chloropus*, Gibbons 1986), and which might be facilitated by the high breeding densities of Hawaiian gallinules at Hanalei National Wildlife Refuge (J. Cosgrove and K. Uyehara, pers. obs.).

Mean hatch rate in this study, (\bar{x} = 50% for meta-analysis, Table 5.2; \bar{x} = 43% for pooled data, Table 5.S1), was much lower than that reported by Greij (1994) in a large study of common gallinules in North America (1974, \bar{x} = 80.2%, n = 2685 nests), and reports for *G. tenebrosa* in Australia (55.5%, Marchant and Higgins 1993). Nest success of Hawaiian gallinules in both our meta analysis and pooled data was similar to that reported by Greij (1994) for North America (\bar{x} = 64.1%, n = 968), and *G. chloropus* in Great Britain (Cramp and Simmons 1980, 65.3%, n = 1,154), but higher than that observed by Jamieson et al. (2000) in nests of *G. angulata* in Namibia (58% failure, n = 33).

O'ahu's higher mean number of chicks produced per nest, and chicks per successful nest in our pooled dataset came as a surprise given the higher clutch sizes on Kaua'i and the absence of one major mammalian predator, the small Indian mongoose. The mongoose is common on O'ahu but rare or not established on Kaua'i (Hays and Conant 2007; USFWS 2011). Because of the scarcity of data on post-hatching survival rates, however, the effect of differences in clutch sizes and hatching rates on recruitment and population growth is unknown. Examining our meta-analysis (Table 5.2), it appears that this higher number of chicks is driven mostly by data from Chang (1990), who had a large sample size and the highest mean number of chicks per nest and chicks per

successful nest; these data came from managed habitats, and so contribute to a trend in our estimates of likely being optimistic for subpopulations in non-managed habitats.

Chang (1990) and Gee (2007)'s estimates of chick survival to fledging among Hawaiian gallinules on O'ahu may fit well with observations of common gallinule (*G. galeata cachinnans*) chicks in the southern United States, for which chick mortality was estimated at >40% in the first ten days post-hatch (Miller 1946; Bell 1976). According to Greij (1994)'s review, Helm (1982) and Matthews (1983) observed reductions in brood size across a 45-day period post-hatch that were similar to values observed here in Hawaiian gallinules (~45% survival). Although the difficulty of marking and resighting chicks is an obvious factor in poor understanding of this life stage, it remains an important research priority. This low chick survival may be evidence of a limiting factor in the population regulation of Hawaiian gallinules; accordingly, management actions focused on improving chick survival are a reasonable priority for wetland managers in Hawai'i. Removal, reduction, and exclusion of predators in refuges is likely the most direct approach to increasing chick survival (USFWS 2011; Vanderwerf, 2012).

Ostensibly high chick mortality in Hawaiian gallinules matches Greij (1994)'s assertion that multiple broods are an important part of population maintenance in common gallinules. Indeed, we observed consistent multiple-clutching in two observed pairs with a maximum of four broods in a year, and Nagata (1983) reported frequent double and triple-brooding at other wetlands on O'ahu. Byrd and Zeillemaker (1981) also observed evidence of multiple broods in a year, noticing family groups with young at two or more distinct stages of development. Bannor (1998) observed a pair of common gallinules in a zoo in Florida hatch five broods in one year under conditions of

supplemental feeding, and Siegfried and Frost (1975) observed common moorhen hatch 33 and 32 broods over a 48 month period, also with supplemental feeding, in South Africa. Given that DesRochers et al. (2010) found that Hawaiian gallinules are not food limited on O'ahu, and that conditions in Hawaiian wetlands are highly consistent year-round, our observation of widespread and frequent multiple brooding is intuitively understandable.

The lack of observed differences in reproductive parameters between managed and unmanaged wetlands in our pooled dataset may be an artifact of the small sample size for unmanaged wetlands ($n = 22$) compared to managed wetlands ($n = 230$). Endangered Hawaiian waterbirds can have large interannual and intersite variation in vital rates, particularly for hatch-year birds (Reed et al. 2015), and we cannot determine if differences observed were due to chance differences in interyear and intersite variation. We acknowledge the possibility that sites not specifically managed for endangered waterbirds might still include activities that decrease predation, such as the presence of guard dogs which do not attack waterbirds (as in the Lotus farms). Some site-specific management activities, like water level controls for aquaculture (as in watercress and shrimp farms) might also reduce nest flooding, which was a notable source of clutch failure for known-fate nests in this study. Nagata (1983) who did much of her work in unprotected areas and a refuge (Hamakua Marsh) at which predator control may have been limited at the time of the study, showed lower nest success and than other studies, reinforcing the notion that our general estimates may be somewhat optimistic for unmanaged wetlands. Unfortunately, we do not yet know what life stage most limits population growth; determining this using population modeling would provide insight for

how to focus management effort and funding on Hawaiian wetlands (e.g., Crouse et al. 1987; Beissinger and Westphal 1998; Fefferman and Reed 2006). In general, wetland managers in Hawai'i would benefit from studies that focus on collecting similar baseline vital rate info in unmanaged habitats for purposes of comparison.

Reported age at first breeding for *G. chloropus* in the literature is one year (Taylor, 2010). Our youngest breeder for the Hawaiian subspecies was almost two years old, but our small sample size of known-age breeders ($n = 7$) does not indicate how representative this observation is. The oldest known bird in our dataset, seven years and eight months, was younger than the oldest reported common gallinule (nine years, 10 months; Clapp et al. 1982). This may be due to comparatively limited sampling of Hawaiian birds, or it could represent a difference for island birds. Longevity data are an important part of population-projection models, which in turn help guide management by estimating the level of risk faced by different populations (Morris and Doak, 2002). Continued monitoring of banded Hawaiian gallinules on O'ahu is necessary to gain a more accurate understanding of the distribution of life spans among birds in managed and unmanaged wetlands.

Our resighting database is the only published account of banding, resighting, and recovery of Hawaiian gallinules of which we are aware. The high performance of survival rate models that varied detection parameters by wetland, year, and their interaction reflects the variation of monitoring effort and ease of detection between wetlands and across time, a product of ad-hoc research efforts by researchers and institutions. Gallinules at JCNWR are behaviorally cryptic due to limited human disturbance, and have flight initiation distances in excess of 75m (C. van Rees pers. obs.).

This makes resightings at JCNWR more difficult than at wetlands like those at Waimea Valley, where birds have frequent exposure to humans, resulting in tolerance of human proximity; they occasionally even approach humans for food. Habitat structure in Waimea Valley, a botanical garden, is also substantially different than that at JCNWR, with more open water areas and paved pathways where gallinules are easily spotted. These differences are likely the strongest drivers of differences in detection between these wetlands. Although a by-wetland annual apparent survival model performed as well as the top model, the 95% confidence intervals of annual apparent survival between the two wetlands overlapped, indicating that the effect of wetland setting on apparent survival is trivial when comparing these two wetlands. Given that the two wetlands included in our reduced dataset (the only ones with sufficient data available) were both managed wetlands, we also have no information on gallinule survival rates outside of managed areas. Such information will be important for understanding the impact of prevailing management strategies on adult survival rates in this subspecies.

Our resighting data set is missing a potentially important period in the gallinule life cycle when survival rates are lower; specifically, the first ~40 days of life between hatching and the point when young birds are large enough to band (Fredrickson 1971). In a study of a different species of endangered Hawaiian waterbird (Hawaiian Stilt, *Himantopus mexicanus knudseni*), Reed et al. (2015) found that this age class had the highest mortality rate. Though our literature research yielded some limited information on chick survival in Hawaiian gallinules, this information is crucial for future work, not only for its likely importance to population dynamics, but also because chick survival is probably among the easiest vital rates to influence via management. Trapping and

exclusion of invasive mammalian predators are a key part of management for Hawaiian waterbirds on wildlife refuges on O'ahu, where they are thought to reduce predation rates on nests and chicks (USFWS, 2011). Better knowledge of the extent to which such management improves this vital rate, and the impact this vital rate has on overall population trends, would be instrumental in improving conservation of this subspecies. The impacts of avian botulism on Hawaiian gallinules are virtually unstudied, though the incidence in this subspecies seems rare (K. Uyehara, pers. obs.). It is also unknown whether botulism has different impacts on juvenile versus adult gallinules, so a major research priority is monitoring incidence of the disease across life stages, to elucidate which parts of the life cycle it impacts most severely.

Though our goodness-of-fit tests indicated that our dataset meets expectations determined by the assumptions of the CJS model, the limitations and asymmetries of this dataset (see Supplemental materials, 5.S1) prevented us from including most of our 14 study sites because the sparseness and short duration of their encounter histories led to overdispersion. The high performance of our null model of annual apparent survival (ϕ constant across both wetlands) is in line with conservative thinking in model selection, particularly where the number of data points per parameter (in this case, encounter histories, $n = 26$) is limited (Harrell 2001). As Beissinger and Snyder (2002) noted, the most complex model is not necessarily the most useful if there is no reliable biological interpretation, and in this context our null model for annual apparent survival, although it does not provide information on annual or habitat-based differences, is our most credible parameter estimate. This estimate can accordingly be used for population viability analysis and for comparative work as data on survival in unmanaged habitats become

available.

Little is known about the movement rates or patterns of Hawaiian gallinules (Dibben-Young 2010), though they are reputed to be highly sedentary (Shallenberger, 1977). Dispersal beyond survey sites can cause underestimation of survival rates (Koenig et al. 1996), raising the potential concern that dispersal has biased estimates in our study. Any impact of dispersal on apparent survival rates is likely to be higher in data from earlier in this study (prior to 2014), when few wetlands were monitored. Banding and surveying for Hawaiian gallinules has occurred opportunistically for the last decade, typically with periods where a cohort of birds was banded, monitored briefly, and then not systematically surveyed for several years. Additionally, bird behavior affecting detectability apparently varies between wetlands; DesRochers et al. (2008) observed a greater proportional response to call playback at sites with more birds. Our mark-recapture study showed minimal evidence of movement (3 confirmed movements), despite exhaustive surveys of 14 sites for four consecutive years, and regular monitoring of four sites (Waimea Valley, James Campbell NWR, Pearl Harbor NWR, and Hamakua Marsh) for 13 years. This corroborates findings by van Rees et al. (2017) that movement may be severely limited in Hawaiian gallinules, reducing the possibility that dispersal has severely impacted our survival and detectability estimates, but reinforcing the notion that habitat connectivity may be a risk factor for subspecies' population dynamics. The problem of poor detectability remains, however, and more in-depth studies on gallinule movement behaviors will be necessary. Radio telemetry studies may be a feasible alternative, although given our low rates of observed movement a very large sample size would be required. A better understanding of gallinule movement behavior would help

managers better predict the effects of habitat management actions (for example, will birds disperse under unfavorable habitat conditions), and would reveal which management units on the island are connected by dispersal between subpopulations.

All of the resighting data analyzed in our reduced dataset came from wetlands that were under active and ongoing habitat management (predator control and removal of invasive plants), and though most of Hawaiian gallinules are currently found in protected areas, our estimates may be optimistic for unmanaged wetlands. Regular and systematic surveys for banded birds at a larger number of wetland sites would make substantial and timely contributions to current knowledge of survival and movement rates of Hawaiian gallinules. The current cohort of banded individuals thus represents a new and unique opportunity to collect valuable information on the behavior and survival of these birds, but consistent, long-term followup is essential to collecting these data. Marking and monitoring of fledglings will also be of value, because poor knowledge of survival rates during this life stage is a major gap in our understanding of the life cycle of the Hawaiian gallinule. Increased nest searching and monitoring, as well as banding and resighting in unmanaged habitats will also be important to quantify the impacts of vegetation management and predator control, the two most commonly-used management strategies, on gallinule vital rates and population dynamics.

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Guidelines to the Use of Wild Birds in Research

(<http://www.nmnh.si.edu/BIRDNET/guide/>), and conducted with the requisite federal and state of Hawaii endangered species and banding permits. Previous drafts of this manuscript were greatly improved by insightful comments from two anonymous reviewers, an anonymous associate editor, and the editor in chief of the Journal of Fish and Wildlife Management.

Table 5.1: We collected unpublished studies on Hawaiian gallinule (*Gallinula galeata sandvicensis*) reproductive vital rates from studies conducted on Kaua’i and O’ahu from 1979-2014. This table shows the study type, location and years of data collection for each of these studies, and whether study sites were managed or unmanaged. All Master’s theses are listed with their date of completion and can be found in the references of this paper; their vital rates data have not been previously published in the peer-reviewed literature. Nagata (1983)’s work at several lotus farms are the only reproductive data from unmanaged wetlands used in this study.

Study	Study Type	Island (Location)	Managed?	Years of Data Collection
Nagata (1983)	Master’s thesis	O’ahu (Hamakua and lotus farms)	Y/N	1979-1980
Chang (1990)	Master’s thesis	O’ahu (James Campbell NWR, Pearl Harbor NWR)	Y	1985-1988
Gee (2007)	Master’s thesis	Kaua’i (Hanalei NWR, Adjacent Taro fields)	Y	2004
Silbernagle (USFWS)	Unpublished data study	O’ahu (James Campbell NWR, Pearl Harbor NWR)	Y	1997-2001, 2004, 2006
Gutscher-Chutz (2011)	Unpublished data	Kaua’i (Hanalei NWR)	Y	2005
Cosgrove (USFWS)	Unpublished data	Kaua’i (Hanalei NWR)	Y	2014

Table 5.2: We reviewed and summarized data on reproduction vital rates of Hawaiian gallinules (*Gallinula galeata sandvicensis*) on the islands of Kaua’i and O’ahu, using data from 1979 to 2014. This table shows the mean, range, and standard deviation of reproduction parameters for each study, and the weighted average and standard deviation from our meta-analysis. Clutch size refers to the number of eggs laid per nest, and nest success is the proportion of nests that hatched at least one chick. Number of chicks per nest is the total number of chicks produced divided by the number of nests, including nests that failed. Number of chicks per successful nest is the total number of chicks divided by the number of successful nests (those which hatched at least one chick). Hatch rate refers to the number of chicks produced per egg among all nests. N = sample size (either nests, successful nests, or eggs). Study averages were derived excluding data from Gutscher-Chutz, which used different methods.

Parameter	Mean (std. deviation)	Range	N
<i>Clutch size</i>			
Nagata (1983)	4.56 (2.19)	1 – 7	9
Chang (1990)	4.91 (1.27)	2 – 8	87
Gee (2007)	6.30 (1.92)	2 – 11	56
Silbernagle (Unpubl. data)	4.18 (1.67)	1 – 7	17
Gutscher-Chutz (Unpubl.data)	5.57 (1.86)	2 – 10	21
Cosgrove (Unpubl. data)	4.42 (1.32)	1 – 8	45
Study Average	5.10 (0.75)	4.18-6.30	5
<i>Nest Success</i>			
Nagata (1983)	0.42 (0.50)	–	31

Chang (1990)	0.77 (0.42)	—	87
Gee (2007)	0.65 (0.48)	—	56
Silbernagle (Unpubl. data)	0.58 (0.50)	—	26
Gutscher- Chutz (Unpubl.data)	0.20 (0.45)	—	19
Cosgrove (Unpubl. data)	0.67 (0.48)	—	43
Study Average	0.660 (0.11)	0.42 – 0.77	5
<i>Number of chicks / nest</i>			
Nagata (1983)	1.68 (2.34)	0 – 8	31
Chang (1990)	3.42 (2.35)	0 – 8	87
Gee (2007)	2.77 (2.58)	0 – 8	56
Silbernagle (Unpubl. data)	1.58 (2.19)	0 – 6	26
Gutscher- Chutz (Unpubl.data)	1.32 (1.83)	0 – 5	19
Cosgrove (Unpubl. data)	1.47 (1.35)	0 – 4	43
Study Average	2.51 (0.94)	1.47 – 3.42	5
<i>Number of chicks / successful nest</i>			
Nagata (1983)	3.71 (2.16)	1 – 8	13
Chang (1990)	4.51 (1.53)	1 – 8	63
Gee (2007)	4.51 (1.99)	1 – 8	36
Silbernagle (Unpubl. data)	2.73 (1.56)	1 – 6	15
Gutscher-Chutz (Unpubl.data)	4.4 (1.03)	1 – 5	6
Cosgrove (Unpubl. data)	2.25 (1.08)	1 – 4	28
Study Average	3.86 (0.83)	2.25 – 4.51	5
<i>Hatch Rate (chicks/egg)</i>			
Nagata (1983)	—	—	—
Chang (1990)	0.65 (0.42)	0 – 1	434
Gee (2007)	0.46 (0.38)	0 – 1	364
Silbernagle (Unpubl. data)	0.56 (0.54)	0 – 1	71

Gutscher- Chutz (Unpubl.data)	0.28 (0.34)	0 – 1	78
Cosgrove (Unpubl. data)	0.34 (0.27)	0 – 0.83	199
Study average	0.52 (0.12)	0.34 – 0.65	4

Table 5.3: We gathered mark-resight and mark-recapture data of banded Hawaiian gallinules (*Gallinula galeata sandvicensis*) between 2004-2017, and ran a suite of models in program MARK to estimate mean annual apparent survival of adults in this subspecies. These models were run on a reduced dataset consisting only of data from wetlands for which data showed goodness of fit for the assumptions of Cormack-Jolly-Seber models (James Campbell National Wildlife Refuge and Waimea Valley Park). This table shows candidate survival models and their number of parameters, ΔAIC_C , model weight, and model likelihood for the reduced dataset. A period (.) is used to denote a null model, in which survival was not allowed to vary (kept constant). ΔAIC_C is the difference in the AIC_C value, a measure of model performance, between a given model and the next-best model. AIC weight describes the explanatory power of a given model relative to all other models compared using AIC_C .

Model design	Number of parameters	ΔAIC_C	AIC weight	Model likelihood
$\phi(.)$ p(wetland*year) ¹	21	0.00	0.65	1.0
$\phi(\text{wetland})$ p(wetland*year)	22	1.21	0.35	0.55
$\phi(\text{wetland*year})$ p(wetland*year)	31	13.12	0.00	0.0
$\phi(\text{wetland})$ p(year)	12	15.73	0.00	0.0
ϕ (year) p(wetland*year)	29	15.87	0.00	0.0
$\phi(\text{wetland})$ p(.)	3	20.38	0.00	0.0
$\phi(\text{wetland})$ p(wetland)	4	20.73	0.00	0.0
$\phi(\text{year})$ p(wetland)	12	28.68	0.00	0.0
$\phi(.)$ p(year)	11	34.01	0.00	0.0
$\phi(\text{year})$ p(year)	19	37.50	0.00	0.0
$\phi(.)$ p(.)	2	38.80	0.00	0.0

¹ (Lowest) AIC value = 353.79

Figure 5.1: In this study, we collected all available information on the vital rates of the Hawaiian gallinule (*Gallinula galeata sandvicensis*) on O’ahu and Kaua’i using mark-resight and nest monitoring data from 1979-2017. These images depict an adult Hawaiian gallinule and gallinule nest at Olomana golf links, Kailua, O’ahu, HI. Photos taken in 2016 by Amanda Sandor.



Figure 5.2: We collected and synthesized unpublished data on the vital rates of Hawaiian gallinules (*Gallinula galeata sandvicensis*) from field work between 1980-2017 on the islands of O’ahu and Kaua’i. This image shows the names and locations on O’ahu where Hawaiian gallinules were banded and resighting surveys were conducted. Nest data were collected at Hanalei National Wildlife Refuge on Kaua’i, and on O’ahu at Hamakua Marsh, Enchanted Lake, Waimea Valley, private agricultural lands (labeled Lotus Farm), and James Campbell National Wildlife Refuge.

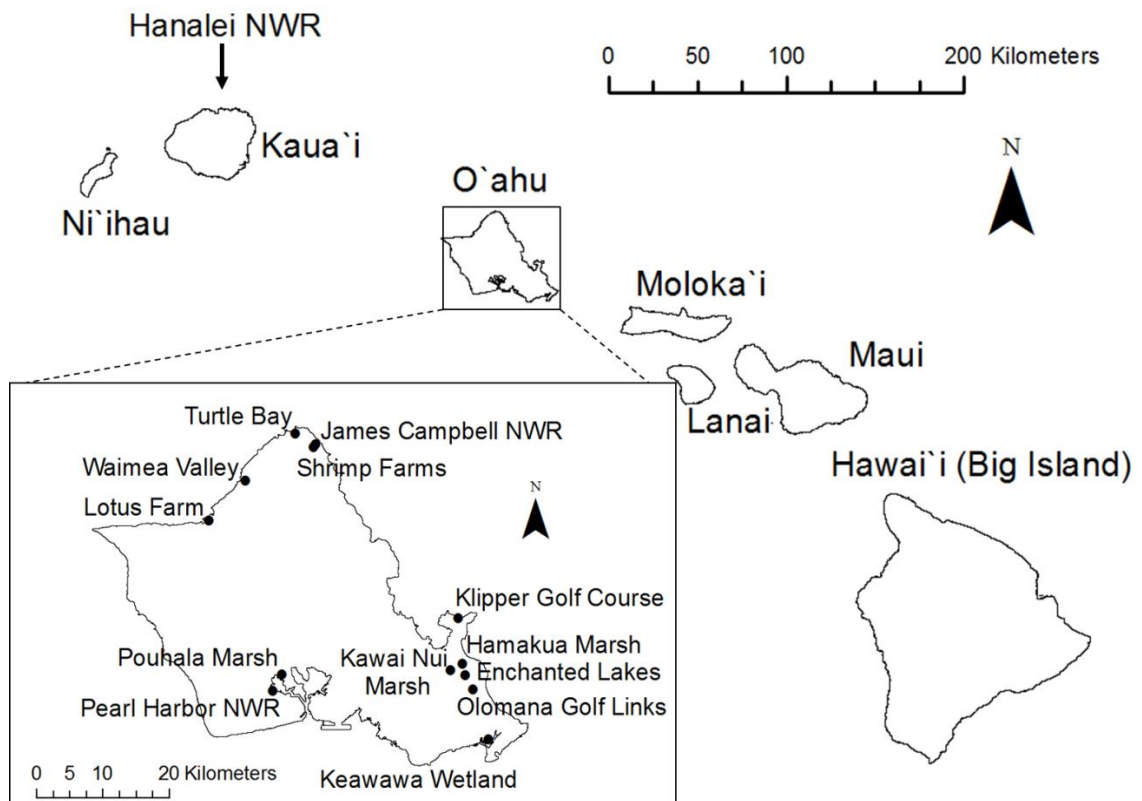
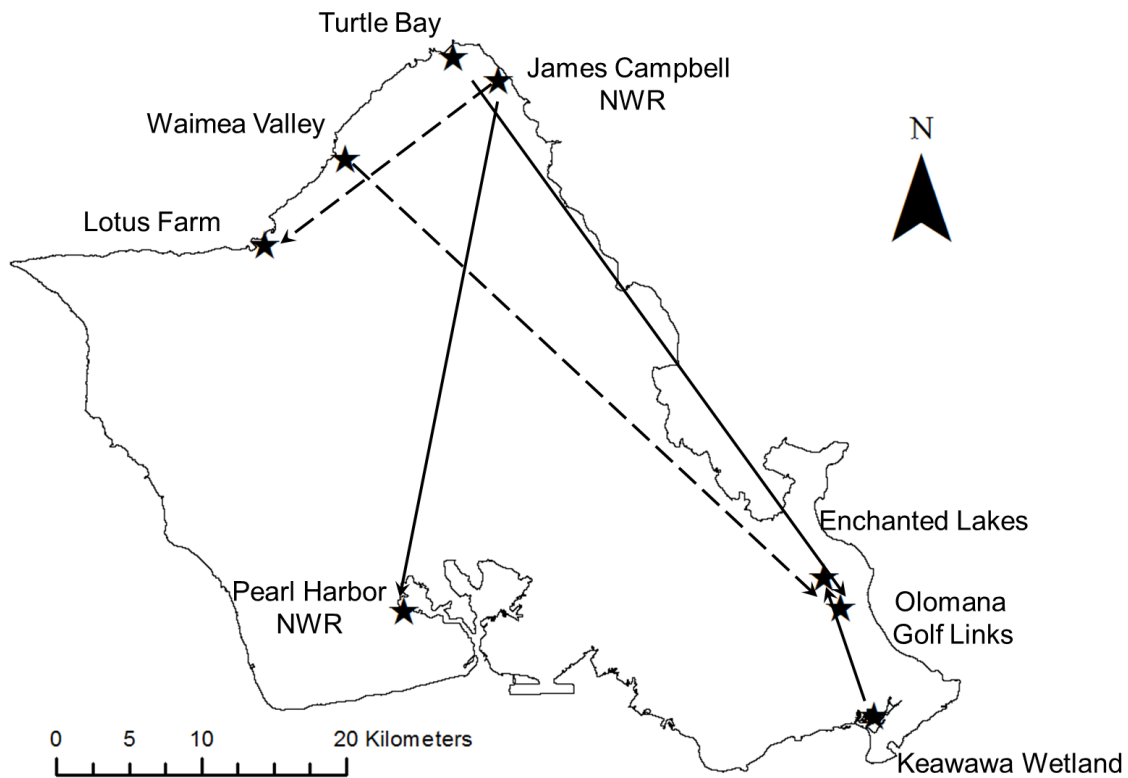


Figure 5.3: We assembled a database of mark-resight and mark-recapture records of Hawaiian gallinules (*Gallinula galeata sandvicensis*) on O’ahu from 2004-2017 and recorded all potential movement events observed during the study period. This figure shows the confirmed (solid arrows) and unconfirmed (dashed arrows) movement detected from 2004-2017.



Supplemental Materials (Chapter 5)

Table 5.S1: Pooled data on the vital rates of Hawaiian gallinules on the islands of Kaua`i and O`ahu. The last column is comparative data from a published study on Kaua`i (not included in our study, Byrd and Zeillemaker 1981). Dashes indicate data that was unavailable or not estimated; * indicates a statistically significant difference in island means ($p \leq 0.05$).

Parameter	Mean (std. deviation)	Range	N	Byrd and Zeillemaker (1981)
Clutch size (all nests) ^a	5.14 (1.84)	2–11	197	
Kaua`i	5.78 (1.85)*		85	5.6 (1.2), N = 64 ^f
O`ahu	4.66 (1.67)		112	
Nest Success ^b	0.62 (0.49)	–	249	
Kaua`i	0.63 (0.48)		101	0.75 (–), N = 61
O`ahu	0.66 (0.47)		148	
Number of chicks / nest ^c	2.49 (2.37)	0–8	225	–
Kaua`i	2.19 (2.19)*		99	
O`ahu	2.73 (2.49)		126	
Number of chicks / successful nest ^d	3.84 (1.86)	1–8	146	
Kaua`i	3.39 (1.83)*		64	4.3 (–), N = 13
O`ahu	4.19 (1.82)		82	
Hatch Rate (chicks/egg) ^e	0.53 (.43)	–	188	
Kaua`i	0.42 (0.36)		85	0.75 (–), N = 53
O`ahu	0.62 (0.46)		103	

^aYears data collected: all data combined: 1979, 1980, 1985–88, 1997–2001, 2004–06, 2014–16;
Kaua`i: 2004, 2005, 2014; O`ahu: 1979, 1980, 1985–88, 1997–2001, 2004, 2006, 2014–2016

^bNest success is the proportion of nests that hatched at least one chick

^cNumber of chicks / nest is the number hatched per nest including nests that failed (no eggs hatched)

^dNumber of chicks / successful nest is the number of hatched chicks per nest only among nests that produce at least one chick

^eHatch rate is the proportion of eggs in successful nests that hatched

^fData come from Kaua`i, 1975–1980

Table 5.S2: Distribution of banding effort, survey effort, and resighting data among wetlands where Hawaiian gallinules were banded and monitored on O’ahu, Hawai’i for all years in our resighting database. Banded Individuals describes the number of individual birds banded at each wetland and years of monitoring describes the number of years in which sites were revisited for resightings. The number of resightings at each wetland includes those resightings of birds banded at that wetland, as well as immigrants banded at other wetlands. Notably, years of monitoring and number of banded individuals vary largely between groups.

Wetland	Banded Individuals	Years of monitoring	Number of Resightings	Proportion of total sightings (%)	Proportion of total individuals (%)
James Campbell National Wildlife Refuge	217	14	963	59.44	51.30
Waimea Valley	43	12	258	15.92	10.02
Hamakua Marsh ^a	47	6	94	5.80	11.11
Keawawa wetland ^a	13	4	96	5.92	3.07
Enchanted Lakes ^a	20	3	51	3.15	4.72
Turtle Bay Resort ^a	13	3	31	1.91	3.07
Hono’uli’uli National Wildlife Refuge ^a	3	5	7	0.43	0.71
Lotus farm ^a	17	3	31	1.91	4.02
Olomana golf links ^a	15	3	29	1.79	3.54
Shrimp farm ^a	7	2	7	0.43	1.65
Pouhala Marsh ^a	9	2	9	0.55	2.12
Kawai Nui Marsh ^a	6	2	11	0.68	1.42
Klipper golf course ^a	13	2	33	2.04	3.07
TOTAL	423	14	1620	100.00	100.00

^a Wetlands excluded from survival analysis due to restricted sample size

Table 5.S3: We reviewed unpublished data on the reproduction vital rates of Hawaiian gallinules (*Gallinula galeata sandvicensis*) collected on the islands of Kaua’i and O’ahu from 1979-2014. We pooled these data to compare reproductive parameter values between managed and unmanaged habitats. N=number of nests. Dashes indicate information not available or not estimated; we detected no statistically significant differences between any of the tested vital rates. Sample sizes in unmanaged wetlands were insufficient for hypothesis testing of clutch size and hatch rate.

Parameter	Mean (std. deviation)	Range	Sample Size
Nest Success			
Managed	0.66 (0.48)	0-1	230
Unmanaged	0.59 (0.50)	0-1	22
Number of chicks / nest			
Managed	2.53 (2.36)	0-8	203
Unmanaged	2.14 (2.47)	0-8	22
Number of chicks / successful nest			
Managed	3.86 (1.86)	1-8	132
Unmanaged	3.62 (2.22)	1-8	13

Chapter 6

The potential effects of habitat connectivity, management, and sea level rise on the extinction risk of an endangered waterbird in a fragmented island landscape

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Abstract

We designed a spatially explicit, stochastic, individually based population viability analysis for the Hawaiian gallinule (*Gallinula galeata sandvicensis*), an endangered subspecies of waterbird endemic to fragmented coastal wetlands in Hawaii. This subspecies persists on two islands, with no apparent movement between them. We assessed extinction risk for birds on O`ahu, where the majority of the gallinule population persists in eight subpopulations. Data on genetic differentiation was used to inform subpopulation status, as well as to estimate dispersal rates. We used sensitivity analyses to gauge the impact of current uncertainty of vital rate parameters on population projections, to ascertain the relative importance of gallinule vital rates to population persistence, and to compare the efficacy of potential management strategies. We used available sea level rise projections to examine the relative vulnerability of O`ahu's gallinule population to habitat loss to this threat. Our model predicted persistence of O`ahu's overall gallinule population at 160 years, but with high probabilities of extirpation of small subpopulations. Sensitivity analyses highlighted the importance of juvenile and adult mortality to population persistence in Hawaiian gallinules, justifying current predator control efforts and suggesting the need for additional research on chick survival. Subpopulation connectivity had

little effect on the persistence of the island population, but a strong effect on the persistence of smaller subpopulations. Our model predicted overall population persistence under current expectations of sea level rise, but with the possibility that O`ahu's largest gallinule populations could lose >40% of current carrying capacity.

6.1. Introduction

Islands are considered a conservation priority (Kier et al., 2009) because of their high species endemism (Alcover et al., 1998) and elevated risks of extinction when compared to mainland ecosystems (Diamond, 1984; Vitousek, 1988). Island populations are typically vulnerable to drivers of deterministic decline due to life history traits that evolved in an island context (Boyer, 2009), and because of their restricted ranges and smaller overall population sizes (MacArthur and Wilson, 1976), which can lead to inbreeding depression (Frankham, 1998). The ecological impacts of introduced invasive predators are a major driver of island species declines and extinctions (Blackburn, et al., 2004 while stochastic factors acting on small remnant populations are typically the ultimate cause of extinction (Caughley, 1994; Hanna and Cardillo, 2013). Avian extinctions on islands are among the best documented recent losses of vertebrate biodiversity (Olson and James, 1982; Steadman 1995, 2006; Duncan et al., 2013), and extant island birds make up a large proportion of threatened avian taxa (Lee and Jetz, 2010).

Although introduced predators have caused most island bird declines and extinctions (Blackburn et al., 2004, 2005; Duncan and Blackburn, 2007), climate change is a rapidly emerging threat to island species in general (Fordham and Brook, 2010) and birds in particular (Sekercioglu et al., 2012). Among climate change threats to island species are lower adaptive capacity to environmental change (Buckley and Jetz, 2007), poorer dispersal rates, resulting in a reduced capacity to relocate in response to changes in local climate, a limited elevational or latitudinal gradient into which to track one's climate envelope (of particular concern for birds, Sekercioglu et al., 2007; Devictor et al., 2008) and habitat inundation with sea level rise, a qualitatively higher risk for island systems (Mimura et al., 2007). Sekercioglu et al. (2012) emphasized that research on climate change impacts on tropical birds in particular was highly

important because of a diverse array of likely impacts, and generally poor knowledge on the subject.

The Hawaiian archipelago is a famous hotspot for extinction, and, having lost the majority of its endemic avifauna to human impacts (Olson and James, 1982). Research has demonstrated climate change is having strong negative impacts on Hawaiian forest birds (Benning et al., 2002; Atkinson et al., 2009), but very little attention has been paid to climate impacts on other endemic Hawaiian bird taxa. Hawai'i's endemic waterbirds, of which 75% have gone extinct since human colonization, include 6 extant species that are all threatened (Scott et al., 2001). The Hawaiian gallinule ('Alae 'ula, *Gallinula galeata sandvicensis*), is among the most threatened of these (USFWS, 2011), with populations below 1,000 individuals (Reed et al., 2011).

We integrated data on vital rates, movement ecology and climate change projections to generate a stochastic simulation model of Hawaiian gallinule population to investigate the potential impacts of management strategies and climate change on their extinction risk. The Hawaiian gallinule, a subspecies of the Common gallinule, is currently found only on the islands of Kaua'i and O'ahu, where it persists after rapid population declines throughout the late 19th and early 20th centuries (Shallenberger, 1977; Griffin et al., 1990). Hunting, habitat loss from wetland reclamation, and predation by exotic invasive species resulted in the extirpation of Hawaiian gallinules from the islands of Hawai'i, Maui, and Moloka'i, and by the 1960s an estimated 60 individuals remained (Engilis and Pratt, 1993). A halt to decline and slow population increases have been achieved since the 1970s, principally attributed to the establishment of protected wetland refuges by state and federal authorities (Reed et al., 2011; Underwood et al., 2013).

Hawaiian gallinules are one of many native Hawaiian bird species, including all of the waterbirds, that are management dependent (Reed et al., 2012; Underwood et al., 2013), requiring continuous management for populations to persist. Management for Hawaii's endangered waterbirds typically includes trapping mammalian, reptile and amphibian predators, pumping fresh water to control water levels and reduce salinity, and regular removal of emergent vegetation through mowing, burning, or flooding to prevent habitat degradation and domination by exotic invasive plants (USFWS, 2011; Vanderwerf, 2012). The distribution of gallinules on each island is naturally fragmented by the subspecies' ecological specialization on limited coastal freshwater wetlands, with greater isolation caused by wetland loss widespread anthropogenic landscape change (van Rees and Reed, 2014; van Rees et al., 2017). Habitat patches, and therefore local subpopulations, are generally small, most supporting fewer than 50 individuals at a site. This highlights the likely importance of dispersal for the persistence of an island's population. Unfortunately, very little is known about Hawaiian gallinule movements, although a population genetic analysis by van Rees et al. (2017) showed strong signs of genetic structure among gallinule populations on O`ahu, indicating that movement may be restricted. This increasing awareness of the fragmented nature of O`ahu's gallinule population has led to suggestions for studying and improving connectivity between the island's isolated subpopulations (van Rees and Reed, 2015; van Rees et al., 2017). The cryptic behavior of Hawaiian gallinules has made field studies of their vital rates and movement behavior difficult; consequently insufficient data have been available to model population persistence for Hawaiian gallinules, or to evaluate alternative management scenarios and threat impacts.

Recent studies of the Hawaiian islands have projected that climate change (Htun et al., 2016), particularly with respect to sea level rise (Kane et al., 2015) may have dramatic effects on

Hawaiian coastal freshwater wetlands (Underwood et al., 2013) raising additional concerns over the long-term viability of O`ahu's Hawaiian gallinule population. The freshwater wetlands upon which Hawaiian gallinules depend are found only along a narrow strip of flat, low-elevation land bordering the coastlines of the islands, and are therefore vulnerable not only to inundation with sea level rise but also to salinization (Vanderwerf, 2012); as sea water rises, it can penetrate the freshwater aquifers that support many palustrine wetlands, as well as provide much of the fresh water used residentially (Lau and Mink, 2006). Hawaiian gallinules appear to have the lowest tolerance for elevated salinity among Hawaii's endangered waterbirds, so they may be threatened by habitat degradation from saltwater intrusion in addition to habitat loss from inundation with sea level rise (USFWS 2011; Underwood et al., 2013).

These numerous sources of uncertainty and risk warrant quantitative assessment, and the U.S. Fish and Wildlife Service's (2011) Recovery Plan for Hawaiian Waterbirds lists population viability analysis as a key part of the process toward Hawaiian gallinule de-listing. Population viability analyses (PVAs) are population models used to project population size and persistence into the future as quantitative assessments of extinction risk (e.g., Seal and Foose, 1989; Taylor, 1995; Catlin et al., 2016). Depending on their structure, PVAs can incorporate a wide variety of demographic and life history information and various types of stochasticity to estimate probabilities of extinction or pseudo-extinction (the probability of declining below a threshold population size) (Beissinger and Westphal, 1998; Morris and Doak, 2002; Beissinger et al., 2006). The objective of PVAs is making the most accurate projections possible using the best available data, which in the case of many declining or rare taxa are often very limited (Boyce, 1992; Beissinger and Westphal, 1998; Morris and Doak, 2002; Zeigler and Walters, 2014). Beissinger and Westphal (1998) present guidelines for the responsible and practical use of PVA,

stressing that their primary utility is in assessing relative impacts (rather than absolute predictions) and trade-offs among organism vital rates, associated management strategies, and their influences on extinction risk.

A major research initiative is understanding and incorporating the role of animal behavior in species conservation (Curio, 1996; Reed, 1999, 2002; Sutherland 1998; Caro, 2007; Berger-tal et al., 2016), including incorporation into PVAs (Reed et al., 2002, Walters et al., 2002). Recent studies have shown that behavioral information can have major impacts on model predictions, in some cases showing higher (Gerber, 2006) and others lower (Grimm et al., 2005; Mortensen and Reed, 2016) extinction risk relative to a behaviorally uninformed model. Movement behavior is an especially important driver of population dynamics for small and fragmented populations, (Hanski, 1998, 1999; Maciel and Lutscher, 2013), mediating population connectivity (Taylor et al., 1993; Reed and Levine, 2002), which in turn may ameliorate extinction risk for small populations via demographic buffering against extinction (the rescue effect, Brown and Kodric-Brown, 1977; Gotelli, 1991; Cosentino et al., 2011), recolonizing extinct populations (Hanski, 1999; Gilpin, 2013), and counteracting loss of genetic diversity through drift (genetic rescue; Keller and Waller, 2002).

The discrete distribution of Hawaiian gallinules on O`ahu makes them an excellent study system for spatially explicit PVA (Walters et al., 2002), and their current existence in many small subpopulations warrants attention to the impacts of stochastic elements of population dynamics as well as to deterministic drivers of decline. The high uncertainty in demographic parameters for this taxon (van Rees et al., in press) and difficulty of studying them in the field necessitates further guidance as to the sensitivity of conservation outcomes to different vital rates. Such information could aid in prioritizing field study and data collection, and provide

insights as to the impacts of parameter uncertainty on projected population outcomes (Morris and Doak, 2002). The management dependence of this subspecies also raises questions about the efficacy of different management alternatives, and which demographic rates would be the most important to manage or improve. Finally, the threat of sea-level rise to Hawaiian gallinule populations, though referenced by several authors, has not been evaluated quantitatively, even in a general and heuristic sense. Here we create a spatially explicit population viability analysis for the Hawaiian gallinule using recently published data on the species' vital rates (van Rees et al. *in press*; Chapter 5 of this thesis) that were assimilated from unpublished research across three decades, as well as using data on microgeographic genetic differentiation on O`ahu (van Rees et al. 2017) to estimate breeding dispersal between wetlands.

6.2. Methods

6.2.1 Study Area

We studied the population of gallinules on the island of O`ahu, Hawai`i (21°28'N 157°59'W), which consists of a number of subpopulations in fragmented coastal freshwater wetlands around the island (Fig. 1). Wetland habitats supporting breeding populations of gallinules include state and federal wildlife refuges that are actively managed for waterbirds, botanical gardens, private lotus, watercress, and shrimp farms, and golf courses. O`ahu is the most populous island of Hawai`i (>70% of state population, State of Hawaii Department of Business, Economic Development & Tourism, 2016), and has experienced rapid landscape change in recent decades (Giambelluca, 1986, 1996; Klasner and Mikami, 2003; van Rees and Reed, 2014), resulting in a highly diverse and increasingly urbanized landscape matrix. Most individual wetlands support small (5-30 individuals) gallinule subpopulations, with the exception

of James Campbell National Wildlife Refuge and Hamakua Marsh Wildlife Sanctuary, which, combined, support an estimated >40% of the island's population. To our knowledge, the O'ahu population of gallinules is an effectively closed system, with no documented inter-island movements in 4 years of monitoring >250 banded individuals (van Rees et al., *in press*). Demographic data used for this study were taken from van Rees et al. (*in press*), and were collected from fourteen wetland sites on the island from 1979-2017.

6.2.2 Baseline Population Model

We used Vortex 10 (Lacy and Pollak, 2014) to generate an individual-based stochastic simulation model of O'ahu's gallinule populations. We chose this approach because the small size of many of our subpopulations makes them vulnerable to demographic stochasticity so we wanted that explicitly modeled, and because it allows movement of individuals between subpopulations, capturing observed population-genetic structure on O'ahu's landscape (Lacy, 2000; Walters et al., 2002). We used a time frame of 160 years, the span of 40 generations recommended by O'Grady et al. (2008) and Reed and McCoy (2014), based on our estimated generation time of approximately 4 years as calculated in Vortex. We defined a subpopulation as extirpated when only one sex remained; the same criterion was used for island-wide extinction. For each scenario, we ran 1000 iterations, and recorded metrics of extinction risk for each subpopulation and for the total island population. Our extinction risk metrics were the (1) probability of extinction at 160 years, (2) mean population size of extant population (and subpopulations) at 160 years, and (3) deterministic and stochastic growth rates for that scenario.

6.2.2.1 Subpopulations and Carrying Capacity

Based on genetic evidence from van Rees et al. (2017), we combined subpopulations that had no evidence of genetic structure (e.g., nonsignificant or near-zero F_{ST}) between them into wetland complexes, which we then treated as a single subpopulation (Figure 6.1). The carrying capacity of each subpopulation was estimated as the maximum recorded count of gallinules in the last 12 years, using data from both Hawaii's biannual waterbird survey and playback surveys (following DesRochers et al., 2008) we made for a separate project (van Rees, unpubl. data). For wetland complexes, we combined the maximum recorded counts of each wetland within the complex for a total carrying capacity (Table 1). The starting size (time = 0) of each subpopulation was set to 80% of K, which is similar to current estimated population sizes.

6.2.2.2 Survival and Reproductive System

We generated baseline model parameters using information on reproduction and survival from van Rees et al. (*in press*), with support and supplementation from data on related taxa (e.g., Common moorhen, *Gallinula chloropus*; Table 2). Even though Hawaiian gallinules do not breed until age 2, there is no evidence of age structure in survival rates beyond year 1 (van Rees et al., *in press*). Therefore, we modeled two age classes: hatch year (hatching to age 1), and after hatch year (age 1+ or adult). For adult (after hatch year, AHY) birds, we used the less conservative of two survival estimates generated by van Rees et al. (*in press*), because it better accounted for the extremely poor detection in this taxon. We calculated first-year survival by combining survival rates to fledging with adult survival rates for the remainder of year 1 (10 months). We used information on fledgling survival from van Rees et al. (*in press*), which suggested ~41% mortality within the 60-day period up to fledging; and compared this to

estimates for *G. g. cachinnans* in North America, which has similar values (Miller, 1946; Bell, 1976; Greij, 1994). Combined with mean adult mortality for the remaining 10 months of year 1, the total mortality in year 1 was estimated as 67% (Table 6.2). We estimated mean adult mortality to be 26.8%, using pooled data from van Rees et al. (*in press*), and calculated variance in adult survival using the binomial equation, because the standard deviation from van Rees et al. (*in press*) appeared strongly inflated by detection errors. We chose a value of 15% for the variance in juvenile survival because we thought that it realistically reflects the large variability in chick survival observed in the field. The sensitivity of our model to this parameter estimate was tested during sensitivity analysis.

We set the age of first breeding for males and females to 2 years, which was the earliest observed breeding of any known-age bird observed on O`ahu (van Rees et al., *in press*; Chapter 5 of this thesis). We used a maximum age of 10, which is the oldest observed Common gallinule (*Gallinula galeata*) from mark-resighting data in the United States (Clapp et al., 1982); the oldest known age-Hawaiian gallinule was recovered at age seven years, eight months (van Rees et al. *in press*). We assumed no reproductive senescence, since no evidence of this has been observed in Hawaiian gallinules (van Rees et al., *in press*). We defined offspring in the model as chicks, and used 8 as the maximum number of progeny per brood; this is the highest observed brood size on O`ahu (van Rees et al., *in press*). We specified the distribution of brood sizes based on data from 103 broods on O`ahu assimilated by van Rees et al. (*in press*; Table 6.2) and assumed a 1:1 sex ratio at hatch in the absence of evidence to the contrary. We set the maximum number of broods in a given year to 4, basing our estimate from field observations of two closely monitored pairs (van Rees et al., *in press*), as well as accounts of this and related subspecies under natural conditions (Benthum, 1931; Nagata, 1983; Smith and Polhemus, 2003). We modeled the

distribution in number of broods produced per female per year using a binomial model with the estimate of nest success for O`ahu (0.65) as the probability parameter, and 4 (the maximum number of broods in a year) as the number of trials (Table 6.2).

6.2.2.3 Density Dependence

Given observations that Hawaiian gallinules are aggressively territorial (van Rees, pers. obs.; Chang, 1990), and population models in other rails that took territoriality into account (Wanless, 2002; Hockey et al., 2011), we added density dependence to our model, using the density dependence function provided by VORTEX, which varies the probability of an individual female breeding in a given year based on the population size with respect to carrying capacity (Lacy and Pollak, 2014):

Equation 6.1:
$$P(N) = (P(0) - [P(0) - P(K) \left(\frac{N}{K}\right)^B]) \frac{N}{N+A}$$

Where $P(N)$ is the proportion of females that breed when the population size is N , $P(K)$ is the proportion that breed when the current population size has reached carrying capacity, and $P(0)$ is the proportion of females breeding at low densities. We used a value of 0 for A (Allee parameter), because we have seen no evidence for behaviors that would lead to Allee effects in this species (e.g., no dependence on group defense from predators, large habitats where finding mates would be difficult), and a value of 20 for the steepness parameter B , which made the function show few density dependent impacts until the population went above $0.8K$ (80% of carrying capacity). We assumed this high ceiling because Hawaiian gallinules are not food limited (DesRochers et al., 2010), and would likely not experience density dependent negative feedback until territorial disputes began negatively affecting survival and reproductive success. We set $P(0)$, the baseline probability of a female breeding in a year at 0.90, and $P(K)$, the probability of a female breeding under maximum density dependence, at 0.33. We estimated

P(K) based on our observations that large family groups in densely populated wetlands typically had at most 4 non-breeding adult helpers, of which 2 were likely females assuming a 1:1 sex ratio, which implies that 1 in 3 adult females per territory would be breeding at high density (van Rees, unpubl. data).

6.2.2.4 Dispersal

We estimated dispersal using unidirectional gene flow data from van Rees et al. (2017) calculated using software MIGRATE (Beerli and Felsenstein, 1999, 2001). For each migration rate, we multiplied the value of M (effective migration rate) by an estimate of mutation rate (10^{-4} , a standard mutation rate for microsatellite dinucleotide repeats; Vigouroux et al., 2002; Marriage et al., 2009) to get the number of migrants per generation, based on the equation $M = m/\mu$, where μ is mutation rate, and m is number of migrants per generation. We then divided this value by 4, the estimated generation time generated by VORTEX (Lacy and Pollak, 2014). Finally, we multiplied this probabilistic value by 100 to convert it to a percentage of individuals per year, which was entered into VORTEX as a matrix of between-wetland movement probabilities. Because of the nature of the data, we were able to estimate separate dispersal rates for each direction for each pair of wetlands.

6.2.2.5 Catastrophes

Generally, wetlands on O`ahu are subject to very few catastrophic events (typically, hurricanes), which we view as unlikely to have significant effects on survival or reproduction of Hawaiian gallinules. Observations indicate that adults are unlikely to be killed by flood events (M. Silbernagle, USFWS ret., pers. comm.); although nests can be lost, birds can re-nest quickly

(van Rees et al., *in press*). Additionally, Hawaiian gallinules are aseasonal breeders, apparently breeding year round (DesRochers et al., 2009), so even widespread losses at a single time point would represent reproductive loss for only one small portion of the total annual breeding window, rather than disrupting some limited breeding season. Three major hurricanes have directly hit the main Hawaiian Islands with enough proximity to affect O`ahu in the last 68 years (Central Pacific Hurricane Center, 2017). We generated a per-year probability using this value (0.04). Because subpopulations are spread across three different coasts of the island, we estimated that a hurricane could cause total reproductive failure due to flooding to a maximum of about 50% of the population. Due to their aseasonal breeding habits, however, such a catastrophe would probably eliminate only about one fourth (25%) of the year's breeding attempts in affected subpopulations, given that the combined nesting, incubation, and fledging time of Hawaiian gallinules is around 90 days. This would result in reducing the reproductive output of 50% of the island's subpopulations by 25%, so we estimated that a hurricane would reduce reproduction by 12.5% in the year that it struck. We set catastrophes to reduce survival by 5% to account for the possibility of a small number of individuals being killed by flooding or during dispersal from flooded areas.

6.2.3 Sensitivity Analyses

We followed the sensitivity analysis protocols of Mortensen and Reed (2016), who conducted sensitivity testing using three approaches: 1) perturbation analysis, 2) relative sensitivity or elasticity, and 3) the logistic regression approach (Cross and Beissinger, 2001). Perturbation analysis in their approach involves systematically changing a single parameter across the range of all feasible parameter values and plotting these values against some

measurement of extinction risk, to see how much a parameter value can be changed until a population either declines to extinction or persists throughout the study period (if it is going extinct under baseline conditions). This threshold can be used to measure how close current estimated parameter values are to values that would cause a major change in population behavior. Relative sensitivity or elasticity analysis is a conventional sensitivity testing procedure in which parameter values are increased and decreased by some small amount from their current mean value, and the percentage change in some metric of extinction risk is scaled by the baseline value of the parameter, to compare the change in outcome created by alterations to different parameters (Cooper et al., 2002; Mortensen and Reed, 2016). The logistic regression approach uses logistic regression to examine the relationship between the value of a given parameter and the probability of extinction given a large number of samples of possible parameter values and a binary outcome of extinct or not extinct at the end of the study period (McCarthy et al., 1995; Cross and Beissinger, 2001). We performed sensitivity analyses on all subpopulations separately, and on the entire O`ahu population as a whole.

We performed perturbation analyses, following Reed et al. (1998), on mean juvenile and adult mortality, percentage of females breeding in a given year, carrying capacity, mean brood size, and dispersal rate (Table 6.2). We varied both survival parameters from 0-1 in increments of 0.1, and percentage of females breeding from 0-100% in increments of 10%. We varied K from 5-100 in increments of 5 for all subpopulations that had probability of subpopulation extinction (hereafter extirpation) > 0 in our baseline model, which included all populations other than the Windward and Kahuku complexes (Figure 6.1). We varied the distribution of brood sizes (which we used as a proxy for reproductive success) based on a normal distribution with a mean which we varied between 1 and 8 chicks (standard deviation of 1), encompassing the range

of observed values on O`ahu (van Rees et al., *in press*), and changed mean brood size by 0.5 chicks at a time. We changed dispersal rate by applying a multiplier across all inter-wetland movement rates, thus keeping relative dispersal rates the same and increasing overall movement and population connectivity on O`ahu. We varied this multiplier from 2 to 100, effectively varying annual probability of individual dispersal by two orders of magnitude, but maintaining relative rates. We used this broad range to reflect current uncertainty over the extent to which connectivity might be altered by management, and uncertainty over the true mutation rate of microsatellite markers used to estimate per-generation movement rates. Each scenario was run for 1000 iterations and 160 years.

We conducted elasticity analysis by changing each parameter by $\pm 10\%$ of its mean value, then calculated a metric of relative sensitivity by dividing the difference between the stochastic lambda (λ) of positive and negative scenarios by 0.2 times the stochastic lambda of the baseline scenario, according to the equation $(\lambda_+ - \lambda_-) / (0.2 * \lambda_0)$ (Cooper et al., 2002), where λ_+ and λ_- are the positive and negative scenarios, respectively, and λ_0 is the baseline scenario. We calculated stochastic lambda using the stochastic instantaneous growth rate (r) provided by Vortex for each scenario (using $\lambda = e^r$). We assessed the relative sensitivity of our modeled populations to mean and variation of juvenile and AHY mortality, the distribution of number of broods per female per year, the average brood size, the percentage of breeding-aged females breeding in a year, the carrying capacity K of each subpopulation, and population connectivity. We varied the distribution of the number of broods per year by subtracting 10% of the percentage of brood numbers falling in each category (0, 1, 2, 3, and 4 broods per year) and adding it either to the next highest or lowest category, depending on the direction being tested. Accordingly, the distribution was shifted to higher or lower values by 10%. We changed the distribution of brood

sizes per year by modeling brood size as a normal distribution, and adding or subtracting 10% from the mean value. We changed dispersal rate by adjusting the overall dispersal multiplier by $\pm 10\%$. We used Cooper et al (2002)'s rule of thumb for assessing the relative sensitivity of model outcomes to changes in parameter values, whereby any parameter with a sensitivity value of >1 or <-1 was considered to have a disproportionate effect on population growth rate.

For logistic regression analysis, we used Latin Hypercube sampling in Vortex to randomly generate parameter sets selected from uniform distributions that we determined using observed and feasible values for Hawaiian gallinules. We ran 10 iterations for each parameter set, resulting in 10,000 total simulations for regression analysis. We then performed logistic regression using the 'car' package (Fox and Weisberg, 2011) in R 3.2.2 (R Core Team, 2015), treating extinction at 160 years as the dependent variable. We conducted logistic regression using carrying capacity, mean juvenile and adult mortality, environmental variation in juvenile and adult mortality, percentage of females breeding, and connectivity as explanatory variables. Each parameter was varied according to a uniform distribution, bounded where needed based on knowledge of feasible values. We varied mean juvenile mortality rate from 0 – 1 because of our extremely poor knowledge of the parameter and its large apparent variation in the field, and adult mortality from 0.02 – 0.65, based on the potential range of annual adult mortality estimates found in van Rees et al. (*in press*). We varied the dispersal multiplier from 2 to 80, again reflecting poor knowledge of possible values (Table 2). We combined these parameters as predictor variables in a single generalized linear model with probability of extinction (PE) as the response variable. We compared the explanatory value of different parameters using their standardized regression coefficients, calculated by dividing the regression coefficient by its standard error.

6.2.4 *Climate scenarios*

We used readily available spatial data on sea level rise and maps of the location and extent of modeled Hawaiian gallinule habitats to estimate the reduction in habitat area expected from future sea level rise on O`ahu. This method assumed that reductions in habitat will respond with a proportional reduction in carrying capacity; in other words, that gallinule population densities are uniform throughout their habitats. The spatial data that we used to approximate sea level rise on O`ahu were created by the National Oceanic and Atmospheric Administration's (NOAA) Office of Coastal Management, and are available through their sea level rise data portal (<https://coast.noaa.gov/slrdata/>). These datasets, consisting of simple rasters of the estimated mean high tide line of O`ahu under different sea level rise conditions, were designed to provide preliminary information on coastal flooding impacts in the United States. They were derived by combining digital elevation models with tidal surface models that approximate regional tidal variability. The sea level rise projections do not account for the impacts of erosion, island subsidence, wetland migration through accretion, or human modification for sea level rise mitigation. We used these models to generate an estimate of the potential magnitude of reduction of gallinule habitat and carrying capacity on O`ahu under projected sea level rise scenarios, and to gauge the relative threat of sea level rise compared to other potential factors affecting extinction risk in this taxon.

We estimated changes in habitat area (carrying capacity) at two scenarios, 0.914m (three feet) and 1.829m (six feet), given a limited number of scenarios for which data were available on the NOAA sea level rise portal. These values correspond approximately to the range of sea level rise projected by Vermeer and Rahmstorf (2009), which other researchers have found to be more

predictively robust than the IPCC (2007) projections (Rahmstorf et al., 2011; Kane et al., 2015). Notably, Vermeer and Rahmstorf's (2009) estimates are only for a 100-year projection, so we chose the highest available sea level rise value from available NOAA maps (1.829m) for our 160 year time frame, representing a highly conservative estimate (estimates for the year 2100, ~80 years in the future, are as high as 1.8m). Our smaller value (0.914m) corresponds to a conservative value for an 80-year projection (Vermeer and Rahmstorf, 2009).

We combined our own maps of gallinule habitats on O`ahu with data from the U.S. Fish and Wildlife Service's National Wetlands Inventory (USFWS 2017) to generate outlines of the habitats supporting all subpopulations modeled in this study. We converted these polygon maps to 3m resolution rasters using the Polygon to Raster tool in ArcMap 10.4.1 (ESRI 2016), and for each subpopulation, added the raster map of its habitats to one of the two sea level rise maps using the raster calculator. We then counted the number of 3m x 3m pixels making up the original habitat map, and subtracted the overlapping pixels revealed by the raster calculation to estimate the proportion of habitat pixels that would be inundated with salt water. Using this value as an ending carrying capacity at either 80 or 160 years, we designed a power function of the form aX^b to approximate the shape of the sea level rise curve depicted in IPCC (2007) and Vermeer and Rahmstorf (2009). We applied this to the carrying capacity of affected populations in Vortex to approximate the change in carrying capacity across time according to equation 6.2:

Equation 6.2:
$$K_t = K_0 - [K_0 * L \left(\frac{at^b}{Y} \right)],$$

where K_t is carrying capacity at time t , K_0 is the original carrying capacity, L is the total proportion of habitat area lost at year 80 or 160 (depending on the simulation), t is the current year, Y is the last year of the simulation (80 or 160), and a and b are shape parameters used to approximate the pattern of projected global sea level rise. We determined values of a and b

separately for 80 year and 160 year scenarios to maintain curve shape while passing through a different point at $t = 80$ or $t = 160$ (for 80 years, $a = 0.06$ and $b = 1.613$; for 160 years, $a = 0.02$ and $b = 1.7385$). We ran sea level rise scenarios using baseline model parameters. Carrying capacities of individual subpopulations were altered independently according to separate analyses of their potential area loss. Both scenarios were run with 1000 iterations, with the ~1m scenario projecting for 80 years, and the ~2m scenario for 160 years (Table 6.3).

6.3 Results

6.3.1 Model Projections

Our baseline model showed that O`ahu's island-wide Hawaiian gallinule population would persist over the 160 year time frame (Table 6.4). Probability of extirpation varied strongly between subpopulations, with the large subpopulations (the Windward and Kahuku complexes) having probabilities near 0, and the small populations (Klipper, Keawawa, and Lotus Farm) having probabilities of near 1. The extirpation of small subpopulations appears to drive the very slight decreases in mean estimated island-wide population size at year 160, though average increases in population size in medium and large populations compensate for much of this loss. The overall stochastic population growth rate (r) was 0.25, indicating rapid growth, although this ranged from 0.09 to 0.24 in different subpopulations. Generally, larger subpopulations had higher stochastic growth rates, although among small populations, Klipper and Keawawa had higher growth rates than Lotus Farm despite having smaller carrying capacities and starting population sizes.

6.3.2 Sea Level Rise Scenarios

Our Hawaiian gallinule habitat maps encompassed ~430 ha. of occupied wetland habitat on O`ahu. In the 80 year and ~1m sea level rise scenario, a total of 36 ha. (8%) was lost due to salt water inundation, with a sharp increase in the 160 year and ~2m sea level rise scenario, in which 239 ha. (56%) was lost. Due to their landscape context, all of the small wetlands (Keawawa, Klipper, and Lotus Farm) and one of the medium wetlands (Waimea Valley) were unaffected by projected sea level rise in either scenario, and Turtle Bay was unaffected in the 80-year scenario. The Windward Complex, Kahuku Complex, and Pearl Harbor Complex lost 5.6%, 17%, and 11%, respectively, of their total carrying capacity in the 80-year scenario. In the 160 year or ~2m sea level rise scenario, the Windward Complex lost 54% of its carrying capacity, the Kahuku Complex 51% (Figure 6.2), the Pearl Harbor Complex ~100%, and Turtle Bay 99%.

Simulated island-wide gallinule populations on O`ahu persisted with 0.0 probability of extinction under both our 80-year and 160-year sea level rise scenarios, though the mean ending population size was 11% lower than the starting size at 80 years and ~1m sea level rise, and 57% lower in 160 years and ~2m sea level rise (Table 6.4). Probabilities of extirpation were not changed by sea level rise at 80 years, although the ending population sizes of the three largest subpopulations were smaller than in the baseline scenario. Pearl Harbor and Turtle Bay had population declines in excess of 80% over the 160-year timeframe, while the Windward and Kahuku complexes showed declines of 40% and 37%, respectively. The probability of extirpation of the Windward and Kahuku complexes remained approximately 0 after 160 years, but increased dramatically for both Pearl Harbor (from 0.05 to 0.77) and Turtle bay (from 0.08 to 0.80). The small subpopulations, which were not predicted to be affected by sea level rise due to

their landscape setting, were equally likely to be extirpated during the 80 year or 160 year time frame as in the baseline scenario (Probabilities of extirpation > 0.99). Waimea Valley was the only subpopulation that maintained population levels similar to its starting population at the end of the simulation and also showed no change in extirpation probability across climate change scenarios. Stochastic population growth rates showed little change between climate change scenarios, both for the overall island population and individual subpopulations.

6.3.4 Model Sensitivity

Because subpopulations of similar sizes behaved similarly, we do not show results for all subpopulations, but instead show those that are representative of particular size classes (Figures 6.3-6.6). Perturbation analysis showed that large and medium subpopulations transitioned rapidly from low probability of extirpation to high ($P = \sim 1.0$) probabilities of extirpation when juvenile mortality rose above 80% (Figure 6.3). Small subpopulations' extirpation probabilities never declined below 1.0, even with 100% juvenile survival. Perturbation of adult mortality showed a transition point among large subpopulations from low to high probability of extirpation at 50% mortality, although this threshold was lower in medium subpopulations. For the Pearl Harbor Complex (Figure 6.4) and Turtle Bay, the transition value was closer to 20-30% mortality. As with juvenile mortality, no levels of adult mortality reduced the extirpation probability of small subpopulations. The range of parameter uncertainty for adult survival encompassed values that were meaningful for medium-sized subpopulations (i.e., there were large differences in probability of extirpation across values ± 1 SD from our parameter estimate), but this was not the case for large or small subpopulations.

Large subpopulations and the overall island population transitioned from near 0 extirpation probability to near 1 extirpation probability when the percent of females breeding decreased below 30% (Figure 6.S4). This transition was more gradual for medium subpopulations, which increased steadily from about 70% of females breeding, reaching an extirpation probability near 1 at 30%. Extirpation probability remained near 1 at all values of this parameter for small populations. For mean brood size, large subpopulations and the overall island population had extirpation probabilities near 1 when mean brood size was 0, but decreased to an extirpation probability of ~0.0 when mean brood sizes were 1 or higher (Figure 6.S5). Medium-sized subpopulations had a probability of extirpation near 1 for mean brood sizes of 0 and 1, but declined to ~0.25 with a mean brood size of 2, and remained near 0 at all higher values. No tested values of mean brood size reduced probability of extirpation in small subpopulations.

Our investigation of management scenarios in which connectivity was increased showed that with large (e.g., 20 to 50 times) increases in the connectivity multiplier, the extirpation risk of small subpopulations could be reduced by 75-80% (Fig. 6.5), but that it had little to no effect on the extirpation risk of medium and large subpopulations, or the overall island population. The probability of extirpation of the two smallest subpopulations, Klipper and Keawawa, declined rapidly from 2-20 times detected dispersal rates, and showed slower declines after that point. For medium-sized subpopulations, extirpation risk declined sharply from 2 to 12 times detected dispersal rates, at which point probability of extinction was near zero. For the habitat management scenario, perturbation of the carrying capacity of small and medium subpopulations showed consistently that carrying capacities above 15 individuals led to rapid decline in extirpation probability, reaching 0 by around ~30 individuals.

Conventional, relative sensitivity analysis showed that none of the tested vital rates had a disproportionate (> 1.0) effect on stochastic annual population growth rate (λ). Juvenile mortality had the largest effect on the overall island population (-0.61 ; Table 6.5), though its effects were smaller for small subpopulations (e.g., -0.46 for Klipper). Mean brood size (a proxy for reproductive success) and percent females breeding had the next largest effects, with 0.30 and 0.23 , respectively, with greater sensitivity to brood size among small subpopulations, and greater sensitivity to percentage of females breeding among large subpopulations. Adult mortality had a moderate effect on population growth rate (-0.17), which was greater for smaller subpopulations (e.g., 0.30 for Keawawa and 0.54 for Lotus Farm). Dispersal rate had a negligible effect on λ for the overall island population, but small populations showed sensitivities up to 0.14 (Keawawa). Environmental variation in adult and juvenile mortality and carrying capacity both also had little effect on λ , with slightly stronger effects (e.g., 0.03 - 0.06) on small subpopulations. Our logistic regression analysis showed that mean juvenile mortality, mean adult mortality, and mean brood size accounted for the most variability in observed extirpation probability of the overall island population (Table 6.5). Variance in juvenile mortality accounted for a greater proportion of variability than variance in adult mortality, and both carrying capacity and dispersal rate explained very little. The importance of dispersal and carrying capacity was much larger for small subpopulations, with standardized coefficients as much as seven times larger than that for the overall island population (Keawawa, -21.73) for dispersal, and three times higher for carrying capacity. The p values for all covariates in our logistic regression model were statistically significant ($p < 0.0001$ in all cases).

6.4 Discussion

We synthesized all available data on the demographic rates, population structure, and movement rates of Hawaiian gallinules to develop a spatially explicit, individually-based, multi-population projection model for this subspecies. Using this model, we assessed the relative effects of potential management strategies and sea level rise scenarios on extinction risk through simulation and sensitivity analysis. This study contributes to a growing and important body of research on the population-level impacts of environmental change (in this case, land use or global climate change) on the viability of wildlife populations (Johst et al., 2011). Reviewing our results, we return to the cautions of Beissinger and Westphal (1998), who emphasized that population projections should be cautiously interpreted and used as tools for assessing relative risks rather than making absolute predictions. Our intention in this study is to provide baseline estimates of the relative sensitivity of O'ahu's Hawaiian gallinule population to different management strategies and potential threats, using the best information currently available. These models and the vital rates estimates from which they are constructed should be updated and validated as new information become available.

6.3.1 Baseline population viability model

Under our baseline scenario, O'ahu's Hawaiian gallinule population had an extinction probability of ~0.0 over 160 years, with a positive stochastic growth rate, but showing small and gradual population decline due to the loss of small populations with some compensation from growth in larger populations. This rapid growth rate indicates that the Hawaiian gallinule's reproductive vital rates make them capable of quickly responding to improving environmental conditions and increased carrying capacity, a promising characteristic for the species' resistance to transient pressures, but the likely extirpation of smaller subpopulations is of concern for the

longer-term viability of the population under present conditions. Although extinction risk is ostensibly low for the overall island population, our projections emphasize that island-wide persistence is largely dependent on the fate of several large and medium-sized subpopulations on the island, because all small subpopulations and some medium-sized subpopulations had high probabilities of extirpation.

The high likelihood of extirpation of the island's smaller subpopulations, even in the absence of wetland-specific demographic rates and explicitly modeled inbreeding depression, illustrates the potentially severe impacts of demographic stochasticity on O`ahu's smaller gallinule subpopulations. An additional risk factor for the island's smallest subpopulations (Keawawa and Klipper) is uncompensated emigration (Fahrig and Merriam, 1985), because estimated gene flow rates out of these subpopulations were much higher than rates into them (van Rees et al., 2017), making emigration much more likely than immigration in our simulation. Such emigration, combined with the potential difficulty of finding mates in small subpopulations and large impact of demographic stochasticity are likely what makes these subpopulations act as sinks in our simulation (Gyllenberg and Hanski, 1992; Lacy, 2000). Although these factors may play a role in actual population dynamics on the island, the degree to which they are mitigated by site-specific vital rates and dispersal is unknown.

Very little is known about the movement rates of Hawaiian gallinules, and compounded with uncertainty in the mutation rates of microsatellite markers used by van Rees et al. (2017), movement between subpopulations on O`ahu may be the most uncertain parameter in our model. Additionally, movement detected using gene flow modeling only detects those movements which led to breeding, and thus does not offer a full picture of actual movement rates amongst O`ahu's subpopulations. Gene flow estimates accordingly give no information on mortality rates during

dispersal, which have important implications for demographic rates (Dale 2001; Fahrig 2001). Empirically-based simulation models on other avian habitat specialists have shown that, even where long distance dispersal is rare, mortality rates during dispersal can have significant impacts on population projections (Cooper et al., 2002). The potential for sex-biased dispersal rates is also of particular interest given the small size of many of O`ahu's populations and the subsequent importance of demographic stochasticity for their persistence. For example, Schiegg et al. (2002)'s spatially explicit, individual-based population model of the Red-cockaded woodpecker (*Picoides borealis*) showed strong dispersal effects on population growth rate driven by sex-specific differences in dispersal tendency. In their simulations, low dispersal success of females resulted in a large number of solitary, unmated males, reducing population growth rate. Where one sex is more likely to disperse or more likely to disperse a greater distance, biased sex ratios will occur in isolated populations, potentially impacting individual fecundity and population growth rate (Milner-Gulland, 2003; Gerber, 2006). Thus, our currently poor understanding of dispersal in Hawaiian gallinules would be improved not only by a general understanding of the frequency of between-wetland dispersal on O`ahu, but also of sex-specific rates and mortality risk among dispersing individuals.

Our simulation model treated dispersal rates as a constant probability for each origin-destination pair (i.e., unidirectional probabilities, where $P(A \rightarrow B) \neq P(B \rightarrow A)$), excluding any density-dependent or habitat quality impacts on dispersal. For example, South (1999) found that dispersal had a smaller effect on population persistence when dispersal only occurred at habitat saturation. If Hawaiian gallinules avoid dispersal until there are no available breeding vacancies, they may reflect a similar pattern. Additionally, habitat quality may affect dispersal rates, with birds more likely to emigrate from lower quality habitats and to immigrate into higher quality

ones (Buechner, 1987; Baguette et al., 2000; Doerr et al., 2006; Pfluger and Balkenhol, 2014). The absence of these factors represents another simplifying assumption of our model which could be overcome with additional research on dispersal behavior in this taxon.

As discussed in van Rees et al. (*in press*; Chapter 5 of this thesis), the vital rates estimates used in our baseline model come almost exclusively from managed populations, which are likely to be optimistic for unmanaged populations, like Turtle Bay, Lotus Farms, and several of those that make up parts of the Windward Complex and the Kahuku Complex. Managed wetlands typically offer favorable conditions due to the removal of exotic invasive plants that reduce habitat quality, and exclusion and trapping of mammalian predators (Vanderwerf, 2012; Underwood et al., 2013). The present population projection model may thus fail to capture important differences in reproductive and survival parameters between modeled subpopulations. Our vital rates data also came from several short (1-5 year) studies spread across a 35-year time period (1979-2014), and accordingly may contain information from different phases of the Hawaiian gallinule's recent population trajectory on O`ahu (Reed et al., 2011), introducing variation that may not be typical of current conditions on the island. van Rees et al. (*in press*) also stress that poor detection rates of Hawaiian gallinules likely impacted survival estimates, which may accordingly result in lower estimates longevity and mean annual adult survival in the parameterization of our baseline models. In using their less conservative estimate of survival, we have attempted to compensate for some of this bias.

Our population model included density-dependent feedbacks despite our lack of empirical evidence for their influence on gallinule populations; it has been shown that incorporating density dependence into population projection models reduces extinction risk by creating compensatory mechanisms that tend to return populations from declines (Ginzberg et

al., 1990). We acknowledge that the inclusion of this phenomenon may produce optimistically-biased projections in our models, although our parameterization of the density dependence curve in Vortex (see Methods) condenses density dependent effects to populations very close to K , and thus may avoid biases toward recovery after perturbation.

6.3.2 Sea level rise scenarios

Our sea level rise scenarios are superficial and heuristic in nature and represent a conservative estimate of the potential impacts of sea level rise on the carrying capacity of O`ahu's freshwater wetland habitats for the Hawaiian gallinule. This analysis was limited by available sea level rise data from the NOAA sea level rise data portal and the assumptions of the models used to generate those data, but we feel that it reflects a sufficient level of precision for the type of generalized, relative risk assessment intended for PVA. Given already poor information on the relative densities of Hawaiian gallinules among known habitats, higher resolution models of sea level rise impacts might not greatly improve the accuracy of model predictions. Consequently, while acknowledging the simplicity of our sea level rise analysis, we suggest that it serves as a blunt instrument to assess the relative impact of sea level rise on extinction risk in Hawaiian gallinules, and have taken precautions where possible to make modeled scenarios conservative.

We used sea level rise values that corresponded with the range of current predictions for increase in mean sea level in Hawaii, and whenever making simplifying assumptions, sought to err on the side of conservatism. Accordingly, both of our modeled sea level rise heights are rather small for the projected time frames, and we did not take into account additional degradation of freshwater wetland habitats through salinization. Coastal freshwater wetlands on

O`ahu could be salinized either by storm surge or by saltwater intrusion in underlying basal aquifers (Kane et al., 2015), which are among the primary sources of fresh water for most of such wetlands on the Hawaiian Islands (Lau and Mink, 2006). The impacts of salinization with sea level rise could thus be quite severe and drive reductions in carrying capacity well beyond the spatial extent modeled our projections.

We assumed that gallinule densities were uniform throughout space within their habitats due to a lack of quantitative data on their spatial distributions. Using preliminary data and field observations from population surveys for another project (van Rees, unpubl. data), we see that many of the areas most threatened by sea level rise are also those with the highest population densities of Hawaiian gallinules. For example, Hamakua Marsh (part of the Windward Complex) and James Campbell National Wildlife Refuge (part of the Kahuku Complex) appear to be the most productive gallinule habitats on the island, with the highest populations overall, and, based on our analysis, will be the first parts of their respective wetland complexes to be lost due to sea level rise. Much of the remaining area of both of these wetland complexes (Kawainui marsh in the Windward Complex, and Shrimp Farms in the Kahuku Complex) is thought to be of much lower habitat value, and lower densities of gallinules are seen there (van Rees, unpubl. data). In our model, for example, Hamakua marsh and James Campbell National Wildlife Refuge account for 51% and 76% of the carrying capacities of their respective wetland complexes. We thus suggest that our assumption of uniform gallinule population density makes our estimates for the loss of carrying capacity especially conservative.

Wetland migration due to accretion is notably neglected in our projections, and has been argued in other systems to be a buffer against habitat loss for some coastal wetland types, which are capable of shifting their distributions inland and upland with rising sea levels (e.g., Traill et

al., 2011). While wetland migration may be a larger influence on continental landscapes, we argue that it may be of little effect on O`ahu, where most areas further inland from wetlands are either densely developed or feature dramatically sloped topography that transitions directly from the coastal plain into the mountains, leaving virtually no room for wetland migration. The unique topography of volcanic islands like O`ahu, coupled with the intense development pressure on the island, greatly limit the capacity of these wetland habitats to migrate inland with rising seas. The persistence of the O`ahu's two major strongholds for Hawaiian gallinules, the Windward and Kahuku complexes, may depend strongly on the migration of wetland habitats to higher elevations and increased management of wetlands that are less vulnerable to rising sea levels. Both Kawainui marsh in the Windward Complex and the Shrimp Farms in the Kahuku Complex are positioned inland and adjacent to high-density managed sites from which gallinules might easily emigrate under sea level rise. Management to increase carrying capacity at these sites (which is currently limited in both cases) could create habitat capable of supporting a large portion of the gallinules currently found in both wetland complexes. Similar inland wetland alternatives are not available for the Pearl Harbor Complex and Turtle Bay, meaning that more intensive and perhaps economically infeasible measures like habitat creation and land acquisition would be necessary to mitigate sea level rise impacts.

While we approximated the gradual loss of wetland carrying capacity using equations that mimic the sea level rise curves predicted by the current best available estimates (Vermeer and Rahmstorf, 2009), the mechanisms by which this change in carrying capacity leads to changes in simulated populations in Vortex bears additional scrutiny. In Vortex, when current population size exceeds K, the mortality of all individuals (across age classes) in the population is increased during that time step such that the population is reduced to carrying capacity in the

following time step. Although this method of population truncation would lead to very small increases in mortality during slower periods of sea level rise early in the simulations, as the rate of sea level rise (and change in K) increases according to equation 6.2, this increase in mortality may become less realistic. Detailed knowledge of the impact of density dependence on survival and reproduction of Hawaiian gallinules is necessary to assess the accuracy of this information, but is not currently available. The apparent prevalence of often physically violent territorial disputes among Hawaiian gallinules at high densities (van Rees, pers. obs.) suggests that crowding from sea level rise might increase mortality, but the apparent tendency of Hawaiian gallinules toward facultative cooperative breeding (Byrd and Zeilemaker, 1981; van Rees et al., *in press*) might alleviate some negative density-dependent impacts, as in Mortensen and Reed (2016). Additional research on Hawaiian gallinule social behavior would contribute substantially to the accuracy of this aspect of our model.

Our future scenarios also exclude the impacts of climate change on other abiotic factors like precipitation, temperature, and nutrient loading of stream flow, which were highlighted as potential influences on Hawaiian gallinule abundance on Kauaʻi by Htun et al. (2016). A poor mechanistic understanding of the relationship between these variables and gallinule vital rates, compounded with uncertainty of how these parameters will change over time, precludes inclusion of these additional threats for the time being, but they will be important to consider pending the future availability of information.

6.3.3 Sensitivity Analysis and Management Strategies

Both conventional and regression sensitivity analysis highlighted the importance of juvenile survival for population persistence in Hawaiian gallinules, a conclusion that matches a

general understanding in the ornithological literature that population regulation in Common and Hawaiian gallinules depends on the production of many young whose survival is generally low (Greij, 1994; van Rees et al., *in press*). This finding is especially relevant to management, given the general belief that exotic invasive predators have larger impacts on juvenile than adult mortality, and that predator management is one of the longest-implemented and logistically feasible management strategies for this subspecies (USFWS, 2011; Vanderwerf, 2012).

Reproductive success (with distribution of broods per year and mean brood size as proxies) and mean adult mortality were also shown to be of generally higher importance, and are affected by the same management strategies. Consequently, the prevailing emphasis on predator control in current management plans for this subspecies should be considered highly justified in light of our population viability analysis. Although the percentage of females in the breeding pool showed some impact on population growth rate, we are not aware of any management strategies to increase this vital rate and accordingly consider it a lower priority for management.

The considerable importance of juvenile mortality in our PVA reinforces the assertion by van Rees et al. (*in press*) that studies on chick and fledgling survival in this subspecies are of great importance for their conservation. At present, although we have a rough idea of the order of magnitude of this vital rate for Hawaiian gallinules, our large degree of uncertainty with respect to this parameter implies that most or all of the scenarios from our perturbation analysis may be possible in some habitats (Figure 6.3). The high importance and uncertainty of this parameter makes it a top priority for future field research on Hawaiian gallinules. Our understanding of adult survival seems to show that large subpopulations are unlikely to be extirpated under present conditions (Figure 6.4), but that medium-sized subpopulations possibly, and smaller subpopulations very likely, will be extirpated within our timeframe of 40 generations.

Interestingly, subpopulations with a carrying capacity above 30 individuals appear to have consistently low probability of extirpation at present, low levels of dispersal (Fig. 6). This result should be interpreted with caution, however, because our model did not include inbreeding effects, which can have strong impacts on reproductive rates in populations below the “rule of thumb” size of 50-100 individuals (Franklin, 1980; Soule, 1980; Frankham et al., 2014). This finding may as a result be optimistic, although present uncertainty about dispersal rates makes it difficult to assess the threat of inbreeding depression to O`ahu’s smaller subpopulations.

The reduced importance of dispersal rates on population growth rate and extinction risk relative to juvenile and adult survival in our study corresponds with findings in other systems (Pulliam et al., 1992; Liu et al., 1995; South, 1999), and reinforces the notion that the contributions of connectivity to population viability are often secondary to the direct effects of demographic rates. Although the degree of connectivity had a generally negligible impact on the extinction risk of O`ahu’s overall population of Hawaiian gallinules, it showed great importance to the persistence of small subpopulations like Keawawa and Klipper, which likely rely on steady immigration from larger subpopulations to maintain their numbers (Pulliam, 1988). In both regression-based and conventional sensitivity analysis, dispersal had substantial impact on the extirpation risk of small subpopulations, amounting to as much as half of the sensitivity value of directly altering carrying capacity for those populations. The extirpation of these subpopulations under low-dispersal scenarios caused a slow, constant decline in overall island population throughout the study period, which was ameliorated by increasing the dispersal multiplier. Interestingly, dispersal multiplier values >10 caused smaller increases in mean island population size at 160 years, indicating that, at a certain point, bird emigration to isolated populations was detrimental to the growth of the overall population. This is similar to

observations by Medici and Desbiez (2012), who examined metapopulation persistence in lowland tapirs (*Tapirus terrestris*). Our perturbation analysis (Figure 6.5) also showed steady decreases in extirpation probability for small subpopulations across a wide range of connectivity values. This implies that even modest increases in connectivity can produce nontrivial changes in the probability of persistence of small Hawaiian gallinule subpopulations. Although management actions that directly increase the carrying capacity of small subpopulations would apparently be more helpful in all circumstances, on islands like O`ahu where space is extremely limited and expansion bears large economic costs, increasing connectivity might be a viable option for decreasing extinction risk where more direct and effective methods are not possible. Recent work by van Rees et al. (*in review*; Chapter 4 of this thesis) suggests that stream networks and green water management infrastructure (e.g., drainage swales) may increase landscape permeability to gallinules, providing a feasible measure of managing connectivity for this subspecies.

van Rees et al. (2017)'s work on the population connectivity of Hawaiian gallinule populations represents foundational but very limited information on current dispersal rates between isolated subpopulations on O`ahu. These estimates rely heavily on assumptions of mutation rate and population genetic conditions under Hardy-Weinberg Equilibrium, which may be violated due to the disproportionate impact of genetic drift in the case of small populations on the island (van Rees et al., 2017), and from the impacts of earlier bottleneck events in the population (Sonsthagen et al., 2017; van Rees et al., 2017). As discussed by van Rees et al. (*in press*), continued monitoring of banded gallinules on O`ahu, and the use of radio telemetry or other higher-detection approaches to studying movement would be very beneficial to our understanding of Hawaiian gallinule population dynamics.

6.3.4 Conclusions

Our population viability analysis highlights the importance of juvenile and adult mortality in the extinction risk of Hawaiian gallinules on O`ahu, and provides the first quantitative evidence of the potential threat posed by sea level rise for this and other endangered Hawaiian waterbirds. Our findings confirm that predator control is rightfully a high priority activity for Hawaiian gallinule management because of its likely effects on juvenile and adult mortality, and that continued vegetation management for carrying capacity will be necessary to maintain current populations. Although population connectivity was only important in the extirpation risk of small, isolated subpopulations these subpopulations are among the only ones not seriously threatened by sea level rise. Their importance to the overall persistence of O`ahu's Hawaiian gallinule population may accordingly increase with time, and if room for wetland expansion and enhancement is limited, connectivity may be the next best option to reduce extinction risk.

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Zoological Society) for their insights for the design of our model and interpretation of simulation results, and Sarah Sonsthagen (USGS) for her help estimating annual dispersal probabilities from gene flow data.

Table 6.1: Names, carrying capacities (K), and size classes of the 8 subpopulations modeled in our study of the population viability of Hawaiian gallinules (*Gallinula galeata sandvicensis*), on O`ahu, Hawai`i.

Subpopulation Name	K	Size Class
Windward Complex	186	Large
Kahuku Complex	105	Large
Pearl Harbor Complex	40	Medium
Turtle Bay	38	Medium
Waimea Valley	27	Medium
Klipper	15	Small
Lotus Farm	14	Small
Keawawa	6	Small

Table 6.2: List of vital rates, their values for our baseline population viability analysis, and range of values used for three sensitivity analysis methods. Letters in superscript indicate the reasons for which a given vital rate was chosen for sensitivity analysis; other parameters were not varied because they did not fit the criteria used. EV stands for environmental variation, the component of variance in vital rate value due to annual variation in environmental conditions.

Parameter	Baseline value (SD)	Source	Perturbation	Conventional	Logistic Regression
<i>Reproduction</i>					
Breeding system	Long-term Monogamy	Bannor and Kiviat, 2002	N/A	N/A	N/A
Min-Max age of reproduction (years)	2-10	Clapp et al., 1982; van Rees et al., <i>in review</i>	N/A	N/A	N/A
Distribution of broods per year ^{U,M}	0 to 4 by binomial dist'n	Nagata, 1984; Gibbons, 1986; Greij, 1994; van Rees, pers. obs.	N/A	± 10% shift	N/A
Mean of brood size ^M	4.19 (1.82)	van Rees et al., <i>review</i>	1-8, by 0.5	± 10%	1-8
Sex ratio at birth	1:1	Assumed	-	-	-
Percent females breeding ^U ± EV	90 ± 10	van Rees, pers. obs.	0-100, by 10	± 10%	-
Males in breeding pool	100%	Assumed	-	-	-

Annual Mortality

Juvenile (HY) mortality \pm EV ^{U,M}	0.67 (0.15)	van Rees et al., <i>review</i>	0-1, by 0.1	\pm 10% (EV: \pm 10%)	0-1 (EV: 10-25)
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Adult mortality \pm EV ^M	0.27 (0.033)	van Rees et al., <i>review</i>	0-1, by 0.1	\pm 10% (EV: \pm 10%)	0.02 – 0.66 (EV: 0.03 – 0.2)
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Population parameters

Carrying capacity \pm EV ^M	See Table 1; \pm 10%	Waterbird surveys, van Rees, unpubl. data.	5-100 individuals, by 5	\pm 10% per population	4 - 25
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Dispersal rates ^{U, M?}	See Supp. Materials	van Rees et al. (2017)	2-100x baseline, by 5	\pm 10%	2-80
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^UVital rate was selected for sensitivity analysis because of uncertainty

^MVital rate was selected for sensitivity analysis because it can be manipulated by existing management strategies

Table 6.3: Scenarios for population viability analysis tested in our population projection model of Hawaiian gallinules on O`ahu. Restoration/creation of habitat involved hypothetical management options increasing carrying capacity at small and medium wetlands, and connectivity involved increasing overall connectivity by increasing the multiplier of baseline dispersal rates between wetlands. The two sea level rise scenarios have reduced K over time according to an equation approximating common projections of sea level rise in 80 and 160 years, respectively. Parameter change represents the amount that each parameter was altered for a given scenario. In the case of sea level rise scenarios, this value represents the maximum reduction in K experienced during the scenario, achieved at the end of the scenario (represented by L in equation 6.2).

Scenario	Parameter change	Time Frame (years)
Baseline	N/A	160
Restoration/creation	As per Table 2	160
Connectivity	As per Table 2	160
Sea Level Rise (~1m, 80 year)		80
Windward Complex	$0.94 * K^a$	
Kahuku Complex	$0.83 * K^a$	
Pearl Harbor Complex	$0.89 * K^a$	
Sea Level Rise (~2m, 160 year)		160
Windward Complex	$0.46 * K^a$	
Kahuku Complex	$0.49 * K^a$	
Turtle Bay	$0.01 * K^a$	
Pearl Harbor Complex	$0.00 * K^a$	

^aDistributed according to equation 6.2 over the total time frame.

Table 6.4: Comparison of population viability of Hawaiian gallinule overall island population and subpopulations on O`ahu across management and sea-level rise scenarios. Probability of extinction is the probability that a given (sub)population went extinct over all simulations of a scenario, and mean r is the mean stochastic growth rate of a population for the scenario. The mean ending population size is the mean number of individuals left in a population when that population was extant at the end of a simulation, and the percent of starting population at ending time is the proportion of the starting population represented by the mean ending population size.

Scenario	Probability of extinction	Mean r (SD)	Mean Ending Population Size (SD)	Percent of starting population at ending time
Baseline	0.0	0.25 (0.38)	336 (46)	97%
Windward Complex	0.0	0.24 (0.51)	171 (25)	115%
Kahuku Complex	0.0	0.23 (0.52)	96 (17)	115%
Pearl Harbor Complex	0.05	0.18 (0.51)	36 (11)	111%
Turtle Bay	0.08	0.18 (0.51)	33 (11)	109%
Waimea Valley	0.79	0.16 (0.51)	22 (10)	100%
Klipper	0.99	0.11 (0.55)	5 (5)	37%
Lotus Farm	0.99	0.09 (0.55)	6 (4)	43%
Keawawa	0.99	0.12 (0.58)	3 (1)	64%
Sea Level Rise	0.0	0.26 (0.37)	311 (35)	89%

(~1m, 80 year)

Windward Complex	0.0	0.24 (0.50)	160 (23)	107%
Kahuku Complex	0.0	0.23 (0.51)	80 (13)	95%
Pearl Harbor	0.06	0.19 (0.51)	31 (7)	96%
Complex				
Turtle Bay	0.00	0.19 (0.51)	32 (7)	106%
Waimea Valley	0.69	0.16 (0.51)	20 (7)	91%
Klipper	0.99	0.09 (0.54)	9 (7)	75%
Lotus Farm	0.99	0.07 (0.54)	5 (3)	35%
Keawawa	0.99	0.10 (0.56)	3 (2)	75%
Sea Level Rise	0.0	0.25 (0.38)	150 (18)	43%

(~2m, 160 year)

Windward Complex	0.0	0.24 (0.50)	90 (14)	60%
Kahuku Complex	0.0	0.23 (0.51)	53 (9)	63%
Pearl Harbor	0.06	0.16 (0.51)	5 (2)	16%
Complex				

Turtle Bay	0.00	0.16 (0.51)	5 (2)	17%
Waimea Valley	0.69	0.16 (0.51)	22 (10)	100%
Klipper	0.99	0.10 (0.55)	9 (7)	75%
Lotus Farm	0.99	0.09 (0.55)	3 (1)	21%
Keawawa	0.99	0.10 (0.56)	2 (0)	50%

Table 6.5: Sensitivity of probability of extinction (PE) and stochastic population growth (λ) of the overall population of Hawaiian gallinules (*Gallinula galeata sandvicensis*) on O`ahu, Hawai`i to changes in various model parameters. Population growth was most sensitive to mean juvenile mortality and mean brood size, while PE was most sensitive to mean juvenile and adult mortality, mean brood size, and variance in adult mortality.

Parameter	Sensitivity to λ	Sensitivity to PE
Mean Juvenile Mortality	-0.61	40.47
Variance in Juvenile Mortality	0.01	10.54
Mean Adult Mortality	-0.17	38.15
Variance in Adult Mortality	0.00	12.69
Dist'n of Broods per Year	0.12	-
Mean Brood Size	0.30	-30.85
Percent females breeding	0.23	-
Carrying capacity	0.02	-5.28
Dispersal rate	0.00	-3.83

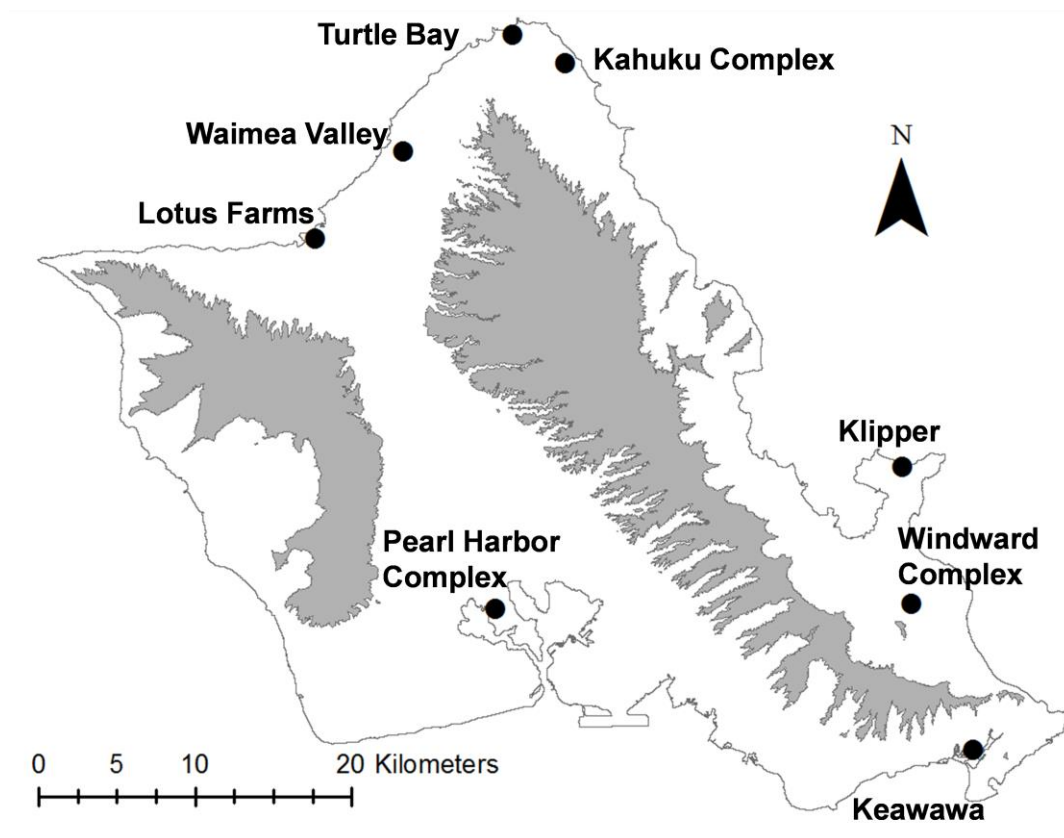


Figure 6.1: Map of O`ahu, Hawai`i, highlighting locations of modeled populations of Hawaiian gallinules. Block dots indicate the approximate centroid of wetland habitats that make up a population; some complexes represent four or more separate wetlands, which were pooled based on population genetic information from van Rees et al. (2017). Gray areas represent the Waianae (left) and Ko`olau (Right) mountain ranges.

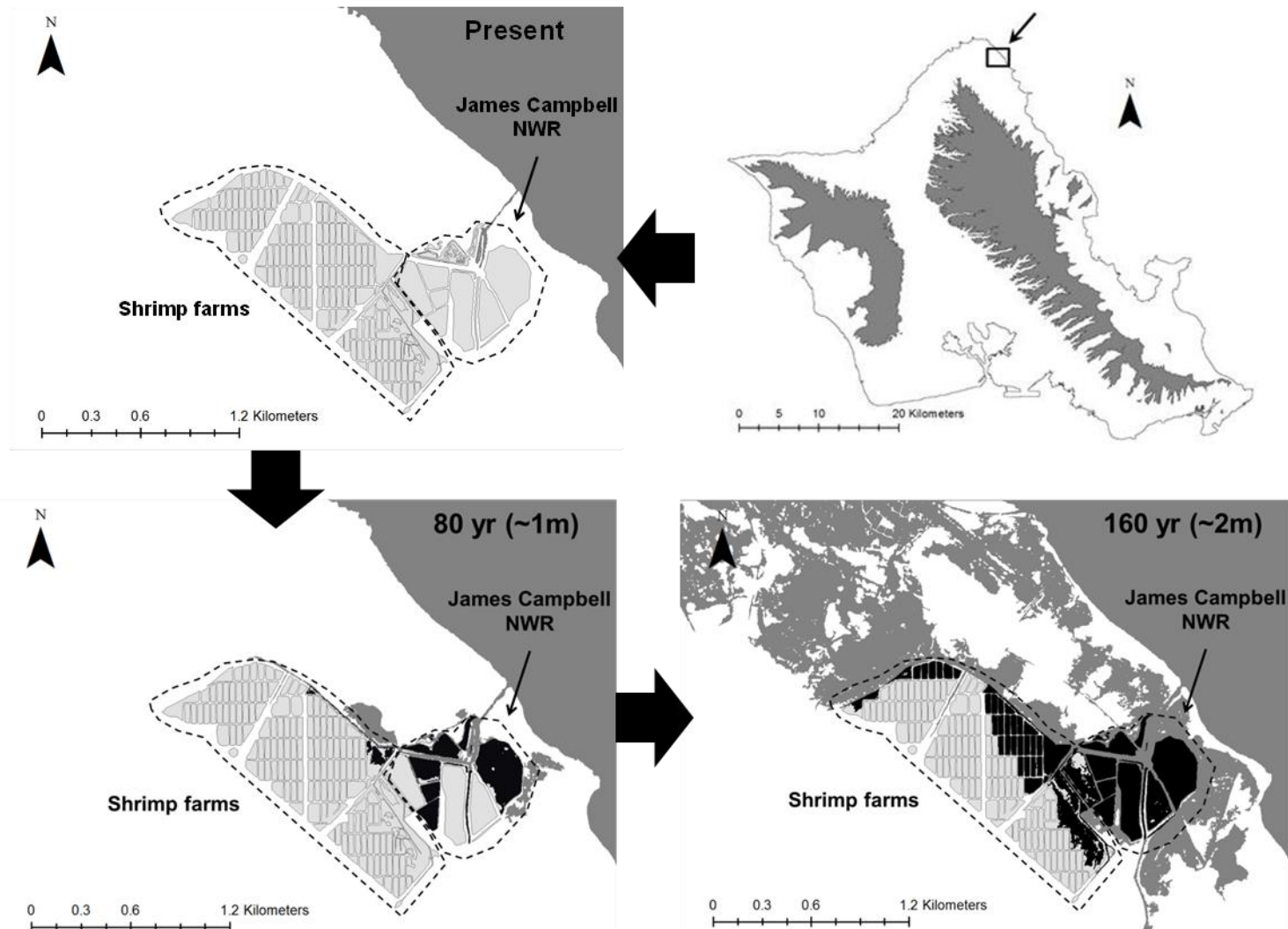


Figure 6.2: Spatial representation of potential Hawaiian gallinule habitat loss due to sea level rise over 80 and 160 year time scales at the Kahuku wetland complex on the North Shore of O`ahu. Light gray areas indicate current Hawaiian gallinule habitat, dark gray indicates seawater. Black areas indicate habitat lost due to seawater inundation. ~17% of habitat in the Kahuku complex is lost with ~1m sea level rise (modeled here as 80 years), and >50%, including the areas of highest gallinule density, may be inundated with ~2m sea level rise (modeled here as 160 years).

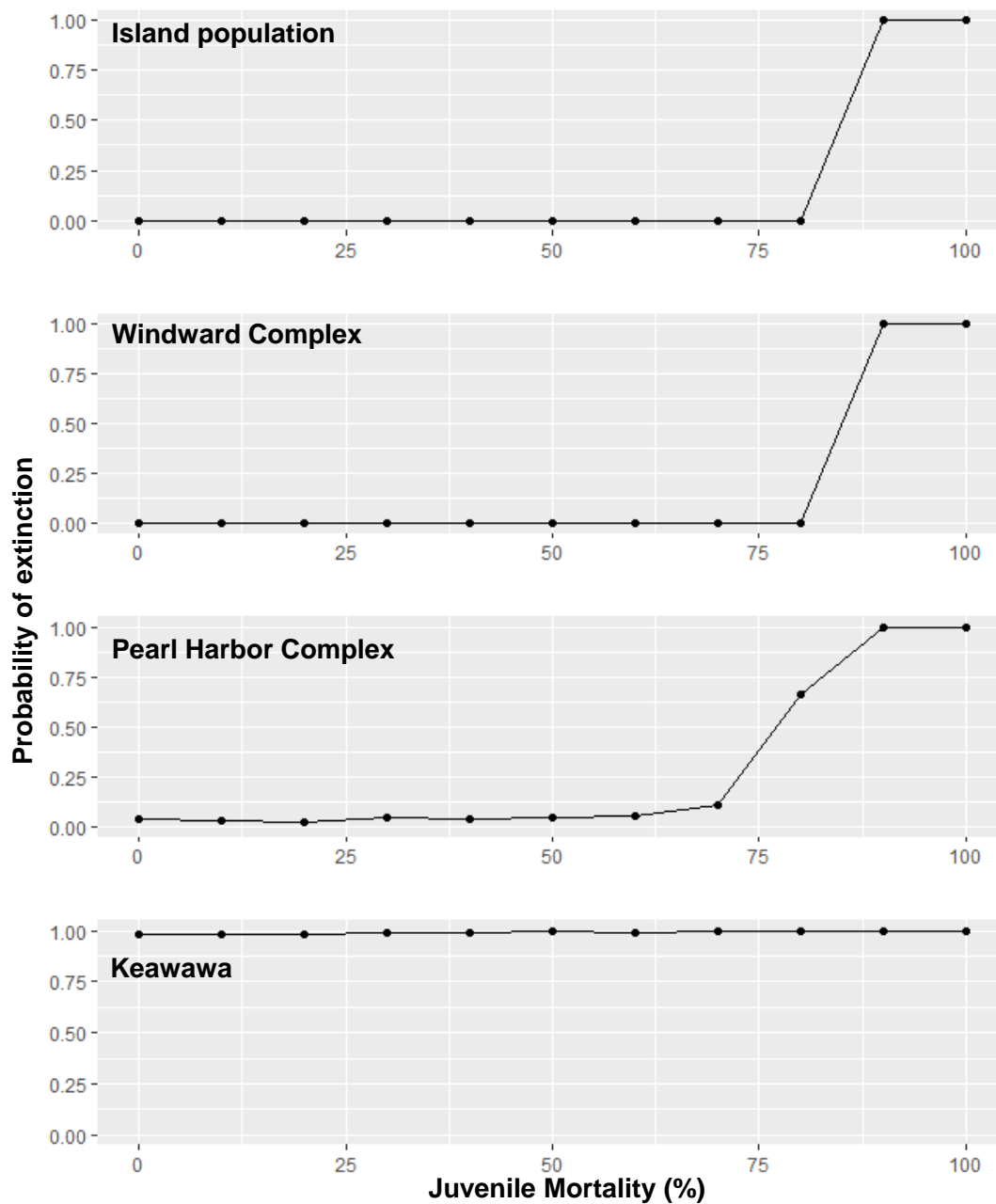


Figure 6.3: Perturbation analysis examining the sensitivity of extinction probability among Hawaiian gallinule populations on O`ahu to varying levels of juvenile mortality. Results are shown for the overall island population and three wetlands whose sensitivity is representative of other wetlands of their size class (in descending size from top to bottom).

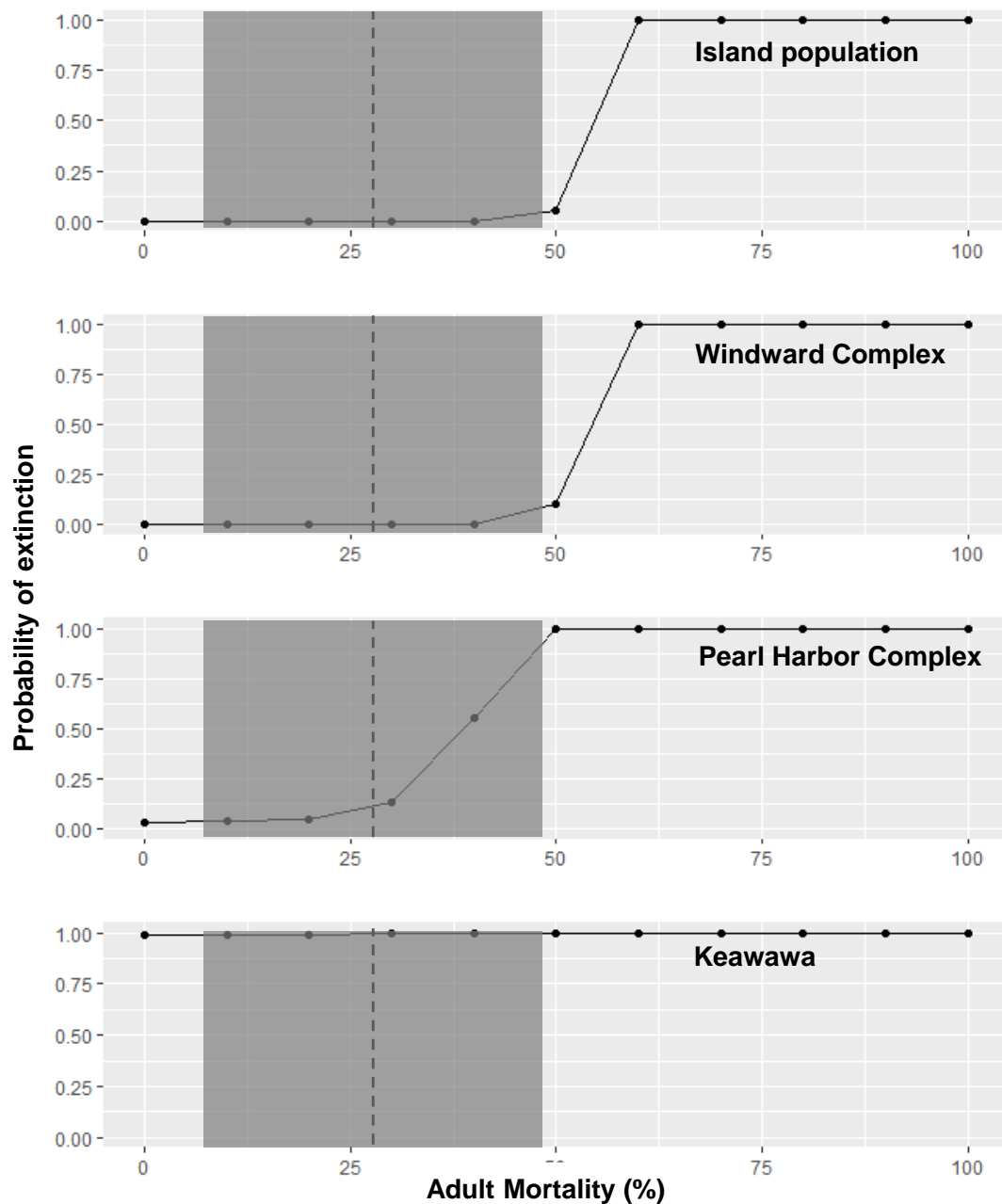


Figure 6.4: Perturbation analysis examining the sensitivity of extinction probability among Hawaiian gallinules populations on O`ahu to varying levels of adult mortality. Results are shown for the overall island population and three wetlands whose sensitivity is representative of other wetlands of their size class (in descending size from top to bottom). The dashed vertical line and shaded boxes indicate the mean survival estimate \pm SD from van Rees et al. (in review).

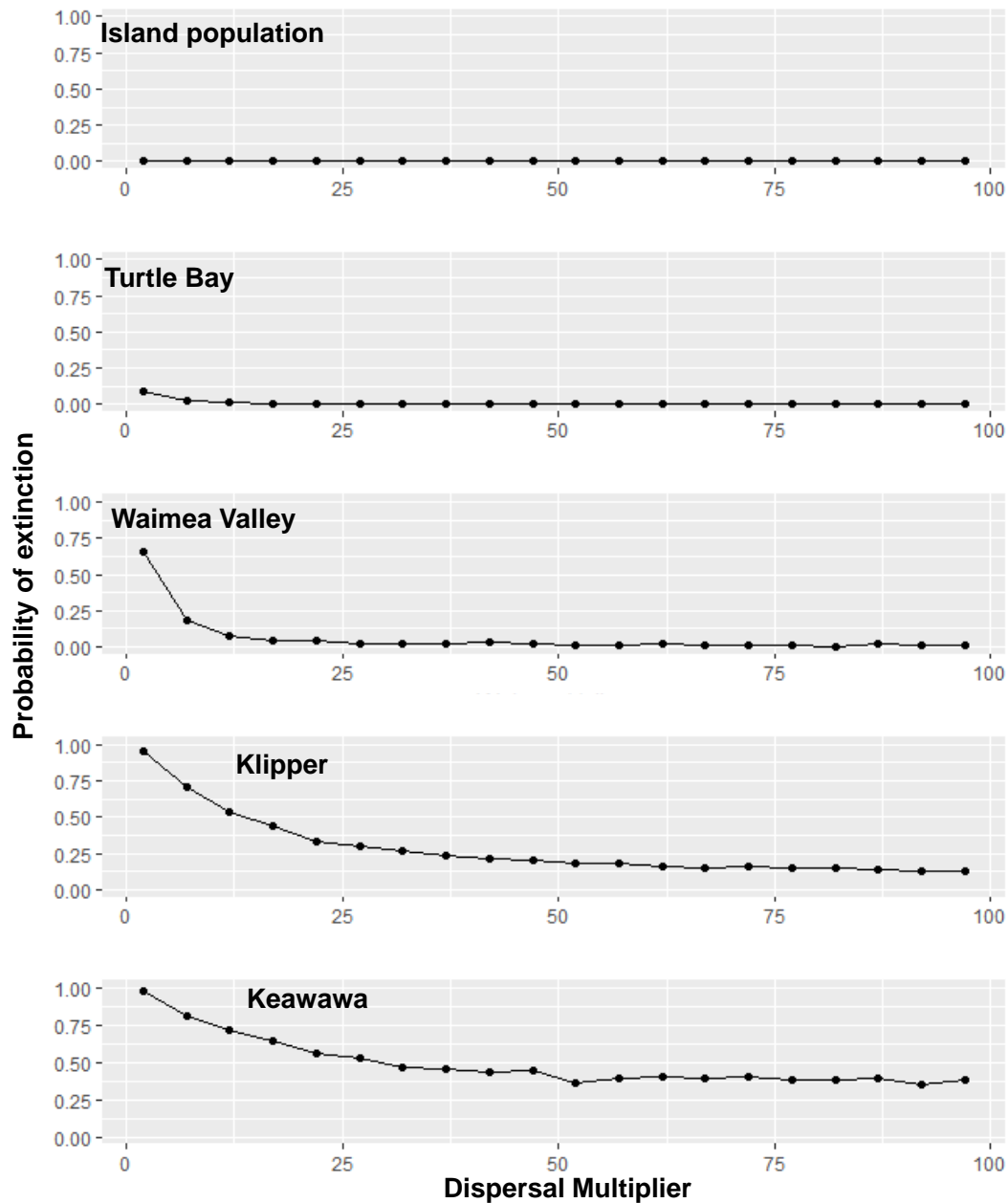


Figure 6.5: Perturbation analysis examining the sensitivity of extinction probability among Hawaiian gallinule populations on O`ahu to varying levels of inter-wetland connectivity. Dispersal Multiplier is the value by which baseline estimated movement rates among wetlands were multiplied for each scenario, simulating increases in movement from connectivity management. Results are shown for the overall island population and all wetlands that showed any changes in extinction probability across the tested connectivity values.

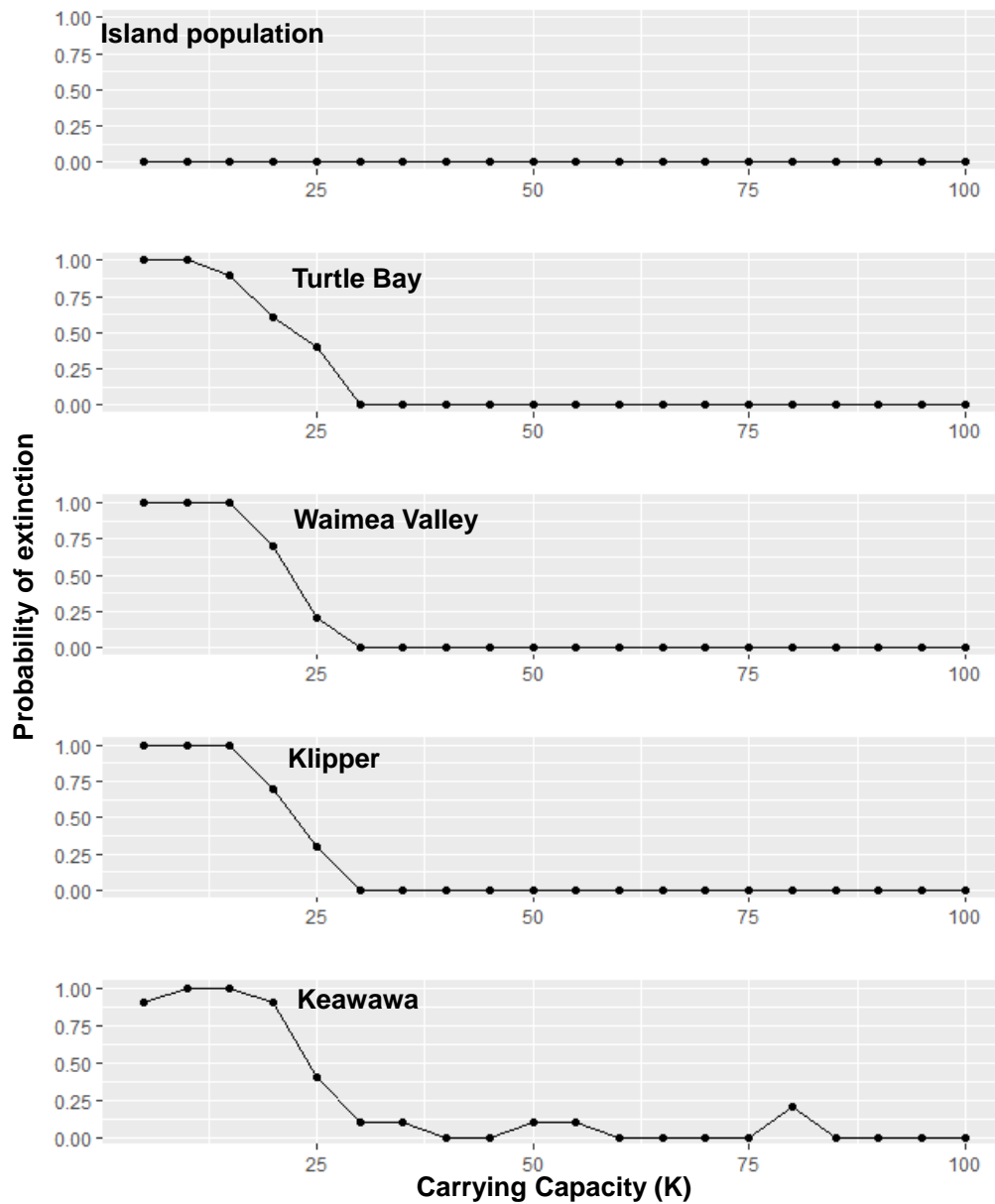


Figure 6.6: Perturbation analysis examining the sensitivity of extinction probability among Hawaiian gallinules on O`ahu to population carrying capacity (K). K values simulate hypothetical changes to carrying capacity due to habitat management. Results are shown for the overall island population and three wetlands whose sensitivity is representative of other wetlands of their size class (in descending size from top to bottom).

Supplemental Materials (Chapter 6)

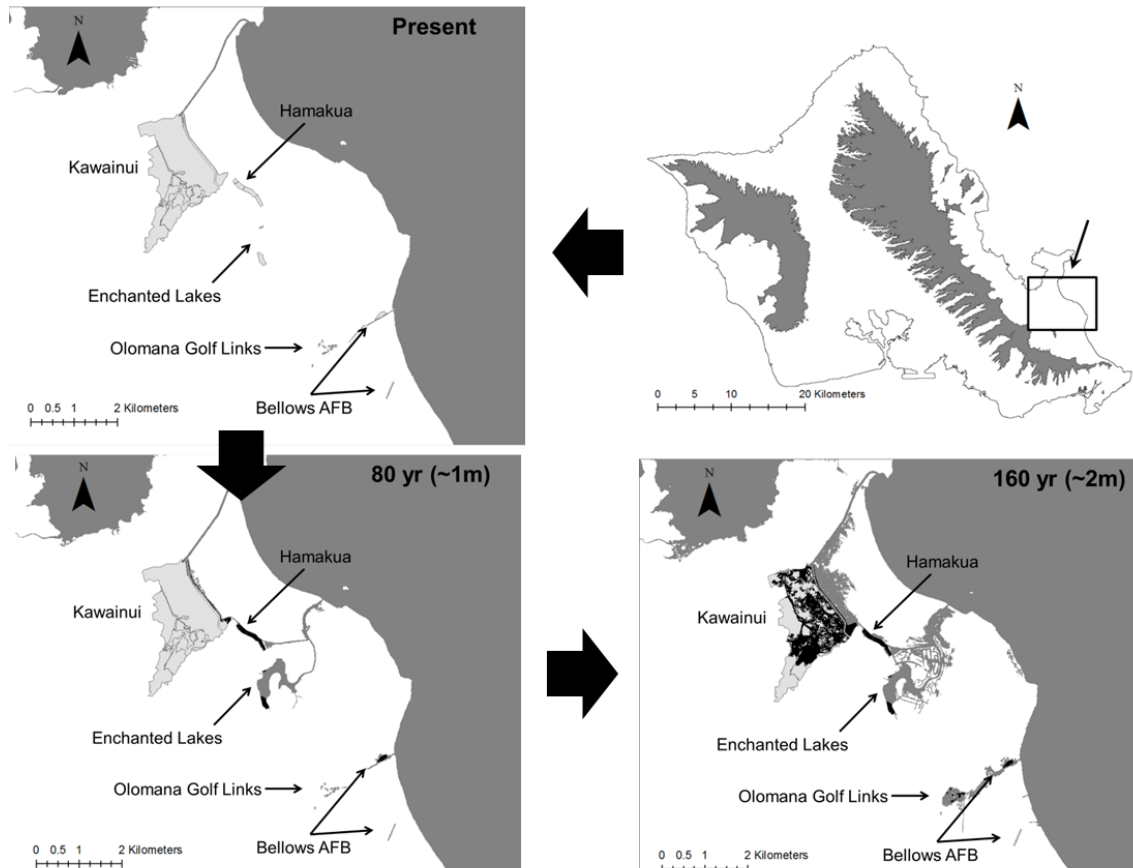


Figure 6.S1: Spatial representation of potential Hawaiian gallinule habitat loss due to sea level rise over 80 and 160 year time scales at the Windward wetland complex on O`ahu. Light gray areas indicate current Hawaiian gallinule habitat, dark gray indicates seawater. Black areas indicate habitat lost due to seawater inundation. ~6% of habitat in the Kahuku complex is lost with ~1m sea level rise (modeled here as 80 years), and >54%, under ~2m sea level rise (modeled here as 160 years).

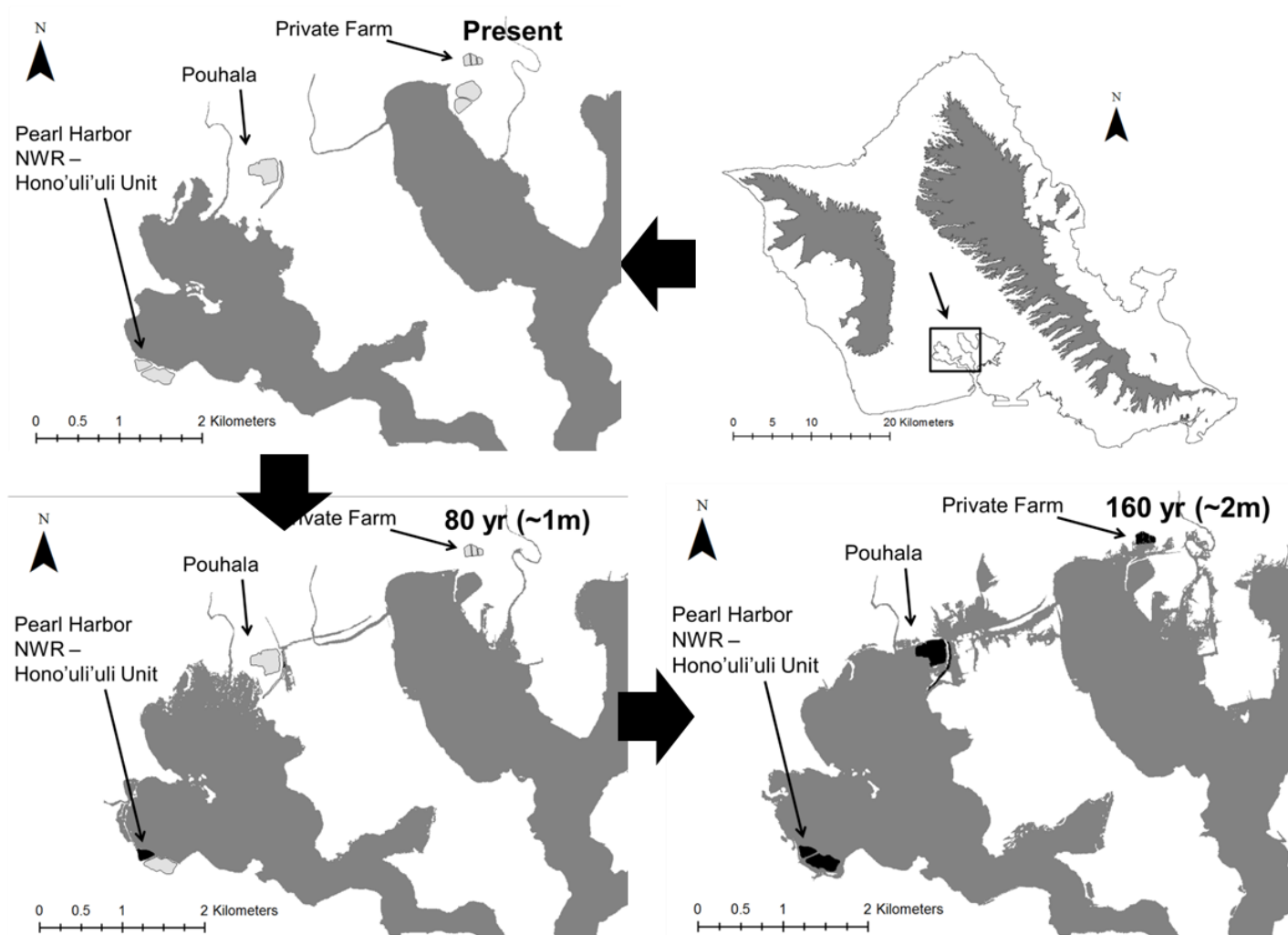


Figure 6.S2: Spatial representation of potential Hawaiian gallinule habitat loss due to sea level rise over 80 and 160 year time scales at the Pearl Harbor wetland complex on O`ahu. Light gray areas indicate current Hawaiian gallinule habitat, dark gray indicates seawater. Black areas indicate habitat lost due to seawater inundation. ~10% of habitat in the Pearl Harbor Complex is lost with ~1m sea level rise (modeled here as 80 years), and >99% under ~2m sea level rise (modeled here as 160 years).

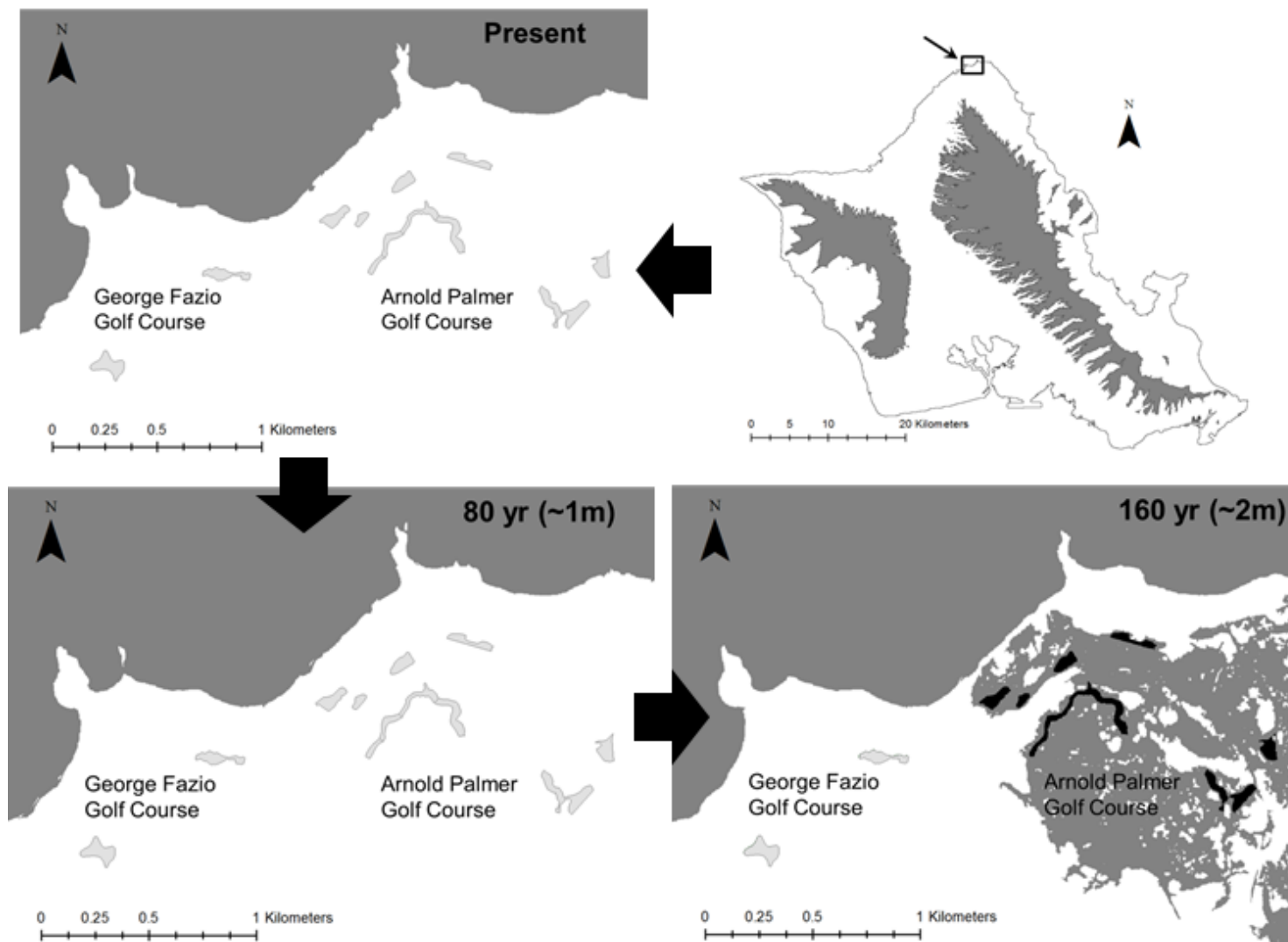


Figure 6.S3: Spatial representation of potential Hawaiian gallinule habitat loss due to sea level rise over 80 and 160 year time scales at Turtle Bay resorts on O'ahu. Light gray areas indicate current Hawaiian gallinule habitat, dark gray indicates seawater. Black areas indicate habitat lost due to seawater inundation. No habitat in Turtle Bay is lost with ~1m sea level rise (modeled here as 80 years), and >99% is lost under ~2m sea level rise (modeled here as 160 years).

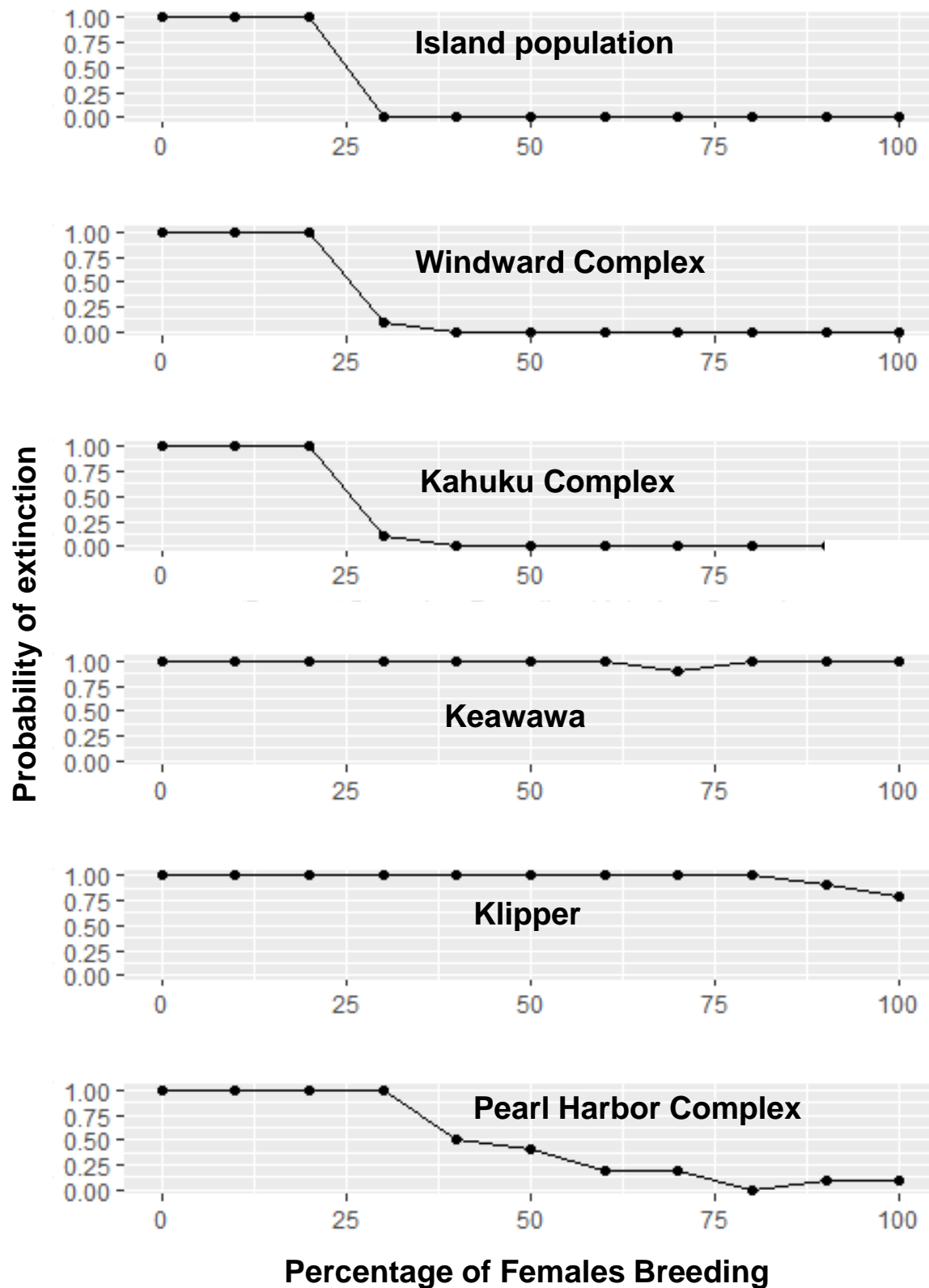


Figure 6.S4: Perturbation analysis examining the sensitivity of extinction probability among Hawaiian gallinule populations on O`ahu to varying proportions of females in the breeding pool. Results are shown for the overall population (top) and 5 subpopulations.

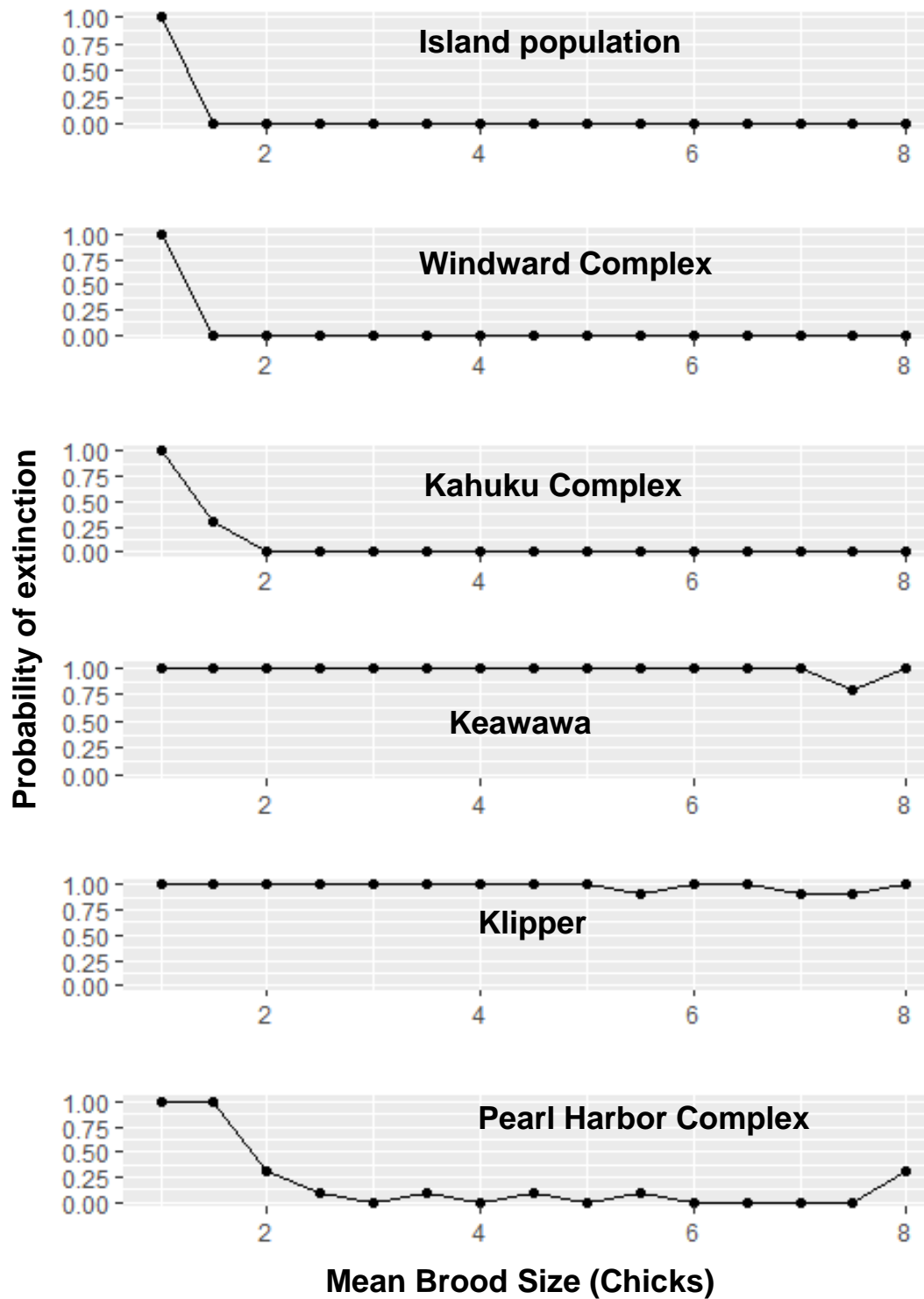


Figure 6.S5: Perturbation analysis examining the sensitivity of extinction probability among Hawaiian gallinule populations on O`ahu to mean brood size. Results are shown for the overall population (top) and 5 subpopulations.

Conclusions and Management Recommendations

7.1 This thesis in context

The Anthropocene extinction crisis is both a situation of critical urgency calling for applied study, and an opportunity to explore the dynamics of extinction, a fundamental part of the process of evolution. Due to continuing anthropogenic pressures, nearly 40% of all species assessed by the IUCN are considered under threat (Vie et al., 2009), and these pressures are only increasing through time (Butchart et al., 2010). Principal among these is land use change (Sala et al., 2000), in which humans fragment and degrade native habitats to suit their needs (Fahrig, 1997; Fischer and Lindenmayer, 2007). While there is a good understanding of the identity of these drivers of extinctions, the actual mechanisms by which these affect vital rates to cause these population changes are less often understood (Ackakaya et al., 2006; Selwood et al., 2014).

Unfortunately, it is precisely this understanding that is necessary for the type of empirically informed, evidence-based conservation (Sutherland et al., 2004) needed to effectively reverse population declines and prevent widespread biodiversity loss through strategic management (Cushman et al., 2006). Although the decline of species richness in general is a typical metric for biodiversity loss, this is driven by the extinctions of individual species, and attention and understanding of this process on a species-level scale is of paramount importance for effective conservation.

This thesis takes a species-level view of the interactions between landscape structure, movement behavior, climate change, and population viability in the Hawaiian gallinule. Focusing specifically on the gallinule has allowed me to ask questions about

how anthropogenic pressures affect the habitat, population structure, and population trends of an organism in the context of an isolated and changing island environment. My research findings contribute to a growing body of literature on the intermediate, mechanistic steps between large scale, anthropogenic environmental change and long-term population trends (Selwood et al., 2014; Hale et al., 2015; Bonte and Dahirel, 2017; Frankham et al., 2017).

7.2 Summary and merit of findings

My wetland loss analysis in Chapter 2 provided an updated and improved perspective on wetland loss in the Hawaiian Islands, a region where research on wetlands ecosystems has been limited. I used an integrated methodology combining hydric soils data, historical maps, and a simple hydrological model to estimate historical wetland distributions; this method and the manuscript in which it was published has been cited by several authors in the last few years. Importantly, this study also highlighted the issue of wetland loss on urbanizing islands, a topic of importance given the disproportionate number of threatened taxa that are island-endemics and wetland specialists (Vitousek, 1988; Edwards et al., 1994; McCullough, 1996; Ricciardi and Rasmussen, 1999), but one that has not yet been thoroughly explored. I am currently collaborating on a literature review on the topic of wetland loss on island landscapes, and the predominant driver in wetland loss appears to be urbanization (J. Rozek and C. van Rees, unpubl. data).

In Chapter 3, I used theory and techniques of population genetics to investigate the impacts of this wetland loss on the population structure of Hawaiian gallinules on O`ahu, one of only two islands upon which the subspecies persists. This analysis

contributed an interesting case study to the population genetics of birds, revealing rapid development of population structure over a short time period of population growth. The observed genetic structuring also occurred at a smaller scale than observed in most avian taxa, especially waterbirds, which are typically highly dispersive (Weller, 1999). Together, these two characteristics of O`ahu's Hawaiian gallinule population make it a powerful cautionary example of the small temporal and spatial scales over which population fragmentation can occur, even in mobile taxa. The infrequent dispersal of Hawaiian gallinules, whose mainland conspecifics are migratory and capable of frequently dispersing long distances (Bannor and Kiviat, 2002), has significant implications for the conservation of other island-dwelling waterbirds, who may have similar differences in their dispersal ability. Reduced dispersal ability is a common characteristic of island syndrome (Adler and Levins, 1994), which has been observed in a variety of taxa including mammals (Goltsman et al., 2005) and reptiles (Novosolov et al., 2013), with some evidence for birds (Prodon et al, 2002). I have been unable to find any accounts of waterbird subspecies on islands showing reduced dispersal behavior when compared to widespread continental conspecifics, so this particular contribution may be novel. If birds as mobile as gallinules can exhibit such dramatic reductions in dispersal over an ostensibly short period of time (Hawaiian gallinules are thought to have recently colonized the islands, Fleischer and McIntosh 2001), then the dispersal ability (and population connectivity) of other island waterbirds may also be of conservation concern.

Although tracking data on gallinule movements was not available in time for inclusion in this thesis, I used a landscape genetics approach to generate preliminary information on the movement behavior of Hawaiian gallinules (Chapter 4). This study is

a large contribution to scant research on the landscape influences on non-migratory movements of waterbirds in general and rallidae specifically. It is also, to my knowledge, the first landscape genetics study done on any waterbird, and a valuable addition to the current landscape genetics literature, in which birds are underrepresented (Zeller et al., 2012; Kozakiewicz et al., 2017).

My synthesis of unpublished vital rates data for the Hawaiian gallinule (Chapter 5) will be the first published report of survival rates in the Hawaiian subspecies and the most comprehensive report on their reproduction rates published to date. It highlights interesting differences between the Hawaiian subspecies and its North American conspecifics, which further illustrate shifts in vital rates between island and mainland populations within a species. These differences in vital rates (particularly clutch size) likely have consequences for population viability, and are worthy of study in other island subspecies and subpopulations. This represents another characteristic by which island populations may be at greater risk of extinction, in addition to the typically-recognized trait of persisting in small, isolated populations (MacArthur and Wilson, 1972).

The population viability model in Chapter 6 is to my knowledge the first full population viability analysis done on any rallid species, and adds quantitative evidence to a small but growing body of literature on the impacts of sea level rise on population viability and their endemic fauna (Aiello-Lammens et al., 2011; Traill et al., 2011). The source-sink dynamics between isolated subpopulations revealed by this study provide additional empirical evidence for commonly-cited theory used in the conservation of habitat specialists in fragmented landscapes (Fahrig and Merriam, 1994; Marzluff and

Ewing, 2001; Ricketts, 2001). I also use a suite of sensitivity analysis methods (also implemented by Mortensen and Reed, 2016) and demonstrate the advantages and utility of each. This work hence provides an illustrative example of a more thorough approach to the sensitivity analysis of population viability analyses which will hopefully guide future projects.

7.3 Recommendations and implications for management of the Hawaiian gallinule

This thesis also contributes to the conservation and management of the focal taxon, which is a federally listed subspecies, including the first research into its movement and population connectivity, as well as a population viability analysis. Both of these are considered research priorities for the subspecies (Bannor and Kiviat, 2002; USFWS 2011). As DesRochers (2010b) suggested, the Hawaiian gallinule is an excellent conservation case-study, not only because of the increasing amount of information readily available on its natural history, population dynamics, and physical environment, but also because of the successful avoidance of its extinction in the mid-20th century (Engilis and Pratt, 1993; Reed et al., 2011). Research on the Hawaiian gallinule is important not only to illustrate an important conservation success story, but also to learn how to “finish the job”. Continued research on the ecology and conservation of the Hawaiian gallinule will demonstrate how to ensure the long-term persistence of a taxon in the context of a changed (urbanized) environment after having averted extinction during the transition from a pre-development to a post-development landscape. As urban landcover continues to spread (McDonald et al., 2008; Seto et al., 2012; Güneralp and Seto, 2013) and natural habitats continue to be fragmented, research on this and other

taxa that are rescued from extinction but must now persist in a permanently altered landscape will become increasingly important.

My synthesis of the vital rate information of Hawaiian gallinules (Chapter 5) has simultaneously increased the accessibility of vital rates information on this taxon, facilitating future population modeling and informing management, while also highlighting areas where knowledge is deficient. This report included some of the earliest information on the movement of Hawaiian gallinules, a subject of great interest to managers on O`ahu and Kaua`i (M. Silbernagle, USFWS Ret., and K. Uyehara, USFWS, pers. comm.). Among the most uncertain vital rates of Hawaiian gallinules are juvenile survival, movement rates, and the number of breeding attempts per year. Sensitivity analysis of an individually-based population model in Chapter 6 revealed that among uncertain parameters, juvenile survival was likely the most important for overall population persistence, while movement rates were important to prevent long-term population declines due to the extinction of smaller subpopulations across time. This analysis also found that adult survival and the distribution of annual numbers of broods had nontrivial effects on persistence. Accordingly, future research on Hawaiian gallinule vital rates should focus on improving estimates of juvenile survival, the distribution of annual number of broods, and movement rates between subpopulations. Continued research on gallinule survival is also of value, and is especially feasible, given that my own banding efforts have left a banded population in excess of 150 living individuals on the island of O`ahu, which can be monitored into the future. Comparative studies of vital rates between managed and unmanaged sites, as well as sites of different sizes, will be important for more accurate population models, since the majority of currently available

vital rates data come from managed habitats only. Given that habitat quality and patch size can have large effects on vital rates (Hokit and Branch, 2003; Horn et al., 2005), differences between current gallinule subpopulations occupying vastly different environments are probably large and have considerable implications for the overall island population.

The population genetics analysis in Chapter 3 revealed the development of rapid population structure among Hawaiian gallinule subpopulations on O`ahu. Subpopulation isolation and limited between-wetland dispersal may be of conservation concern, due to the risk of inbreeding depression affecting demographic rates (Young et al., 2000; Keller & Waller, 2002), the potential for skewed sex ratios and the disruption of behavioral mating systems (Harrisson et al., 2012), and the loss of a demographic rescue effect (Brown and Kodric-Brown, 1977). Comparative research on vital rates (as discussed above) might elucidate the possibility and severity of inbreeding effects in Hawaiian gallinules, and would be feasible in small, highly isolated habitats where breeding pairs have already been genotyped and sampled (e.g., Klipper).

Population viability analysis (Chapter 6) has indicated that movement rates and a demographic rescue effect are very important to the persistence of O`ahu's smaller subpopulations, so a better understanding of the behavioral and landscape determinants of gallinule dispersal rates is needed to better assess current movement rates, their potential limitations, and options for management. My landscape genetics analysis (Chapter 4) gave strong support to the hypothesis that water features like canals and rivers facilitate inter-wetland dispersal of Hawaiian gallinules. Interestingly, the presence of roads and

urban cover, strongly thought to be limiting connectivity in this taxon, has little explanatory value for patterns of observed genetic differentiation. While this study offers the management possibility that drainage swales and other green water management infrastructure could improve connectivity between gallinule subpopulations and improve long-term population viability (described in Appendix I), validation through other means of movement-study are needed. Continued monitoring of the current cohort of banded Hawaiian gallinules will provide a good comparison with genetic data for the degree of dispersal limitation among subpopulations on O`ahu, and telemetry using automated telemetry towers (e.g., Kays et al., 2011), which has already been implemented, could make major contributions to this goal. Further population genetics analyses should use genetic markers of higher spatial and temporal resolution to overcome the potential limitations of the gene pool of gallinules on O`ahu (low genetic variability, the potential for founder effects among recolonized wetland habitats). One particularly useful study might be an examination of the population genetics of feather lice (order Phthiraptera) among gallinule subpopulations. Research has shown that genetic distance patterns in dispersal-limited parasites are parallel to their hosts (Riley et al., 2006; Liu et al., 2008), and can potentially reveal more than analysis on host genetics, due to their faster generation time and typically higher abundance (Nieberding and Olivieri 2006; Whiteman et al., 2007). I have repeatedly observed philaptherid lice on gallinules during handling, and note that several wetlands on O`ahu have such a small number of breeding gallinules that sample sizes are prohibitive to population genetic analysis (e.g., Keawawa). Accordingly, population genetics on gallinule ectoparasites might be an excellent way to gain a better understanding of population structuring on O`ahu without

the continued expense and difficulty of telemetry research. Unfortunately, although I tried to begin this project myself, I was unable to obtain U.S. Fish and Wildlife permits in time for my final field season, due to delays caused by legislations from the new presidential administration.

I joined a project started by USGS-PIERC (Pacific Island Ecosystems Research Center) researchers attempting to track waterbird movement rates between wetlands on O`ahu using automated telemetry systems. My colleagues and I outfitted >30 Hawaiian gallinules with coded radio nanotags which were tracked by between 4 and 10 automated telemetry receiving towers over the last two years, but these data are still forthcoming; their analysis may make additional contributions to current knowledge of gallinule movement rates, especially with regard to non-breeding or temporary movements. Validation of the findings of my landscape genetics analysis (Chapter 4) will require, in addition to inter-wetland movement rates, data on the pathways taken when moving between subpopulations. Collaborating with USFWS researchers in 2014-15, I outfitted several Hawaiian gallinules with two different types of GPS dataloggers, but due to the gallinule's small size (relative to the types of animals typically tracked with dataloggers, primarily large mammals) and associated restrictions on datalogger size, the costs of tags were prohibitive to large sample sizes. Additionally, the gallinule's tendency to spend most of their time concealed in dense vegetation led to poor-quality spatial fixes, which could not provide specific information on the gallinule's whereabouts or travel paths beyond confirming that they were still on the island of O`ahu. As the technology for GPS dataloggers continues to improve, especially in terms of longer battery life, greater

storage capacity, higher-resolution locational fixes, and lower costs, this future study will become increasingly feasible and no less important.

My population viability analysis chapter (Chapter 6) provided preliminary evidence that the largest and most important gallinule subpopulations on O`ahu may face significant reductions in carrying capacity due to sea level rise in the next 100-200 years. Although I chose a conservative sea level rise estimate for the 160-year (40 gallinule generation), approximately 1.8m, this scenario is considered feasible within a 100 year time frame (Vermeer and Rahmstorf, 2009) in less conservative analyses and represents a realistic threat. Among those subpopulations most threatened by sea level rise were the three largest on the island, which combined support an estimated 76% of the island's total carrying capacity. Within these subpopulations, the areas with the highest densities of Hawaiian gallinules and largest per-wetland population estimates (James Campbell National Wildlife Refuge and Hamakua marsh) are the parts likely to be inundated first (i.e., at even lower levels of sea level rise). Notably, however, my analysis was superficial, using simple models to estimate changes in coastline which assumed a static landscape with no changes in human infrastructure or inland wetland migration through accretion. The dynamics of coastal change under sea level rise, especially with regard to wetland habitats, are highly complex and require computationally expensive models parameterized with high-resolution spatial data to account for additional factors like groundwater dynamics, storm surge, and wave action (Titus, 1988; Nicholls et al., 1999; Kirwan and Megonigal, 2013; Kane et al., 2015). More thorough simulation of sea level rise dynamics on O`ahu using models like the Sea Level Affecting Marshes Model (SLAMM; Park et al., 1986) will be necessary to gain a more informed understanding of

the potential threat of sea level rise to Hawaiian gallinule populations. To my knowledge, however, the inclusion of these additional dynamics may only result in more dramatic predictions of habitat loss, because groundwater changes and storm surge will only increase the salinity of near-shore freshwater wetlands, lowering their habitat quality to Hawaiian gallinules (which are not found in more saline waters) beyond the spatial extent of projected inundation.

This climate change analysis, combined with my updated estimate of wetland loss for the state of Hawai`i (Chapter 2) has helped to clarify the past, present and future distribution and threats of wetland ecosystems on O`ahu. In my experience, wetland ecosystems are a highly under-recognized feature of Hawai`i's natural history and ecology, which are typically unknown or disliked by the general public and sought out only by researchers. Although the hydrology of Hawaiian streams and wet forests is being extensively studied (A. Strauch, Hawaii Commission on Water Resources Management, pers. comm.; e.g., Sutherland, 2000; McIntosh et al., 2002; Sahoo et al., 2006), the hydrology of many of the state's palustrine wetlands is apparently poorly understood. I have been unable to find published research on the hydrological functions of these wetlands or any estimate or quantification of their ecosystem services, but given their coastal location and the hydrological challenges faced by Hawai`i in general and O`ahu in particular (reviewed in Appendix I, section A1.4), these are likely to be substantial. Better models of the past and future distribution of Hawaiian wetlands, improving upon the limited technical knowledge and resources with which I undertook my own analyses, will be greatly valuable for wetland conservation on Hawai`i and on other oceanic islands. Information on the hydrological and ecological functions of these

wetlands, and how they are tied to particular wetland characteristics, is an equally important task for understanding the present value of wetlands and how this might be impacted in the future.

From an applied perspective, the conservation of wetland ecosystems on O`ahu will likely not be achieved without public and political support, which, based on my discussions with directors of local conservation non-profits and government agencies as well as members of the general public on O`ahu, is at present is minimal at best. DesRochers (2010b) noted that the Hawaiian gallinule, an important figure in Hawaiian mythology (Thrum and Forbes, 1879; Henshaw, 1902; Westervelt, 1910) is an excellent flagship species for wetland conservation on O`ahu because of its cultural importance, the power of native Hawaiian culture to influence public opinion in Hawai`i, and its specialization on wetlands and sensitivity to small changes in habitat quality. During my time on O`ahu, I have taken this possibility seriously, and sought to cultivate this flagship status by working closely with conservation non-profits and other partners on the island to improve outreach around Hawaiian gallinule ecology and wetland ecosystem services. This work has culminated recently in a \$25,000 grant and offer of continuing support from the Disney Conservation Fund, that I secured with the help of non-profit partners. The U.S. Fish and Wildlife Service has expressed interest in providing additional funding to support continued outreach in coming years. In addition to several interviews on public television, I have given outreach talks and seminars at urban wetlands on O`ahu to audiences of diverse age and educational background. On February 3, 2018, my collaborators and I have organized a World Wetlands Day celebration (Figure 7.1), that includes 11 partners from the state and federal government, non-profit organizations, and

even a local restaurant. Plans for the event include educational workshops and talks on endangered waterbird ecology, wetland ecosystem services, and the importance of citizen science in continued research on Hawaiian wetlands and waterbirds. Interest in wetland conservation is already growing, with the recent establishment of Hawaii's state office of climate resilience, who will be participating in our World Wetlands Day event. With increasing public and political recognition, wetland conservation in Hawai'i will have the capacity to contribute dramatically to the protection of endangered Hawaiian waterbirds and other threatened wetland taxa (e.g. two damselfly species, *Megalagrion nesiotes* and *M. pacificum*), and potentially to the future sustainability and climate security of the Hawaiian archipelago.

World Wetlands Day

Urban wetlands making cities liveable

February 3, 2018

9:00 a.m. – 1:00 p.m.

(Saturday) Free Public Event

Wetlands for a Sustainable Urban Future



Livable Hawaii Kai Hui



the Oahu Club

"Wetlands for Sustainable Urban Future" is the theme for 2018 World Wetlands Day.

Livable Hawaii Kai Hui with Conservation Council for Hawaii'i, US Fish & Wildlife Service, Pacific Islands, Hawaii Audubon Society and partners invite the public to participate in raising global awareness about the value of wetlands for society by offering a day of cultural and natural resources activities on the grounds of a unique East Oahu cultural heritage preserve.

A COMMUNITY DRIVEN, VOLUNTEER-BASED RESTORATION PROJECT.

Hāwea Heiau Complex & Keawāwā Wetland

CELEBRATE THE CULTURAL AND NATURAL RESOURCES OF YOUR COMMUNITY!

A Day of FREE Activities for the Whole Family

Keiki crafts and games * Hula * 'Alae'ula (Hawaiian moorhen) bird watching * Outreach education activities for other Oahu wetlands * Planting native Maunaloa grown plants * Tours of Hāwea heiau and Keawāwā wetland * Maunaloa talk story * Sustainability information tables * Guest speakers * Prizes Giveaways and more.

Location: 6888 Hawaii Kai Drive, Honolulu 96825 and neighboring property, The Oahu Club.
E-mail: KeawawaWetland@aol.com **PH:** 864-8081



#KeepUrbanWetlands
#WorldWetlandsDay
www.worldwetlandsday.org

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I.C.L.E.I
Local Governments
for Sustainability



World Wetlands Day
2 February 2018
Wetlands for a sustainable urban future



World Wetlands Day
is made possible by the
Danone Fund for Water.



Figure 7.1: Flier for the 2018 World Wetlands Day wetland conservation and education event at Keawawa Wetland, Honolulu, Hawai'i. Continued outreach and education on the unique wildlife, value and functions of wetland ecosystems in Hawai'i are necessary to build the political will to overcome current inertia and protect these threatened ecosystems for societal benefit.

Appendix I

Water Diplomacy from a Duck's Perspective: Wildlife as Stakeholders in Water Management

Charles van Rees and J. Michael Reed

A manuscript version of this appendix was published in the *Journal of Contemporary Water Research and Education* in 2015.

Abstract

Contemporary water management strategies call for the inclusion of ecological research in the decision-making process and emphasize environmentally sustainable management solutions. Most ecological information used in water management shares two problematic characteristics; 1) simplistic, phenomenological approaches and aggregated data that may not properly describe system behavior, and 2) a “zero-sum” perspective treating ecological water needs as constraints to management. We argue that the newly devised Water Diplomacy Framework (WDF) can help overcome these shortcomings. We also provide a simple and intuitive method for integrating ecological factors into the WDF. We suggest that treating ecological phenomena as “surrogate stakeholders” in water negotiations increases opportunities for discovering mutual-gains solutions and encourages a hypothesis-based approach to research on the ecology of water management. By differentiating between the “positions” and “interests” of ecological stakeholder surrogates, decision-makers can make greater use of the potential added value of ecosystem services in water management and avoid costly misunderstandings of the behavior of relevant ecological systems. We outline how the WDF can be applied to better integrate ecological factors into water management, and

show how our approach could create synergies between endangered waterbird conservation and sustainable water management on the island of Oahu, Hawaii.

A1.1 Introduction

Water management problems in the new millennium increasingly involve multiple stakeholders with competing interests, managing shared and limited water resources under a high degree of technical and scientific uncertainty (Molle et al. 2008; Wagener et al. 2010; Islam and Susskind 2013). Interdisciplinary approaches are essential to create sustainable and effective solutions for this new generation of complex water problems. Frameworks like Integrated Water Resources Management (IWRM) encourage integration of knowledge across fields like water resources engineering, economics, and political science to generate effective solutions to modern water resources problems (Al Radif 1999; GWP 2000; Biswas 2004; Molle et al. 2008). For the last 25 years, increasing global awareness of the importance of ecosystems and biodiversity for human well-being (ICWE 1992; Millennium Ecosystem Assessment 2005; Duffy 2009; Hough 2014) has prompted the developers of leading water management strategies to incorporate ecological factors into the decision-making process (Tharme 2003; Arthington 2012; Liu et al. 2013). We define ecological factors as any ecological phenomenon (e.g., a species, population, habitat, ecosystem function, ecosystem structure, etc.) that is of interest for water management. It is now widely acknowledged that ecological factors are important to consider in water management, because they are influenced strongly by management action (e.g., Kingsford and Johnson 1998), and can greatly affect management outcomes by affecting the provision of ecosystem services (Postel and Carpenter 1997; IUCN 2000; Richter et al. 2003; Poff et al. 2003). The growing impetus to include ecological factors in water management is made especially clear by their explicit inclusion in the core principles of IWRM

(ecological sustainability, GWP, 2000).

Recognition of the need to include ecosystems in water management decision-making motivated the creation of theoretical frameworks capable of internalizing ecological factors into the water management equation. Such frameworks include natural or environmental flows (Poff et al. 1997; Tharme 2003; Arthington 2012) and environmental water (Beesley et al. 2014), ecosystem services valuation (Postel and Carpenter 1997; Brauman et al. 2007), and blue and green water (Falkenmark and Rockstrom 2004, 2006). Including ecological factors advances the water management process by forming the conceptual nexus between the alteration of natural water regimes, the resulting degradation of ecosystems, and the potential negative effects of such degradation on human populations and stakeholders. In practice, however, most contemporary approaches to ecologically informed water management share two characteristics that we view as problematic:

Problem 1) Ecological factors used in water management research most often consist of coarse-scale ecological data (e.g., species richness), that are spatially aggregated, or they describe the behavior (response) of only one taxon or guild in an ecosystem, and thus may not adequately characterize the dynamics of the ecosystem.

Problem 2) Ecological factors are typically presented or integrated into decision-making in the form of constraints on water management solutions, resulting in a focus on trade-offs and allocation of water exclusively for ecosystems.

Problem 1 arises when data are collected at large ecological or spatial scales in order to summarize the characteristics of the ecological systems affected by water management decisions, such as when the condition of a river is measured by the number

of fish species within it (e.g., Cui et al. 2010). Such data are often used because they are relatively easy to collect and interpret, and they operate on scales similar to the hydrological models developed by engineers for comparing management strategies (Mollinga et al. 2006; Xenopoulos and Lodge 2006). Thus, these data are a convenient way to integrate ecological factors into management via hydrological models. Basing decisions of scale and resolution of ecological data on convenience increases the probability of mischaracterizing the behavior of the ecological system in question and missing important system dynamics that may have profound effects on management outcomes. For example, using the abundance of a single fish species as an indicator of ecological health and basing minimum flows for a river on that information might fail to detect shifts in community structure that occur independently of the abundance of the indicator species. Some animal species will shift their diets or feeding habits in different environmental contexts, thus having different impacts on other species in the system (e.g. Kushlan 1986); others cannot make such shifts, and are thus especially sensitive to hydrological alteration (Rubega and Inouye 1994). For example, Balcombe et al. (2005) found that some fish species in a floodplain river in Queensland, Australia dramatically changed their diets depending on river flow (flooding vs. non-flooding). Failure to detect such shifts in community structure might lead to unanticipated management outcomes, for example trophic cascades that affect ecosystem processes like primary productivity and nutrient retention (Brett and Goldman 1996; Baxter et al. 2004). Although this problem is of interest and will be touched upon in this paper, we are more interested in Problem 2, and will save a more in-depth analysis of Problem 1 for a later publication.

Problem 2 is driven by the process by which water management decisions are

made, and the point at which ecological information is used in that process. Generally, ecological information is used later in the decision-making process, after management strategies have been decided upon, and it is used to place limits on operations or present ecosystem trade-offs that must be weighed (Mollinga et al. 2006; e.g., Chisolm 2010; Sanon et al. 2012; Willaarts et al. 2012). In the case of water diversions for agricultural irrigation, for example, the infrastructure for irrigation will already have been decided upon, but the needs of riparian ecosystems for in-stream flow are considered post-hoc as a means of constraining withdrawals and ensure a minimum in-stream flow to support ecosystems (Richter et al. 2003; Mollinga et al. 2006). While this is one way to ensure that enough water is provided for specific ecological systems, such hard and fast rules fail to convey *why* constraints like minimum flows are set, and what role the allotted minimum flow plays in the affected ecosystem. There is little room for leeway or more creative solutions, particularly when water is scarce; furthermore, the “constraints”, or zero-sum mindset can create negative public attitudes toward environmental water needs (Moore et al. 1996; Votteler 1998; Wallace et al. 2003). Zero-sum thinking can also become a self-fulfilling prophecy, whereby decision-makers ultimately create management that results in situations where benefits to stakeholders are mutually exclusive (Islam and Susskind 2013). For example, water management of the Danube River in Europe led to two failed management plans, the first favoring economic gain at the expense of ecological integrity, and the second favoring ecological restoration over economic development (Islam and Susskind 2013).

It should be noted that both problems 1 and 2 are natural results of the complexity and urgency of the water management issues faced by decision-makers; decisions are

often made with limited monetary resources and time, leading to simplification of ecological metrics, and constraints are used as a precautionary measure to avoid unacceptable losses that might occur from misunderstanding ecological dynamics. This simplification of both options and data are considered necessary steps to include ecological factors in management when decision-makers may have poor understanding of ecological dynamics (Schiller et al. 2001). We do not question that decisions must be made under uncertainty—this is nearly a defining characteristic of modern water management—but we do not want water managers to limit themselves to low quality information and hard constraints when available knowledge may offer better solutions. Improved frameworks for integrating ecological information into water management should thus contribute to overcoming these problems while also making ecological data more accessible to decision-makers.

Water Diplomacy is an emerging water management framework that operates from a negotiations-based approach to decision-making in the context of complex water problems (Islam and Susskind 2013). Several of its core principles provide potential solutions to the problems outlined above, and we assert that methods integrating ecological factors into the Water Diplomacy Framework (WDF) can lead to improved solutions in water management. Currently, the WDF has no formal protocol to integrate ecological information. In this paper, we propose that ecological factors, especially focal species, can be easily integrated into the WDF when treated as “surrogate stakeholders”; that is, when such variables are treated in a functionally similar manner to actual stakeholders in the negotiations process of Water Diplomacy. We suggest that considering ecological factors early in water allocation decision-making, and treating

water allocation as a non-zero sum game (i.e., allowing for mutual gains), expands options for creating sustainable management solutions. Ecological factors like focal species (those of economic, cultural, ecological, or conservation importance), entire ecosystems, and indices of ecological integrity (e.g. Karr 1991; DePhilip and Moberg 2010; Clapcott et al. 2012) can act as surrogate stakeholders. We support this surrogate stakeholder approach for the sake of practicality, and not with any normative intention of asserting that species, ecosystems, or other natural phenomena are capable of having interests or have their own ethical standing; such philosophical questions are outside the scope of this paper. We do suggest, however, that this method makes complex ecological information more readily attainable to decision-makers and expands its possible use in creating feasible management solutions. We describe this approach below and illustrate how it expands management options in the case of water management on the island of O`ahu, Hawai`i (USA).

A1.2 Advantages of the Water Diplomacy Framework (WDF)

The core tenets of the WDF include I) the use of network and complexity theory to define the scale of analysis and boundaries of the water management problem; II) an emphasis on “actionable” knowledge—that which is easily grasped by stakeholders and answers research questions crucial to decision-making—and applied research; III) treatment of water as a “flexible resource”, acknowledging the potential importance of water throughout the hydrological cycle and the role of order of use in maximizing benefits to stakeholders; and IV) using a negotiations approach based in mutual gains (Susskind and Islam 2012; Islam and Susskind 2013).

Tenet IV is perhaps the most novel for water use negotiation and it is the most

important of the concepts for overcoming Problems 1 & 2 identified above. The negotiations framework convenes stakeholders with potentially competing interests and uses mutual gains negotiations to create and highlight solutions that benefit the interests of all stakeholders (Islam and Susskind 2013). Mutual gains negotiations avoid zero-sum thinking and shift the dynamics of stakeholder interaction from competition to value creation, such that stakeholders can find mutually beneficial outcomes without sacrificing their self-interest (Fisher and Ury 1991; Susskind 2008). A chief goal of mutual gains is disabusing stakeholders of the notion that their interests can only be met at the expense of other stakeholders (Fisher and Ury 1991; Islam and Susskind 2013). Mutual gains or non-zero sum thinking is viewed by some as the best approach to overcoming water management issues, especially in the case of transboundary water resources (Islam and Susskind 2013; Dema 2014). As an ecologically-relevant example, a zero-sum view is that water can either remain in a wetland to support fishing or can be diverted for agricultural irrigation; a non-zero sum view recognizes that rainfall can be captured in a wetland for use by fish, and then infiltrate into groundwater for subsequent human uses (e.g. Musu 2001; cf. Dema, 2014).

Mutual gains negotiation differentiates between the *positions* and *interests* of stakeholders with respect to the shared resource—this allows stakeholders to view one another not as constraints but as entities with flexible needs resulting from a particular set of values. Interests are the direct product of a stakeholder's values, defining what they actually need to get out of the negotiations process; this might be sufficient water to support agriculture, or the need for a diplomatic official to maintain face and protect the reputation of his or her constituents (Fisher and Ury 1991; Islam and Susskind 2013).

Interests are the needs and values that motivate *positions*, the spoken, manifest demands or perspectives presented by a stakeholder during negotiations over the management of a shared resource. Positions might include an unwillingness to allow dam releases at certain times of year, or a request that a specific amount of water be set aside for irrigation (Fisher and Ury 1991; Islam and Susskind 2013). Interests, by contrast are tacit, often hidden, and ultimately less flexible—for example, it might be culturally or politically unacceptable to force farmers to abandon their lifestyles simply due to water demands—the positions that arise from these interests are often much more negotiable. If irrigation releases cannot be increased to match the position of rural farmers, the underlying interests of that position—that of making greater profit from the management of their land, and maintaining their livelihoods and lifestyles—might be satisfied by subsidizing transitions to more profitable crops with lower water demand, higher-efficiency watering equipment, or alternate forms of income through farmland management (e.g. ecotourism; Pooler 2013). These could sustain income—satisfying basic interests—while altering the farmers’ position. Creative alternatives can satisfy the interests of a stakeholder while circumventing the problematic aspects of their original position; in this case, a demand for water diversions that might be untenable considering the rest of the system. This process of meeting interests—rather than positions—by providing benefits from sources originally external to the system is called “adding value” (Islam and Susskind 2013). Applying this framework to ecological systems would enable decision makers to treat ecological factors as potential opportunities for added value among stakeholders and not as constraints on available options (Problem 2).

Tenets I and III relate most strongly to the beginning stages of the WDF

workflow, particularly in the process of convening stakeholders, defining the boundaries of the water resources problem, and exploring potential solutions (Islam and Susskind 2013). Using a network or systems approach (Tenet I) emphasizes functional linkages, be they ecological, economic, political, or social, between various stakeholder groups. Linkages might include economic benefits of water purification provided by a riparian wetland to a downstream city, the cultural importance of a fish migration to a First Nations people, or the exchange of virtual water between two countries through agricultural commerce (Allan 1998). The network approach can thus be used to model and internalize interest groups that might normally be overlooked or managed separately—such as endangered or economically important species. Understanding the relationships between stakeholders also helps recognize the broader boundaries of the water problem. While most traditional engineering approaches to water management delineate the watershed as the boundary of any water management problem, the effects of water management can be felt far beyond watershed boundaries. As an example, if pollution in a coastal city affects its fishing yields, neighboring states are affected even if they are not using that water but are sharing the economic burden through trade. This expanded view of the problem's boundaries identified through non-hydrological variables is known as the “problemshed”. Ecological problemsheds might be limited to the watershed, or can extend far beyond it. Many waterbird species cross continents in annual migrations, passing through many watersheds, effectively linking the impacts of management within each of those areas (Bauer and Hoyer 2014). Migratory birds have become a key driver in encouraging transboundary cooperation throughout the world, including U.S.A-Canada (Dorsey 1998), Israel-Palestine (Leshem et al. 2003), and

U.S.A-Cuba (Boom 2012).

Expanding viewpoints to the problemshed level seems at first overwhelming and counter-productive, as though it might add too many constraints to the system. However, as part of the WDF, framing the problemshed and acknowledging the complex interactions of various system components in a network actually aids the process of adding value by increasing the pool of potential interests that can be aligned and satisfied.

Once the problemshed has been identified, Tenet III becomes important in designing integrated management solutions by expanding the ways in which water is viewed and valued within the system. Water is most often viewed as a finite resource—particularly as a sum of fresh surface or groundwater to be divided amongst interested parties. However, water has many other values and functions in ecosystems and economies that are often unacknowledged. Taking a narrower view reduces opportunities for mechanistic understanding of system behavior and for adding value in mutual gains negotiations. Following Tenet III, researchers should pay attention to the role that water plays in stakeholder interests throughout the hydrological cycle, and not focus only on, for example, water provision as its sole function. For instance, evaporating water from irrigation can influence regional meteorology, changing rainfall patterns in nearby but separate watersheds (Lo and Famiglietti 2013). Water is also a highly effective transporter of nutrients, sediments, salt, and other chemical agents that may be beneficial or detrimental to human or natural systems, and failure to recognize this function can have severe consequences (e.g., Harris 1991; Schepers et al. 1991; Jaeger et al. 1999). For example, many wetland ecosystems provide under-recognized hydrological benefits to adjacent human settlements in the form of meteorological “oasis effects” (Polcher et al.

2008) and by recharging groundwater (e.g., van der Kamp and Hayashi 1998).

Employing Tenet III further enlarges the problemshed created by Tenet I, leading to a more holistic understanding of the system being managed and the impacts of potential management actions. Ultimately, these two tenets internalize stakeholders and processes that were formerly treated as external to water management problems, and could help to resolve Problem 2 (treating target species and ecosystem water needs as constraints), by facilitating mutual gains negotiation and including species as stakeholders, and Problem 1 (inadequate ecological metrics), by requiring a more systematic and thorough understanding of ecological dynamics than is typically considered.

Finally, Tenet II demands that data collected for water management are actionable (Islam and Susskind 2013). Actionable knowledge comes from applied research designed to answer questions about system dynamics that are of concern to stakeholders. Once previously-external stakeholders and linkages have been internalized (via Tenets I & III), targeted research creates a shared knowledge base for all stakeholders. This joint fact-finding process either reduces or clarifies and quantifies uncertainty about the dynamics of the system to be managed (Islam and Susskind 2013). It can also build trust and enhance cooperation for later mutual gains negotiations. To be actionable, research must be adequately detailed to describe important elements of the system's behavior, but also be in a format that can be easily integrated into the negotiations process. Thus, Tenet II could address Problem 1 by ensuring that ecological research is focused on processes important to the functioning of the ecological system(s) in question, thus enhancing integration into the decision making process. Finally, it addresses Problem 2 by

necessitating that ecological data take a form amenable to a negotiations approach.

A1.3 Ecological factors as Surrogate Stakeholders

Although the Water Diplomacy Framework (WDF) has characteristics that would improve how ecological factors can be integrated into water management, there remains the problem of fitting ecological factors conceptually within the framework in such a way as to be implementable. We propose that this can best be done by treating ecological factors as surrogate stakeholders; that is, as entities that have specific interest and position analogs that can be integrated into mutual gains negotiations and potentially used to add value, rather than simply act as constraints.

For actual stakeholders, positions are the external manifestation of internal interest; an ecological factor's position is a combination of its response to manipulations of the water resource, and societal and cultural values attributed to that response. In other words, a surrogate stakeholder's position is its observed reaction to changes in the hydrological regime, as indicated by a chosen set of ecological indicators, plus some social determination of whether those changes are good or bad for the system. Examples of ecosystem positions may include an increase in native emergent aquatic plant cover, an increase in dissolved oxygen or aquatic nutrient load, increased salmon abundance, or decreased sediment transport. In the case of a target or focal species approach, a species' position might be described by increased or decreased abundance—perhaps with respect to the fulfillment of an ecological role (e.g. Soulé et al. 2003), increased reproductive success, an expanded range, etc. The positions of ecological surrogate stakeholders are products of a purely phenomenological understanding of ecosystem dynamics; they are

based on simple observations of how a target species or ecological indicator responds to changes in the system. What an ecosystem is observed to do in response to a management action dictates its position with respect to a resource. However, the implications of this behavior—that is, its value, whether it is considered good or bad—cannot be provided by the surrogate stakeholder.

Unlike real stakeholders that can articulate their own values, the value of management outcomes with respect to surrogate stakeholders' positions must be based on values attributed *a-priori* by some external agent. In other words, it is unclear whether the behaviors listed above (increases in abundance, changes in dissolved oxygen) are considered negative or positive until they are given some value in the context of the socio-ecological system. In a given hydrological system, if 95% of avian diversity is lost when water levels rise more than 60 cm in a pond, that is the ecosystem's response, but it is not an informative position unless given some value by society at large or some subset within it. If decision-makers and other stakeholders have decided that avian declines are unwanted, then the behavior described above shows a negative consequence to be avoided. The position of the ecosystem is thus that the pond's water should not rise beyond that threshold. In this way, the "position" of an ecological factor is a combination of its observed behavior and cultural values that specify whether certain behaviors are desirable or undesirable. This level of analysis is where most water management frameworks stop ecological analysis, and incorporate these dynamics into water management plans as direct constraints. The Water Diplomacy Framework encourages ecological research to proceed to deeper levels of analysis when treating ecological factors as surrogate stakeholders.

Because they are not actual stakeholders that can be consulted directly, ecological surrogate stakeholders' positions and interests are determined by empirical ecological research. The "interests" of an ecological system are causal, mechanistic relationships that explain the observed phenomena of position analogs. Just as a farmer's interests explain the underlying values that bring about their manifest positions, ecological interests are the actual causes that generate an ecological factor's observed response to changes in the hydrology of the system. A wetland's position might be that marshgrass diversity (a desirable trait of the system, in this case) decreases after water levels are reduced by residential water use. The wetland's interest is the mechanism causing this response; perhaps lower water levels allow competitive exclusion of some marshgrass species by others. Other means of maintaining marshgrass diversity—perhaps the use of occasional floods or physical disturbance like mowing—might satisfy the wetland's interests (i.e., the need to maintain species diversity, a desired trait in the ecosystem) without compromising residential water needs as apparently necessitated by its original position. Focal species' interests are typically behavioral and more analogous to the interests of human stakeholders; for example, beavers build dams to increase their reproductive fitness and survival (Naiman et al. 1988). Mechanistic understandings of these behaviors can lead to better management of human-wildlife conflicts caused by such behaviors. Several devices have been designed to prevent beaver dams from flooding roads and residential areas using detailed knowledge of the behavioral cues beavers use for dam-building (Payne and Peterson 1986; Nolte et al. 2000; Jensen et al. 2001). These devices save managers the energy and expense of beaver control alternatives like killing or relocation, while beavers are able to perform their natural

behaviors undisturbed and without causing destructive floods.

Because Water Diplomacy is an emerging framework, and because our suggested role for ecology within this framework is particularly new to water management, we are unable to find any concrete examples of our suggested approach in action. However, cases exist that validate different aspects of our approach. One of the most famous examples of the enhanced, mutual-gains outcomes that can be created using a negotiated approach is the New York City Watershed collaboration. In the 1990's, the City of New York was getting about 90% of its water from the rural Catskill-Delaware watershed, and due to land practices within the watershed, the quality of this water was at risk (Hoffman 2010). Rather than forcing cooperation from farmers in the Catskill-Delaware, the city negotiated a memorandum of agreement with them that led to mutual gains (Daily and Ellison 2002; Postel and Thompson 2005). Instead of spending an estimated \$6 billion on a water filtration plant with \$300 million annual operating costs, the city spent \$1.5 billion on helping farmers improve their lands to prevent erosion and contaminated runoff. Landowners were able to voluntarily participate in a program they helped design and received funding for restoration and enrichment of their properties (Postel and Thompson 2005).

The recent trend among conservation biologists toward including more detailed, mechanistic research (especially regarding behavior) in wildlife conservation (Reed 2002; Blumstein and Fernandez-Juricic 2004; Caro 2007) illustrates the increased utility of seeking ecological "interests" when solving environmental problems. Inquiry into the behavioral and physiological mechanisms of observed species responses has led to improved predictions of species distributions in response to climate change (Kearney et

al. 2010), risk of pest establishment (Kumar et al. 2014), and effectiveness of protected areas (Kujala et al. 2011).

The ability of ecological factors to provide added value in negotiations is readily apparent in recent research on ecosystem services; the services provided by wetlands are especially relevant to water conservation. While constructed wetlands have been used for decades to treat wastewater effluent and simultaneously provide wildlife habitat (e.g., Worrall et al. 1997), more recent developments like the Qunli stormwater park (Saunders 2012) and the reconstruction of the Bezai community in China (Wang et al. 2006) extend the concept to impressive scales. These integrated eco-urban environments require an understanding of wetland ecology, and yield simultaneous benefits in wildlife support and stormwater treatment (Campbell and Ogden, 1999; Wang et al. 2006; Scholz et al. 2007).

To illustrate specifically how our proposed framework might lead to better water management solutions, we describe below a hypothetical application of our framework to water management on O`ahu, Hawai`i.

A1.4 Case Study: O`ahu, Hawai`i and endangered waterbirds

The island of O`ahu, Hawai`i supports a rapidly-growing human population under vulnerable hydrological conditions. Nearly 100% of the island's natural freshwater is stored in basal aquifers that are threatened by overdrafting and sea level rise (Lau and Mink 2006; Liu 2007). Intense urban development and recent declines in agriculture have reduced infiltration and increased runoff (Ridgley and Giambelluca 1991; Giambelluca et al. 1996). This leads to floods and the contamination of offshore waters, which threatens

tourist beaches, offshore fisheries of cultural importance, and coral reefs (Banner 1974; U.S. EPA et al. 2004; Leone 2006; U.S. Bureau of Reclamation 2008). The island's limited freshwater originally supported extensive coastal freshwater marshes, of which 70% have been lost to development (van Rees and Reed 2014), leading to declines in the island's endemic waterbird species, of which only 6 of the original 27 species remain (Scott et al. 2001). Four of these species still persist in breeding populations on O`ahu, where increasing habitat protection is considered a key part of ensuring the persistence of their populations (Reed et al. 2011; USFWS 2011).

Water resources management on the island has until recently been considered inefficient and possibly inequitable (Derrickson et al., 2002; Gopalakrishnan 2007), and has focused primarily on addressing only one aspect of the hydrological cycle—the availability of freshwater—at the expense of other important factors like runoff and infiltration (Oceanit et al. 2007; U.S. Bureau of Reclamation 2008;). Additionally, it has largely neglected the ecological systems, like near-shore fisheries, coral reefs, and coastal wetlands, which are all affected by water and land management on the island. The resulting water management plans focus only on a single group of stakeholders—those interested in increased groundwater and freshwater availability—and suggest management techniques like deep injection wells, desalination plants, or diversions of highly contested river flows to meet increasing water needs (Oceanit et al. 2007; U.S. Bureau of Reclamation 2008). These strategies are likely to be very costly, have potential environmental impacts, and are unlikely to be socially acceptable in the context of past water resources disputes on the island (Gopalakrishnan et al. 2005).

By expanding the problemshed to include the island's historical context of

wetland loss due to land development and water diversions (van Rees and Reed 2014) and the economic and cultural importance of coastal and near-shore ecosystems (Birkeland 2004; Carl 2010), one can add a suite of ecological surrogate stakeholders and their relevant ecological processes (services) to the decision-making process (Tenets I & III). Their positions—for example, endangered waterbirds require increased wetland habitat, and coral reefs and fisheries require less-polluted runoff—might not be met by currently supported methods of increasing freshwater availability. Including these surrogate stakeholders in the decision-making process can yield added value to certain management strategies that are capable of meeting multiple needs simultaneously (Tenet IV).

For example, constructed wetlands are an increasingly popular and highly successful water management tool for reducing floods, increasing groundwater infiltration, and filtering sediment and nutrients from runoff (Magmedov et al. 1996; Mitsch and Gosselink 2000; Thompson 2002). Such wetlands may be an excellent solution to many of O`ahu's water management problems, and would cost a fraction of the expense of alternatives under consideration (Oceanit et al. 2007; U.S. Bureau of Reclamation 2008). Increased coastal wetland cover could reduce and purify runoff that is harming offshore ecosystems, while serving other stakeholder interests in reducing floods and potentially increasing groundwater recharge. At the same time, they could provide habitat for endangered waterbirds and offer opportunities for ecotourism and environmental education. Wetlands are often constructed specifically as habitat for waterbirds (Davis 2008; Rajpar and Zakaria 2013) and wetlands designed for hydrological benefits could likely be easily managed to provide habitat for endangered

waterbirds at the same time (Zhang 2008). Applied ecological research into the habitat use and selection by endangered waterbirds (e.g., their movement habits and indicators of habitat quality), or the effects of different types of runoff on coral reefs and culturally important fish would yield further information on how best to implement mutual-gains solutions. If, for example, endangered waterbirds had less need for larger wetlands for breeding, but instead benefitted more from smaller “stepping-stone” wetlands to facilitate movement throughout the landscape (Amezaga et al. 2002), a smaller, more decentralized approach to wetland design might be used while de-centralizing runoff control benefits. This higher level research into the interests of relevant ecological factors would clarify the feasibility of targeted, integrated solutions to multiple water management problems on the island.

While it is beyond the scope of this paper to quantitatively evaluate the economic, social and political benefit of such an integrated solution, it does provide a clear example of how the inclusion of ecological surrogate stakeholders expands water management options to include mutual gains solutions that might ultimately result in more sustainable outcomes. Detailed analysis of the economic and social benefits of such a proposal would be necessary before choosing such integrated methods over more traditional approaches.

A1.5 Discussion

Treating ecological factors as surrogate stakeholders would allow decision-makers and water managers to take advantage of the benefits of the WDF, especially the ability to develop mutual gains solutions. Understanding the interests of ecological

surrogate stakeholders requires hypothesis-driven, rather than purely observational research, and thus involves the integration of ecological theory into data collection for water management decision-making. Such hypothesis-driven research, performed in the context of established theory, is generally thought to be a more effective form of scientific inquiry than purely observational studies (Platt 1964). In this way, viewing ecological factors as surrogate stakeholders can create the impetus for more rigorous scientific inquiry into the dynamics of hydrological and ecological systems, and drive progress in the ecology of water management. This research is also encouraged by the tenets of the WDF (Tenets I, II, & III) that call for internalization of ecological surrogate stakeholders characteristically left out of water management, recognition of the complete problems created by ecological linkages within the managed system, and the need for research to be targeted to important applied issues. Finally, viewing ecological factors as surrogate stakeholders simplifies their involvement to a format that may be more accessible to decision-makers with no background in ecological science. Ecological information then becomes packaged in a way that is more familiar to politically-trained professionals and can be integrated into their general workflow. This method also shifts the integration of ecological factors in engineering approaches from a constraint near the end of the decision-making process to a surrogate stakeholder at the beginning of the process, when there is greater flexibility in the selection of management options.

As noted earlier, constraints with regard to ecological systems are often part of a precautionary approach to water management employed under conditions of uncertainty. The difficulty of actionable ecological research in water management problems is partly responsible for this uncertainty; studies often have a limited timeframe and budget.

Additionally, the type of large-scale ecological manipulations needed to anticipate the effects of management decisions are often infeasible, and comparative studies can be confounded by differences between different ecological and hydrological systems (e.g., Mazzacano and Black 2008). The precautionary approach is typically the most prudent approach under such circumstances of forced uncertainty, but it should be acknowledged that opportunities for mutual-gains outcomes can be missed if this precautionary approach becomes a default, even in cases where better ecological information is available.

While our goal is to emphasize how more effective management solutions can be discovered by taking a mutual-gains negotiations approach reaching beyond such constraints, it should be acknowledged that for all natural systems there exist certain boundaries and constraints that are non-negotiable. That is, there is always a point at which ecological systems can no longer sustain processes and services, and no amount of ecological research or negotiation with surrogate stakeholders can circumvent such constraints. Our suggestion is not that our methodology allows ecological limitations to be bypassed altogether, but instead that receptiveness to new information and an adaptive approach to decision-making can yield superior management outcomes where time and information are available. Understanding the ecological positions and interests—especially those which are entirely non-negotiable—is at the core of this process, and empirically-supported environmental regulations that delineate the ecological “bottom line” greatly facilitate its functioning.

Additionally, the role of the environmental negotiator deserves careful attention; individuals that represent the interests or positions of environmental factors may not be at

liberty to negotiate freely on the condition of natural resources that are often held in the public trust. It is consequently important to give adequate consideration to the social values we described that ultimately attribute positive or negative value to ecological interests, and insure that the needs of affected parties are acknowledged therein.

We do not claim that advocating the use of ecological factors as surrogate stakeholders in water management is novel or unique. The idea has been thoroughly discussed in business ethics literature, with specific regard to the more philosophical questions avoided in this text (Starik 1995; Jacobs 1997; Phillips and Reichart 2000; Driscoll and Starik 2004). Additionally, the idea of integrating human and wildlife resource needs has been prominent and heavily debated for some time, gaining special attention with the creation of reconciliation biology in the early 2000's (Rozenzweig 2003; Geisler 2010). We propose that our more formalized approach may provide a convenient theoretical framework for implementing the type of ecological thinking generated by reconciliation biology in cases where resource-sharing is both necessary and unavoidable. This is especially important in cases where natural systems are given lowest priority among many stakeholders competing for use of a water resource. The growing emphasis on integrated water resources management requires constant improvement of the contributions of various disciplines to the process of water management, and we believe the approach outlined above may be the next step forward for the successful interaction of ecological science and water management. In order to implement this new perspective, further research is needed to define the types of ecological metrics that are most amenable to understanding surrogate stakeholder positions and interests while minimizing cost and effort. Additionally, applied, hypothesis-driven research will help

inform more contextually appropriate water policy and strengthen ties between ecological experts and the decision-makers who govern water management.

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Table. A1.1: (A) *Reference list of potential problems with current interdisciplinary water management approaches* and (B) *four selected tenets of the Water Diplomacy framework that are useful for improving use of ecological research in water management.*

Problems with contemporary water management	Selected tenets of the Water Diplomacy Framework
<p>1) Information on ecological factors is often spatially aggregated or based on assumptions of surrogacy, and focuses on correlative rather than mechanistic relationships.</p> <p>2) Ecological factors are typically integrated late in the decision-making process, or treated only as constraints to management options.</p>	<ul style="list-style-type: none"> I. Defining analytical scale and boundaries using network and complexity theory II. Prioritizing actionable knowledge III. Treating water as a flexible resource IV. Using a negotiations approach based on mutual gains

Appendix II

Identifying and Prioritizing Ecological Stakeholder Surrogates in Water Resources Management

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Abstract

Water resources are a key nexus between societal and ecological systems, and an increasing awareness of this notion has spawned a new paradigm of ecologically informed water management. The elevated profile of ecological variables in integrated water resources management has coincided with a burgeoning of stakeholder-based approaches to solving water problems. However, applied understanding of how ecological information can inform such approaches has lagged behind theory. We present and elaborate upon a conceptual framework that acts as an adapter between ecological research and stakeholder-based water resources management. The Ecological Stakeholder Surrogate (ESS) concept is a tool for formalizing the organization and prioritization of ecological phenomena in the context of complex water resources management by treating species and ecological phenomena as analog stakeholders. We review the potential advantages of this framework and, by reviewing foundational literature in stakeholder theory, illustrate how the ESS framework is readily compatible with existing methods for the identification and prioritization of stakeholders. We also discuss how the ESS concept can improve the integration of ecological science with water management decision-making by increasing the transparency of the process of integrating ecological data,

aiding prioritization of ecological research, and by promoting recognition of mutual-gains outcomes. Finally, we illustrate the potential utility of this framework by applying it to a famous water resources case study, the Klamath River Basin in Oregon and California (USA).

A2.1 Introduction

Water is an essential but flexible resource of fundamental importance to human societies (Islam & Susskind, 2012), and upon which the biosphere is ultimately reliant (Ripl, 2003). However, water policy and management decisions have until recently excluded ecosystems and wildlife beyond their commodification. Contemporary accords and agreements in water policy and governance (e.g., Pigram, 2000; United Nations [UN], 1997; UN Economic Commission for Europe, 2013), in contrast, have explicitly included ecological systems in their consideration of freshwater resources. At the same time, wildlife conservation organizations have started to prioritize water resources management at a large scale (e.g., International Union for the Conservation of Nature [IUCN], 2002; IUCN, 2012; IUCN Global Water Programme; The Nature Conservancy Water for Life; World Wildlife Fund, 2013; WWF Water Stewardship). The increasing overlap of water governance and biodiversity conservation is testament to water's role as a major nexus between human society and ecosystems. Indeed, the water needs of society (e.g., residential, industrial, agricultural) and the environment (hydrological regimes supporting intact ecological communities) interact strongly and can come into conflict (Chapman et al., 2003; Islam & Susskind, 2012; Poff et al., 2003; Richter et al., 1997). There is an increasing urgency to recognize and understand how anticipated scenarios of global change (e.g., a shifting climate, landscape changes, a growing human population) will impact the natural and societal domains and their interdependencies (Basnyat et al., 1999; Green et al., 2017; Malmqvist & Rundle, 2002; Vorosmarty et al., 2000, 2010). By 2050, for example, the world's population is predicted to reach 9.7 billion, with more

than 40% of that population living in water-stressed areas (Organization for Economic Co-operation and Development, 2015; UN, 2015).

Ecology is accordingly a growing component in the management of water systems, and plays a key role in well-established frameworks for water management (e.g., Integrated Water Resources Management [IWRM] [Agarwal et al., 2000]; or Water Diplomacy [Islam & Susskind, 2012; Susskind & Islam, 2012]). Indeed, at least six of the eight “key challenges” identified by Bernhardt et al. (2006) for the water management community involve ecological variables, and might therefore be addressed by improved integration and collaboration between the disciplines of ecology, conservation biology, and water management. The Association of California Water Agencies (ACWA), a coalition of water management groups in the state of California (USA), has adopted policy principles that specifically include language relating to ecological integrity and sustainability, describing these as “embracing environmental and economic sustainability as co-equal priorities for water-management” (ACWA, 2009). Because California uses more than 10% of all freshwater in the USA (Maupin et al., 2014), the inclusion of this language indicates a major shift toward acknowledging the critical intersection of water management to meet human needs and biodiversity conservation.

The relevance of ecological knowledge to water management stems from decades of research demonstrating that ecological phenomena (populations, communities, ecosystems) can be strongly affected by anthropogenic forces in any part of the natural hydrological cycle (e.g., precipitation and evapotranspiration (Rovito et al., 2009); natural flooding regimes (Arthington & Balcombe, 2011); groundwater availability (Bernadez et al., 1993); aquatic connectivity (Sheer & Steel, 2006)). Ecological systems

also can exert strong influences on water management objectives; for example, where human impacts affect species of conservation concern, or species of ecological, aesthetic, cultural, or ecosystem service value, constraints caused by ecological systems can greatly complicate decision-making in water management (e.g., National Research Council [NRC], 2004).

More recently, research has demonstrated that many non-human species, ecological communities, and their associated processes, can have strong direct effects on the regulation and availability of water resources (e.g., Acreman, 2012; Griebler & Avramov, 2014). For example, there are ecosystem services provided by some species, such as the reed *Phragmites australis*, that purify water, thus increasing its availability to humans (Vymazal & Brezenova 2015). Some of these services are being harnessed ex situ for phytoremediation (e.g., Rezanian et al. 2015). Indeed, there are commonly known water-related examples of all four types of ecosystem services (ecological processes that benefit human societies) classified by the Millennium Ecosystem Assessment (MEA) (2000), such as fresh water storage (Provisioning, e.g., Notter et al., 2012), water purification (Regulating, e.g., Brix, 1987), dissolving and transporting nutrients and sediment (Supporting, e.g., Orr et al., 2007), and increasing aesthetic value of natural areas (Cultural, e.g., Luttik, 2000). Extensive research has shown the strong regulating influences of terrestrial vegetation on atmospheric moisture and rainfall dynamics (reviewed by Pielke et al., 2007). In the arid West of the United States, beavers (*Castor canadensis*), and hydrological changes associated with their dams, increase the residence time of water in glacial river systems, thereby maintaining natural stream channel morphology, increasing groundwater recharge, and prolonging the availability of

freshwater throughout the year (Pollock et al., 2003, 2007, 2014). As climate change reduces snowpack in the same region, water availability is temporally reduced over the dry season, but hydrological modifications by beavers are considered so effective that many organizations now seek to mimic their effects with artificial beaver dams (Pollock et al., 2015). Hydrological ecosystem services have been synthesized in a number of comprehensive reviews (e.g., MEA, 2005; Sanderson, 2006) that have established a paradigm for acknowledging the interconnectedness of water and ecological systems and their importance to human well-being.

The proliferation of thought on the connection between social and environmental needs for water necessitates the development of conceptual frameworks that improve the applied integration of related disciplines to enhance water management (Biswas, 2008; Poff et al., 2003). The development of implementation aids and applied frameworks for IWRM and other forms of water management have lagged behind theory (Borchardt et al., 2011; Hering and Ingold, 2012; United Nations Environment Programme, 2012). To begin addressing this gap, van Rees and Reed (2015) proposed an approach based on stakeholder theory and the Water Diplomacy Framework (Islam & Susskind, 2012) in which ecological phenomena were integrated into water management as “surrogate stakeholders” in the decision-making process. This is in contrast to treating species and ecological processes as constraints to available options of water use (see below). They illustrated how this approach allows decision-makers to take advantage of key aspects of the Water Diplomacy Framework to better include ecological information in water management. Chief among these aspects are the recognition of possible mutual-gains outcomes and the use of a process- and value-based understanding of stakeholder

interests to achieve better results with more actionable and targeted information (Islam & Madani, 2017; Islam & Repella, 2015; Islam & Susskind, 2012). Though the framework of ecological surrogate stakeholders (ESS) is intuitively appealing, no formal method has been proposed for identification and prioritization of ecological stakeholders. Faced with a complex water management problem, decision makers and managing entities have no formalized approach to select ecological processes or species to include in their decisions. Thus, implementation is unstandardized and potentially inaccessible to water resources decision makers and practitioners. Our aim is to integrate literature from the fields of ecology, conservation biology, and business ethics to provide guidelines for identifying ecological surrogate stakeholders and prioritizing among their varied respective positions and interests as part of the established decision-making process.

A2.2 The Ecological Surrogate-Stakeholder (ESS) Framework

We begin by reviewing the basic concepts of stakeholder approaches to management, specifically relating these to the framework put forward by van Rees and Reed (2015). Stakeholder theory is an approach to organizational management with a well-established literature in the field of business ethics (Freeman, 1984, 1994; Weiss, 1994). Over the last three decades, stakeholder-based methods have become the dominant paradigm for confronting complex water management problems and other recalcitrant issues of environmental decision-making. For example, stakeholder consultation is a major part of Integrated Water Resources Management (Mollinga et al., 2006), and the approach of major government agencies to complex environmental issues (e.g., National Oceanic and Atmospheric Administration [NOAA], 2015a, 2015b). The principal

processes informed by stakeholder theory are identifying and prioritizing the needs of stakeholders (defined loosely as parties that may affect or be affected by management decisions) and optimizing decision-making through an awareness of their values, interests, and positions (see Supporting Information for a glossary of key terms).

van Rees and Reed (2015) highlighted the utility of stakeholder theory in general and ESS in particular as a solution to two issues that they identified as being pervasive in the use of ecological information in water management.

- 1) A focus on phenomenological information (simple metrics) without inquiry into the mechanisms of ecological response to water management.
- 2) A zero-sum perspective, wherein ecological phenomena are viewed exclusively as constraints on water management (e.g., National Academy of Engineering, 1996), and the focus is on trade-offs and balance (Falkenmark & Rockstrom, 2004), ignoring the possibility of synergy.

Drawing a parallel with the increase in stakeholder participation in water management, they argued that treating ecological phenomena with relevance to the water management problem as stakeholder-surrogates offered distinct advantages over the prevailing - but not formally recognized - model of indicators and constraints. They used the term “ecological factors” to refer to any ecological phenomenon (e.g., a species, population, habitat, ecosystem function, ecosystem structure, etc.) that is of interest for water management, where factors of interest are those that affect or are affected by a water management decision (van Rees & Reed, 2015). Accordingly, an ESS might be a coastal estuarine salt marsh, a population of economically important migratory waterfowl, an assemblage of emergent hydrophytes in a marsh, or a species of

endangered damselfly. Notably, this definition is deliberately imprecise, and any water system large enough to be faced with complex management problems is likely to contain an overwhelming number of candidate ecological factors. Formal guidance on how to decide which ecological factors are of interest is needed in order to make the ESS framework practicable. The approach described in this paper provides this additional guidance.

van Rees and Reed (2015) made it clear that their framework makes no ethical or philosophical claim that ESS constitute actual stakeholders. Rather, they are treated as “stakeholder analogs” in order to integrate more detailed and pertinent ecological information into an approach that was easier for decision-makers and participants to implement. Their motivation is thus a practical one, as opposed to a moral one. The ESS concept consequently avoids the contentious philosophical issue of whether or not the environment should be considered a stakeholder per se (Driscoll & Starik, 2004; Gibson, 2012; Haigh & Griffiths, 2007). The idea of species or some component of nature as a stakeholder is not a new one, but the primary contribution of van Rees and Reed (2015) was an effort to apply the idea to enhancing the integration of ecological information into water management. One of the principal advantages of the ESS framework is that it allows ecological factors to be included directly in water management approaches like IWRM or the Water Diplomacy Framework, which include formal steps for collecting stakeholder information, thereby streamlining the process for the inclusion of ecological information.

In the context of the Water Diplomacy Framework, another major advantage of treating ecological phenomena as stakeholders is the opportunity to employ principles of

mutual gains negotiations. Mutual gains negotiation is an approach to decision-making and conflict resolution focused on differentiating between the positions of stakeholders (i.e., their outward demands) and their interests, the underlying values that drive those demands (Fisher & Ury, 1981). By bypassing demands to a more direct understanding of interests, mutual gains negotiation seeks to achieve mutually beneficial solutions that satisfy the interests of previously competing stakeholders while avoiding potential incompatibilities of their positions or demands.

In the context of ESS, van Rees and Reed (2015) defined a position as the ecological factor's observed or predicted response to a given water management decision (or associated hydrological change), combined with the value attributed to that response based on the prevailing and accepted set of values amongst decision makers and (non-surrogate) stakeholders in the system (Figure 1). For example, the observed response of rainbow trout *Oncorhynchus mykiss* to reduced streamflow can be reduced growth rate (Harvey et al., 2006), which can have population-level impacts because body size ultimately limits reproductive output. Stakeholder positions can be viewed as positive or negative according to either anthropocentric or intrinsic value ethics of the stakeholders, surrogate stakeholders, and decision-makers involved. In the case of conflicting ethical systems, the values of different actual stakeholders with respect to the response of an ESS are subject to the same analysis and consideration as any of their other positions or interests in the decision-making process, and so integrate with existing frameworks for natural resources decision-making (e.g., IWRM [Mollinga et al., 2006]).

The interests of ESS are defined as the underlying ecological, biological, hydrological, or geophysical mechanisms responsible for observed or predicted responses to hydrological alterations. ESS interests necessitate a deeper understanding of the ecological factors under consideration.

The principal benefits of recognizing ESS interests are: 1) replacing the “constraints” mindset, which involves viewing ecosystem positions as being potentially problematic restrictions for decision making, 2) creating the potential for mutual gains outcomes, in which the interests of ESS can be met (i.e., preservation or restoration of certain ecological processes) while also meeting the interests of other stakeholders, or, preferably, in which these interests can be made synergistic, and 3) better characterization of the ecological factor involved, by looking beyond phenomenological observations to the inherent mechanisms and processes involved with its observed behavior. Ultimately, this results in a better understanding of the hydrological-ecological system, creating a mechanistic, rather than just phenomenological, understanding.

Another major contribution of the ESS framework is that it formalizes to a greater degree the process of including ecological variables in water management. The utility of the framework is not limited to practitioners of Water Diplomacy, but extends to any stakeholder-based approach to wildlife conservation (Decker et al., 1996; Sterling et al., 2017) or water management (e.g., IWRM; Sustainable Urban Water Management [Kahil et al., 2016]; or Eco-engineering Decision Scaling [Poff et al., 2016]), to which the framework adds an increased degree of repeatability and transparency to the decision-making process. In effect, the ESS framework acts as a two-way adapter between ecological research and stakeholder-based management strategies (Figure 2). Because

ecological research is often undertaken at a level of detail and complexity that can complicate decision-making, ESS can help clarify the implications of research findings, improving their integration into the process of reaching a management decision. In the other direction, ESS can be used to highlight the most salient or important ecological factors in a system. The criteria and framework needed to select such high-priority ESS have not yet been developed, and are explored in the following sections.

As discussed earlier, the ESS approach is also independent of the issue of whether the environment deserves ethical consideration as a stakeholder, offering a practical, argument for the inclusion of ESS regardless of prevailing views of their potential to have ethical standing. For in-depth discussion of the merits and potential problems of the ESS approach, we refer readers to van Rees and Reed (2015), and here we focus our efforts on a clear conceptual gap in the paper: a formal method of including ESS in making water management decisions.

A2.3 Stakeholder Identification

Freeman's (1984) work on strategic management provided the foundation for stakeholder analysis in business management. The definition of a stakeholder, which began as "[a]ny group or individual who can affect or is affected by the achievement of the organization's objectives" (Freeman, 1984), has been steadily revised over the last thirty years (Bryson, 2004; Mitchell, 1997; Wagner Mainardes et al., 2011), with a growing literature on resolving key issues via stakeholder-based approaches (Bendjenna, 2012; Parent and Deephouse, 2007; Poplawska, 2015; Starik, 1995). The aim of this

literature is to provide guidelines for managers to understand which parties should be included and consulted for important and complex management decisions, in order that resulting decisions result in successful management, avoid costly litigation or settlements, and satisfy the interests of the organization (Neville et al., 2011).

Stakeholder research has focused primarily on two sets of theoretical guidelines: the identification, and prioritization, of stakeholders. Normative stakeholder theory addresses the former (Who should be included?), while both descriptive (Mitchell et al., 1997) and normative (Neville et al., 2011) theories of salience have been developed to address the latter (Who tends to be prioritized? vs. Who should be prioritized?). We address both sets of guidelines here, and illustrate how protocols used to identify and prioritize actual stakeholders can be applied to ecological surrogate stakeholders. Mitchell et al. (1997) outlined three criteria - power, legitimacy, and urgency - by which relevant stakeholders tend to be identified by managers, and proposed a system of classifying stakeholders according to these criteria (Figure 3).

A2.3.1 Power

Power is defined in a number of ways by different authors (Blau, 1964; Freeman, 1984; Weber, 1947), but generally refers to the stakeholder's ability to influence the managers' interests, the decisions made by the managers, or the outcomes of those decisions. Power is particularly relevant if those stakeholders have resources needed by the organization, or some manner of coercive or normative power that can be exerted over the organization or manager. In the context of human stakeholders, power can manifest as economic power over the organization, or the potential for force or violent action (both forms of coercive power), legal power (the ability to threaten by a lawsuit),

or social authority or popularity sufficient to create a prevailing cultural pressure on the organization (normative power; Mitchell et al., 1997).

Because ESS do not have their own political agency, they do not have direct or coercive power, but instead they derive power from the evaluation of their position, which in turn consists of their observed behavior and societal evaluation of that behavior, including, for example, legal protection or economic interest. Specifically, if some aspect of an ESS is altered by a management decision in a way that is perceived as strongly negative or positive by society at large, or that impacts the interests of other involved stakeholders, the surrogate stakeholder has some form of power to influence the outcome of a water management decision. Because power in ecological surrogate stakeholders is derived indirectly, and does not involve agency, ESS tend to have lower power than do other stakeholders in a system. Power among ESS can be derived from their economic value, political or cultural importance, legal status, or connections to other ecological factors that have characteristics of influence or value. For example, trout (*Oncorhynchus* spp.) and other coldwater fish that inhabit montane streams in the American Northwest have substantial power as an ESS due to their economic importance for fisheries, as well as some species being legally protected by the US Endangered Species Act, and are accordingly given explicit consideration in water management (Gosnell et al., 2007). Legal protection alone can give power to ESS, especially in the case of endangered species. For example, a single Say's phoebe (*Sayornis saya*) nest in California delayed repairs on a highway overpass for weeks (while waiting for the bird to complete its nesting cycle) due to the species' legal protection (Ghori, 2015).

A2.3.2 Legitimacy

Legitimacy refers to how the positions and interests of a stakeholder are viewed in the context of the cultural norms and expectations created by the society in which management is taking place (Mitchell et al., 1997). In short, legitimacy pertains to how much a stakeholder deserves to be part of a management conversation, or whether they have any right to be considered in the decision-making process. Suchman (1995) divided legitimacy into three types based on the source from which it was derived. Moral legitimacy is based on the cultural norms under which the organization or decision-makers are operating; pragmatic legitimacy is derived from the instrumental importance of the stakeholders to the decision system at hand; and cognitive legitimacy is derived from common assumptions or beliefs that are taken for granted by those involved. Accordingly, legitimate stakeholders are ones that society at large sees as rightful in their claims to consideration in the decision-making process of a management issue, usually because they are strongly affected by those decisions. As an example of moral legitimacy, in the context of permitting the construction of an energy plant that might contaminate local aquifers, water users (such as fish) living in the affected area would have high legitimacy in the issue, while property owners with separate water supplies concerned about the factory blocking their view of a nearby mountain range would have lower legitimacy.

Moral legitimacy for ESS is strongly tied to the origins of an ESS's involvement in a water management issue; in particular, its historical ecology and distribution with regard to the affected area. For example, species or ecosystems that are part of the native or natural ecology of a region -- those for which there is strong evidence for their prior

existence in the region before substantial human disturbance -- are considered to have greater legitimacy, because much of society perceives that they have an intrinsic value or right to exist in a place (Driscoll et al., 2015). Thus, most ESS have high moral legitimacy. By contrast, non-native or introduced species, recent invaders, or artificial habitats created by recent land-use changes, have decreased moral legitimacy, because they may be perceived as less natural. Introduced species that are used or valued for other reasons (e.g., mute swans *Cygnus olor*, and ring-necked pheasants *Phasianus colchicus*, which were introduced for aesthetic reasons and hunting, respectively, in North America; Long, 1981) may derive pragmatic legitimacy from their utility or value to other stakeholders, or power from their economic or cultural value, despite having decreased moral legitimacy.

Paradoxically, when permanent changes have occurred to an ecosystem to the extent that an ecological factor is no longer supported by ambient conditions, its legitimacy may be decreased. Legitimacy in this case may also be dependent on the amount of time elapsed since an ecological factor naturally occurred in an area. For example, although gray wolves (*Canis lupus*) were once found throughout the Northeastern United States, their reintroduction was and still is a contentious subject because of the substantial landscape and societal changes since their extirpation (Mech, 1995; Mladenoff et al., 1997). Intense management to reduce human-wildlife conflicts would be needed to facilitate the persistence of a wolf population in the proximity of such dense developments, as evidenced by conflicts in much less developed parts of North America (Wydeven et al., 1998). Similarly, conservation-reliant species (Reed et al., 2012; Scott et al., 2010) may also suffer reduced legitimacy in this context, because they

can no longer survive without active management in a previously occupied environment due to potentially irreversible changes. Decision-makers may be reluctant to accommodate a species in a watershed that would not survive there under current circumstances, or that would require substantial assistance to do so.

A2.3.3 Urgency

Urgency refers to the magnitude of impact a decision could potentially have on the stakeholder, and the timeframe of those impacts. Urgency is the degree to which a decision is critical for a stakeholder's interests, or the degree to which their interests are time sensitive. In water management cases, urgent stakeholders might be those whose health or well-being is currently being impacted by a given situation, such that potentially irreversible damage is being incurred during the decision-making process. Alternatively, the magnitude of the potential effect may add urgency, as in cases where a stakeholder's lives or health are in jeopardy. Stakeholders with high urgency warrant or typically gain attention from managers because their interests will be very strongly affected by management decisions, or because they can be directly violated by a lack of action. In high-urgency cases, decisions must be made in a short amount of time, or else the delay alone will cause harm to stakeholders.

Urgency for ESS is relatively intuitive, referring to ecological factors that are under direct and current threat by present conditions in a water management system, for which action is needed within a given time frame to avoid damage, or for which the potential impacts are irreversible or unacceptable (e.g., extinction, extirpation, significant declines in function). Ecological factors that are already impacted by current conditions

in a watershed have higher urgency, because they are being impacted continuously throughout the decision-making process. The concept of temporal urgency can be somewhat problematic for ESS, which often operate at very different time scales than do human systems. For example, a number of ecosystems and taxa have been shown to be in extinction debt (Tilman et al., 1994), a state where already-completed, anthropogenically induced environmental changes have doomed a population or ecosystem to extinction or loss of function, but only after some considerable lag time, possibly 50 to hundreds of years delayed (e.g., Hylander & Ehrlen, 2013). This lag time is typically the product of ecological or demographic processes delaying the visible effects of environmental disturbance (Tilman et al., 1994). For example, habitat loss and fragmentation in Europe resulted in delayed extirpations of forest plant species up to a century after forest clearing (Vellend et al., 2006). In such cases, although contemporary water management decisions are causing severe harm to an ESS in the form of legacy effects, the apparent temporal urgency of the stakeholder would be lost, reducing stakeholder salience according to Mitchell et al. (1997). Driscoll and Starik (2004) criticized this potential shortcoming, emphasizing that the different time scales at which ecological factors operate must be accounted for in stakeholder identification and prioritization. They cautioned that decision makers must evaluate management actions with respect to “current and future generations and both the short- and long-term impacts of decisions on the natural environment.” (pp. 62). Consequently, in the context of ESS, the definition of urgency may need modification to account for inevitable, time-delayed effects of some actions.

A2.4 Stakeholder Prioritization

The concept of stakeholder identification is closely related to stakeholder salience (*sensu* Mitchell et al., 1997), which we refer to as stakeholder prioritization. Although two types of stakeholder salience -- normative (Neville et al., 2011), *who should count*, and descriptive (Mitchell et al., 1997), *who typically does count* -- are described in the literature, we do not distinguish between these here, arguing that for the purposes of our work the distinction is unimportant. While relevant or important stakeholders can be identified by the possession of any of the criteria outlined above, they must be (or typically are) prioritized for the decision making process. Stakeholder priority or salience takes into account the magnitude of legitimacy, power, and urgency possessed by a given stakeholder or stakeholder group as well as how many of these criteria are possessed simultaneously.

Mitchell et al. (1997) identify eight qualitative classes of stakeholders based on which and how many stakeholder identification attributes they possess. Stakeholders that possess only one attribute are known as latent stakeholders, while stakeholders with two attributes are termed expectant stakeholders, and those with all three attributes are highly salient stakeholders or definitive stakeholders. These stakeholder classes are further subdivided based on the attributes that contribute to them; Mitchell et al. (1997) describe these in great detail, though for the sake of brevity we describe only a sample of these that are particularly relevant to ESS.

Dependent stakeholders are those possessing legitimacy and urgency, but potentially no direct power. In the context of ecological surrogate stakeholders, this might include ecological factors that are not protected by laws and are not economically

valuable, but that are strongly affected by the management decision in question and with high legitimacy for its presence in the system. These stakeholders must rely on other, more powerful stakeholders (e.g., dominant stakeholders) to represent their interests. In referencing the Exxon Valdez oil spill, Starik et al. (1993) identify ecological factors like marine mammals and their natural environment as examples of dependent stakeholders.

Dominant stakeholders are those with both power and legitimacy, but potentially not urgency in their claims. ESS that are associated with ecosystem services, or are protected by law, or are of cultural or economic importance, but that will not be immediately or critically impacted by a management decision, fall under this category. Dominant non-surrogate stakeholders in environmental conflicts are often governmental or non-profit conservation organizations, which are tasked with or interested in protecting the interests of dependent ESS.

An additional factor to consider in stakeholder prioritization is the interactions and relationships that a given stakeholder shares with other stakeholders. A stakeholder-issue interrelationship diagram is often created to place stakeholders and issues of interest in a conceptual map contextualizing their relationships with other stakeholders (Bryson, 2004). Technically, such a map is a graph (*sensu* West, 2001) that can be directional and weighted. Arrows on the map connect stakeholders to relevant issues and to other stakeholders with whom they share some relationship, which may include social ties and interdependencies, as well as competitive relationships.

Conveniently, a long-standing and well-established framework in ecology, the trophic web, shares this essential structure and purpose, and summarizes the ecological relationships between organisms in an ecological system (McDonald-Madden et al.,

2016; Pimm et al., 1991). Arrows depict the flows of energy that connect ecological factors in a system. Although they are a simplified view (or model) of a complex system, trophic webs yield insights on system structure, such as the potential vulnerability of a given species to a disturbance (e.g., loss of a species in the network) or the centrality (a measurement of a given node's role in the context of its network) of a given species to the stability of the system.

Converting a trophic web, whether hypothetical or empirically derived, into a stakeholder-issue interrelationship diagram is a simple analytical step that requires the integration of variables from the social and political domains that affect ecological factors in the system. Two types of network models can be constructed using ecological factors, each serving a distinct purpose: 1) Trophic webs among ecological factors, which allows prioritization and selection of ecological factors as ecological surrogate stakeholders based on their relationships to one another, and 2) Stakeholder-issue-interrelationship diagrams, in which ESS are related to actual stakeholders to better understand how their interests and positions in the water management issue align with those of other parties.

Several authors have asserted that stakeholder salience may be better analyzed with respect to coalitions or groups of stakeholders (Neville & Menguc, 2006, Neville et al., 2011). The explicit mapping of relationships between ESSs using the approach outlined above would enable easy grouping of ESS based on trophic interactions, ecological similarities (e.g. habitat use, feeding guild), or taxonomic relatedness. Similarly, Medema et al. (2017) emphasized the importance of bridging organizations, which are stakeholder groups that unite sets of stakeholders according to some common interest, even if this interest is outside of the issue under decision. In the context of actual

stakeholders, these organizations are often created especially for facilitating collaboration and social ties between stakeholders to simplify and strengthen the decision-making process. Examining trophic webs and interactions between ecological factors or ESS takes advantage of existing ecological knowledge to better understand the interconnectedness of the stakeholder network at a larger scale and may assist in prioritization.

In addition to selecting ESSs based on economic importance and social values, a number of well-established approaches in ecology can be employed to examine the interconnections among ecological factors (i.e., potential ESS) in the same way decision-makers would normally approach conventional stakeholders. Our framework takes advantage of the ecological toolbox for selecting study species based on species-specific characteristics, co-dependencies, and ecological relationships, and applies the techniques for integrating ESS in water management decisions. Classifications of especially important focal species might include umbrella species (Lambeck, 1997), keystone species (Mills et al., 1993) including ecosystem engineers (Jones et al., 1994), foundation species (Dayton, 1972), flagship species (e.g., Dietz et al., 1994), and bioindicators (e.g., Bourgoin, 1990), some of which can be identified using trophic webs or basic knowledge of ecological interactions (Noss, 1990). All of these classifications reference species that represent ecological factors beyond themselves. If protecting species diversity is a concern, for instance, protecting umbrella species is intended to protect other species (the ‘umbrella’) largely because their protection requires managing large areas of habitat on which many other species depend.

A network-based ecological approach also allows for the identification of aggregate groups that are united by common ecological functions or requirements (e.g., foraging or functional guilds [Simberloff & Dayan, 1991]), or factors or ESS that link multiple other ecological factors or ESS, functioning as bridging organizations. If their ecological positions and interests are similar or aligned, combining such ecological factors might greatly simplify system analysis.

Results from a network analysis of stakeholder relationships can also inform the stakeholder identification process, contributing to the power and legitimacy of ESS. For example, some species like ecosystem engineers directly affect and provide services to a contingent of other ecological factors (e.g., beavers build dams, thus creating habitat for lentic wetland specialists). These ESS have greater power, and should be prioritized because they represent a number of other stakeholders. Identification of ecological factors such as these might simplify the process of selecting ESS by reducing the number of stakeholders necessary to capture the ecological dynamics that are important for a management problem.

It is also important to note that criteria of salience are dynamic, so a given ESS can alternately gain and lose power, legitimacy, or urgency throughout a decision-making process. For example, increased media coverage might add power to an ecological stakeholder, while newly published population projections might increase or decrease urgency. Accordingly, stakeholders can switch between different levels of salience and classification based on the number of criteria they possess, and the relative influence of those criteria on other stakeholders in the system (Figure 3). For example, ESS with high legal power (e.g., species given legal protections) may be highly salient by that single

criterion alone, simply because of the power it holds over other stakeholders. Though, legal listing is typically associated with one or more other attributes (e.g., urgency necessary for listing, social legitimacy due to listing), and the contribution of these attributes also increases salience.

Just as ESS can be identified using similar criteria to those used for societal stakeholders, the same attributes and processes can be used for their prioritization. Ecological surrogate stakeholders can thus be organized based on the number of stakeholder attributes that they possess, and further prioritized and associated based on their relationships to one another and other stakeholders, which might simplify analyses through the use of stakeholder groups. By matching established ecological theory to concepts of stakeholder salience and prioritization, the ESS framework allows for a more comprehensive analysis of the risks and opportunities for ecologically-informed water management and reduces the risk of system oversimplification. The techniques and criteria for prioritizing and grouping specific ecological factors can be easily integrated into identification, prioritization, and grouping of ESS, thereby promoting further inclusion of key ecological concepts and information in water management. In the next section, we apply the ESS approach to a well known water resources conflict to provide a concrete example of the process and results of ESS identification and prioritization.

A2.5 Case Study: ESS in the Klamath River Basin

The Klamath River Basin is a region encompassing the watersheds of the Upper Klamath Lake (UKL), the Klamath River, and its tributaries, which pass through the states of Oregon and California. The region can be divided between the Upper Klamath

and Lower Klamath, where the former is characterized by headwater conditions and a large lake, and the latter by downstream conditions and an estuarine connection with the ocean (NRC, 2008). These subregions are separated by a series of dams built for river reclamation in the early 20th century. Dams, as well as irrigation projects started in the late 19th century, facilitated agricultural development in the Upper Klamath, which is now home to rural communities dependent on irrigation infrastructure (Doremus & Tarlock, 2008). Water use in the Lower Klamath is characterized by traditional and cultural rights of several First Nations tribes (including the Hoopa Valley, Karuk, and Yurok), as well as commercial and recreational fishers (Chaffin et al., 2014). Water demand for irrigation by Upper Klamath agricultural communities impacts streamflow in the Lower Klamath, while UKL is affected by shifts in the nutrient and sediment content of runoff from the surrounding landscape, which has largely been converted by agricultural development and wetland reclamation (Eilers et al., 2004; Ray et al., 2012). Impoundment of the Klamath River has drastically reduced the hydrological connectivity of the Klamath River system, impacting anadromous fish populations (Hamilton et al., 2005; National Resource Council 2008; Schlosser, 2011), while lowered water levels and nutrient inputs in the UKL are affecting endemic resident fish species, including the Lost River (*Deltistes luxatus*) and shortnose suckers (*Chasmistes brevirostris*; hereafter suckers; Bortleson and Fretwell, 1993; Martin & Saiki, 1999; National Resource Council, 2004). Both of these species were listed as endangered in the 1980s due to large population declines. Among other drivers for these declines were the loss of hydrological connectivity with spawning grounds in lake tributaries and the loss of wetland habitats to support young fish (National Research Council, 2004; Scoppettone & Vinyard, 1991;

Stubbs and White, 1993). Large-scale fish die-offs occurred in the early 2000s, attributed to blooms of the alga *Aphanizomenon flos-aquae* due to nutrient loading in the watershed (Kann & Smith, 1999). Larger water conflicts began when irrigation was restricted in 2001 to maintain water levels in the Upper Klamath for the protection of these listed species. The legislation coincided with a drought year in which irrigation-reliant farmers incurred large economic losses (Chaffin et al., 2014; Doremus & Tarlock, 2008).

Identification of ESS in this water management context is straightforward and intuitive, but closer analysis is required for selecting and prioritizing ESS that would contribute to improving management solutions. Given that ESS can apply to phenomena across ecological scales (van Rees & Reed, 2015), decision-makers are faced with a number of potential ESS that might promote sustainable management. These could include UKL, the Klamath river, and their tributaries as one or separate ecosystems, anadromous fish populations affected by conditions in the Lower Klamath, and migratory bird populations using the remaining wetlands around UKL, and at the species scale, the two suckers. This list is by no means exhaustive, and indeed could theoretically include any ecological factor trophically or ecologically linked to these, but starting with a bounded list is an essential practical step for analysis.

The species scale may be the most approach to ESS, because species are often the unit of ecological inquiry, and because they are easier to grasp for decision-makers than are concepts like ecosystems, populations, or processes. Species are also most commonly the subject of legal protections because of the Endangered Species Act (ESA, 1973, as amended), as well as other wildlife protection laws. Their frequent centrality to litigations and management decisions, as in the Klamath, makes them especially useful ESS. Indeed,

the suckers became the central ecological figure in the Klamath debates due to their legal protections, but numerous other factors contribute to their strong salience as ESS. The shortnose and Lost River suckers possess high legitimacy from their endemism to the region (i.e., the two species do not occur anywhere else [National Resource Council, 2004]). Fish die-offs in associated waters contributed to a sense of urgency to the “claims” of these ESS for sufficient water to carry out their life cycles. The suckers also derive additional power from their social and cultural importance to First Nations tribes of the Upper Klamath (Chaffin et al., 2014). The combination of these characteristics make the suckers definitive stakeholders. These two ESS could easily be combined into a coalition or stakeholder group based on basic knowledge of their shared habitat needs and life history traits. An understanding of their trophic relationships and habitat needs within the UKL (both are largely planktivorous, and rely on shoreline wetlands at parts of their life cycle [Markle & Clauson, 2006]) reveal their potential to represent other, less-salient ESS including the UKL as a lentic ecosystem, and migratory birds relying on associated wetlands. Because downstream portions of rivers are dominated by upstream hydrological conditions (Gordon, 2004; Vannote et al., 1980) management decisions favoring suckers would likely benefit less-salient ESS in the lower Klamath, (e.g., anadromous fish) that are not protected under the Endangered Species Act. Thus, according to the three categories of salience, as well as their ecological and hydrological relationships with other potential ESS, the suckers are important ESS worth formal consideration in water management decisions in the basin.

A2.6 Conclusion

This paper provides conceptual clarification and elaboration on the concept of Ecological Stakeholder Surrogates. In particular, we explore the foundational literature of stakeholder theory and show how the formal processes of stakeholder identification and prioritization are directly applicable to the framework. This guidance will facilitate effective implementation of the ESS framework in managing complex water resources problems.

The ESS framework is a structured approach to organizing the integration of ecological data into water management decisions, or in prioritizing research on the specific ecological factors that will most inform decision-making in a water resources system. In some circumstances, the framework can reveal previously unrecognized mutual gains outcomes capitalizing on ecosystem services and hydro-ecological interactions (van Rees & Reed, 2015), while in others (as with the Klamath example) it may help decision-makers integrate and compartmentalize information on ecological factors while clarifying the interactions and values attributed to them. This explicit treatment of the formerly “black-box” process of selecting ecological information is especially valuable because numerous water conflicts are between societal needs and some ecological factor. Framing these factors as ESS may help improve interpretations of ecological information and simplify the decision-making process, thereby increasing the trust in, and credibility of, the decision-making process. This framework also clarifies the role of scientists in a management context, employing them as translators of ecological positions and interests (‘honest brokers’; sensu Pielke, 2007), who can potentially deliver information with greater objectivity while not being treated as a special interest group.

This role facilitates the joint-fact-finding approach adopted in many modern water management frameworks like water diplomacy (Islam & Susskind, 2012).

The ESS framework adds much needed organization and rigor to the interface of ecological data and the new paradigm of stakeholder-based water resources management (Poff et al., 2015; Schoeman et al., 2014). Our hope is that by illustrating the ease with which existing stakeholder theory can be applied to the ESS concept, we can facilitate its use and increase its utility in enhancing the continued integration of ecology into modern water resources management.

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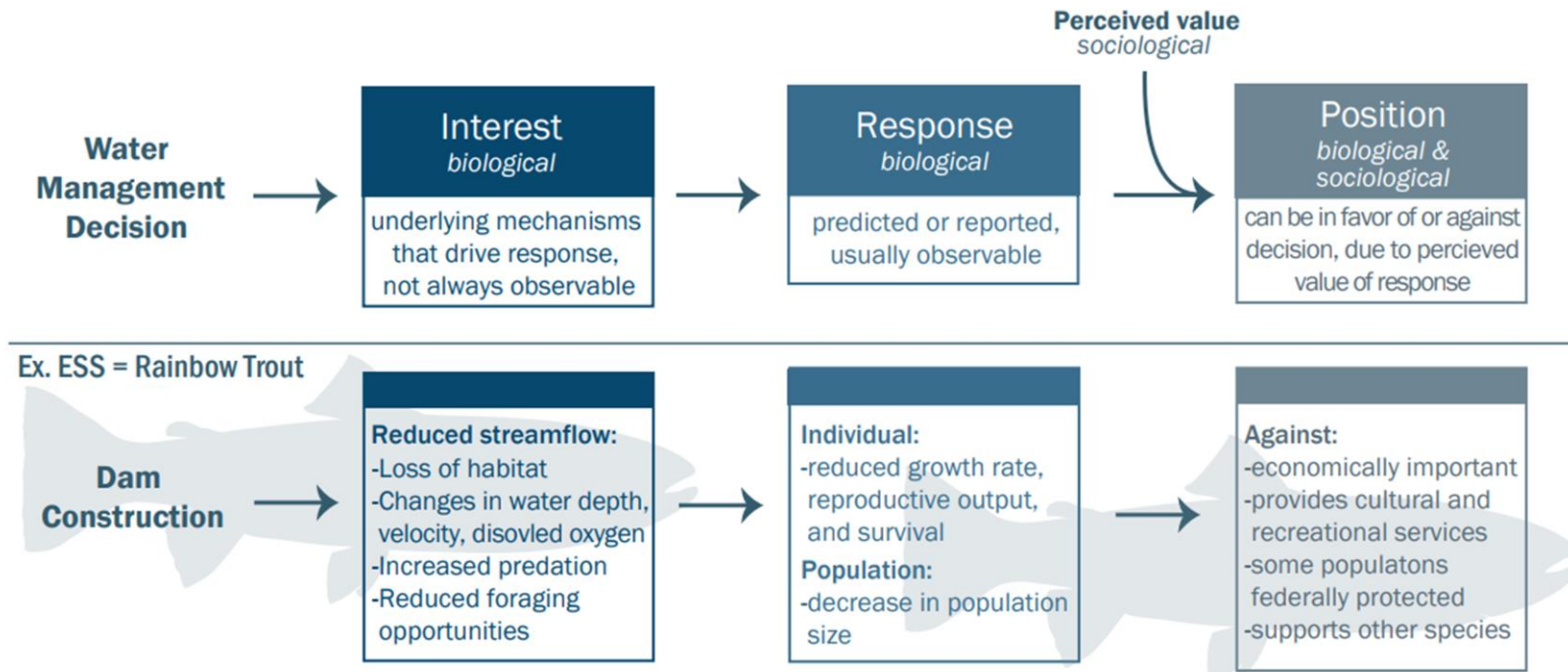


Figure A2.1. The position of an ESS, an integral component of stakeholder negotiation, is the result of the biological response to a water management decision combined with the perceived value (anthropocentric or intrinsic) of that response. Observed responses are produced by underlying biological or ecological mechanisms, which are treated as the interests of an ESS. Rainbow trout example adapted from Harvey et al., 2016.



Figure A2.2. The ESS framework acts as a two way converter as it: 1) allows for the distillation and selection of useful ecological research and its incorporation into stakeholder-based decision-making, and 2) identifies salient ecological factors as research priorities to improve management.

Salience	No		Low		Moderate		High	
Stakeholder Class	Potential		Latent		Expectant		Definitive	
Attributes	0	None	1	Power or Legitimacy or Urgency	2	Power & Legitimacy or Power & Urgency or Legitimacy & Urgency	3	Power, Legitimacy & Urgency
Dynamism	<p>Increase salience by gaining attributes</p> <p>Decrease salience by losing attributes</p>							

Figure A2.3. The number of attributes (power, legitimacy, and urgency) a stakeholder possesses informs its salience. For example, stakeholders having all three attributes are classified as “Definitive Stakeholders” and those with none as “Potential Stakeholders.” Salience is dynamic and stakeholders may gain or lose attributes at any time. Adapted from Mitchell et al., 1997.

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