

Diet and Selectivity of *Porphyrio porphyrio* (Purple Swamphen) in Florida

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Abstract - We tested whether *Porphyrio porphyrio* (Purple Swamphen) in South Florida selected particular types of food and whether their diets differed among 3 geographically separate wetlands (northern Everglades, a stormwater treatment marsh, and Lake Okeechobee littoral zone). We found that the Purple Swamphens we collected from the treatment marsh were larger than those from the other sites. The primary food item of the Purple Swamphen at all 3 sites was *Eleocharis cellulosa* (Gulf-coast Spikerush), comprising 79%, 72%, and 49% mean dry weight of total gut contents for the northern Everglades, littoral zone, and treatment marsh, respectively. Accounting for availability, Purple Swamphens were strongly selective for Gulf-coast Spikerush, which is a common plant in the southeastern US. The availability of this plant is not likely to be a factor limiting the spread of this bird northward.

Introduction

The spread of nonnative and invasive species is a major problem for US policy makers (USFWS 2006), costing billions of dollars nationally every year (USFWS 2012). Aware of the limited funds available for control efforts, scientists have responded to threats posed by the growing number of invasive species by developing screening tools to focus management actions on the most harmful species. Screening tools typically require basic ecological and life-history information about the invasive species and its effects on the invaded ecosystem. We conducted this study to fill gaps in basic information for *Porphyrio porphyrio* L. (Purple Swamphen; hereafter Swamphen) in south Florida.

The Swamphen is a member of the Rallidae family, which ranges widely across Europe, Australia, Asia, Africa, and New Zealand (Pranty 2012, Pranty et al. 2000). Like other rallids, Swamphens are secretive and spend the majority of their time in marshes. However, they occupy a wide diversity of habitats, including freshwater and brackish wetlands dominated by emergent vegetation, pastures, and disturbed areas (del Hoyo et al. 1996, Freifeld et al. 2001, Sanchez-Lafuente et al. 2001).

In 1996, a population of Swamphens was discovered in Pembroke Pines in Broward County, FL (Pranty et al. 2000). In the subsequent 2 decades, the Swamphen expanded its range northwest, through the northern Everglades, and Lake Okeechobee (Pearlstine and Ortiz 2009, Pranty 2013), a distance of approximately 60 km (Fig. 1). Individual Swamphens have been documented moving more than 300 km to colonize new habitats and territories within their native range (Sanchez-Lafuente et al. 2001). Additionally, their widespread occupation of oceanic islands demonstrates their capability as dispersers (Garcia-Ramirez and Trewick 2015).

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Diet studies from other continents suggest Swamphens are generalists that can exploit a variety of local plant species (Johnson and McGarrity 2009). Swamphens are known to be predominantly herbivorous (Balasubramaniam and Guay 2008),

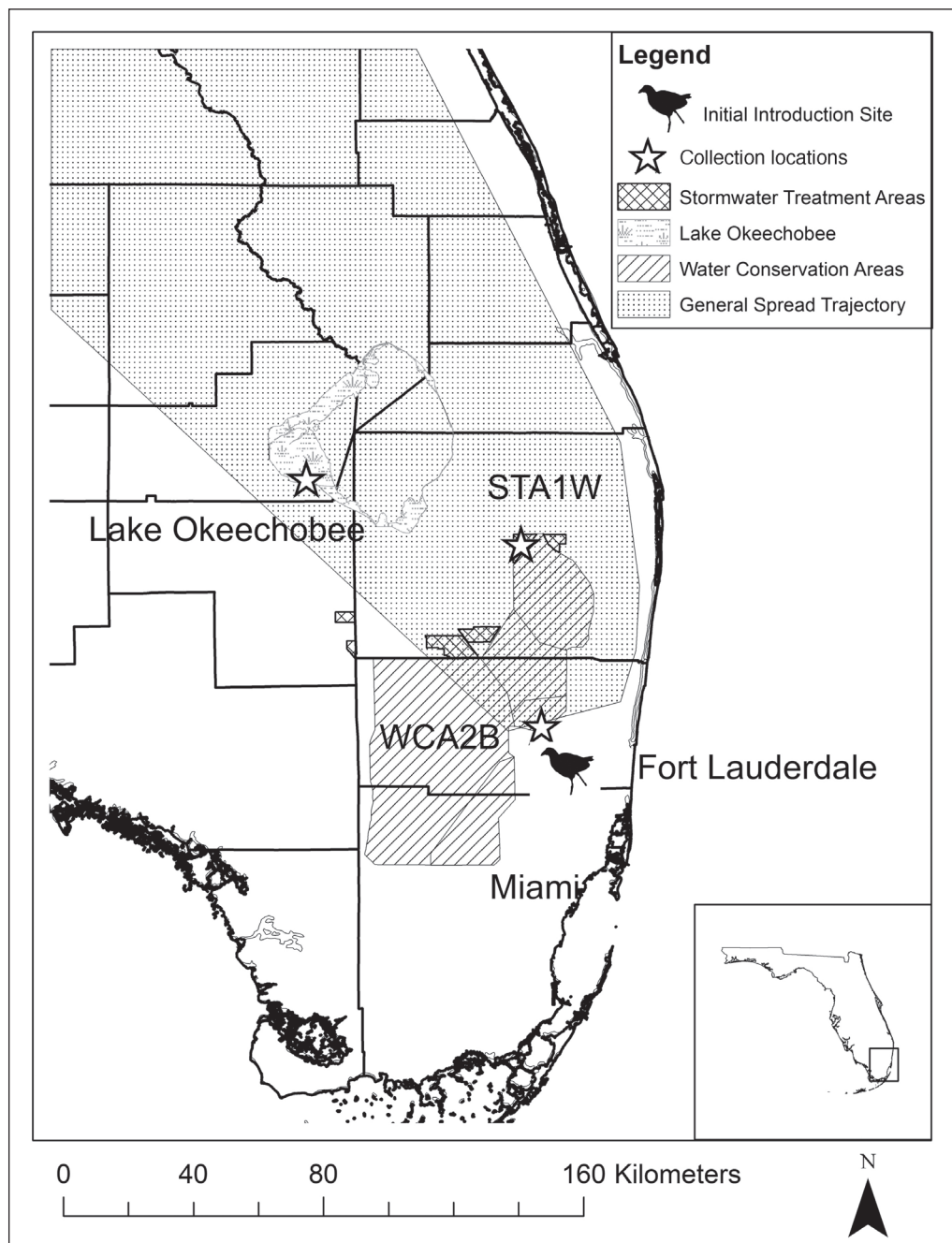


Figure 1. A map of south Florida, showing the the initial introduction location, 3 locations where Purple Swamphens were collected, and the anticipated general spread of the Swamphens, 2014.

but are also opportunistic, consuming a wide range of taxa, including birds, amphibians, reptiles, fish, eggs, insects, arthropods, and mollusks (Balasubramaniam and Guay 2008, del Hoyo et al. 1996). Although little is known about their diet in Florida, Swampheens are generally found there in places dominated by herbaceous wetland plants (Pranty 2012).

Swampheens invading novel habitats provide a unique opportunity to study processes such as habitat selection and range expansion (Duncan et al. 2003), which is especially relevant in our rapidly changing climate. Phenotypic divergence from source populations, as well as any divergence among different Florida populations could provide insight into how these invaders are adapting to their new environment. One way to study this expansion is to compare morphological changes that may have taken place among populations.

In Florida, the Swampheens are likely still at an early stage in its invasion trajectory (*sensu* Simberloff 2001); thus, wildlife management agencies need additional information on the resources used by this species. In particular, more detailed information is needed on the basic biology and life history of the Swampheens in its invaded ecosystem. Our goals were to support management of the Swampheens in Florida by (1) quantifying the diet of Swampheens, (2) determining the selectivity of food items by Swampheens, and (3) comparing morphology of Swampheens in 3 regions of South Florida.

Methods

From January to March 2014, Florida Fish and Wildlife Conservation Commission (FWC) personnel used shotguns and steel shot to collect sample birds from 3 geographically separate wetlands across south Florida—water conservation area 2B in the northern Everglades (WCA2B), stormwater treatment area 1W (STA1W), and the littoral zone of Lake Okeechobee (Fig. 1). The birds were collected from areas of emergent marshes at all 3 sites.

Diet

We removed and stored in 70% ethanol the stomach contents from the sample birds. Prior to analysis of stomach contents, we created macro- and micro-level reference collections of plant material from the WCA2B site. We prepared slides (Dusi 1949) to create a reference collection at the microscopic (cellular) level. We identified food items in a hierarchical manner through a macroscopic and microscopic level of sorting and identification (Ward 1968). We sorted stomach contents at the macroscopic level by aggregating items with the same texture and structure visible to the naked eye. We retained the remaining smaller particles, termed homogenate, for subsequent microscopic analysis. We conducted the microscopic analysis by spreading the homogenate evenly across one hundred 0.8 cm x 0.8 cm cells arranged in a 10 x 10 grid. We randomly selected 10 cells and identified the contents by their cellular structure.

After sorting and identification, we placed food items in a drying oven at 55 °C for ~48 h until they reached a constant weight (Free et al. 1971); each macroscopic

and homogenate sample was then weighed. We used the proportion of each food item identified in the subsamples to determine its dry mass in the homogenate.

Swanson et al. (1974) recommended using an aggregate percentage approach rather than an aggregate volume approach. Therefore, we employed the former method, and we present the diet data as (1) the average percent of dry weight, (2) the percent occurrence of food items, and (3) the percent occurrence in the Swampghens (i.e., the number of Swampghens that consumed a particular item from that particular area; Preveit et al. 1979). The average percent of dry weight is defined as $\Sigma W_i / n$, where W_i is the weight of the i^{th} food item expressed as a percentage of all food items in the sample, and n is the total number of Swampghen samples for a particular site. The percent occurrence of food items is defined as $\Sigma F_i / \Sigma F_s$ and the percent occurrence in the Swampghens is defined as $\Sigma F_i / n$, where F_i = occurrence of food item i in a sample, and F_s = number of food items in a sample.

We investigated differences in diet by performing a multidimensional scaling (MDS) ordination with a Bray-Curtis similarity matrix and an analysis of similarity (ANOSIM) to test for significant differences among sites. ANOSIM provides a global R -value that indicates the degree of discrimination among sites. We also conducted a similarity percentages procedure (SIMPER) to determine the percentage each food item contributed to any differences among sites. All techniques were performed in PRIMERV6 software (Clarke and Gorley 2006).

Selectivity

We employed Chesson's index of selectivity (Chesson 1978) to determine whether Swampghens in WCA2B showed a preference for any particular plant species. Plant-availability data were not available for the other 2 study sites. Chesson's index quantifies selectivity and determines food preference by comparing the proportions and distribution found in the environment to those found in the diet. This technique assumes that prey abundance is large compared to the amount of food consumed. It also assumes that the ability of the organism to consume a particular item is equal for each item (Chesson 1983). The index is calculated by using the formula:

$$\alpha_i = (r_i / p_i) / \left(\sum_{i=1}^n [r_i / p_i] \right), i = 1, \dots, m$$

where α_i is the selectivity index for prey type i ; r_i is the relative abundance of prey type i consumed by the Swampghen; p_i is the percent of prey type i in the environment calculated from the vegetation surveys; and m is the number of prey types available in the environment ($m = 7$ prey types encountered during the vegetation surveys). In order to interpret Chesson's index, values of α_i are related to $1/m$. Random feeding occurs when $\alpha_i = 1/m$. Preferential selection of a prey type occurs when $\alpha_i > 1/m$, and avoidance of a prey type occurs when $\alpha_i < 1/m$. We calculated the α_i at the individual level and then we arrayed the mean indices of all individuals to create a mean selectivity index (Rudershausen et al. 2005); 95% confidence intervals surrounding the mean selectivity index were also calculated.

We defined a vegetation sampling area as the approximate spatial ranges of the Swampheens collected for our study. We determined the spatial range by plotting the coordinates of the locations from which each bird in the study was initially flushed. We applied a 1.03-ha buffer to each location, which represents the average home-range size of the *Porphyrio martinicus* L. (Purple Gallinule; West and Hess 2002), a congener of the Swampheens; the home range of the Swampheens in Florida is unknown. We created a minimum convex polygon around the buffered locations to delineate the extent of the area from which to sample vegetation. We generated random points within this defined area such that each point represented the northeast corner of 3 nested vegetation-sampling plots. The 3 plots were 5 m x 5 m, 3 m x 3 m, and 1 m x 1 m in size (Ross et al. 2003). We used a modified Braun-Blanquet scale to determine the percent cover of each species within each of these subplots (Mueller-Dombois and Ellenburg 1974). We sampled vegetation at 10 random points, but added no new species in the last 4 plots; thus 6 random points were adequate to characterize the available plant species (Cain 1938).

We calculated vegetation available to Swampheens in the environment as the plot averages for the 3 nested-plot sizes at each of the 10 random points. We determined percent cover of each plant type by converting each Braun-Blanquet value to the midpoint of the corresponding percentage range.

Morphology

FWC staff collected 30 birds from Lake Okeechobee, of which 25 were intact enough to be used for morphometric analysis. Twenty-nine birds were collected from STA1W, of which 28 were intact and included in the morphometric analysis. Thirty-two birds were collected from WCA2B, all of which were included in the morphometric analysis. Only 2 of the birds collected were juveniles, both from Lake Okeechobee; these were excluded from all analyses.

We measured body mass, bill length to gape, exposed culmen, bill width, bill depth, tarsus length, wing chord, and tail length of each bird carcass (e.g., Pyle et al. 2008). Swampheens are sexually dimorphic (Marchant and Higgins 1993), and therefore, sex determination is an important factor in considering morphologic differences among sites. Hence, we determined sex with a genetic analysis of feathers plucked from each individual. Sex could not be determined for 2 of the birds, and we excluded them from the morphology analysis. We employed PRIMERV6 software for multivariate statistics (Clarke and Gorley 2006) to quantify morphometric differences among sites. We used multi-dimensional scaling (MDS) with a Euclidian-distance similarity matrix to visualize similarities or differences among sites, and analysis of similarity (ANOSIM) to determine if there were significant differences among groups (Clarke and Gorley 2006). The data were normalized via a base-10 log-transformation before performing the analysis to account for the difference in morphological measurement types.

Results

Diet

The macroscopic-level sorting procedure showed a low diversity of food types, which we confirmed with microscopic analysis. *Eleocharis cellulosa* Torr. (Gulf-coast Spikerush) was the dominant plant consumed (Table 1), comprising more than 70% of the average dry weight of birds' diets from Lake Okeechobee and WCA2B, and about 50% from STA1W. Gulf-coast Spikerush also occurred in 100% of Swampshen samples from both WCA2B and Lake Okeechobee, and 96% of samples from STA1W. Birds from STA1W had a more diverse diet than birds from other sites. Only 3.3% of the average dry weight was unidentified (Table 1). Additionally, we observed no grit in the stomachs of birds from WCA2B, whereas 25% and 59% of samples from Lake Okeechobee and STA1W, respectively, contained grit. Six birds consumed insects, but all specimens were small and presumed to have been consumed incidentally. Two birds consumed lepidopterans. Fifty percent of Swampshens from WCA2B had mollusks in their stomachs, whereas only 1 sample from STA1W had a mullosk, and we found no mollusks in samples from Lake Okeechobee.

Purple Swampshen diets differed among the 3 sites ($R = 0.525$, $P < 0.001$; Fig. 2). The SIMPER analysis uses dissimilarity to demonstrate the degree to which food items contribute to the difference of diet among sites; therefore, 2 pairwise tests

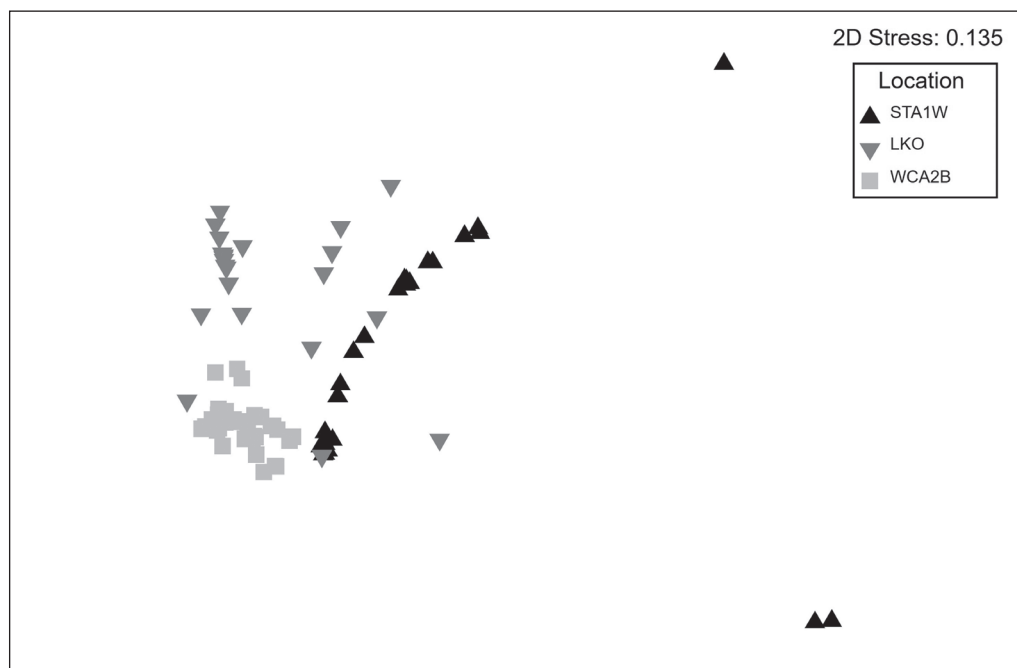


Figure 2. An MDS plot demonstrating the similarity/dissimilarity of Purple Swampshen diets for STA1W = Stormwater Treatment Area 1W, WCA2B = Water Conservation Area 2B, and LKO = Lake Okeechobee in south Florida of samples collected from January to March 2014. The ordination was performed using a Bray-Curtis similarity matrix.

Table 1. Biomass estimates of food items in Purple Swamphen stomachs from Stormwater Treatment Area 1W, Water Conservation Area 2B, and Lake Okeechobee in south Florida January to March 2014. The numbers in parentheses indicate the sample size for the corresponding area. % of PUSW = the percent occurrence in the Swamphens (i.e., the number of Swamphens that consumed a particular item from that sampling site). + indicates that the item was present but comprised less than 1.0% of the mass.

| Items in diet | Water Conservation Area 2B (n = 32) | | | Lake Okeechobee (n = 24) | | | Stormwater Treatment Area 1W (n = 27) | | |
|---------------------------------|-------------------------------------|---------------------------|-----------|--------------------------|---------------------------|-----------|---------------------------------------|---------------------------|-----------|
| | Average % dry wt | % occurrence of food item | % of PUSW | Average % dry weight | % occurrence of food item | % of PUSW | Average % dry weight | % occurrence of food item | % of PUSW |
| Plant material | | | | | | | | | |
| <i>Eleocharis cellulosa</i> | 79.6 | 27.8 | 100.0 | 72.5 | 44.4 | 100.0 | 49.3 | 32.9 | 96.3 |
| <i>Typha</i> sp. | | | | | | | 1.2 | 19.0 | 55.6 |
| <i>Cladium jamaicense</i> seeds | 9.4 | 22.6 | 81.3 | + | 3.7 | 8.3 | + | 3.8 | 11.1 |
| <i>Panicum</i> spp. seeds | 5.3 | 14.8 | 53.1 | | | | | | |
| <i>Eleocharis</i> spp. seeds | + | 2.6 | 9.4 | 21.8 | 33.3 | 75.0 | | | |
| <i>Typha</i> seeds | | | | | | | 3.6 | 2.5 | 7.4 |
| Insecta spp. | + | 4.3 | 15.6 | + | 1.9 | 4.2 | | | |
| Lepidoptera spp. | + | + | 3.1 | | | | + | 1.3 | 3.7 |
| Mollusk sp. | 3.3 | 13.9 | 50.0 | | | | + | 1.3 | 3.7 |
| Grit | | | | 5.1 | 11.1 | 25.0 | 35.3 | 20.3 | 59.3 |
| Shot pellets | | | | | | | 7.1 | 2.5 | 7.4 |
| Unknown plant matter | 2.1 | 13.0 | 46.9 | + | 5.5 | 12.5 | 3.3 | 16.5 | 48.1 |

were conducted for each site location (Table 2). *Panicum* spp. (panic grasses) seeds, only present in WCA2B, accounted for 46% of the dissimilarity between WCA2B and Lake Okeechobee, whereas they accounted for 30% of the dissimilarity between STA1W and WCA2B. Likewise, grit, only present in STA1W and Lake Okeechobee, accounted for 42% of the dissimilarity between WCA2B and STA1W.

Selectivity

We identified 6 species of emergent aquatic plants—Gulf-coast Spikerush, panic grasses, *Nymphaea odorata* Aiton (American White Water-lily), *Cladium jamaicense* (Crantz.) Kük. (Jamaican Swamp Sawgrass), *Typha* spp. (cattails), and *Pontedaria cordata* L. (Pickerelweed)—and 1 submerged aquatic plant (*Utricularia* spp. [bladderwort]) in the 10 plots. The 2 most-abundant emergent species were Gulf-coast Spikerush (10.5%, 9.3%, and 9.0% cover) and American White Water-lily (7.3%, 7.0%, and 8.0% cover) at the 5 x 5-m, 3 x 3-m, and 1 x 1-m plots, respectively.

Swamphens at WCA2B selected Gulf-coast Spikerush at each of the 3 hierarchical levels at which we carried out the vegetation surveys (Table 3). We also found that Swamphens selected Jamaican Swamp Sawgrass seeds, but that selection was weaker than selection for Gulf-coast Spikerush. Swamphens consumed Jamaican Swamp Sawgrass much less often than Gulf-coast Spikerush.

Table 2. Dissimilarity in food items between pairs of study sites from samples collected from January to March 2014. STA1W = Stormwater Treatment Area 1W, WCA2B = Water Conservation Area 2B, and LKO = Lake Okeechobee, in south Florida. Food items are listed in order of decreasing contribution. Cum. % dis. = cumulative percent dissimilarity.

| STA1W vs. LKO | | WCA2B vs. LKO | | STA1W vs. WCA2B | |
|-------------------------|-------------|-------------------------|-------------|----------------------|-------------|
| Food items | Cum. % dis. | Food items | Cum. % dis. | Food items | Cum. % dis. |
| Grit | 41.94 | <i>Panicum</i> seeds | 46.57 | <i>Panicum</i> seeds | 30.41 |
| <i>Eleocharis</i> | 64.34 | <i>Eleocharis</i> | 63.10 | Grit | 57.66 |
| Shot pellets | 75.46 | <i>Eleocharis</i> seeds | 73.81 | <i>Eleocharis</i> | 82.25 |
| <i>Eleocharis</i> seeds | 83.86 | Grit | 82.69 | Shot pellets | 90.24 |
| <i>Cladium</i> seeds | 88.91 | <i>Cladium</i> seeds | 88.50 | | |
| <i>Typha</i> flower | 93.67 | Unknown | 93.75 | | |

Table 3. Mean food-type selectivity (Chesson's index, a_i ; 95% CI) across all 32 individuals from Water Conservation Area 2B for each of the 3 plot sizes. All values for Gulf-coast Spikerush are greater than 1/m, which indicates selection of this prey type at all levels. Refer to the methods for a further explanation of how to interpret Chesson's index.

| Food item | Plot size | | | 1/m |
|-----------------------------|----------------------------|----------------------------|----------------------------|-------|
| | 5 m x 5 m Mean (95% CI) | 3 m x 3 m Mean (95% CI) | 1 m x 1 m Mean (95% CI) | |
| <i>Eleocharis cellulosa</i> | 0.587 (0.463–0.680) | 0.554 (0.429–0.680) | 0.350 (0.232–0.468) | 0.143 |
| <i>Cladium jamaicense</i> | 0.290 (0.185–0.394) | 0.385 (0.265–0.505) | 0.534 (0.404–0.665) | 0.143 |
| <i>Panicum</i> spp. | 0.124 (0.048–0.199) | 0.061 (0.011–0.111) | 0.115 (0.037–0.194) | 0.143 |

Morphology

In total, we sampled 83 Swampheens across the 3 sites; STA1W ($n = 27$), WCA2B ($n = 31$), and Lake Okeechobee ($n = 25$). The morphology of adult Swampheens differed significantly among study sites (Global $R = 0.164$, $P < 0.001$; Fig. 3), and all pairwise differences were significant. However, based on estimates of R , the magnitude of the differences was much larger between birds from STA1W and WCA2B ($R = 0.236$, $P < 0.001$) than between those from STA1W and Lake Okeechobee ($R = 0.154$, $P < 0.008$) or WCA2B and Lake Okeechobee ($R = 0.098$, $P < 0.01$). Birds in STA1W had the largest mean body mass, bill length to gape, exposed culmen, bill depth, bill width, and wing chord (Table 4).

Discussion

Diet

Prior to this study, the diets of Swampheens in Florida had not been quantified. Pranty (2012) reported that the birds were predominantly herbivorous but that they also took some small invertebrate prey. A diet study of Swampheens from their native range in Australia found that they primarily ate plants from the Poaceae (59%), Cyperaceae (17%), and Hydrocharitaceae (11%) families (Norman and Mumford 1985). Our study confirmed that Swampheens in Florida are also predominantly herbivorous. However, as opposed to a generalist diet, we found a strong selection for Gulf-coast Spikerush (Cyperaceae). At 2 of the 3 study sites, Swampheens

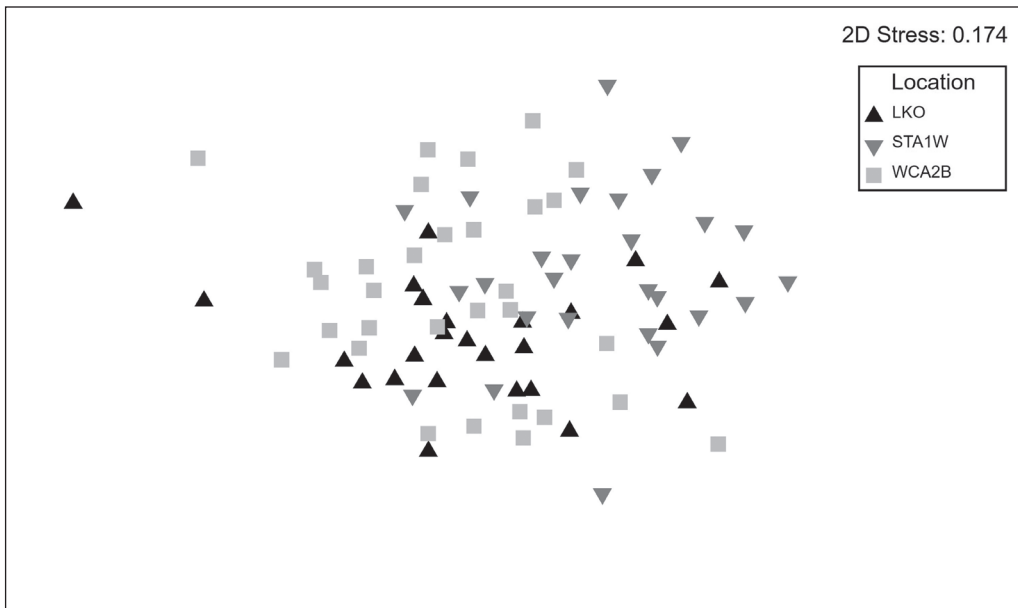


Figure 3. An MDS plot showing the morphometric similarity/dissimilarity of individual Purple Swampheens from STA1W = Stormwater Treatment Area 1W, WCA2B = Water Conservation Area 2B, and LKO = Lake Okeechobee in South Florida of samples collected from January to March, 2014. The ordination was performed using a Euclidean distance similarity matrix.

Table 4. Morphological characteristics of 85 Purple Swamphens collected from Stormwater Treatment Area 1W, Water Conservation Area 2B, and Lake Okeechobee in south Florida, January to March 2014. The number of decimal places present in the table corresponds to the level of accuracy that was achieved while measuring that particular morphological characteristic.

| Morphological characteristic | Water Conservation Area 2B (n = 31) | | | | Lake Okeechobee (n = 25) | | | | Stormwater Treatment Area 1W (n = 27) | | | |
|------------------------------|-------------------------------------|--------|-------|------|--------------------------|--------|-------|------|---------------------------------------|--------|--------|------|
| | Min | Max | Mean | SD | Min | Max | Mean | SD | Min | Max | Mean | SD |
| Body mass (g) | 505 | 730 | 621 | 57 | 555 | 850 | 689 | 81 | 570 | 815 | 702 | 66 |
| Bill length to gape (mm) | 21.48 | 32.47 | 25.28 | 2.57 | 21.73 | 27.72 | 24.84 | 1.74 | 23.34 | 29.61 | 26.07 | 1.61 |
| Exposed culmen (mm) | 25.59 | 39.85 | 33.68 | 2.87 | 32.49 | 38.41 | 34.73 | 1.72 | 32.02 | 39.41 | 35.45 | 1.91 |
| Bill depth (mm) | 20.13 | 24.52 | 22.40 | 1.24 | 20.79 | 25.71 | 23.33 | 1.57 | 21.42 | 27.17 | 24.32 | 1.32 |
| Bill width (mm) | 10.86 | 15.74 | 13.47 | 1.32 | 12.01 | 15.84 | 14.19 | 0.82 | 11.63 | 16.17 | 14.39 | 1.23 |
| Tarsus length (mm) | 84.93 | 109.12 | 96.32 | 6.28 | 84.38 | 106.04 | 95.77 | 5.63 | 93.16 | 112.54 | 102.90 | 4.88 |
| Wing chord (mm) | 22.3 | 25.9 | 24.0 | 0.8 | 22.4 | 25.0 | 23.7 | 0.8 | 21.5 | 26.7 | 24.5 | 1.3 |
| Tail length (mm) | 7.3 | 9.2 | 8.2 | 0.6 | 6.9 | 8.7 | 7.7 | 0.5 | 7.2 | 9.4 | 8.2 | 0.5 |

consumed predominantly 1 plant species rather than a more even mix of species. The higher use of Cyperaceae in Florida than in Australia likely reflects the availability of plants in the environment. However, the narrower range of plant species consumed by birds in Florida demonstrates that across their range, Swampheens have the ability to specialize on specific plant species to different degrees.

Although we found a small percentage of animal matter in the diet of Swampheens, caution in interpretation is warranted because the birds were collected during a single dry season; inferences about diet should be restricted to that period. It is possible that we missed seasonal switches from one food item to another. For instance, Balasubramaniam and Guay (2008) noted that in their native range, Swampheens consumed *Cygnus atratus* (Latham) (Black Swan) eggs. Indeed, the closest relative of the Swampheens here in south Florida, the Purple Gallinule, has a diet that varies greatly with seasonality and locality (West and Hess 2002). More than 50% of the diet of Gallinules during spring and summer is animal material such as arthropods, annelids, and mollusks (Mulholland and Percival 1982). We did not investigate spring and summer diets.

A broad diet is a trait associated with successful establishment by exotic species (Blackburn et al. 2009). Swampheens have successfully established in a number of locations and, although they are reported to be generalists, diets in our study had a narrow breadth. There are several possible reasons for this apparent inconsistency. Swampheens in Florida are already well established, which makes it possible that the species initially had a wider diet breadth which narrowed once they were successfully established (Overington et al. 2011). If true, this pattern would support Wright et al.'s (2010) "adaptive flexibility hypothesis" in which they predicted a decline in behavioral diversity during the establishment of a population due to successful strategies being learned and taught.

Similar to diets of Purple Gallinule and *Gallinula galeata* (Lichtenstein) (Common Gallinule), the diet of the Swampheens in our study was dominated by plant, not animal matter (Bannon and Kiviat 2002, West and Hess 2002). Both of these gallinule species have been known to feed on exotic plants (Mulholland and Percival 1982), demonstrating that they are generalists and can shift their diet in response to the available plant community. The Swampheens' and gallinules' shared ability to be generalists and to sometimes specialize on certain species could lead to high diet overlap.

Selectivity

Resource selection occurs in a hierarchical fashion. First-order selection is the physical or geographical range of a species, 2nd-order selection represents the home range of an individual or group of individuals, 3rd-order selection is the use of habitat components within a home range, and 4th-order selection is the use of particular food items (Johnson 1980). Based on anecdotal evidence that showed large "eat-outs" of Gulf-coast Spikerush from Lake Okeechobee (T. Beck, FWC, pers. comm.), we hypothesized a priori, and subsequently confirmed, that Swampheens selected the spikerush in the WCA2B site at the 4th-order selection level. We

utilized 3 different-sized plots due to the hierarchical process of habitat selection. However, we did not sample vegetation at lower-order levels of selection, so we do not know whether Swampheens were selecting Gulf-coast Spikerush at those levels as well. In addition, we found weak selection for *Cladium* seeds, which we would expect to vary seasonally because of plant phenology, and thus, availability.

Morphology

Body size in birds is often related to habitat quality (Johnson 2007), suggesting that the STAs may provide better habitat for Swampheens than the other sites. Given how quickly Swampheens have expanded their range across the region, it is surprising to find significant differences in morphological measurements among the study sites. This pattern is puzzling because Swampheens were clearly selecting for Gulf-coast Spikerush, but they were largest in STA1W, where the spikerush made up the smallest proportion of their diet. The strong selection for this plant in the area where the birds were smallest suggests that factors other than plant species may play a role in habitat quality, or alternately, the benefit of the spikerush is not reflected in body size but rather some demographic response, such as productivity. If Swampheens habitat quality is determined by plant-community characteristics and trophic status, then quantification of these effects could be used to model future range-expansion in Florida. Alternatively, body size differences could result from some form of character displacement (Grant and Grant 2006); there may have been slight differences in the avifauna present at each of the 3 study sites.

Conclusion

This study provides a quantitative basis for the perception that the Swampheens in south Florida utilize Gulf-coast Spikerush as a main food resource. Given that the spikerush is widespread and fairly abundant throughout Florida and the southeast US, it is not likely to limit the Swampheens' distribution. It is uncertain how this preference for Gulf-coast Spikerush and the likely expansion of Swampheens throughout Florida might impact native species. Potential effects of resource competition could be evident for other species that rely heavily on this plant species. Gulf-coast Spikerush is generally known to provide habitat and food for a variety of fish, invertebrates, and waterfowl. Additionally, our study presents observations that suggest that divergent evolution may have taken place among 3 different populations of Swampheens in a short period of time. The combination of the Swampheens' diet as well as this potential divergent evolution make this species an excellent candidate for future studies of potential impacts to the native fauna in south Florida.

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