Wetlands
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ARTICLE

Impacts of Mute Swans (*Cygnus olor*) on Submerged Aquatic Vegetation in Illinois River Valley Backwaters

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Abstract Wetland loss in North America has been considerable and well documented, and the establishment of exotic species in remaining wetlands can further reduce their ability to support native flora and fauna. In the Chesapeake Bay and Great Lakes ecosystems, exotic mute swans (*Cygnus olor*) have been found to negatively impact wetlands through degradation of submerged aquatic vegetation (SAV) communities. Mute swan populations have expanded into many areas of mid-continental North America outside the Great Lakes ecosystem, but the environmental impact of these populations is not well known. Mid-continental wetlands in North America differ in physical characteristics (e.g., size, depth, and permanency) and aquatic vegetation species composition compared to wetlands in other areas where mute swans have been studied and, thus, may be more or less susceptible to degradation from swan herbivory. To investigate the impact of mute swan herbivory on SAV communities in mid-continent wetlands, we used exclosures to prevent swans from foraging in 2 wetland complexes in central Illinois. Above-ground biomass of vegetation did not differ between exclosures and controls; however, mean below-ground biomass was greater in exclosures (52.0 g/m^2, SE=6.0) than in controls (34.4 g/m^2 SE=4.0). Thus, although swan densities were lower in our study region compared to that of previous studies, we observed potentially detrimental impacts of swan herbivory on below-ground biomass of SAV. Our results indicate that both above-ground and below-ground impacts of herbivory should be monitored, and below-ground biomass may be most sensitive to swan foraging.

Keywords Competition · Degradation · Exotic species · Foraging · Wetlands

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Introduction

Wetland loss in North America has been considerable and well documented, with >50 % of pre-settlement wetlands in the United States lost and losses >90 % in some states (Tiner 1984; Dahl 1990). Exacerbating these losses, many remaining wetlands in the Upper Midwest have been degraded or lack productivity due to extensive sedimentation, eutrophication, and colonization by exotic plants and animals, which reduces their ability to support native flora and fauna (Bellrose et al. 1983; Havera 1999). For example, contemporary backwater wetlands in the Illinois River valley (IRV) are largely devoid of submerged aquatic vegetation (SAV), which was historically abundant (Stafford et al. 2010). Loss or degradation of SAV can dramatically impact the value of wetlands to native organisms by reducing refugia for aquatic invertebrates and fish and forage for invertebrates, fish, waterbirds, and aquatic mammals (Kiorboe 1980; Jonzen et al. 2002).

Introduced species may have unique life-history traits that lead them to become detrimental and considered invasive (Sakai et al. 2001). Several introduced species have been cited as major sources of wetland degradation in North America, notably the zebra mussel (*Dreissena polymorpha*), common carp (*Cyprinus carpio*), and mute swan (*Cygnus olor*). Exotic zebra mussels have impacted the Great Lakes ecosystem by altering the trophic structure, increasing water

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clarity, and increasing infiltration depths (Ludyanskiy et al. 1993; Effler et al. 1996). Similarly, common carp were introduced to the U.S. as a sport fish and are now found throughout North America. Carp can degrade wetlands through their destructive feeding behavior, which increases turbidity and decreases light penetration, which negatively impacts SAV (Mills et al. 1996; Angeler et al. 2001). In both the Chesapeake Bay and Great Lakes ecosystems, exotic mute swans have been found to negatively impact wetlands through degradation of SAV communities (Allin and Husband 2003; Petrie and Francis 2003; Tatu et al. 2007).

The mute swan has become recently established in central Illinois and is a concern to natural resources due to their rapid population growth and destructive herbivorous behavior. Mute swans are native to Eurasia and were introduced to the Atlantic coast in the late 1800 s, mostly through private collections (Bellrose 1980; Petrie and Francis 2003). Feral populations grew rapidly due in part to low predation and high reproductive rates, and populations now persist throughout the eastern half of the U.S. (Hindman and Harvey 2001; Petrie 2004). In the Atlantic Flyway, the mute swan population increased 147 % between 1987 and 2003 (Atlantic Flyway Council 2003), though it subsequently declined from a peak of 14,344 individuals in 2002 to 10,541 in 2008 (J. Osenkowski, Rhode Island Department of Environmental Management, personal communication). In the Mississippi Flyway, a similar trend has been documented, with the population increasing from 175 individuals in 1982 to >13,000 in 2006 (Mississippi Flyway Council Technical Section 2006). In areas where SAV is abundant and foraging habitat conditions are particularly attractive to mute swans, the trend is even more pronounced. In the Chesapeake Bay, the mute swan population increased by 1,200 % between 1986 and 1999 (Perry et al. 2004).

Regarding mute swan foraging, Bailey et al. (2008) reported that 94 % of mute swan diet samples contained SAV, most (72.4 % of biomass) of which were above-ground parts; however, they also consumed roots and tubers (Bailey et al. 2008). Mute swans can consume ~3.8 kg (wet weight) of SAV daily (Willey and Halla 1972). While foraging, mute swans rake the substrate to dislodge plants and roots leaving many parts of the plant unconsumed yet unable to regenerate (Tatu et al. 2007). Because mute swans are generally sedentary and do not migrate unless required (e.g., due to lack of open water or density-dependent dispersal), impacts from their diet and feeding methods can be concentrated and severe (Reese 1975; Perry et al. 2004). Sustained grazing pressure can inhibit SAV regeneration and has resulted in localized depletions of aquatic plants in the Chesapeake Bay (Perry et al. 2004; Tatu et al. 2007).

We are unaware of research investigating impacts of mute swan herbivory on below-ground plant material such as roots and tubers, and most evidence of below-ground herbivory comes from other, similar herbivores. For example, Badzinski et al. (2006) reported no difference in below-ground biomass of SAV in areas where tundra swans (*Cygnus columbianus*) and Canada geese (*Branta canadensis*) had been feeding compared to areas where they were excluded. Conversely, LaMontagne et al. (2003) found that trumpeter swans reduced biomass of sago pondweed (*Potamogeton pectinatus*) rhizomes and tubers by 24 % in Alberta wetlands. However, trumpeter swans (*Cygnus buccinator*) consume more below-ground structures than mute swans, and it is uncertain if mute swan herbivory would reduce below-ground biomass (LaMontagne et al. 2003; Bailey et al. 2008).

Mute swan populations have expanded into many areas of mid-continental North America outside the Great Lakes ecosystem, but the environmental impact of these populations have not been well studied. However, wetlands in mid-continent North America differ in physical characteristics (e.g., size, depth, permanency) and aquatic vegetation species composition compared to wetlands in other locales where mute swans were studied. To investigate if mute swan herbivory impacted SAV communities in mid-continent wetlands, we excluded mute swans from feeding in specific areas using an exclosure experiment on 2 wetland complexes located in the IRV of central Illinois. Specifically, we quantified and compared above-ground and below-ground SAV biomass in areas where mute swans were able to feed freely and in areas where exclosures were erected to exclude mute swans. If mute swans were detrimentally impacting habitat in our study area, we predicted lower SAV biomass in areas where mute swans fed freely compared to areas where they had been excluded for 1.5 years.

Methods

Study Area

The Illinois River valley is an important mid-continent migratory stopover for waterfowl and other waterbirds. The original 172,000 ha floodplain was comprised of mast-producing hardwood bottomlands, moist-soil, emergent marsh, and open water habitats (Bowyer et al. 2005). These habitats flood seasonally and provide foraging and loafing areas during spring, an important time for waterbirds as they acquire nutrients for migration and breeding (e.g., Devries et al. 2008). During the breeding season, variable water levels encouraged growth of moist-soil plant species that provided forage and energy during the fall and winter. Less than 74,000 ha of wetland habitats remain, however, as a result of formation of drainage and levee districts and conversion to agriculture. Of the remaining habitat types, 39.9 % was open water, 34.9 % bottomland forest, and the remaining 25.2 % included moist-soil (8.6 %), scrub-shrub (3.6 %), and emergent vegetation (2.8 %; Havera 1999).

Banner Marsh State Fish and Wildlife Area

Banner Marsh is located approximately 40 km southwest of Peoria, Illinois in Fulton County (N 40.53, W 89.86) (Fig. 1) and is bordered by the Illinois River to the east. The site encompassed 1,765 ha of which approximately 208 ha were bottomland forest, and 1,595 ha were wetland or open water habitats depending upon the time of year. Banner Marsh was comprised of many bodies of water of varying shapes and sizes, a result of previous coal mining activities prior to ownership by the Illinois Department of Natural Resources (IDNR). Water depths were mostly <1.5 m.

The abundance and distribution of SAV at Banner Marsh has not been quantified. However, several species of SAV were present, including coontail (*Ceratophyllum demersum*), sago pondweed, brittle naiads (*Najas minor*), and waterweed (*Elodea canadensis*). Eurasian water milfoil (*Myriophyllum spicatum*) also appeared to have increased in abundance during the past decade and was likely the most abundant species at the site during this study (A. Phillips, personal observation).

Natural resource managers noted the first pair of mute swans at Banner Marsh in 1999. In July 2007, an unofficial survey estimated 120 mute swans (including cygnets) at Banner Marsh, including ≥30 nesting pairs (Bill Douglass, IDNR, personal communication). The swans mostly used marshes in the southern part of the property and this is where we concentrated sampling efforts.

Spring Lake State Fish and Wildlife Area

Spring Lake is located in Illinois, 40 km southwest of Peoria in Tazewell County and is bordered by the Illinois River to the west (N 40.46, W 89.87; Fig. 1). The lake was once a meander of the Illinois River and stretches 13.7 km and covers 520 ha as a single open body of water. Water depths vary throughout the lake and can reach >3 m. Spring Lake supported a diverse aquatic plant community, because of its clear, eutrophic, spring-fed water source (Havera 1999). During the summer, about half of the lake's surface area is typically covered by water lily (*Nymphaea tuberosa*) and American water lotus (*Nelumbo lutea*). These floating broadleaf plants provided understory conditions conducive to shade-tolerant species, such as coontail and bladderwort (*Utricularia* spp.) (Wayne Herndon, IDNR, personal communication). Some of the firmer substrates of the lake bottom supported SAV species, such as chara (*Chara* spp.), sago pondweed, waterweed, brittle naiads, southern naiads (*Najas guadalupensis*), leafy pondweed (*Potamogeton foliosus*), and Illinois pondweed (*Potamogeton illinoensis*). The aforementioned exotic Eurasian water milfoil was the most abundant species of SAV at Spring Lake and another exotic species, curly-leaf pondweed (*Potamogeton crispus*), has been recently documented (Stan Weimer, IDNR, personal communication). An estimated 100 mute swans (adults and

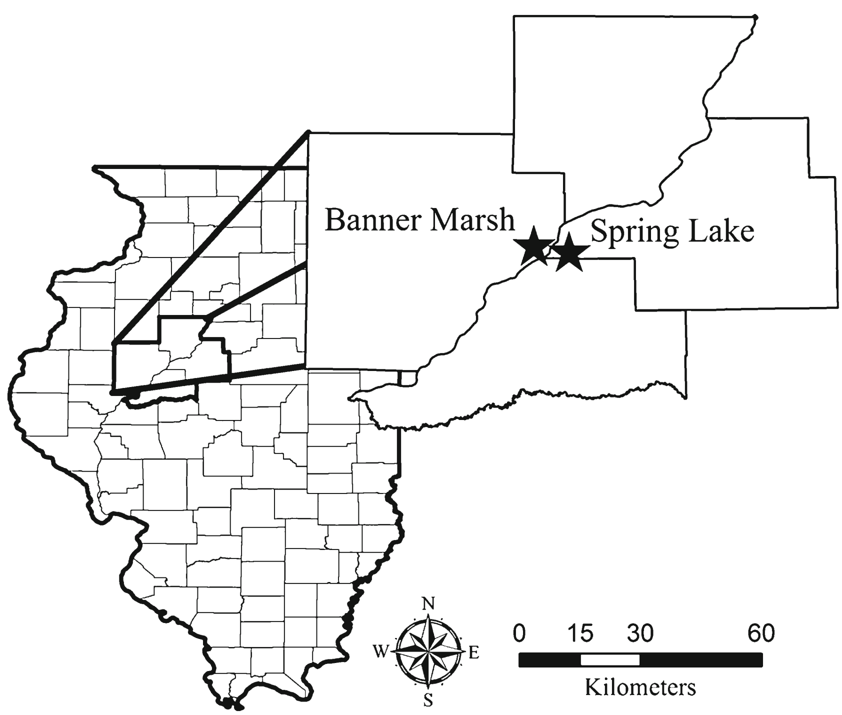

Fig. 1 Banner Marsh and Spring Lake site locations in counties of central Illinois where submerged aquatic vegetation was sampled in 2009

cygnets) inhabited Spring Lake, including about 15 nesting pairs (Stan Weimer, IDNR, personal communication).

Experimental Design

We used 20 pairs of vegetation exclosures and control plots to investigate the impacts of mute swan herbivory on SAV at our study areas. We constructed exclosures from 3 m sections of metal fence post, 1 m tall wire mesh, and cable ties. By securing the wire 0.5 m above the water surface, exclosures were expected to prevent swans from feeding in a 9 m^2 core area, but allow other aquatic animals access to the vegetation (Badzinski et al. 2006). We did observe instances of small waterbirds and turtles inside our exclosures (A. C. Phillips, personal observation). We monitored exclosures at least weekly to ensure that the 0.5 m wire height was maintained if water levels fluctuated.

Because the maximum feeding depth of mute swans is approximately 1.5 m (Holm 2002), we excluded areas with water depths >1.5 m as potential exclosure and control sites. We used ArcGIS to randomly select locations within the remaining area to construct exclosures. If no SAV was present at a randomly selected site, we selected another random location for exclosures and controls. We constructed exclosures (10 at each site) between February and April 2008. Each exclosure was associated with a control plot of the same size located randomly within 10 m of the exclosure where vegetation structure and composition were visibly similar. Swans at our study sites were habituated to humans and objects, such as boats, so the exclosures did not deter use of areas; in fact, we observed some individuals feeding next to or reaching inside the periphery but not entering the exclosures. Control plots were not marked, and swans were able to feed freely in them for the entire study period. We delineated control plots after we sampled SAV within exclosures, selecting a random bearing and distance from a random numbers table.

Sampling Design and Procedure

We sampled SAV during 10–11 September 2009, which was near the end of the SAV growing season in Illinois; thus, sites were subjected to herbivory for 2 growing seasons (1.5 years). We divided each exclosure and control into 32, 0.25 m^2 sections and excluded the outermost 16 sections from sampling to prevent bias associated with an exclosure effect (e.g., shading, reduced flow) or swans reaching to feed inside the exclosure. We randomly selected 5 of the remaining 16 interior sections to sample. To remove all above and below-ground biomass, we used a plastic trash can modified to encompass 0.25 m^2, placed it over the selected section and pressed it into the substrate, and used gardening clippers to clip all vegetation at ground level. Without moving the trash can, we removed all below-ground biomass by hand to a depth of 13 cm (e.g., about the distance from the tip of a mute swan bill to the eye). Samples were refrigerated at 4.5 °C and were processed within 3 weeks of collection.

We separated all above ground biomass by species, removed detritus or foreign materials, and gently washed samples to remove sediment. We were unable to identify below-ground biomass to species. We dried samples at 50 °C until they reached a constant mass and weighed them to the nearest mg on an electronic balance (Bailey et al. 2008).

Statistical Analyses

We compared above and below ground biomass (g/m^2; dependent variable) of vegetation collected in September 2009 between exclosures and controls using separate paired t-tests, with α=0.05 to evaluate significance. Each sampled unit (n= 5 samples each) was a paired exclosure and control (18 pairs) that had been monitored for the entire study period (1.5 years). We conducted all analyses using SAS v9.1.

Results

We positively identified 9 species of SAV in exclosure and control plots, and 2 others were unidentifiable (Table 1). The 2 unidentified species were found in very low abundances (<1 % total biomass). We excluded data from 2 exclosure-control pairs from analyses because 1 exclosure (Banner Marsh) was missing a side panel and 1 (Spring Lake) contained no vegetation due to water lotus encroachment. Therefore, our sample size was 18 paired units.

Above-Ground Biomass

Biomass of above-ground vegetation was not different between exclosures and controls (t_{17}=0.39, P>0.05).

Table 1 Common names, scientific names, and locations of submerged aquatic vegetation encountered in exclosures and controls in Banner Marsh (B) and Spring Lake (S), Illinois in September 2009

Common name	Scientific name	Site
Eurasian water milfoil	*Myriophyllum spicatum*	B,S
Coontail	*Ceratophyllum demersum*	B,S
Bladderwort	*Utricularia macrorhiza*	B,S
Sago pondweed	*Potamogeton pectinatus*	B,S
Curly-leaf pondweed	*Potamogeton crispus*	B
Muskgrass	*Chara* spp.	B,S
Illinois pondweed	*Potamogeton illinoensis*	B
American waterweed	*Elodea canadensis*	B,S
Brittle naiads	*Najas minor*	B,S

However, there was considerable variation in the dataset and mean exclosure biomass ranging from 1.2 to 486.8 g/m^2 and mean control biomass ranging from 2.4 to 506.4 g/m^2. Eurasian water milfoil was the most common species, occurring in 78 of 90 subsamples (enclosures and controls combined) and representing 45 % of the total above-ground biomass. Coontail was the most common native species, occurring in 71 of 90 subsamples and representing 47 % of total biomass. Despite lack of significance, we note that there was a trend to greater mean biomass in exclosures than controls (13 of 18, Table 2).

Below-Ground Biomass

Mean below-ground biomass was 51 % greater in exclosures (52.0 g/m^2, SE=6.0) than in controls (34.4 g/m^2, SE=4.0) (t_{17}=2.88, P=0.01). At the sample-unit level, 13 of 18 exclosures contained greater mean root biomass than the associated control (Table 3).

Discussion

Mute swans have the potential to degrade wetland habitats by overgrazing and uprooting plants, and where their abundances are substantial they can locally deplete SAV (Tatu et al. 2007). Monitoring the impacts of mute swans on wetland vegetation may provide data for managers to decide if actions are warranted to prevent wetland degradation. In Illinois, mute swans were recently established and presented the opportunity to monitor their impacts on wetland health early, as their populations increase. This scenario should also allow for management of mute swan populations if and when their abundance increases to a level were their impacts are detrimental (e.g., significant local depletion of SAV).

After 1.5 years of exclusion, above-ground biomass of SAV did not differ statistically between areas where swans were able to feed and those where they were excluded. Mute swan abundances in our study were lower than those reported in studies that found swans degraded SAV. An estimated 150 mute swans inhabited our 2 study areas, which encompassed >1,500 ha of potential habitat (0.1 swans/ha). In Maryland, Tatu et al. (2007) documented mute swan herbivory decreased SAV percent cover, shoot density, and canopy height when >1,500 mute swans inhabited their study areas (i.e., >10 times that in our study). O'Hare et al. (2007) also found that mute swans reduced SAV biomass, but swan density was estimated at approximately 29 swans/ha; more than 2 orders of magnitude greater than in our study area. Alternatively, because few wetlands exist with SAV in the IRV, swans could have impacted vegetation differentially compared to other areas where alternate foraging sites exist. Nonetheless, relative to the amount of

Table 2 Mean biomass and SE of above-ground SAV biomass collected in exclosures and controls, September 2009. B: Banner Marsh; S: Spring Lake

Pair number	Site	Exclosure mean (g/m^2)	SE	Control mean (g/m^2)	SE
1	B	65.6	5.6	27.6	6.8
2	B	148.8	45.6	91.6	31.2
3	B	486.8	116.0	351.2	81.2
4	B	38.0	10.4	113.6	25.6
5	B	149.2	42.4	138.8	29.6
6	B	54.8	9.6	33.2	9.2
7	B	259.2	52.8	101.6	22.8
8	B	279.6	43.6	506.4	237.2
9	B	110.8	30.0	137.6	30.8
10	S	204.4	51.6	166.0	54.0
11	S	99.2	17.2	107.2	34.8
12	S	148.0	26.8	107.2	12.4
13	S	136.4	13.6	149.2	19.2
14	S	234.8	23.2	107.2	11.2
15	S	1.2	0.4	4.8	2.0
16	S	3.2	0.8	2.4	0.8
17	S	210.8	68.4	209.6	16.4
18	S	5.2	3.2	4.0	2.0

Table 3 Mean biomass and SE of below-ground SAV biomass collected in exclosures and controls, September 2009. B: Banner Marsh; S: Spring Lake

Pair number	Site	Exclosure mean (g/m^2)	SE	Control mean (g/m^2)	SE
1	B	68.4	46.4	60.4	11.6
2	B	114.0	36.4	67.6	21.2
3	B	72.4	32.0	32.0	10.0
4	B	34.0	9.2	3.2	0.8
5	B	92.4	19.6	42.0	8.0
6	B	48.4	14.0	89.6	28.8
7	B	58.4	13.2	31.6	10.0
8	B	11.2	5.2	4.8	2.4
9	B	74.8	22.8	25.6	10.0
10	S	8.0	2.4	7.6	2.0
11	S	25.6	3.2	10.4	3.6
12	S	50.8	8.8	58.4	5.6
13	S	110.0	29.6	46.4	10.0
14	S	90.8	28.8	40.0	14.4
15	S	0.4	0.0	1.6	1.2
16	S	0.4	0.0	0.4	0.0
17	S	74.8	11.2	60.8	20.0
18	S	0.4	0.0	33.2	32.8

wetland habitat available at Banner Marsh and Spring Lake, our data indicate that mute swans are not yet abundant enough to significantly deplete above-ground biomass.

Although we did not detect a reduction in above-ground SAV biomass, results of the below-ground biomass comparisons (i.e., lower in control than exclosure plots) suggested that mute swans had some detrimental impact on SAV in our study wetlands. The most obvious way that mute swans could reduce biomass of below-ground plant structure is by direct consumption; that is, intensely foraging on roots and tubers during winter, when above-ground biomass has recessed and is less nutritionally valuable (Jonzen et al. 2002). Below-ground foraging has been documented in trumpeter swans, a close relative of mute swans (LaMontagne et al. 2003). In a study of mute swan foraging, however, Bailey et al. (2008) found that mute swan diets were comprised of 72 % above-ground SAV parts and 22 % below-ground SAV parts. Because below-ground parts comprised a significantly smaller proportion of mute swan diets, reduction of below-ground biomass by consumption of below ground parts alone seems unlikely.

Responses of aquatic vegetation to waterbird herbivory have been thoroughly studied (e.g., Jonzen et al. 2002; LaMontagne et al. 2003; Nolet 2004; Rodriguez-Villafane et al. 2007), and results of such research suggest an alternative hypothesis may explain the difference in below-ground biomass we observed. If mute swan foraging defoliated SAV, plants may have invested additional energy into shoot regeneration which may have, in turn, reduced below-ground stores and biomass. Indeed, plants in general, and aquatic vegetation in particular, often compensate for grazing by diverting energy from below-ground structures to increase photosynthesis and above-ground biomass growth rate (Richards 1984; Mulder and Ruess 1998; Person et al. 2003). Compensation can occur at the scale of individual plant or at the community scale, although compensation by individual plants is rare (Nolet 2004). In some cases, above-ground biomass of SAV can be greater following herbivory pressure (i.e., over-compensation), depending on the intensity and duration of herbivory (Nolet 2004). In other cases, however, plants are unable to compensate for energy lost to herbivory, and community structure can change (i.e., under compensation; Nolet 2004; Tatu et al. 2007).

Under compensation can result in decreased densities of competing plants and increased light penetration (LaMontagne et al. 2003; Nolet 2004). Normally this would be neutral or favorable, as similar species could recolonize areas where conditions were adequate. Across North America, however, exotic species of SAV are becoming more abundant and widespread (Smith and Barko 1990; Mills et al. 1993; Engel 1995). Bare substrates left from reduced densities of native SAV may promote colonization and spread of exotic species, such as Eurasian water milfoil. Milfoil has the ability to create dense monocultures, partly because it begins growing earlier in the spring and outcompetes native species. Furthermore, milfoil does not constitute a significant portion of mute swan and other waterbird diets, with the exception of American coots (*Fulica americana*) and gadwall (*Anas strepera*) (Benedict and Hepp 2000; Bailey et al. 2008). With little grazing pressure and more colonization potential, Eurasian water milfoil has the potential to become a greater problem for natural resources in Illinois as a result of mute swan herbivory on native vegetation.

Impacts of herbivory can be cumulative, manifesting over years instead of months. In our 1.5 year study we were able to document some precursory impacts of mute swan grazing on SAV in Illinois River valley wetlands. If mute swan abundances increase in the IRV it is likely that herbivory pressure on above and below-ground structures will increase, thereby influencing SAV community structure and abundance. Future efforts should focus on monitoring above and below-ground biomass and identify what the threshold for SAV grazing pressure is, so managers can initiate compensation or swan restriction measures if necessary. A variety of options exist for managing mute swan populations, including impacting reproduction (e.g., egg oiling), relocation, or direct control (e.g., euthanization), and appropriate methods must be based on local conditions, management objectives, and logistics.

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