

**Evaluating the Relationship Between Habitat
Interspersion and Abundance of the Hawaiian Gallinule
(*Gallinula galeata sandvicensis*)**

An Honors Thesis for the Department of Biology

M. Alejandra Muñoz

Tufts University, 2018

Acknowledgements

This research was supported by Tufts Institute of the Environment, Tufts Summer Scholars, and the Tufts Biology Department which made two field seasons in Hawaii financially possible for me. I'd like to thank my mentor and advisor, Dr. Charles van Rees and Dr. Michael Reed who have guided me through this process and have been invaluable role models to me, setting me on a career path that I used to only dream of. Thank you to all the other role models that have shaped my experience at Tufts, the Reed & Romero Lab, and in Hawaii, Marty Kawasaki. I am incredibly grateful and fortunate to have been a part of Team Gallinule and I thank Annie Miller, Amanda Sandor, and Matt Pedrotti for all their hard work and contributions!

TABLE OF CONTENTS

ABSTRACT	1
INTRODUCTION	2
METHODS	6
RESULTS	13
DISCUSSION	19
LITERATURE CITED	IV

ABSTRACT

Habitat selection is a crucial behavioral process that affects fitness and reproductive success in animal species. Understanding habitat selection also has strong implications for the success of habitat management plans and the conservation of endangered species. The endangered Hawaiian Gallinule (*Gallinula galeata sandvicensis*) is a wetland specialist endemic to two islands in Hawaii. It has suffered extensive habitat loss, particularly through conversion for agriculture and by extensive urbanization; the remaining habitat has a fragmented distribution. This loss is severe on the island of Oahu, where 75% of its wetlands have been lost since human arrival to the island. Despite its importance, little research has been published for this species and little is known about the details of Hawaiian gallinule habitat requirements beyond basic associations, mostly garnered from studies of other subspecies. My research focuses on understanding the effect of interspersion, defined as the intermixing of water, emergent vegetation, floating vegetation, and bare ground, on the abundance of the Hawaiian gallinule. We gathered abundance and interspersion data at freshwater coastal wetlands along the coast of the island of Oahu between the months of May and August 2015-2017. We determined the relationship between five interspersion metrics (Contagion, Edge Density, Edge Length, Edge Index, and Simpson's Diversity Index) and gallinule abundance using general linear models. Our analyses revealed that, among the interspersion metrics we evaluated, edge length is the best predictor of gallinule abundance in ponds on the island of Oahu. We therefore believe that the direct creation of interspersion with an emphasis on

maximizing emergent/water edges could be an indispensable management tactic at increasing gallinule numbers.

INTRODUCTION

Habitat selection is a crucial behavioral process that affects fitness and reproductive success in animal species, and understanding this process is a central problem in ecology (Hildén 1965). Selecting habitat that maximizes fitness depends on the ability of individual organisms to discriminate among alternative sites to favor its survival and reproductive opportunities as well as to provide resources for its offspring (Mayor et al. 2009). Explicit in its name, habitat selection involves a response to perceived environmental characteristics. Individuals seeking a breeding site will cue on a variety of proximate environmental characteristics, ranging from coarse structure such as forest and grassland, to more specific features such as habitat openness or particular structures such as suitable nest-holes for hole-nesting species (Hildén 1965, Haartman 1956, Cunningham & Johnson 2006). By investigating the features associated with habitat selection, one can answer questions about expected species distributions and species-specific habitat requirements, both of which involve an understanding of how organisms respond to the composition of landscapes (Wiens 1995). This type of knowledge is central to explaining or predicting community structure, population dynamics, and the effects of climate change on future species' distributions (e.g., Weller 1999, Morris 2003, Jensen et

al. 2012). In fact, habitat management and restoration ecology have been central to managing populations of game birds for centuries, and many of the same tools are being used now to improve populations of endangered species (Payne 1992).

Recently, ecologists have come to recognize the critical role of spatial scale and landscape context on habitat selection, affecting how ecologists understand, quantify, and analyze habitat quality (Mayor et al. 2009, Cunningham & Johnson 2006). In particular, local habitat quality is important in species distributions (Bruton et al. 2016) and might be particularly important for species that are geographically isolated or are sedentary habitat specialists that tend to have an absence of behavioral plasticity in habitat selection (Hagan et al. 1997). Birds, in particular habitat specialists, are excellent subjects for habitat selection studies because they are highly mobile yet breed and forage in predictable habitats. There is a large body of evidence for the effect of local scale habitat quality on avian habitat selection in habitat restricted species such as waterbirds (Rehm & Baldassarre 2007, Roach & Barrett 2015, Weller & Spatcher 1965, Jones 2001). Our interest here is in habitat selection by wetland specialists.

Wetland-dependent species are often specialists of habitats containing both water and emergent vegetation (Weller & Spatcher 1965). Within this particular mix of requirements, however, there can be further specialization on particular habitat features. For example, North American rails (family Rallidae) respond to water depth, as well as the configuration of water and vegetation (spatial distribution or interspersed) within in the wetland (Rehm & Baldassarre 2007, DesRochers 2010, Robertson & Olsen 2015, Weller & Spatcher 1965). The

interspersion of water and emergent vegetation increases macroinvertebrate abundance (e.g. isopods, planorbid and physid snails) and has been hypothesized to increase the abundance of waterbirds dependent on invertebrates as an important food source (Voigts 1976). Interspersion can also reduce interspecific and intraspecific competition through visual isolation (Murkin et al. 1982). Studies of habitat selection by wetland species have been integral to developing successful conservation and wetland management plans (Weller 1999). Most of the work on waterbirds, however, has been done on continental species, especially game birds, and very little work has been done on the habitat selection of more geographically isolated wetland species.

My research focuses on habitat selection of an island marsh bird. The Hawaiian Gallinule (*Gallinula galeata sandvicensis*) is a subspecies of the Common gallinule that is endemic to Hawaii (USFWS 2011). In addition to its global isolation on the Hawaiian Islands, the gallinule is also being increasingly isolated within its own range (Griffin et al. 1989). Hawaiian gallinules live year-round in shallow coastal wetlands dominated by emergent vegetation. These areas on the Hawaiian Islands are particularly favored by human settlement for agriculture and housing (Griffin et al. 1989). This subspecies once occurred on the five main islands in Hawaii; because of habitat loss via habitat conversion/development and exotic invasive plants, and predation by exotic invasive mammals, it now remains in isolated wetlands only on Oahu and Kauai (USFWS 2011). Oahu, the island with the largest human presence, has lost ~65% of its wetlands since human settlement (van Rees & Reed 2014). The remaining

wetlands on Oahu are relatively isolated, and the Hawaiian gallinule, which depends on them, is now endangered. In fact, over 200 species listed under the U.S. Endangered Species Act depend on Hawaiian wetlands (van Rees & Reed 2014). The Hawaiian gallinule is the most endangered and least studied of Oahu's water birds (USFWS 2011). Despite the importance of understanding habitat selection in managing and protecting endangered habitat specialists, no research has been published for this species and little is known about the details of Hawaiian gallinule habitat requirements beyond basic associations, mostly garnered from studies of other subspecies (Bannor & Kiviat 2002). Without a detailed understanding of habitat suitability for the Hawaiian gallinule, habitat maintenance and restoration will be based only on anecdotal evidence and optimal only by accident, and predictive modeling of gallinule populations will have unknown accuracy. My research focuses on understanding the effect of interspersed, defined as the intermixing of water, emergent vegetation, floating vegetation, and bare ground, on the abundance of the Hawaiian gallinule. I selected this habitat feature because it is well-known to be important for other wetland bird abundances (Rehm & Baldassarre 2007, Weller & Spatcher 1965, Tacha & Braun 1994). This research is one component of a more comprehensive study of habitat selection by Hawaiian gallinules. Our ultimate goal is to better inform the conservation and management of this endangered subspecies.

METHODS

Study Sites

We gathered habitat data at freshwater coastal wetlands along the coast of the island of Oahu (21.45°N – 158.038°W; Hawaii, USA) between the months of May and August 2015-2017. We defined a wetland as a hydrologically independent land unit in which gallinules have the potential to feed, reproduce, and nest. A wetland might be composed of only a single pond, or it might encompass numerous potentially hydrologically connected ponds that are delineated as separate territories that gallinules establish and defend. All data were analyzed at the individual pond level because gallinule territories are most often linked to specific pond features, like dikes, large vegetation barriers, or pond edges. Both occupied and unoccupied ponds were sampled; all were potential habitat for the species; i.e., freshwater coastal wetlands at low elevations with some emergent vegetation. Wetlands were under a variety of ownerships and degrees of habitat management, and included federally or state protected restored wetlands (Kawainui Wetland), wetlands from commercial activities such as farming (Shrimp Farm and Lotus Farm), as well as wetlands on golf courses (Klipper Golf Course and Olomana Golf Course). All wetlands were managed wetlands with human maintained ponds, that ranged from two (Waiawa National Wildlife Refuge) to eleven separate ponds (Lotus Farm).

Abundance Data Collection

The Hawaiian gallinule is behaviorally cryptic, spending a great deal of its time moving quietly through deep emergent vegetation. Habitat surveys of species that live in this type of habitat have high uncertainty because of low detectability, so we used a protocol employing playbacks of species' calls to elicit a behavioral response (Conway & Gibbs 2005, Conway & Nadeau 2010). Accordingly, gallinule abundance at each pond was sampled using a call-playback protocol developed to enhance detections for this subspecies (DesRochers 2008). This protocol consisted of a playback of the distress call of a gallinule chick, which elicits a defensive response from adults in the form of alarm calls and occasionally aggressive charging. It must be noted, however, that playback calls did not always elicit individual responses (Pers. Obs.), so the sampled abundance is still only an estimate. A one minute call playback was amplified with a commercial portable speaker (UE Roll), and playback was followed by a minute of silence. All gallinules seen or heard during the playback and one minute afterwards were counted. This protocol was repeated every 20 meters around the perimeter of a pond in order to minimize the likelihood of double counting individuals. Abundance data were only sampled between 0600-1000 hours because bird activity and responsiveness tends to decrease in birds in the late morning and afternoon.

Quantification of Interspersion

We defined interspersion as a measure of the degree of mixing of different land cover types within a pond. These include emergent vegetation, open water, short floating vegetation, scrub, forest, and bare ground. Google Earth (7.1.7.2606) and false-color Digital Orthophoto Quarter Quadrangle (DOQQ) images were used to convert in-field hand-drawn interspersion maps into spatially referenced interspersion maps of each pond on ArcGIS 10.4 (Figure 1). DOQQ images alone were not sufficient for creating maps to determine interspersion because the shallow wetlands gallinules inhabit are dynamic, and their characteristics can change weekly. To account for this, we collected all habitat characteristic information on the same day that abundance and occupancy surveys were conducted. The Rubber Sheeting tool with images from Google Earth was used when the DOQQ images could not provide up-to-date details on wetland boundaries, for example in newly constructed wetlands (e.g., Kawainui Marsh). Each pond was treated as a separate data layer in ArcGIS, where land cover types and their interspersion were manually drawn as polygons. Each polygon was given an attribute depending on the land type it represented (open water, bare ground, etc.). The resulting vector maps were converted into raster maps, with each pixel representing a land cover type. This raster image allowed for the quantification of interspersion for each pond using FRAGSTATS 4 (McGarigal et al. 2012). We used six commonly used interspersion metrics (Table 1). We retained each of these metrics in our analysis because we detected fairly low correlation among them (Spearman correlation, mean: 0.41, range: 0.14 - 0.81).

All metrics have been used in previous literature as a measure of interspersion. We calculated Interspersion and Juxtaposition Index (IJI) and Contagion (CONTAG) which determines the interspersion or intermixing of patch (land cover) types (Constible et al. 2006, Torio & Chmura 2015, McGarigal et al. 2012). We also calculated Edge Density, Edge Length, and Edge Index, all of which measure the amount of edge between different habitat types (O'Connell & Nyman 2010, Nielson 2016, Rehm & Baldassare 2007, Chabot & Bird 2013), and Simpson's Diversity Index which analyzes the diversity of habitat types within a landscape (Alexander & Hepp 2014).



Figure 1. Google Earth (7.1.7.2606), vector interspersions map, and raster interspersions map of James Campbell National Wildlife Refuge on ArcGIS 10.4. Each polygon or pixel represents a land cover type (emergent vegetation, water, bare ground, etc.) and its location within a pond. Raster images allowed for the quantification of interspersions for each pond using FRAGSTATS 4 (McGarigal et al. 2012).

Table 1. Interspersion metrics.

Interspersion Metric (Units)	Calculation	Definition	Citation
Interspersion and Juxtaposition Index (IJI; %)	$IJI = \frac{-\sum_{i=1}^m \sum_{k=i+1}^m \left[\left(\frac{e_{ik}}{E} \right) \cdot \ln \left(\frac{e_{ik}}{E} \right) \right]}{\ln(0.5[m(m-1)])}$	IJI approaches 0 when the distribution of adjacencies among unique patch types becomes increasingly uneven. IJI = 100 when all patch types are equally adjacent to all other patch types (i.e., maximum interspersion and juxtaposition)	McGarigal et al. 2012
Contagion (CONTAG, %)	$CONTAG = \left[1 + \frac{\left(\sum_{i=1}^n \sum_{k=1}^n (P_i) \left(\frac{B_k}{\sum_{k=1}^n B_k} \right) \cdot \ln(P_i) \left(\frac{B_k}{\sum_{k=1}^n B_k} \right) \right)}{2\ln(m)} \right] (100)$	CONTAG approaches 0 when the patch types are maximally disaggregated (i.e., every cell is a different patch type) and interspersed (equal proportions of all pairwise adjacencies). CONTAG = 100 when all patch types are maximally aggregated; i.e., when the landscape consists of single patch.	McGarigal et al. 2012
Edge Density (ED; m/HA)	$ED = \frac{E}{A} (10,000)$	ED = 0 when there is no edge in the landscape	McGarigal et al. 2012
Edge Length (EL; m)	EL = ED x Pond Area	A linear measure of the amount of edge between habitat types within a pond extrapolated from Edge Density.	This study
Edge Index (EI)	Edge Index = $\frac{\ell}{2\sqrt{A\pi}}$ where: ℓ = edge length, A= area of pond	Edge index between emergent vegetation and open water (a ratio to determine the amount of edge between emergent vegetation and open water).	Allen 1985
Simpson's Diversity Index (SIDI)	$SIDI = 1 - \sum_{i=1}^m P_i^2$	SIDI = 0 when the landscape contains only 1 patch (i.e., no diversity). SIDI approaches 1 as the number of different patch types (i.e., patch richness, PR) increases and the proportional distribution of area among patch types become more equitable.	McGarigal et al. 2012

Data Analysis

All habitat and abundance data were analyzed using R (x64 3.2.0; R Core Team, 2018). First, Spearman correlations were run on all interspersions metrics to check for correlation; this was done using the `cor` function from the package MASS (Venables & Ripley 2002). We then wanted to know the underlying distribution of the count data of gallinule abundances to inform further analyses. We performed goodness-of-fit tests to evaluate Poisson and Negative Binomial distributions – common distributions for count data – using the `fitdist` function from the `fitdistrplus` package (Delignette-Muller & Dutang 2015) and the `goodfit` function from the `vcd` (Visualizing Categorical Data) package (Meyer et al. 2017) in R. The count data fit the negative binomial distribution, which was used in subsequent analyses.

We determined the relationship between each of the interspersions metrics and gallinule abundance using general linear models with the `glm.nb` function from R package MASS (Venables & Ripley 2002). Subsequently, we created a model that included all interspersions metrics, and we reduced the model in single steps, removing the covariate with the largest p-value until only statistically significant metrics were left in the model.

RESULTS

We conducted abundance surveys at 86 ponds at 15 freshwater coastal complexes on Oahu. Of the 86 ponds sampled, 54 had at least one gallinule detection. The mean number of gallinules per pond was 3.6 birds (standard deviation: ± 5.93 ; range: 1-32), and within occupied ponds, 5.6 birds (standard deviation = ± 6.99). Count data were not statistically significantly different from a negative binomial distribution ($\chi^2=19.74$, $df = 30$, $p = 0.92$) (Figure 2); consequently, general linear models (GLM) used this as their underlying distributions.

There was a great deal of variation in interspersions (Figure 3), predominantly between water and emergent vegetation. The distribution of Edge Density (ED) had a right skew with a mean density of 2604.06 m/ha (SD: +1976.18; range: 482.309-13197.72). There was also a right skew for the distribution of Edge Length which had a mean value of 1324.16 meters (SD: +1082.65; range: 63.03 – 5265.53). IJI had a platykurtic distribution with a mean value of 62.67 percent (SD: + 21.25; range: 17.12 – 99.89) for ponds containing three or more land cover types (water, emergent vegetation, bare ground, etc.). Because IJI is incapable of calculating an interspersions value for ponds with less than three land cover types (its denominator reduces to zero when less than two land cover types are present), nearly one fourth of sampled ponds could not be assigned a value, and subsequently, IJI was left out of further analyses. CONTAG had a left skewed distribution with a mean value of 56.95 percent (SD: + 16;

range: 0-87.25). Edge Index (EI) distribution was skewed to the right and had a mean value of 415.15 m/ha (SD: + 162.5; range: 150.04 – 916.64). Simpson's Diversity Index (SIDI) was also skewed to the right with a mean value of 2.55 (SD: +2.40; range: 0-16.23).

The reduced GLM model contained only a single variable, Edge Length (Table 2b), and explained 25% of the variation in gallinule abundance ($p < 0.0001$, $\beta = 1.00$) with a positive relationship (Figure 4). That is, ponds with greater EL had more birds. We found that a model of gallinule presence-absence also contained only a single statistically significant variable, Edge Index ($p = 0.028$); this model, however, explained little variation in the data ($r^2 = 0.05$).

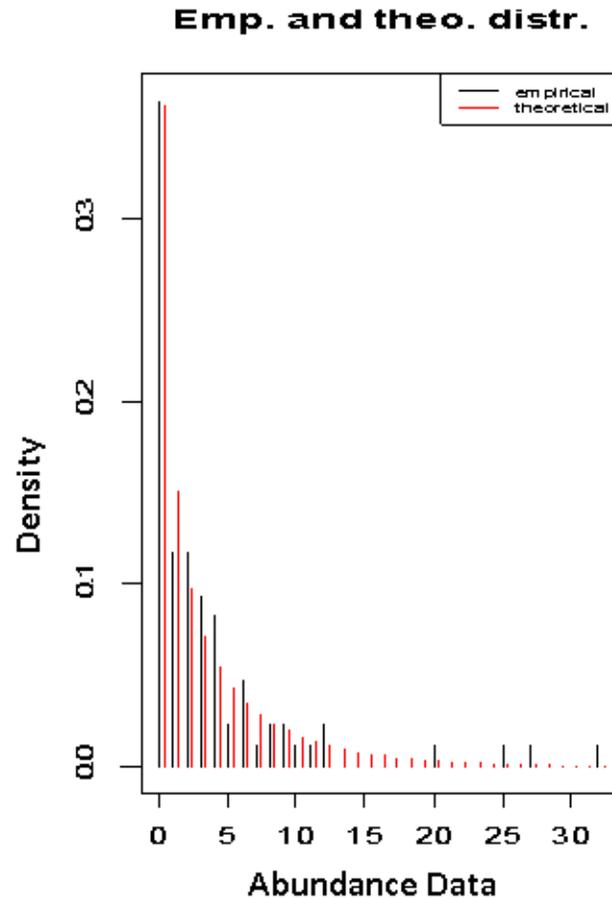


Figure 2. Fit of gallinule count data to the negative binomial distribution. The plot was generated using the `fitdist` function from the `fitdistrplus` package in R (Delignette-Muller & Dutang 2015). The density axis is proportion of wetlands having each of the count values. Count data were not statistically significantly different from a negative binomial distribution ($\chi^2=19.74$, $df = 30$, $p = 0.92$); consequently, general linear models (GLMS) used this as their underlying distributions.

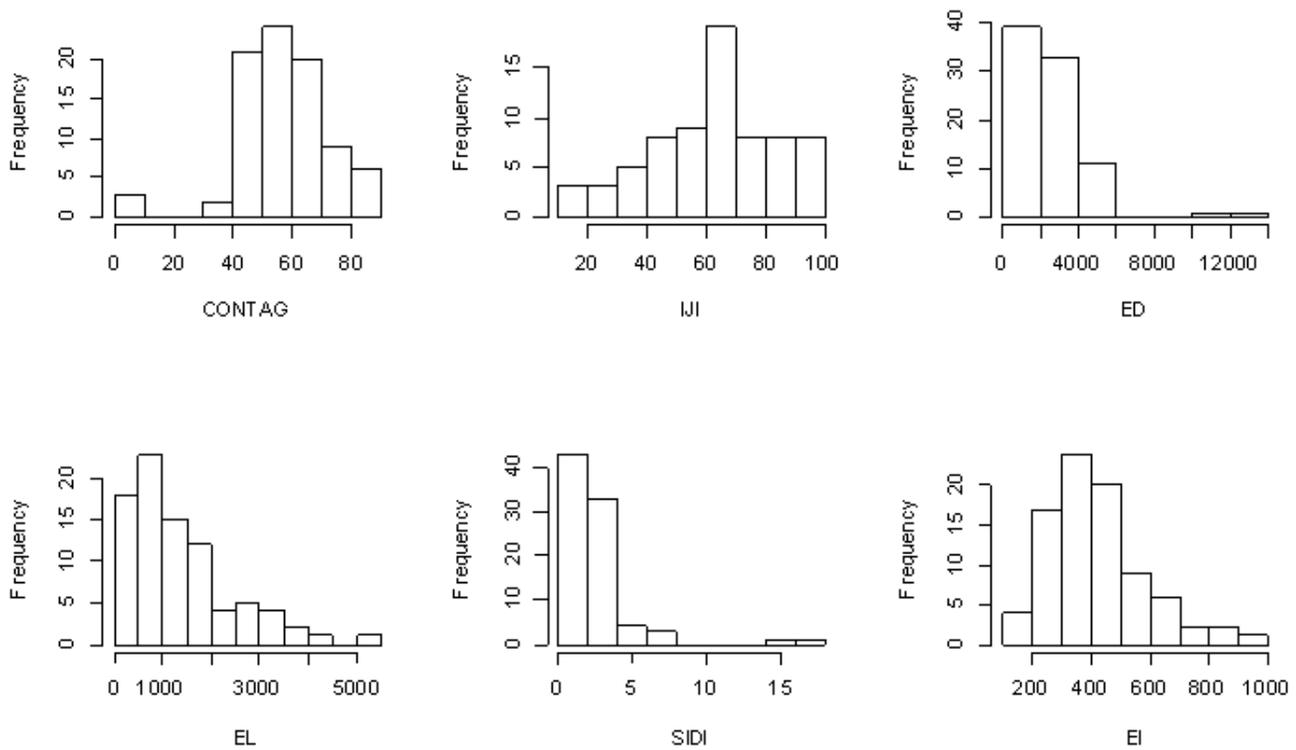


Figure 3. Frequency histograms of interspersed metric used to predict the abundance of the Hawaiian gallinule. Interspersion was visually estimated on site and spatially accurate interspersed maps were made on ArcGIS 10.4 and analyzed using FRASGSTATS 4 (McGarigal et al. 2012). Calculations described in table 1.

Table 2. a) Analysis of deviance table of a multivariable general linear model describing gallinule abundance. An all-inclusive general linear model was run with an underlying negative binomial distribution using the `glm.nb` function in the MASS package of R (Benables & Ripley 2002) and an analysis of deviance using the `anova` function in R (R Core Team, 2018). **b) Analysis of deviance table of the best-fit model describing gallinule abundance.** A step wise regression analysis of an all-inclusive general linear model presented edge length as the best predictor for gallinule abundance ($r^2=0.25$).

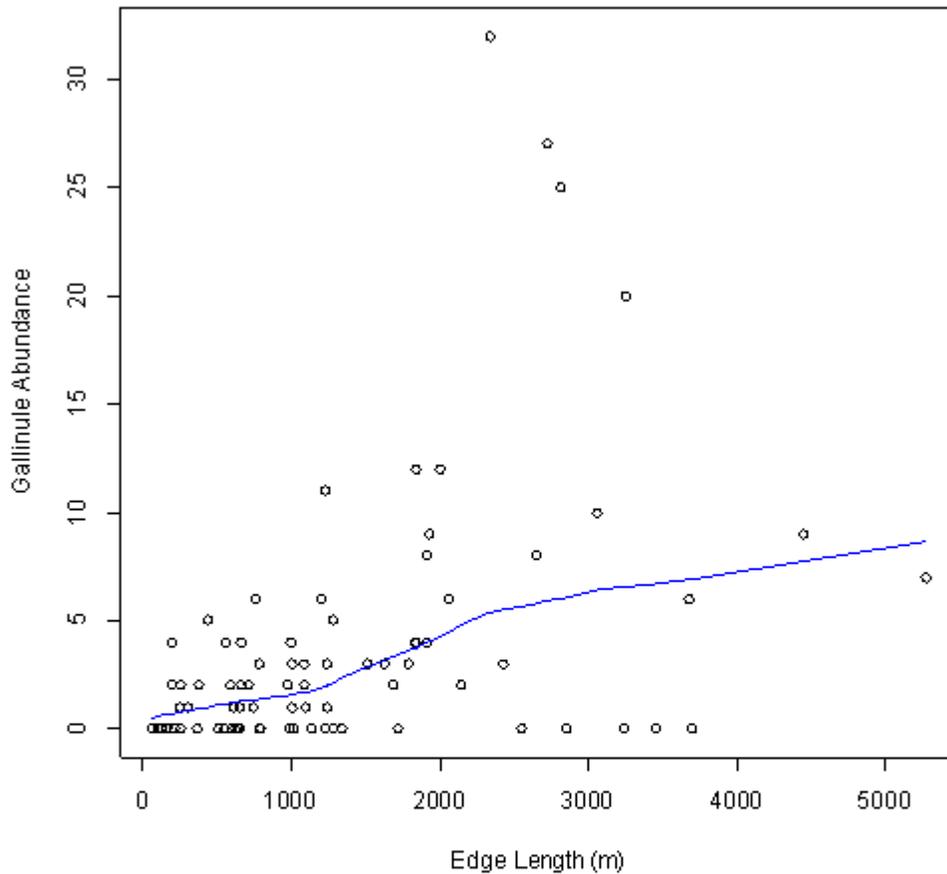
a)

Source of Variation	df	Residual Deviation	Pr (>Chi)
CONTAG	1	124.77	0.09
ED	1	106.03	<0.0001
EL	1	91.61	<0.0001
SDI	1	91.08	0.46
Edge Index	1	90.03	0.31

b)

+

Source of Variation	df	Residual Deviation	Pr (>Chi)
EL	1	89.66	<0.0001



DISCUSSION

Our analyses revealed that, among the interspersion metrics we evaluated, edge length is the best predictor of gallinule abundance in ponds on the island of Oahu. Edge length quantifies the amount of edge at the interface between landscape cover types; in our setting, this was primarily where open water and emergent vegetation abut). Our results suggest that the amount of these edges within ponds correlates positively with abundance of Hawaiian gallinules, making it a potential indicator of habitat quality. Water-emergent vegetation edge length might also be an environmental cue influencing the gallinules “decision” to settle and breed in ponds with higher amounts of edges present. Proximate factors such as environmental cues are known to affect settlement (Hildén 1965) and results from this study may inform our understanding of the habitat selection process of the Hawaiian gallinule and avian habitat selection in general, particularly in waterbirds. Along with habitat quality, information on habitat selection can have direct implications on the management and conservation of this endangered subspecies and other waterbird species (Weller 1999, Naef-Daenzer 2012).

Evaluating interspersion as a linear measurement of the amount of edge within a pond instead of a spatial analysis of the intermixing of habitat patches may be a more accurate measure of interspersion or may measure aspects of interspersion that are more important indicators of habitat quality to waterbirds. A key advantage of edge length or density as metrics of interspersion is that they directly correspond with the intermixing of habitat types (habitat configuration;

O'Connell & Nyman 2010). The amount of edge between emergent vegetation and open water within wetlands has been used as a metric for interspersion in several studies of the habitat use and abundance of waterbirds (Nielson 2016, Bolenbaugh et al. 2011, O'Connell and Nyman 2010, Rehm & Baldassare 2007). Some studies were unable to find statistically significant relationships between interspersion and abundance (Nielson 2016) while others found strong associations between these variables (Bolenbaugh et al. 2011, O'Connell & Nyman 2010, Rehm & Baldassare 2007). Many other studies have cited the importance of a 50:50 ratio of emergent vegetation to water to maximize waterbird abundance (Tacha & Braun 1994; Weller & Spatcher 1965; Weller & Fredrickson 1974; Chang 1990, Nagata 1983, Rehm & Baldassarre 2007), but this ratio only defines habitat composition (the relative amounts of habitat types) as opposed to habitat configuration (the spatial arrangement of those habitat types) and may not be as biologically relevant as edges between habitat types. For example, Hawaiian coots and gallinules both select habitat with high emergent vegetation cover, but coots appear to select wetlands where the emergent vegetation is along pond edges (Swift 1982), while gallinules appear to select wetlands where it is interspersed throughout the wetland. It may be that waterbirds have less use for uninterrupted stands of water and emergent vegetation and are instead using vegetation/water edges for its use or as a cue for other environmental conditions.

We hypothesize that waterbirds use emergent vegetation/water edge as a physical boundary between territories and to reduce both inter- and intraspecific

competition. Hawaiian gallinules are highly territorial and aggressive (Tacha & Braun 1994; Chang, 1990), quick to attack unrelated conspecifics, and may be excluded by the Hawaiian coot with which they share considerable niche overlap and show interspecific aggression (DesRochers et al. 2010). Interspersion has been hypothesized to create visual barriers between individuals and competitors (Murkin et al. 1982) and an increase in edge may help with the physical allocation of gallinule territories with clear boundaries making territorial defense easier, reducing conflict, and ultimately increasing gallinule densities within a pond.

Edges within a landscape can also help organisms access a variety of resources and habitats at a much smaller spatial scale, positively associating with increased abundances for many species (Lidicker & Peterson 1999). Hawaiian gallinules tend to forage in open, grassy areas (Pers. Obs.) and nest within patches of emergent vegetation (Nagata 1983) and these sites tend to be in close proximity to each other (USFWS 1985, USFWS 2005). Hawaiian gallinules are more likely to nest closer to the edge between open water and emergent vegetation and are less likely to nest in the interior of large patches of emergent vegetation (Chang 1990). Interspersion has been shown to positively affect nest survival and success in other waterbirds as well (Robertson & Olsen 2015). Increased availability of both foraging and nesting areas within a smaller spatial scale, and more importantly within a single territory, represent a likely mechanism for the positive effects of emergent/water edges present in a landscape on gallinule abundances within ponds. It has also been argued that edge densities also increase the abundance of food available to waterbirds (Voigts 1976). Gallinules, while

primarily herbivorous, supplement their diet with invertebrates which have been shown to correlate positively with edge density, increasing both in abundance and diversity (Voigts 1976). This might have less of an impact on Hawaiian gallinules, however, since they are not known to be limited by food availability (Desrochers et al. 2010).

Another potential mechanism for the effects of habitat edges on gallinule abundance pertains to their predator escape behavior. The Hawaiian gallinule is behaviorally cryptic, fleeing towards water and stands of emergent vegetation (Pers.Obs) when disturbed, and related species have been found to be increasingly alert at increasing distances from water features (Dear et al. 2015). At a local habitat scale, a pond with a large amount of edge between emergent vegetation and other habitat types where gallinules tend to forage (i.e. bare ground and floating vegetation) and open water may allow a decrease in perceived risk of predation through easy access to emergent vegetation to hide in and open areas of water that can expose approaching predators. Such behavior and tendency to stay in close proximity to water has been hypothesized to drive Hawaiian gallinule movements across larger landscapes through the use of streams and canal ditches as a movement corridor between wetlands (van Rees et al., *in review*).

Psychological factors have also been known to play a role in the habitat selection of birds (Hildén 1965). We hypothesize that gallinules may be attracted to edges within ponds because it feels safer from predators and these individuals tend to have a higher fitness as they are able perceive a predator across an open expanse

of water and flee into a thick stand of emergent vegetation leading to increased densities of gallinules within ponds with high amounts of edge.

While our results and the natural history of the gallinule and related taxa indicate that edge length is an important correlate of habitat quality and predictor of abundance, other local and landscape characteristics could be affecting the abundance and presence of the Hawaiian gallinule. There have been no formal studies analyzing of the influence of local habitat factors, or larger landscape features, on the abundance of Hawaiian gallinules; however some research has found common gallinule nesting initiation to be positively correlated with vegetation height (Brackney 1982). Studies on other waterbirds have tied many other habitat variables to abundances and nesting sites including hydrologic variability, percent water and vegetation cover, vegetation density, water depth, salinity, and average vegetation height (Tacha & Braun 1994, Roach & Barrett 2015, Robertson & Olsen 2015, Lor & Malecki 2006, Gee 2007). Edge length only explained a quarter of our abundance variation, and analyzing these additional habitat characteristics may very well serve to paint a more comprehensive picture of what a suitable habitat is for the Hawaiian gallinule.

Spatial scale is another critical factor that must be taken into account. Habitat selection studies must address the perception of an individual organism to their landscape and scale of their environment (Wiens 1976). Ecosystems must also be viewed and understood in the context of the movement and processes occurring between ecosystem boundaries (McGarigal 2002). To our knowledge only one study has analyzed and acknowledged the effects of landscape level

features on the abundance of Hawaiian gallinules finding that high cover of high grass and shrubland was positively associated with gallinule numbers (DesRochers 2010). Understanding the habitat requirements of the Hawaiian gallinule therefore involves an understanding of landscape level processes and an expansion of local habitat studies to involve a larger spatial extent. Future studies combining both more in-depth local habitat characteristics with landscape level features are critical for a truly comprehensive, well-rounded, and empirical-based conservation plan for the Hawaiian gallinule. Since it is not clear what limits Hawaiian gallinule population size, this would also identify features that could be manipulated in future studies to get at this problem.

Many management strategies for endangered species threatened by habitat loss and fragmentation are focused around the creation of artificial habitats and managed ecosystems to support viable or increase populations (Wiens 1995). Habitat loss of estuarine environments has played a critical role in diminishing historical coastal rail populations (Eddleman et al. 1988) and the creation of marsh impoundments has been critical to preserving waterbird populations (e.g. Roach & Barrett 2015). Hawaiian gallinules in particular require intensive habitat management as the threat of habitat loss is also coupled with continuous threats of invasive plant and predator species (Reed et al. 2012; Underwood et al. 2013). The importance of habitat creation and management for gallinule persistence is evident in the coincidence of established national wildlife refuges with long-term population recovery (Reed et al., 2011). Our results suggest the importance of interspersions and in particular the creation of edges between emergent vegetation

and open water, as a management tool for increasing gallinule densities and abundance. The current recovery plan for Hawaiian gallinules acknowledges the importance of a 50:50 emergent to water ratio within a wetland (USFWS 2011), this ratio, however, should be created with the specific interest of maximizing edges within the wetland. For example, Chang (1990) physically manipulated Hawaiian ponds by creating a 50:50 cover of emergent vegetation and water and then an irregular mowing of vegetation to create islands and strips and found an increase in gallinule abundance post manipulation. We therefore believe that the direct creation of interspersion with an emphasis on maximizing emergent/water edges could be an indispensable management tactic at increasing gallinule numbers.

LITERATURE CITED

- Alexander, B. W., & Hepp, G. R. (2014). Estimating Effects of Habitat Characteristics on Abundances of Three Species of Secretive Marsh Birds in Central Florida. *Waterbirds*, 37(3), 274–285.
<https://doi.org/10.1675/063.037.0306>
- Allen, A. W. (1985). Habitat Suitability Index Models: American coot (Federal Government Series No. 82/10.115). U.S. Fish and Wildlife Service. Retrieved from
http://pubs.er.usgs.gov/publication/fwsobs82_10_115
- Bannor, B.K., & Kiviat, E. (2002). Common Gallinule (*Gallinula galeata*). In Rodewald PG, editor. The birds of North America. Ithaca. The Cornell Lab of Ornithology (New York, USA).
- Bolenbaugh, J. R., Krementz, D. G., & Lehnen, S. E. (2011). Secretive Marsh Bird Species Co-Occurrences and Habitat Associations Across the Midwest, USA. *Journal of Fish and Wildlife Management*, 2(1), 49–60.
<https://doi.org/10.3996/012011-JFWM-001>
- Brackney, A., & Bookhout, T. A. (1982). Population Ecology of Common Gallinules in Southwestern Lake Erie Marshes. Retrieved from
<http://hdl.handle.net/1811/22880>
- Bruton, M. J., Maron, M., Franklin, C. E., & McAlpine, C. A. (2016). The relative importance of habitat quality and landscape context for reptiles

in regenerating landscapes. *Biological Conservation*, 193, 37–47.

<https://doi.org/10.1016/j.biocon.2015.11.004>

Chabot, D., & Bird, D. M. (2013). Small unmanned aircraft: precise and convenient new tools for surveying wetlands. *Journal of Unmanned Vehicle Systems*, 01(01), 15–24. <https://doi.org/10.1139/juvs-2013-0014>

Chang, P.R. (1990). Strategies for managing endangered waterbirds on Hawaiian national wildlife refuges. Master's thesis, University of Massachusetts at Amherst.

Constible, J. M., Chamberlain, M. J., & Leopold, B. D. (2006). Relationships Between Landscape Pattern and Space Use of Three Mammalian Carnivores in Central Mississippi. *The American Midland Naturalist*, 155(2), 352–362. [https://doi.org/10.1674/0003-0031\(2006\)155\[352:RBLPAS\]2.0.CO;2](https://doi.org/10.1674/0003-0031(2006)155[352:RBLPAS]2.0.CO;2)

Conway, C. J., Gibbs, J. P., & Haukos, D. A. (2005). Effectiveness of call-broadcast surveys for monitoring marsh birds. *The Auk*, 122(1), 26–35. [https://doi.org/10.1642/0004-8038\(2005\)122\[0026:EOCSFM\]2.0.CO;2](https://doi.org/10.1642/0004-8038(2005)122[0026:EOCSFM]2.0.CO;2)

Conway, C. J., & Nadeau, C. P. (2010). Effects of Broadcasting Conspecific and Heterospecific Calls on Detection of Marsh Birds in North America. *Wetlands*, 30(2), 358–368. <https://doi.org/10.1007/s13157-010-0030-1>

Cunningham, M.A., & Johnson D.H. (2006). Proximate And Landscape Factors Influence Grassland Bird Distributions. *Ecological Applications*,

16(3), 1062–1075. [https://doi.org/10.1890/1051-0761\(2006\)016\[1062:PALFIG\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[1062:PALFIG]2.0.CO;2)

Dear, E. J., Guay, P.-J., Robinson, R. W., & Weston, M. A. (2015). Distance from shore positively influences alert distance in three wetland bird species. *Wetlands Ecology and Management*, 23(2), 315–318. <https://doi.org/10.1007/s11273-014-9376-0>

Delignette-Muller, M. L., Dutang, C. (2015). fitdistrplus: An R Package for Fitting Distributions. *Journal of Statistical Software*, 64(4), 1-34. URL <http://www.jstatsoft.org/v64/i04/>.

DesRochers David W., Gee Hugo K. W., & Reed J. Michael. (2008). Response of Hawaiian Moorhens to broadcast of conspecific calls and a comparison with other survey methods. *Journal of Field Ornithology*, 79(4), 448–457. <https://doi.org/10.1111/j.1557-9263.2008.00190.x>

DesRochers, D. W., McWilliams, S. R., & Reed, J. M. (2010). Evaluating if Energy and Protein Limit Abundance of Hawaiian Moorhen. *Journal of Wildlife Management*, 74(4), 788–795. <https://doi.org/10.2193/2009-278>

Eddleman, W. R., Knopf, F. L., Meanley, B., Reid, F. A., & Zembal, R. (1988). Conservation of North American Rallids. *The Wilson Bulletin*, 100(3), 458–475.

Fuller, R. J. (2012). *Birds and Habitat: Relationships in Changing Landscapes*. Cambridge University Press.

- Gee, H. (2007). Habitat Characteristics of Refuge Wetlands and Taro Lo'I Used By Endangered Waterbirds At Hanalei National Wildlife Refuge, Hawai'i. *Electronic Theses and Dissertations*. Retrieved from <https://openprairie.sdstate.edu/etd/432>
- Griffin, C. (1989). Hawaii's endangered waterbirds : a resource management challenge. *Freshwater Wetlands and Wildlife*, 1165–1175.
- Haartman, L.v. (1956). Territory in the pied flycatcher *Muscicapa hypoleuca*. *Ibis*, 98(3), 460–475. <https://doi.org/10.1111/j.1474-919X.1956.tb01431.x>
- Hagan, J. M., McKinley, P. S., Meehan, A. L., & Grove, S. L. (1997). Diversity and Abundance of Landbirds in a Northeastern Industrial Forest. *The Journal of Wildlife Management*, 61(3), 718–735. <https://doi.org/10.2307/3802179>
- Hildén, O. (1965). Habitat selection in birds: A review. *Annales Zoologici Fennici*, 2(1), 53–75.
- Jensen, R. A., Sunde, P., & Nachman, G. (2012). Predicting the distribution of Tawny Owl at the scale of individual territories in Denmark. *Journal of Ornithology*, 153(3), 677–689. <https://doi.org/10.1007/s10336-011-0785-z>

- Jones, J. (2001). Habitat Selection Studies in Avian Ecology: A Critical Review. *The Auk*, 118(2), 557–562. [https://doi.org/10.1642/0004-8038\(2001\)118\[0557:HSSIAE\]2.0.CO;2](https://doi.org/10.1642/0004-8038(2001)118[0557:HSSIAE]2.0.CO;2)
- Lidicker, W. Z., & Peterson, J. A. (1999). Responses of Small Mammals to Habitat Edges. In *Landscape Ecology of Small Mammals* (pp. 211–227). Springer, New York, NY. https://doi.org/10.1007/978-0-387-21622-5_10
- Lor, S., & Malecki, R. A. (2006). Breeding Ecology and Nesting Habitat Associations of Five Marsh Bird Species in Western New York. *Waterbirds*, 29(4), 427–436. [https://doi.org/10.1675/1524-4695\(2006\)29\[427:BEANHA\]2.0.CO;2](https://doi.org/10.1675/1524-4695(2006)29[427:BEANHA]2.0.CO;2)
- Mayor, S. J., Schneider, D. C., Schaefer, J. A., & Mahoney, S. P. (2009). Habitat Selection at Multiple Scales. *Ecoscience*, 16(2), 238–247. <https://doi.org/10.2980/16-2-3238>
- McGarigal, K., S. A. Cushman, and E. Ene. (2012). FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. University of Massachusetts, Amherst, Massachusetts, USA. <http://www.umass.edu/landeco/research/fragstats/fragstats.html>
- McGarigal, K. (2015). Introduction to Landscape Ecology. (Accessed March 1, 2016). <http://www.umass.edu/landeco/about/landeco.pdf>.

- Meyer, D., Zeileis, A., & Hornik, K. (2017). vcd: Visualizing Categorical Data. R package version 1.4-4.
- Morris, D. W. (2003). Toward an ecological synthesis: a case for habitat selection. *Oecologia*, *136*(1), 1–13. <https://doi.org/10.1007/s00442-003-1241-4>
- Murkin, H. R., Kaminski, R. M., & Titman, R. D. (1982). Responses by dabbling ducks and aquatic invertebrates to an experimentally manipulated cattail marsh. *Canadian Journal of Zoology*, *60*(10), 2324–2332. <https://doi.org/10.1139/z82-299>
- Naef-Daenzer, B. (2012). Understanding individual life-histories and habitat choices: implications for explaining population patterns and processes. 408-431.
- Nagata, S. E. (1983). Status of the Hawaiian Gallinule on lotus farms and a marsh on Oahu, Hawaii (Doctoral dissertation, Colorado State University).
- Nielson, P. (2016). Secretive Marshbirds of Urban Wetlands in the Washington, DC Metropolitan Area (Doctoral dissertation).
- O’Connell, J. L., & Nyman, J. A. (2010). Marsh Terraces in Coastal Louisiana Increase Marsh Edge and Densities of Waterbirds. *Wetlands*, *30*(1), 125–135. <https://doi.org/10.1007/s13157-009-0009-y>

- Payne, N. F. (1992). Techniques for wildlife habitat management of wetlands. McGraw-Hill. Retrieved from <http://agris.fao.org/agris-search/search.do?recordID=US201300700262>
- R Core Team (2018). R: A language and environment for statistical computing. Vienna, R Foundation for Statistical Computing. <https://www.R-Project.Org/> (January 2018).
- Reed, J. M., Elphick, C. S., Ieno, E. N., & Zuur, A. F. (2011). Long-term population trends of endangered Hawaiian waterbirds. *Population Ecology*, 53(3), 473–481. <https://doi.org/10.1007/s10144-011-0262-9>
- Reed, J. M., DesRochers, D. W., Vanderwerf, E. A., & Scott, J. M. (2012). Conservation reliance and long-term persistence of Hawaii’s endangered avifauna. *Bioscience*, 62, 881-892.
- van Rees, C.B., Reed, J.M., Wilson, R.E., Underwood, J.G., and S.A. Sonsthagen. *In review*. Landscape genetics implicates stream and drainage infrastructure as corridors in the dispersal of an endangered wetland bird.
- Rehm, E. M., & Baldassarre, G. A. (2007). The influence of interspersions on marsh bird abundance in New York. *The Wilson Journal of Ornithology*, 119(4), 648–654. <https://doi.org/10.1676/06-060.1>

- Roach, N. S., & Barrett, K. (2015). Managed Habitats Increase Occupancy of Black Rails and May Buffer Impacts from Sea Level Rise. *Wetlands*, 35(6), 1065–1076. <https://doi.org/10.1007/s13157-015-0695-6>
- Robertson, E. P., & Olsen, B. J. (2015). Behavioral plasticity in nest building increases fecundity in marsh birds. *The Auk*, 132(1), 37–45. <https://doi.org/10.1642/AUK-14-73.1>
- Swift, J. A. (1982). Construction of rafts and islands. *Managing Wetlands and their Birds. Slimbridge*, 200-203.
- Tacha, T.C. & Braun, C.E. (1994). Migratory shore and upland game bird management in North America. Allen Press, Lawrence, Kansas.
- Torio, D. D., & Chmura, G. L. (2015). Impacts of Sea Level Rise on Marsh as Fish Habitat. *Estuaries and Coasts*, 38(4), 1288–1303. <https://doi.org/10.1007/s12237-013-9740-y>
- U.S. Fish and Wildlife Service (USFWS). (1985). Hawaiian waterbirds recovery plan. U.S. Fish and Wildlife Service, Portland
- U.S. Fish and Wildlife Service (USFWS). (2005) Draft revised recovery plan for Hawaiian waterbirds, second draft of second revision. U.S. Fish and Wildlife Service, Honolulu
- U.S. Fish and Wildlife Service (USFWS) (2011). Recovery Plan for Hawaiian Waterbirds, Second Revision. U.S. Fish and Wildlife Service (Portland, Oregon).

- Underwood, J. G., Silbernagle, M., Nishimoto, M., & Uyehara, K. (2013).
Managing Conservation Reliant Species: Hawai'i's Endangered
Endemic Waterbirds. *PLOS ONE*, 8(6), e67872.
<https://doi.org/10.1371/journal.pone.0067872>
- van Rees, C. B., & Reed, J. M. (2014). Wetland Loss in Hawai'i Since
Human Settlement. *Wetlands*, 34(2), 335–350.
<https://doi.org/10.1007/s13157-013-0501-2>
- Venables, W. N. & Ripley, B. D. (2002) Modern Applied Statistics with S.
Fourth Edition. Springer, New York. ISBN 0-387-95457-0
- Voigts, D. K. (1976). Aquatic Invertebrate Abundance in Relation to
Changing Marsh Vegetation. *The American Midland Naturalist*, 95(2),
313–322. <https://doi.org/10.2307/2424396>
- Weller, M., & Spatcher, C. (1965). Role of habitat in the distribution and
abundance of marsh birds. *Special Report*. Retrieved from
<https://lib.dr.iastate.edu/specialreports/42>
- Weller, M. W., & Fredrickson, L. H. (1974). Avian ecology of a managed
glacial marsh. *The Living Bird, Twelfth Annual of the Cornell
Laboratory of Ornithology, Cornell University, Ithaca, New York* p 269-
291, 1973. 16 Fig, 7 Tab, 13 Ref.
- Weller, M. W. (1999). Wetland Birds: Habitat Resources and Conservation
Implications. Cambridge University Press.

Westervelt, W. D. (1910). Legends of Ma-ui -- a Demi God of Polynesia, and of His Mother Hina. *Hawaiian Gazette*.

Wiens, J. A. (1976). Population Responses to Patchy Environments. *Annual Review of Ecology and Systematics*, 7(1), 81–120.

<https://doi.org/10.1146/annurev.es.07.110176.000501>

Wiens John A. (1995). Habitat fragmentation: island v landscape perspectives on bird conservation. *Ibis*, 137(s1), S97–S104.

<https://doi.org/10.1111/j.1474-919X.1995.tb08464.x>