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THE EFFECTS OF VERTEBRATE HERBIVORY ON PLANT COMMUNITY STRUCTURE IN THE COASTAL MARSHES OF THE PEARL RIVER, LOUISIANA, USA

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Abstract: In this study, we investigated the impacts of herbivory by the introduced aquatic herbivore, nutria (*Myocastor coypus*), on three marsh communities of the Pearl River using fenced exclosures and control plots. Although total community above-ground biomass was reduced by 30% in the plots exposed to herbivory as compared to those protected from herbivory, we found species richness to be unaffected. When individual species were examined within each community, *Panicum virgatum* and *Aster subulatus* were found to be significantly reduced by herbivory in the freshwater community, *Panicum virgatum* and *Vigna luteola* were significantly increased by herbivory in the oligohaline community, and no species were significantly affected in the mesohaline community. We conclude that this herbivory has some specific effects on some plant species as well as having a general community effect.

Key Words: coastal marsh, freshwater marsh, herbivory, mesohaline marsh, *Myocastor coypus*, nutria, oligohaline marsh, *Panicum, Spartina*

INTRODUCTION

Herbivores may affect plant communities in a variety of different ways. Selective herbivory may create an environment in which one species is particularly favored, herbivory may be a type of "disturbance" which may prevent competitive exclusion from occurring, and selective grazing on certain species may limit or extend the distributions of certain plant species.

Herbivory may be thought of as a disturbance, which at intermediate levels, might be expected to promote species richness within a given plant community. At higher levels of herbivory, a decrease of species richness might be expected as the species most susceptible to herbivory would be removed from the system. At low or negligible levels of herbivory, species diversity or richness might be expected to be less than that at intermediate levels because of competitive exclusion.

In addition to affecting total species richness, herbivory has been shown to be an important factor in limiting the distributions of some individual plant species (Parker and Root 1981, Louda 1983). Herbivores may selectively eat certain plant species, thus driving preferred food species to local extinction. Alternatively, the gaps in vegetation created by herbivore activity may allow certain species to exist in an area in which they would otherwise be competitively excluded. Within a single plant community, it is possible that some species may be absent because herbivory has restricted their distributions while other species that are present in the community would not exist there without the presence of herbivores (Louda 1989).

Nutria, (*Myocastor coypus* (Monina)), an introduced herbivore, have been found to convert marsh to open water in the United Kingdom (Boorman and Fuller 1981), and in Louisiana, nutria have been reported to be ". . . a dominant force in destroying desirable vegetation and preventing revegetation" (Conner 1989). Several studies of the effect of nutria on Louisiana marshes have concluded that nutria herbivory may be an extremely important force governing community structure in some marsh communities (Chabreck 1959, Fuller et al. 1985, Rejmanek et al. 1990, Shaffer et al. 1990). Nutria are large, semiaquatic rodents that inhabit many of the wetlands of Louisiana. Lowery (1974) places nutria in the Capromyidae, but other sources (Packard 1967, Woods and Howland 1979) place nutria in the monotypic family Myocastoridae. Nutria are native to South America and have been introduced to North America repeatedly since 1899 (Evans 1970). Nutria were brought to the U.S. both by fur ranchers for pelt production and by state and federal governments (Kinler et al. 1987). Wild populations have existed in Louisiana since at least the 1940s (Lowery 1974). Nutria reach sexual maturity at 4-8 months, depending on season of birth. They breed at all times of the year, have a mean gestation period of 130-132 days, and produce about five young per litter (Kinler et al. 1981).

In this study, the effect of herbivory, mainly by nutria, was studied by experimentally creating plots with and without herbivory in three different marsh communities along an elevational and salinity gradient. The specific questions asked in this study were:

1. Is total aboveground biomass in areas that are exposed to natural herbivory less than, equal to, or greater than areas from which herbivores have been excluded?
2. Does species richness increase, decrease, or remain constant when vertebrate herbivory is removed from the community?
3. Does the abundance of any plant species change when herbivores are excluded from the community?

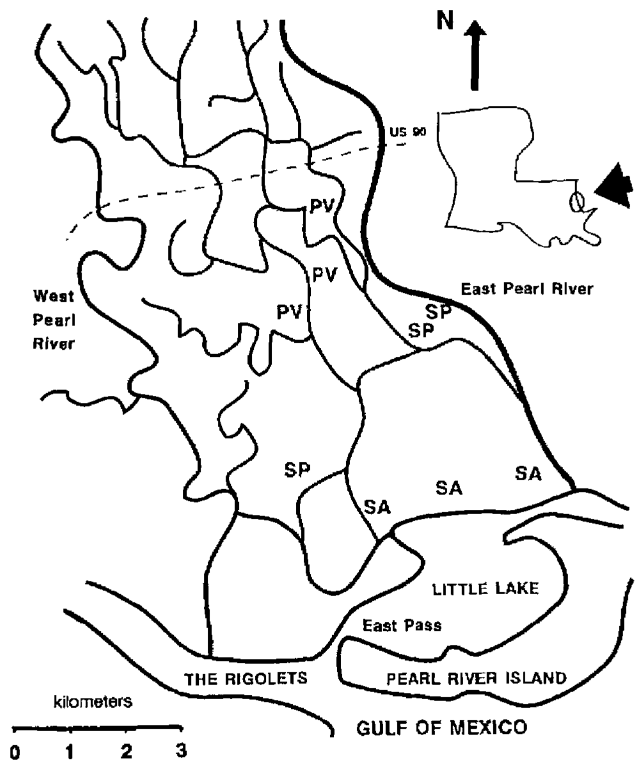

Figure 1. Location of research sites. PV = freshwater community dominated by *Panicum virgatum*, SP = oligohaline community dominated by *Spartina patens*, SA = mesohaline community dominated by *Spartina alterniflora*.

METHODS

Plant Communities and Study Sites

This study was designed to examine the effects of herbivory on representative fresh, oligohaline, and mesohaline marshes of the lower Pearl River basin located at the boundary of Mississippi and Louisiana. Representative community types were chosen for each marsh type based on general field surveys.

The freshwater community type chosen was dominated by *Panicum virgatum* L. (Figure 1). Numerous subdominant species were present, and the mean species richness of vascular plants in this marsh type was relatively high (13 species per square meter). The salinity of the water in this community always measured near zero. This community had the highest elevation of the three communities studied. Relative elevation was determined by visual observation and comparison of water depths.

The oligohaline community type chosen was dominated by *Spartina patens* (Ait.) Muhl. (Figure 1). Numerous subdominant species were common, and mean species richness of vascular plants was 10 species per square meter. The salinity of the water ranged from 0 to 4 ppt. The elevation of this community was intermediate to the other two communities studied.

The mesohaline community type chosen was dominated by *Spartina alterniflora* Loisel. and was located at the mouth of the Pearl River (Figure 1). Very few species were found coexisting in this community, and the mean species richness of vascular plants was two species per square meter. The salinity of the water ranged from 0 to 6 ppt. This community had the lowest elevation of the three studied.

Experimental Design

This experiment was designed to study the overall effects of nutria herbivory on the marshes of the Pearl River (as opposed to the effects of localized "eat-outs"). Sites were selected using a restricted randomization procedure. First, within the appropriate region of the river basin, points were chosen randomly from a map. Second, in the field, these points were located and the nearest area characterized by the appropriate dominant species was identified. Third, areas were selected so as to avoid recent human disturbance and to permit ready access. Within each of the nine research sites, four 1-m^2 study plots were located, and treatments were randomly assigned among plots.

In order to exclude large herbivores, a 2-m by 2-m fence (exclosure) was constructed around two of the four plots at each site leaving a 1-m buffer zone be-

Table 1. Model, degrees of freedom (df), mean square (MS), F value (F), and probability of a greater F under the null hypothesis (P > F) for the split plot analysis of total biomass of all species taken together in the exclosed plots and the control plots. The site (within community) by treatment interaction was tested and found to be nonsignificant so was pooled into the error term. Response variable = mean total above-ground biomass (g m^{-2})

Source	df	MS	F	P > F
Community	2	927400	6.73	0.0293
Site (Community)*	6	137801	2.74	0.0361
Treatment	1	800064	15.88	0.0005
Treatment•Community	2	7054	0.14	0.8700
Error	26	47040		
Corrected total	35			

* Error term used to test Community effects.

Table 2. Model, degrees of freedom (df), mean square (MS), F value (F), and probability of a greater F under the null hypothesis (P > F) for the split plot analysis of species richness in the exclosed plots and the control plots. The site (within community) by treatment interaction was tested and found to be nonsignificant so was pooled into the error term. Response variable = species richness (species m^{-2})

Source	df	MS	F	P > F
Community	2	385	27.72	0.0009
Site (Community)*	6	14	10.83	0.0001
Treatment	1	1	0.78	0.3864
Treatment•Community	2	0.08	0.06	0.9374
Error	26	1.2		
Corrected total	35			

* Error term used to test Community effects.

tween the fence and the plot. The buffer zone was intended to minimize any effect of the fence on the experimental plot. Exclosures were constructed with plastic-coated welded wire and were supported by corner posts of 2.54-cm-diameter PVC pipe. The plastic coating prevented the corrosion of the fence. The exclosures were 2 m by 2 m and rose 1.5 m above the marsh surface. Exclosure bases were sunk into the marsh to a depth of approximately 50 cm. Observations confirmed that this procedure excluded all large herbivores during this study. All exclosures were completed by 31 March 1990.

Although the exclosures were designed to prevent the major herbivore of this system, nutria, from entering the experimental plots, other herbivores were also excluded. Any walking or swimming animal larger than 2.54 cm in diameter was excluded from the protected plots. It has been reported (Bazely and Jefferies 1986) that small fenced exclosures also exclude waterfowl. Although other vertebrate herbivores were present, nutria was clearly the dominant herbivore during the course of this study.

Fires occur frequently in the marshes of the Pearl River. Any particular area of land may burn as frequently as once every two years. In order to reduce the variation between sites that would be attributable to the time since the site last burned, all sites were burned between 12 February and 17 March 1990, prior to initiating the experiment.

Each of the plots was maintained and monitored for the subsequent two growing seasons. At the end of the experiment in September of 1991, all of the above-ground biomass in each of the plots was clipped, sorted by species, dried at 70°C, and weighed.

Total biomass of all species (g m^{-2}) and species richness (species m^{-2}) were tested for differences between treatments and between communities using a split plot analysis with a completely randomized design on the whole plot (Sokal and Rohlf 1981). The treatment-by-site interaction was tested for significance, found to be nonsignificant in each case ($P>0.4$), and was pooled into the error term. Data were tested for normality and found to be normal. The alpha level used to determine significance in these tests was 0.05. All analyses were performed using PC-SAS statistical software programs (SAS 1987).

Biomass data for each major species in each community were analyzed separately using a randomized complete block design blocked on site (Sokal and Rohlf 1981). Major species were defined as those species that occurred in over 50% of the plots and had a mean dry biomass of over 30 g m^{-2} in at least one of the treatments at the end of the experiment. Since each treatment was replicated at each site, the treatment-by-site interaction was tested. This interaction was found to be nonsignificant in each case and was pooled into the error term. The biomass data for each species were tested for normality and, when found to be non-normal, were log-transformed. To avoid discounting the effects of herbivory on non-major species, a Wilcoxon Sign-Rank Test was performed using data from all species (Sokal and Rohlf 1981).

RESULTS

Mean total above-ground biomass of the community differed significantly between communities (Table 1, Figure 2, $P=0.0293$). The freshwater community had the greatest total mean biomass, the mesohaline community had the least, and the oligohaline community had an intermediate total mean biomass. Species richness also differed between communities (Table 2, Figure 3, $P=0.0009$). Species richness was highest in the freshwater community and decreased along the ele-

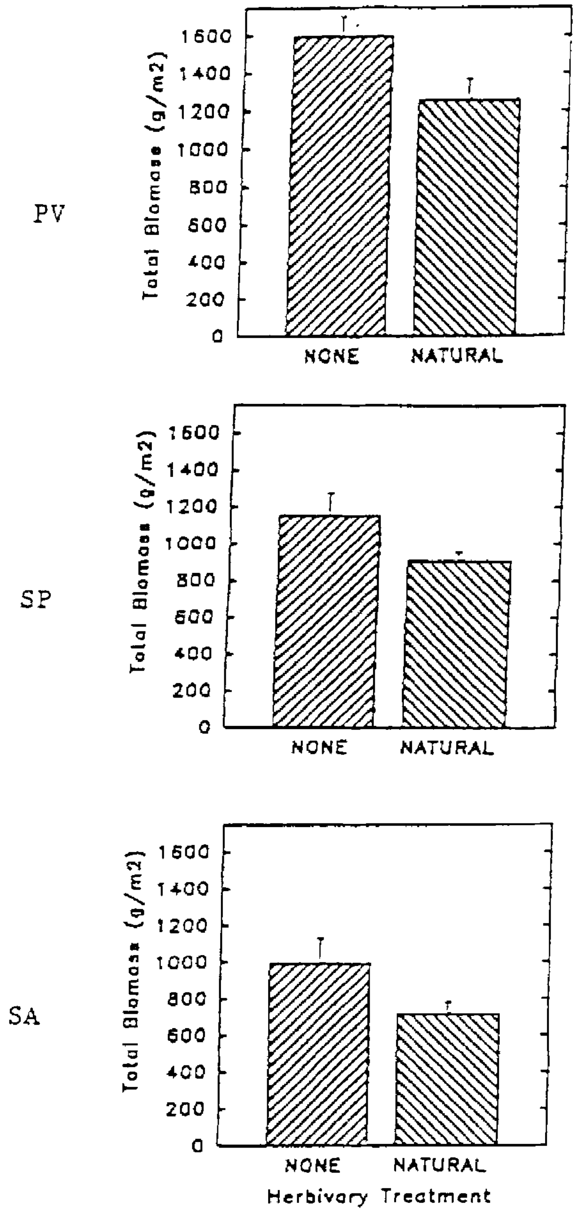

Figure 2. Mean total above-ground biomass and standard error of the mean for plots exposed to natural herbivory levels (NATURAL) and for plots from which herbivores have been excluded (NONE) in each of the three community types. PV = freshwater community dominated by *Panicum virgatum*, SP = oligohaline community dominates by *Spartina patens*, SA = mesohaline community dominated by *Spartina alterniflora*.

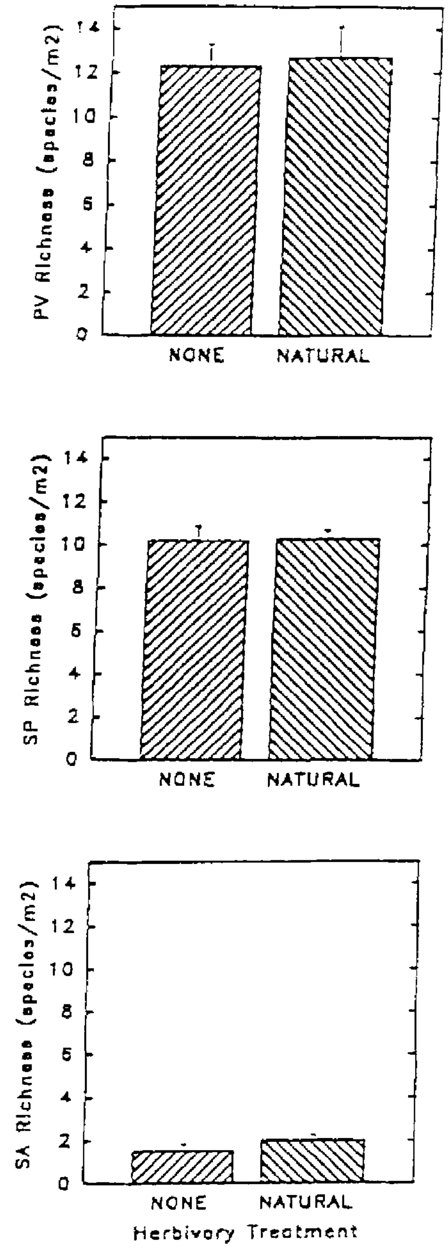

Figure 3. Mean species richness and standard error of the mean for plots exposed to natural herbivory levels (NATURAL) and for plots from which herbivores have been excluded (NONE) in each of the three community types. PV = freshwater community dominated by *Panicum virgatum*, SP = oligohaline community dominates by *Spartina patens*, SA = mesohaline community dominated by *Spartina alterniflora*.

vational and salinity gradient to be lowest in the mesohaline community.

Mean total above-ground biomass was reduced by herbivory (Table 1, P=0.0005). The mean total biomass in the exclosed plots was 130% of that in the control plots (Figure 2). However, species richness was not significantly affected by herbivory (Table 2, Figure 3, P=0.38).

In the *Panicum virgatum*-dominated community, *Aster subulatus* Michx.(P=0.05) and *Panicum virgatum* (P=0.08) were both negatively affected by herbivory (Table 3). The mean above-ground biomass of *Aster subulatus* was 3 times greater and the mean above-ground biomass of *Panicum virgatum* was 1.5 times greater in the plots that were protected from herbivory.

Table 3. Mean total biomass (standard error of the mean) of major species in the *Panicum virgatum*-dominated freshwater community in the plots protected from herbivory and those exposed to natural herbivory and the P-value associated with the test for differences in biomass between treatments. Response variable = individual species biomass (g m^{-2}).

Species	Protected	Natural	P > F
Aster subulatus	32 (6)	11 (5)	0.0506
Panicum virgatum	771 (152)	517 (109)	0.0821
Spartina cynosuroides	381 (94)	355 (86)	0.6598
Vigna luteola	23 (8)	32 (7)	0.3310

Table 4. Mean total biomass (standard error of the mean) of major species in the *Spartina patens*-dominated oligohaline community in the plots protected from herbivory and those exposed to natural herbivory and the P-value associated with the test for differences in biomass between treatments. Response variable = individual species biomass (g m^{-2}).

Species	Protected	Natural	P > F
*Mikania scandens**	168 (51)	96 (50)	0.8410
Pnaicum virgatum	11 (7)	59 (30)	0.0874
Sagittaria lancifolia	108 (29)	120 (29)	0.6664
Spartina patens	501 (153)	290 (86)	0.1380
Vigna luteola	37 (10)	65 (10)	0.0720

* Test for this species was performed on log transformed data.

The above-ground biomass of the other major plant species, *Spartina cynosuroides* (L.) Roth (P=0.66) and *Vigna luteola* (Jacq.) Benth. (P=0.33) were not significantly affected by vertebrate herbivores (Table 3). An overall trend of greater biomass in the protected plots was found (Wilcoxon Sign-Rank Test, P<0.01).

In the community dominated by *Spartina patens*, the above-ground biomass of *Panicum virgatum* was over 5 times greater (P=0.087) and the biomass of *Vigna luteola* was 1.75 times greater (P=0.072) in the plots exposed to herbivory as compared to the protected plots (Table 4). No significant differences were found in the above-ground biomass of the other major species in this community (*Sagittaria lancifolia* L. and *Mikania scandens* (L.) Willd.) (Table 4). A Wilcoxon Sign-Rank Test showed no significant difference in species biomass between treatments.

In the *Spartina alterniflora*-dominated community, the above-ground biomass of the only major species, *Spartina alterniflora*, was not significantly different between treatments (Table 5, P=0.118). A Wilcoxon Sign-Rank Test showed no significant difference in species biomass between treatments.

DISCUSSION

Species richness was unaffected by herbivory, which indicates that herbivory in this system may not be a strong enough force to act as an "intermediate disturbance" (sensu Connell 1978). Rather, herbivory in the marshes of the Pearl River during this study might be thought of as a low level disturbance. The lack of effect that the removal of herbivory had on species diversity in this system contrasts with the results of some other studies. Bazely and Jefferies (1986) found that species richness of a salt marsh community increased when snow geese were excluded. Bakker (1985) also found an increase in species richness when cattle were excluded from a salt marsh. However, several studies on the effect of nutria in Louisiana coastal marshes conducted for two growing seasons have found that the exclusion of vertebrate herbivores resulted in a reduction of species richness (Fuller et al. 1985, Rejmanek et al. 1990, Shaffer et al. 1990). The findings of this study, that herbivory had no effect on species richness, agrees with those of Smith (1988), who found no effects of herbivory in a playa wetland, and Gibson et al. (1990), who found no effects of herbivory on species richness in a tallgrass prairie.

Gibson et al. (1990) write that "... small mammal herbivory is of lesser importance in the later successional tallgrass prairie than compared with earlier successional...". It is possible that herbivory also has different effects on Louisiana marshes, depending on successional stage. Fuller et. al (1985) studied an early successional marsh community and found an increase in species richness and total biomass in areas protected from herbivory. However, the marshes studied were relatively mature and had a dense layer of rhizomes below the substrate surface. Our study found no effect of herbivory on species richness in the marshes of the Pearl River.

Although species richness was unaffected, herbivory had a pronounced effect on total above-ground biomass in two of the three marsh communities. Although not measured in this study, our observations indicate that the effects of herbivores on vegetation were even greater during the winter period when plant regrowth

Table 5. Mean total biomass (standard error of the mean) of major species in the *Spartina alterniflora*-dominated mesohaline community in the plots protected from herbivory and those exposed to natural herbivory and the P-value associated with the test for differences in biomass between treatments. Response variable = individual species biomass (g m^{-2}).

Species	Protected	Natural	P > F
Spartina alterniflora	993 (139)	713 (66)	0.1180

was minimal. The fact that the plots which were protected from herbivory had 30% more above-ground biomass than the plots subjected to natural herbivory may have ecological implications in this system. Because less biomass is present in the areas subjected to natural herbivory, the accumulation of organic material in the marsh sediment may be less than if nutria were not present. This lessening of organic matter accumulation may further affect the microbial and faunal components of the marsh.

The results for individual species are generally consistent with reports of nutria feeding behavior. In the freshwater community, *Panicum virgatum* and *Aster subulatus* were reduced by herbivory. In the oligohaline community, *Panicum virgatum* and *Vigna luteola* were increased by herbivory, but no species were significantly reduced. In the mesohaline community, no species were affected. To understand these results more completely, it is important to realize that even though nutria are thought to prefer to eat certain plant species (Kinler et al. 1987), nutria have been observed to be remarkably wasteful feeders (Harris and Webert 1962). This aspect of nutria's effect on marsh communities may help explain why their effects were found to be of a general nature.

In conclusion, herbivore activities reduced biomass equally in all three communities. Additionally, the effects of nutria herbivory in the Pearl River seem to be less dramatic than in some other Louisiana marshes, and further work is needed to determine the causes of this difference. Lastly, although herbivory seems to have some specific effects, the herbivores seem to have a general effect on the system, which may be attributable to their destructive use of the vegetation for purposes other than food.

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