

DIPTERAN STANDING STOCK BIOMASS AND EFFECTS OF AQUATIC BIRD PREDATION AT A CONSTRUCTED WETLAND

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Abstract: We studied the relationship between benthic invertebrates and aquatic birds at a newly constructed wetland using an avian exclosure experiment combined with counts of aquatic bird use. We measured the standing stock biomass of benthic dipterans both inside and outside exclosures. Chironomidae was the most abundant dipteran family present. Maximum chironomid standing stock biomass per pond ranged from 3.62 to 27.82 g/m² and was comparable to that found in a number of natural systems. We monitored the abundance of ten aquatic birds species. Abundances of three aquatic bird species [American avocet (*Recurvirostra americana*), Wilson's phalarope (*Phalaropus tricolor*), and cinnamon teal (*Anas cyanoptera*)] were significantly correlated with chironomid and total dipteran densities. Our experiment, however, found no significant effect of predation on invertebrate densities.

Key Words: constructed wetland, diptera, aquatic birds, chironomid, American avocet, Wilson's phalarope, predation

INTRODUCTION

Wetlands are critical habitats for many avian species (Schneider 1978). By the 1980s, wetlands in the United States had been reduced by 53% (Johnston 1994), with California the most severely affected (Dahl 1990, Johnston 1994). In response to such habitat losses, wetland construction has become a common strategy for wildlife enhancement (Salverson 1990).

Monitoring the value of constructed wetlands for avian species is typically based on the number of birds present (McKinstry and Anderson 1994). However, a clearer picture of the ecological value of a constructed wetland may be gained by studying critical avian food resources, for example, aquatic invertebrates (Hothem and Ohlendorf 1989).

Chironomids spend the majority of their life cycle in the aquatic larval stage (Oliver 1971, Pinder 1986). The larvae are mostly infaunal but can be epibenthic or pelagic. They must ascend to the surface after pupation to emerge (Oliver 1971, Pinder 1986). They are thus available, during different life stages, to aquatic birds with different feeding behaviors. Chironomid larvae are an important dietary component for American avocets (*Recurvirostra americana* Gmelin) (Hothem and Ohlendorf 1989), Wilson's phalaropes (*Phalaropus tricolor* Vieillot), and cinnamon teal (*Anas cyanoptera* Vieillot). American avocets were the predominant breeding bird of ten species that foraged at our research site.

We studied wading bird response to aquatic dipteran

larvae in constructed wetlands and the effect of avian predation on aquatic dipteran abundance. Our primary objectives were to (1) quantify the standing stock biomass of aquatic dipterans, chironomids in particular; (2) determine if presence of aquatic birds was related to density of their invertebrate prey; and (3) to assess if aquatic bird predation affected invertebrate densities. A secondary objective was to use these quantitative measures to make a qualitative assessment of the ecological function of the constructed wetland.

METHODS

Study Area

Sampling was conducted in 1993 at the Jay Dow, Sr. Wetlands (JDW), a field research facility of the University of Nevada, Reno, which was constructed during 1991 and 1992. JDW is located in Lassen County, California, USA (40°3'N, 120°12'W) within the historic reaches of Pleistocene Lake Lahontan (Benson 1978).

The overall wetland site consists of 13 ponds, divided into four complexes (A–D) of interconnected ponds supplied with water from three wells. Pumping from these wells allows for maintenance and manipulation of water levels. The ponds we sampled were filled for six to eight months beginning in February 1992. Natural, ephemeral ponds existed at this site prior to wetland construction. The land formerly was in alfalfa production, as is much of the surrounding area. These wetlands were ideally suited for experimentation on avian invertebrate consumption because there were no fish and few amphibians at the time of the study. The system is shallow (<1 m), with nearly complete access to benthic invertebrates by wading and dabbling aquatic birds. The study ponds were free of emergent macrophytes, and all experienced filamentous algae blooms.

Field Methods

The primary research goal at the wetlands is the study of American avocet life history traits and behavior. Therefore, we chose our study ponds and study sites within ponds based primarily upon lowest potential disruption of avocet nesting behavior. Other factors regarding pond selection were accessibility of sediments to foraging aquatic birds and vehicular access (Figure 1). Even though some ponds were excluded due to high nesting densities, we did not consider this problematic as nesting birds moved freely among the ponds for feeding. The study ponds varied somewhat in size: Pond 1 (Complex A) area = 7.28 ha, Pond 5 (Complex B) area = 8.90 ha, Pond 10 (Complex D)

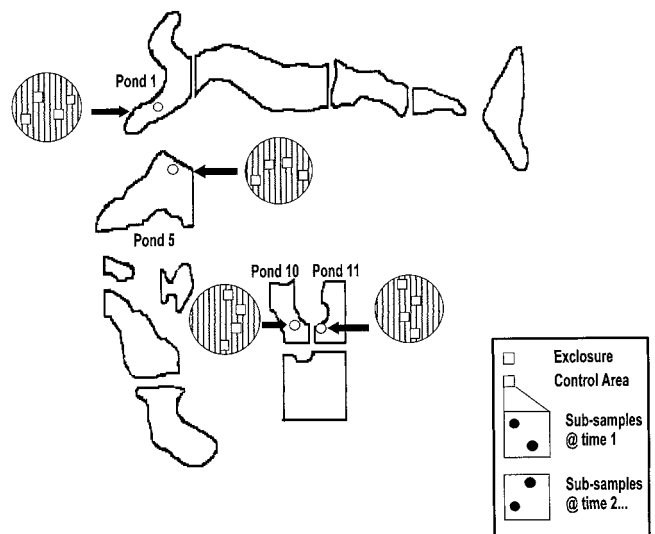


Figure 1. Relative positions of four ponds at the Jay Dow, Sr. Wetlands. Shaded circles indicate general position of control and experimental plots in study ponds. Inset shows example of sub-sampling pattern to prevent overlaps.

area = 6.48 ha, and Pond 11 (Complex D) area = 9.71 ha. Estimated Avocet nest density (nests/ha of ponds) also varied between complexes: Complex A = 10.8, Complex B = 2.4, Complex C = 6.0, Complex D = 6.8.

We identified study areas at each study pond that met our minimum disturbance and sampling criteria and that were characterized by continuous habitat type, eliminating the need to stratify sampling (Murkin et al. 1994). The experimental plots were placed centrally, with control plots ≥ 15 m away to reduce the potential negative effect of cage presence on foraging at control plots. We constructed 1-m \times 1-m \times 95-cm-high exclosures with 2.54 cm polyvinyl chloride (PVC) tubing covered with 2.54 cm mesh wire. Control plots were marked with a PVC stake, delineating the southwest corner of an imaginary quadrat having the same dimensions as exclosures. Invertebrates were sampled weekly between 13 April and 13 July 1993 with the exception of one two-week interval in June.

We collected benthic invertebrates with a transparent plastic coring tube (15.2 cm² sample cross section, 28 cm long), externally marked at one-centimeter intervals. Samples were taken by pressing the sharpened tube into the substrate until substantial resistance was met. The tube was capped and manually withdrawn. The pond substrate and the overlying water were retained within the tube. Substrate samples and water were transferred to labeled glass bottles and fixed with 10% formalin. We felt that this technique ensured accurate sampling of benthos, as primary substrates differed in hardness (Pond 5 > Pond 10 = Pond 11 > Pond 1), and it is unlikely that many invertebrates bur-

rowed below sampling depth because of the dense clay present in ponds. Average core depth was 10.5 ± 1.0 cm. Two subsamples were collected from each cage and control plot on each sampling date. We selected the subsampling locations within each plot to prevent overlap with previous extractions. We recorded water depth at each plot each sampling period.

Avian counts were conducted weekly in the morning (0800–1100 h) using a team approach (one person spotting and another recording species counts). Observers counted all the birds using high quality 20–60× spotting scopes or binoculars, usually from the bed of a truck. Census activities posed no significant disturbances. Care was taken to avoid counting birds twice by having different sets of ponds counted simultaneously by the three teams. Eleven of the 13 benthic sampling dates coincided with the aquatic bird censuses.

Laboratory Methods

We washed substrate samples with tap water in a 425 μm USA Standard Testing Sieve (No. 40) to remove fine sediment and other detritus. Invertebrates were separated by flotation on a saturated sucrose solution (Wetzel and Likens 1991). We washed floated invertebrates and organic matter with deionized water and stored them in 70% isopropanol. To test efficiency of the flotation method, we examined 18 random samples of residue and found that we recovered >97% of the dipterans.

We manually sorted samples using a 30× binocular dissecting microscope. Dipterans were identified to family according to Merritt and Cummins (1984). We counted all dipteran larvae. We dried the ten largest control plot samples of chironomids from each pond at 90°C for >48 hours and weighed them to the nearest 0.1 mg to determine standing stock biomass. These samples were representative of peak abundances and spanned the period 19 April to 22 June. We analyzed chironomid standing stock biomass as a function of water depth and pond area using the GLM module in Systat 7.0 (SPSS 1996).

We conducted analyses of variance for the enclosure experiment using SAS (SAS 1988). We tested the null hypothesis of no effect of avian predation on dipteran abundance by comparing the number of dipterans within enclosures to the number in control plots. Blocking by pond was conducted to partition habitat effects.

We constructed F-tests for a design including repeated measures and subsampling. As such designs can be prone to pseudoreplication, we followed the approach to complex designs advocated by Milliken and Johnson (1992). This design consisted of three levels of analysis

with different errors forming the denominator degrees of freedom for each level. The first level of variance was treatment ($df = 1$) and was tested over error(cage), which is equivalent to ponds(treatment) in a nested design ($df = 14$). We then evaluated the variance due to time (i.e., the repeated measures portion of the design). The factors time ($df = 12$) and time*treatment ($df = 12$) were tested over error(time), which is equivalent to time*pond(treatment) and has 152 degrees of freedom. Finally, we tested variance due to subsampling. Factors for this level of analysis were subsamples ($df = 1$), subsamples*treatment ($df = 12$), subsamples*time ($df = 1$), and subsamples*treatment*time ($df = 12$). All subsampling factors were tested over the error (subsamples), which is equivalent to subsamples*time*pond (treatment) and had 166 degrees of freedom.

After analyzing the complete design, we evaluated the contribution of subsampling and all interaction effects containing subsampling. If they were not significant, we used the mean of the two subsamples as a new response variable to collapse the design into a typical repeated measures analyses of variance (SAS 1988), blocking by pond. Thus, the re-analysis after averaging the two subsamples had half the total number of observations. The use of the repeated measures design prevented pseudoreplication in the testing of main effects. To avoid exclusion of an entire experimental unit when data for one sampling date were missing from the time series (four cases), we approximated missing values as the means of response variables taken during previous and subsequent weeks.

We compared avian abundance to both chironomid and total dipteran abundance using correlation analyses. Those bird species that showed a significant correlation were used as dependent variables in a repeated measures analysis of covariance, ANCOVA (SPSS 1996). The first ANCOVA tested avian abundance against pond with chironomid density as a covariate; the second analysis tested avian abundance against pond with total dipteran density as a covariate. We also tested avian density (birds/hectare) against chironomid density with a repeated measures ANOVA to control for pond size. These analyses were limited to those eleven dates on which we had both avian and dipteran abundance measures.

RESULTS

We collected four families of aquatic dipterans during the sampling period. Chironomidae, Tabanidae, and Tipulidae were found in all four ponds, while Ceratopogonidae were only found in Ponds 1 and 10. Chironomids were relatively abundant in all four ponds at the start of sampling, but their numbers decreased during the study (Figure 2). Conversely, tabanids were

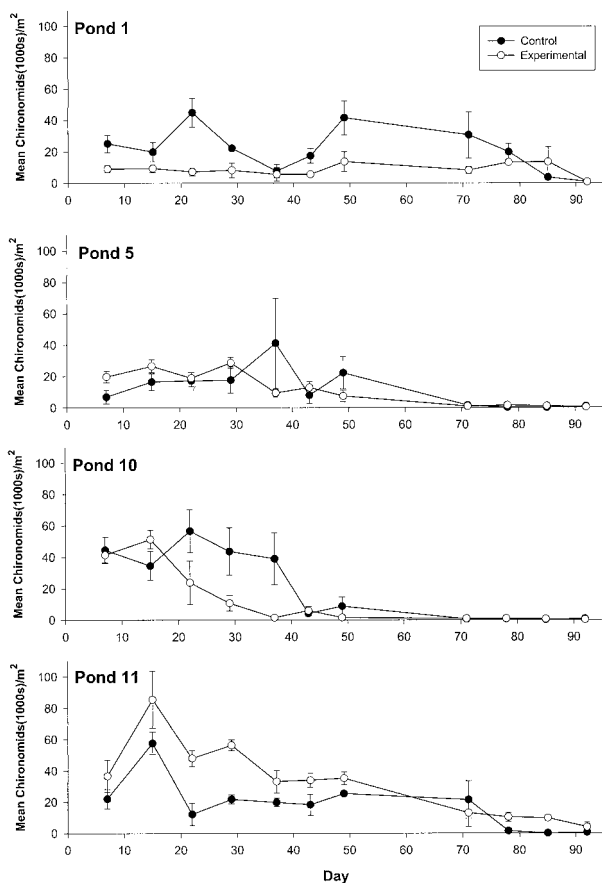


Figure 2. Average benthic chironomid density by pond and treatment for the eleven periods coinciding with avian counts. Error bars represent one standard error.

rare until the latter part of the study (Figure 3), and their increase correlates with the decrease in chironomid densities ($F = 2.48$, $df = 42$, $P = 0.002$). The remaining two dipteran families were rare overall.

Water depth ranged from 17 to 28 cm at the start of the study. Water level fluctuated from week to week. The direction of change was the same across ponds except when well water was added to one pond and not the rest ($n = 1$). Average water depths across the study were 16.5 cm for Pond 1, 16.1 cm for Pond 5, 17.7 cm for Pond 10, and 25.5 cm for Pond 11.

Chironomids varied in length from 1 to >15 mm within weighed samples, suggesting that a number of instars were present in the ponds. Adults midges were present at the ponds, and emerging adults were regularly found in the samples throughout the study period. There was considerable variation in average dry mass of chironomid larvae among ponds (Table 1). Maximum standing stock biomass was sensitive to water depth ($R^2 = 0.29$, $df = 1$, $P = 0.001$) but not to pond area ($R^2 = 0.06$, $df = 1$, $P = 0.15$). Estimated maximum chironomid dry mass varied from 3.62 (Pond 5) to 27.82 g/m² (Pond 10) (Table 1), yielding a maxi-

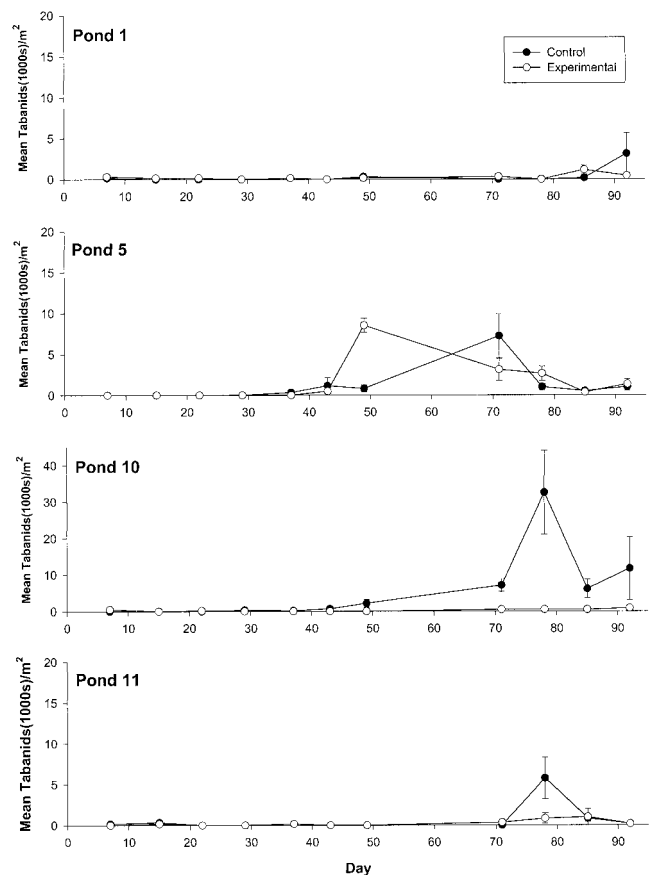


Figure 3. Average benthic tabanid density by pond and treatment for the eleven periods coinciding with avian counts. Error bars represent one standard error.

imum potential caloric value of these larvae ranging from 18.46 to 141.88 k-cal/m² (Maxson and Oring 1980).

American Avocet, American coot (*Fulica americana* Gmelin), black-necked stilt (*Himantopus mexicanus* Müller), cinnamon teal, gadwall (*Anas strepera* Linnaeus), killdeer (*Charadrius vociferous* Linnaeus),

Table 1. Average maximum standing stock biomass and estimated maximum standing stock biomass of chironomids per square meter based on ten samples with the highest chironomid counts for each pond. The ranges and standard errors reflect the temporal variability of chironomid density.

	Pond	Mean	Range	SE
Average Maximum Biomass (µg/individual)	1	0.15	0.30	0.04
	5	0.05	0.12	0.01
	10	0.25	0.46	0.05
	11	0.32	0.79	0.07
Estimated Maximum Biomass (g/m ²)	1	8.92	22.89	2.58
	5	1.39	3.16	0.34
	10	15.86	25.19	3.15
	11	13.08	22.36	2.15

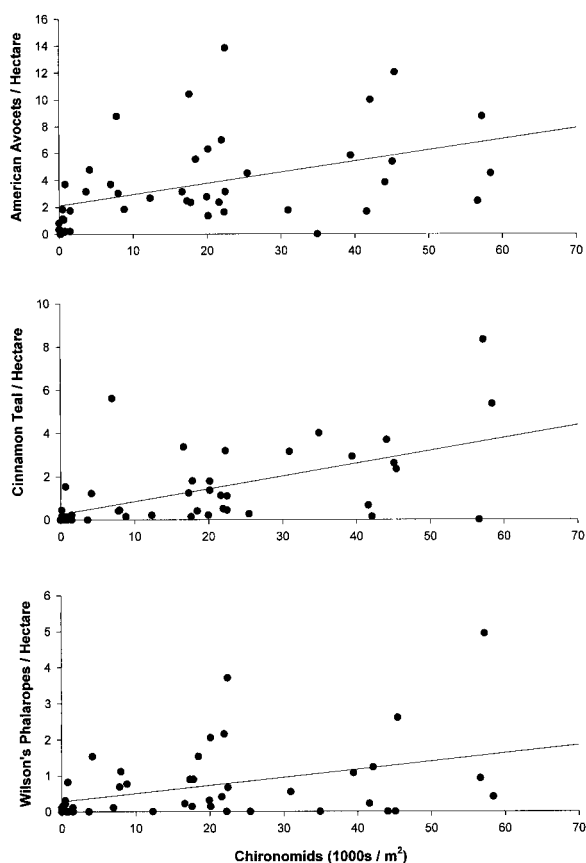


Figure 4. American avocet, cinnamon teal, and Wilson's phalarope density relative to Chironomid density.

mallard (*Anas platyrhynchos* Linnaeus), northern pintail (*Anas acuta* Linnaeus), willet (*Catoptrophorus semipalmatus* Gmelin), and Wilson's phalarope were present throughout the study. Avian abundance varied for all species both among ponds and across time. American avocet ($\rho = 0.59$, $df = 42$, $P = 0.002$) and Wilson's phalarope ($\rho = 0.47$, $df = 42$, $P = 0.04$) counts showed significant positive correlations while cinnamon teal ($\rho = 0.42$, $df = 42$, $P = 0.06$) did not show a significant correlation with chironomid densities (Figure 4). The P-values for the Spearman correlations (ρ) are minimum simultaneous significances, corrected for test non-independence and to control for the experiment-wise error rate (Rice 1989). Avian abundance by pond was significantly positively correlated to chironomid ($F = 11.56$, $df = 1$, $P = 0.002$) and total dipteran abundance ($F = 10.02$, $df = 1$, $P = 0.003$). American avocet ($F = 9.76$, $df = 1$, $P = 0.003$), cinnamon teal ($F = 13.95$, $df = 1$, $P = 0.0001$), and Wilson's phalarope ($F = 7.25$, $df = 1$, $P = 0.01$) densities (birds/hectare) were significantly related to chironomid density (Figure 4).

Subsample densities within both exclosures and control plots were not significantly different for any of

the invertebrates measured. There was a significant subsample*treatment interaction for tabanids, but given the pattern for other invertebrate measures and the number of samples, this probably represents a Type I error. Therefore, we used means of subsamples and repeated measures analyses to compare exclosure to control plot dipteran abundances. Time was a highly significant factor of both chironomid ($F = 11.95$, $df = 12$, $P = 0.0001$) and total dipteran variability over the length of the study ($F = 11.89$, $df = 12$, $P = 0.001$). Pond was a necessary blocking factor and accounted for a significant amount of the weekly variability for chironomids and total dipterans. There were, however, no significant treatment (exclosure) effects on either chironomid ($F = 0.247$, $df = 1$, $P = 0.621$) or total dipteran densities ($F = 0.252$, $df = 1$, $P = 0.617$).

DISCUSSION

Two years post-construction, JDW supported a variety of aquatic dipterans and a relatively high maximum standing stock biomass (SSB) (Table 1). The chironomid SSB maxima of the wetland complex exceeded average estimated SSB of chironomids in a southeastern United States wetland study by up to an order of magnitude (Duffy and LaBar 1994). Average dipteran abundances were comparable to those from studies in a variety of freshwater habitats (Thorpe and Bergey 1981, Benke et al. 1984, Batzer and Resh 1992, Duffy and LeBar 1994, Rader and Richardson 1994). Given differences in abundances among different ponds that we observed and the variation observed in the aforementioned studies, experimental comparisons of constructed and natural wetlands are extremely difficult to conduct, and they require logistical arrangements that are not generally available for most wetland restoration projects. However, one component of the aquatic bird habitat value of a constructed wetland can be qualitatively evaluated by comparing observed densities of aquatic dipteran populations with values measured in other studies.

Differences in dipteran abundances among ponds suggest that factors such as pond-filling history, chemical characteristics of water from different wells, substrate composition, water depth, aquatic and emergent vegetation, and bottom slope might be significant factors influencing invertebrate abundance in these constructed ponds (Murkin et al 1994). Variation in timing of invertebrate population maxima may have reflected responses to differing water temperature, proportion of algal cover, age of the ponds, and food availability (Danks 1978). Adult chironomids were observed and pupae were present in core samples throughout the study, suggesting continued development during the

period. Even with the variability observed among ponds, dry SSB figures of chironomids alone indicate the potential forage value for aquatic birds that can be achieved in constructed wetlands (Table 1).

Of many experiments assessing predator impacts on benthic invertebrates, some have shown no impact by predation on macroinvertebrate populations (Bay 1974, Virnstein 1978, Quammen 1984, Schneider 1985), while others have demonstrated significant reductions of prey densities by predation (Schneider 1978, Quammen 1981, Schneider and Harrington 1981, Wilson 1989, Wilson 1991, Székely and Bamberger 1992, Mercier and McNeil 1994). Our results support the idea that American avocets, Wilson's phalaropes, and cinnamon teal behaviorally tracked the abundance of chironomid and dipteran densities and were likely foraging on these invertebrates. Despite this foraging pressure, chironomid and total dipteran numbers seemed resilient to predation.

The lack of a detectable impact may have been an artifact of the exclosures themselves as evidenced by the number of periods when abundance within exclosures was lower than controls. Wrubleski and Rosenberg (1984) noted that devices that remain in the environment for long periods, such as emergence traps, can, depending upon their composition, cause overestimates of chironomid abundance by providing a favorable substrate for larvae. Unlike that example, few chironomid larvae were observed on the submerged portions of our cages during sampling. Conversely, exclosures may have made the internal environment less amenable than external conditions for dipterans, as large masses of filamentous algae occasionally accumulated on the mesh and potentially altered food-particle distribution (Virnstein 1978). Because of this, the abundance of chironomids within cages may have been decreased by outward migration. Davies (1976) noted that many chironomid species are able to disperse short distances in lacustrine habitats. As density within the cages increased, larvae may have migrated outward, seeking greater food availability.

The constructed wetland we studied provided nesting and foraging habitat for numerous aquatic birds, suggesting that constructed wetlands can be an effective form of mitigation of aquatic bird habitat loss due to development. Such wetlands can support a variety of aquatic invertebrates that provide food for aquatic birds. Invertebrate densities were similar to those measured in other studies of natural and constructed wetlands, suggesting natural ecological function in the constructed wetland. Our simultaneous study of benthic invertebrate densities and avian use indicated that several species of birds were responding to resource availability by feeding on ponds with the highest densities of invertebrates.

Although we did not detect a significant increase in invertebrate density when aquatic birds were excluded, two changes could be implemented in future studies that would improve the exclosure experiment. First, an alternative exclosure design should be considered. Second, given the nonsignificant impact of subsampling observed here, future studies could eliminate subsampling and increase the numbers of ponds and exclosures in the design. This would increase the power of the experiment to detect exclosure effects.

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