

Keddy, P.A., L. Gough, J.A. Nyman, T. McFalls, J. Carter and J. Siegrist. 2009. Alligator hunters, pelt traders, and runaway consumption of gulf coast marshes. p. 115-133 in B.R. Silliman, E.D. Grosholz and M.D. Bertness (eds.) *Human Impacts on Salt Marshes, A Global Perspective*. University of California Press, Berkeley, CA.

7

Alligator Hunters, Pelt Traders, and Runaway Consumption of Gulf Coast Marshes

A TROPHIC CASCADE PERSPECTIVE ON COASTAL WETLAND LOSSES

*Paul A. Keddy, Laura Gough, J. Andy Nyman, Tiffany McFalls,
Jacob Carter, and Jack Siegrist*

The rate of loss of Gulf Coast marshes in general, and the Louisiana coastline in particular, is now a national issue, particularly following the 2005 hurricanes in the region. We suggest that current management paradigms for marsh restoration may focus too exclusively on plants and sediment, with a bottom-up view of coastal wetlands. Top-down processes also merit consideration and may expand the array of potential tools for coastal management and restoration. Here we propose an alligator trophic cascade hypothesis incorporating a top-down approach: that alligator hunting, by reducing the density and mean size of alligators, removes a natural control on the primary herbivores in wetlands, enabling the runaway consumption of coastal marshes. We present current evidence to support this hypothesis. Mammalian grazing can directly remove plant biomass and make plants less tolerant to flooding and salinity, therefore increasing erosion of sediments. Both muskrats and nutria have been implicated in this process, with the larger, nonnative nutria of greater current concern. Annual aerial surveys beginning in 1998 indicated that 321 to 415 square kilometers of Louisiana's 14,164 square kilometers of coastal wetlands were severely damaged by nutria. Adult alligators eat muskrats and nutria, but the role of alligators as potential controllers of mammal populations, and thus as controllers of marsh damage, has received minimal consideration. Our hypothesis cannot be tested with existing data because almost no numbers exist for nutria populations, and data on marsh integrity, plants, nutria, and alligator densities are not being collected in a systematic way across multiple sites. However, we explore these relationships with a modeling exercise and propose several different ways to test these relationships empirically. If the hypothesis is supported, reducing the alligator harvest or closely controlling the size of the animals being harvested may prove a valuable management tool in conserving coastal wetlands. Adopting multiple working hypotheses, including a top-down approach, may be crucial to adequately managing and restoring coastal areas.

Should I say, that the river (in this place) from shore to shore, and perhaps near half a mile above and below me, appeared to be one solid bank of fish, of various kinds, pushing through this narrow pass of St. Juans into the little lake, on their return down the river, and that the alligators were in such incredible numbers, and so close together from shore to shore, that it would have been easy to have walked across on their heads, had the animals been harmless.

William Bartram (1791, 123)

The rapid loss of wetlands along the Gulf Coast of North America poses a serious threat to wildlife populations, human infrastructure, and local and regional economies (Boesch et al. 1994). Coastal wetland loss in Louisiana averaged one hectare a day from 1978 through 1990 (Barras, Bourgeois, and Handley 1994). Estimates of one-time conversion of marsh to open water caused by Hurricane Katrina in 2005 approach seventy-five square kilometers in one area of coastal Louisiana (20 to 26 percent of the study area; U.S. Geological Survey [USGS] 2005). Some marsh loss is natural in the Mississippi Deltaic Plain, where the river has changed drainage patterns over millennia, instigating natural cycles of construction and degradation (Teller and Thorleifson 1983; Boyd and Penland 1988). Humans have accelerated this loss in several ways, including building levees on the Mississippi River that prevent spring floods from delivering fresh water and sediments to the marshes, constructing canals and spoil banks that alter salinity and hydrology (Boesch et al. 1994; Turner 1997), controlling the amount of water (and associated sediment) in the Mississippi River that enters the Atchafalaya River basin, and introducing an exotic herbivore, nutria, *Myocastor coypus* (Keddy et al. 2007; figs. 7.1 and 7.2). These human alterations have reduced rates of vertical accretion that would otherwise offset the effects of global sea-level rise and local subsidence (Day and Templet 1989; Boesch et al. 1994).

Nutria, and to a lesser degree muskrats (*Ondatra zibethicus*), are implicated in accelerat-



FIGURE 7.1 Coastal marshes, such as these along the Mississippi River, have been lost and fragmented by the dredging of canals and creation of spoil banks. About 12 percent of Louisiana's coastal wetland loss is attributable to this cause, while an additional 32 percent is due to factors such as hydrological changes and sedimentation reduction resulting from dams and levees.

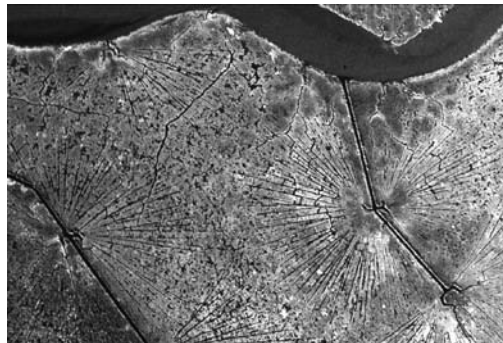


FIGURE 7.2 A modern aerial view of the coastal marshes in the Manchac area, northwest of New Orleans, showing the scars left by pullboat logging of the former cypress swamp. Channels dredged for the boats and ditches gouged out by the logs have altered the marsh hydrology, facilitating saltwater intrusion and organic decomposition.

ing the loss of coastal wetlands in Louisiana (Coastal Wetlands Planning, Protection, and Restoration Act Task Force [CWPPRA] 2008) (and in Chesapeake Bay; Patuxent Wildlife Research Center [PWRC] 1999). Nutria were introduced into Louisiana in the 1940s and soon became abundant and widespread (Lowery 1974; Bernard 2002). Marsh damage by nutria accelerated after the mid-1980s when the fur industry declined and trapping efforts similarly lessened. Recently, Louisiana has attempted to increase nutria harvest to reduce marsh

damage. The state promotes human consumption of nutria in the United States and elsewhere (particularly in China) to try to dispel the local image of nutria as “swamp rats,” unfit to eat. Beginning in 2002, Louisiana implemented an incentive payment program of an additional \$4 per nutria (increased to \$5 in 2006) for registered trappers (since the 1990s a pelt has normally been worth \$1) for up to four hundred thousand animals a year for five years (CWPPRA 2008; Louisiana Department of Wildlife and Fisheries [LDWF] 2008). The cost of this program was initially estimated at \$69 million statewide (CWPPRA 2008). The extent of marsh area damaged has consistently declined since the program was introduced, with the lowest levels detected in 2008 (LDWF 2008). These results, along with documented recovery of marsh in areas where many animals have been removed, suggest the control efforts are working. This success may be attributable to harvest goals being set to levels similar to the late 1970s when pelt prices were higher and to procedures that focus on lands with the most intense nutria damage.

Governments in other areas to which nutria have been introduced, such as Maryland and England, chose to completely eradicate their nutria populations through systematic hunting and trapping programs subsidized by the state and federal governments (Carter and Leonard 2002). In the Chesapeake Bay region of Maryland, 53 percent of the marsh remaining at Blackwater National Wildlife Refuge was damaged by nutria (PWRC 1999), and an \$8.2 million study of the effects of trapping on nutria density was initiated. In late 2004, the refuge was declared “nutria-free” in the popular press after the state of Maryland paid trappers to kill every animal they encountered (Fahrenthold 2004). Nonetheless, nutria still persist in low numbers on the refuge and adjacent lands (D. Birch, Blackwater National Wildlife Refuge, personal communication). In all, approximately 8,300 nutria were killed by 2004, although the original population on the refuge was estimated to be closer to 50,000 animals. For perspective,

in just one of the heavily nutria-populated parishes in Louisiana, more than one hundred thousand nutria were killed in one season (CWPPRA 2008). Louisiana officials have not taken a similar eradication approach, partly because the more extensive marshes in the state make eradication logistically very difficult, and they instead encourage trapping as part of the state’s fur industry (Louisiana Fur and Alligator Advisory Council [LFAAC] 2004). Control of nutria through harvesting by humans in the absence of a sustainable commercial market, even if effective, will require continued government inputs, not only through incentive payments but also through the costs of management itself, such as the staff required to monitor nutria, regulate hunting activity, and pay incentives.

Natural predation may be a more cost-effective means to control nutria and ultimately protect marshes from damage if a strong trophic cascade exists among marsh vegetation, herbivores, and predators (figs. 7.3 and 7.4). The term *trophic cascade* refers to a situation where a predator controls the abundance of herbivores, thereby indirectly controlling the biomass and species composition of plant communities. When such predators are reduced in numbers, the herbivores may increase in population size, become limited by food availability rather than predation, and cause significant damage to vegetation. Recent reviews (e.g., Schmitz, Krivan, and Ovadia 2004; Borer et al. 2005) suggest that trophic cascades occur in a variety of ecosystems—aquatic, wetland, and terrestrial. They may be more important in food webs that resemble linear food chains with only one or two species of consumers in each trophic level (Borer et al. 2005), similar to what is found in Louisiana marshes. In southern U.S. salt marshes, blue crabs are important predators on snails that consume marsh vegetation, and crabs may thereby protect salt marshes from overgrazing (Silliman and Bertness 2002). In northern marshes in North America, exploding geese populations have damaged nearly two-thirds of the approximately fifty-five thousand

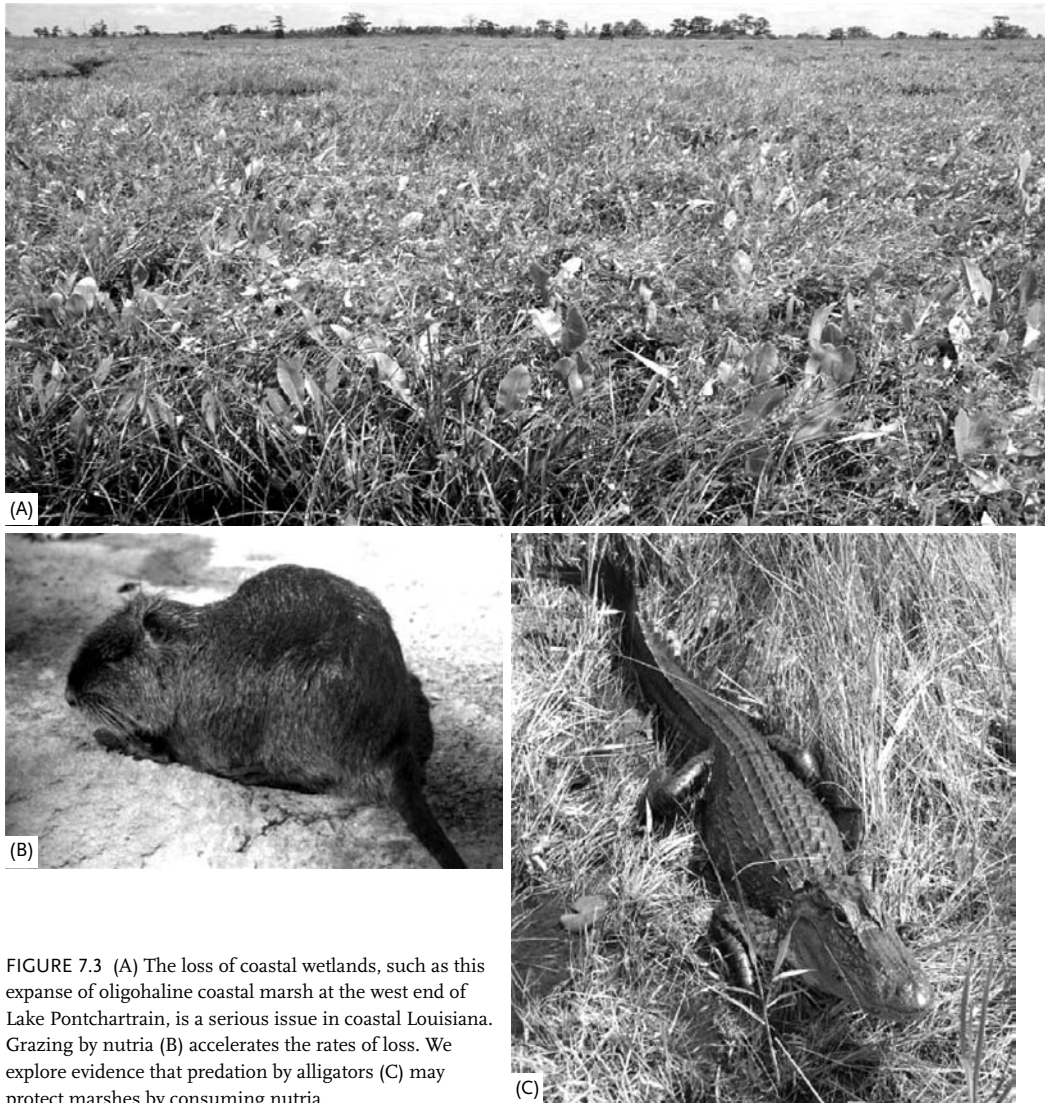


FIGURE 7.3 (A) The loss of coastal wetlands, such as this expanse of oligohaline coastal marsh at the west end of Lake Pontchartrain, is a serious issue in coastal Louisiana. Grazing by nutria (B) accelerates the rates of loss. We explore evidence that predation by alligators (C) may protect marshes by consuming nutria.

hectares of salt marsh along the coast of Hudson and James bays (Jefferies and Rockwell 2002; Abraham and Keddy 2005). To our knowledge, the potential of alligators to create a trophic cascade in the Gulf Coast region and thus protect marshes from herbivory has not been examined.

Previous explanations of the ecological significance of alligators in wetlands have largely addressed their role in digging alligator holes

that increase the variation in plant communities and provide deep-water refuges for many wetland species in the Florida Everglades (Loveless 1959; Craighead 1968; Gunderson and Loftus 1993; Palmer and Mazzotti 2004). Dundee and Rossman (1989) observed similar behavior in Louisiana, where holes one to three meters in diameter and one to two meters deep were connected to underground dens used as retreats during the winter.

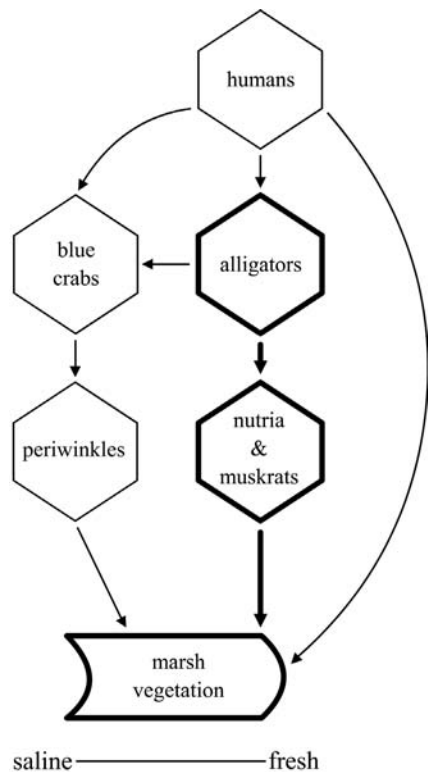


FIGURE 7.4 Alligators may have a positive indirect effect on marsh vegetation by their negative direct effect on nutria and muskrats. There is also a possible link to the blue crab–periwinkle–vegetation food web, depending on salinity.

Reliable data on the effects of alligator predation on herbivore abundance are not available. Here we review some of the evidence consistent with the alligator trophic cascade hypothesis. We propose that herbivore damage to Louisiana coastal wetlands results, at least in part, from the release of predation by alligators on nutria; we present the results of a model that supports the hypothesis; and we explore what is needed to empirically test this hypothesis. Our review is limited to the available data, including evidence from the effects of nutria and muskrats on marsh vegetation, evidence from the diet of alligators, and largely anecdotal evidence regarding the relative abundance of alligators and herbivores in Louisiana wetlands over the past one hundred years. Our goal is to suggest to wetland

researchers and managers the possibility that these relationships exist, and to advocate for properly designed field experiments to test the hypothesis.

EFFECTS OF NUTRIA AND MUSKRATS ON MARSH VEGETATION AND WETLAND LOSS

Annual aerial surveys beginning in 1998 provide a conservative estimate that 321 to 415 square kilometers of Louisiana's 14,164 square kilometers of coastal wetlands were severely damaged by nutria (LDWF 2008). This damage occurred almost exclusively in the Mississippi Deltaic Plain, rather than in the Chenier Plain (unpublished map, LDWF 2008; CWPPRA 2008). Marshes in the Mississippi Deltaic Plain probably are more sensitive to nutria damage because submergence (i.e., the combination of local subsidence and global sea-level rise) exceeds 1 centimeter a year in the Mississippi Deltaic Plain but averages only 0.57 centimeter a year in the Chenier Plain (Penland and Ramsey 1990), and because nutria increase the sensitivity of vegetation to flooding and salinity stress (Gough and Grace 1998a; Grace and Ford 1996). Also, nutria may prefer the vegetation and habitat found in the Mississippi Delta; fewer nutria are harvested in the western coastal areas, likely reflecting lower abundance.

Nutria and muskrats affect marsh plants directly by reducing the biomass of vegetation (Evers et al. 1998; Fuller et al. 1985), sometimes creating "eat-outs" (fig. 7.5), areas of marsh denuded of vegetation (Lynch, O'Neil, and Lay 1947). Removal of plant biomass increases the sensitivity of marsh soils to erosion because of the loss of living roots that trap and hold sediment (McGinnis 1997). Indirectly, grazing may also increase the sensitivity of plant species to flooding or salinity stress (Gough and Grace 1998a, 1998b; Grace and Ford 1996) and reduce organic matter necessary for vertical accretion (McCaffrey and Thomson 1980; Bricker-Urso et al. 1989; Gosselink, Hatton,

and Hopkinson 1984; Nyman et al. 1993; Callaway, DeLaune, and Patrick 1997). Ford and Grace (1998a) observed that soil elevation increased less in nutria-grazed than in ungrazed plots. Models for Louisiana wetlands (e.g., Reyes et al. 2000) include a term for the rate by which plants contribute to accretion. That model has a term for herbivory partly because, if such grazing is omitted, the model shows that rates of accretion exceed those observed in nature (G. P. Kemp, personal communication). Nutria grazing may also be a factor in the conversion of thick mat floating marshes to thin mat floating marshes and then to shallow open water (Visser et al. 1999).

These effects may extend to forested landscapes. The regeneration of coastal swamps with bald cypress (*Taxodium distichum*) may have been slowed or even halted by herbivores (fig. 7.6). When bald cypress trees are planted in experiments or for restoration, they are frequently eaten by nutria. Saplings under a half-meter tall may be cut off at ground level, while larger saplings may be killed when their bark is removed. Myers, Shaffer, and Llewellyn (1995) planted four hundred young bald cypress trees in the Manchac Wildlife Management Area in Louisiana; trees exposed to ambient herbivory suffered 100 percent mortality.

Manipulative studies of the interactive effects of soil nutrients, fire, and herbivory illustrate



FIGURE 7.5 Nutria can strip marsh vegetation from large areas of coastal wetland, creating openings called eat-outs. These areas become more vulnerable to further disturbances. From U.S. Geological Survey 2000.



FIGURE 7.6 Where a vast cypress swamp with trees a thousand years old once stood, coastal marsh dominates today. While succession might have restored such a sight, it is highly unlikely now because hydrological alteration and herbivory by nutria prevent cypress from establishing.

how nutria may affect plant species composition as well as biomass in Louisiana marshes. Ford and Grace (1998b) found that the abundance of *Spartina patens*, a frequently dominant perennial grass, was reduced by the combination of burning and herbivore exclusion in two marsh communities but not in a third, while other common species responded favorably to the same treatments. In particular, the sedge *Schoenoplectus americanus*, the preferred food species of muskrats and nutria, increased in relative abundance when mammalian herbivores were excluded. In a similar brackish marsh, Gough and Grace (1998b) documented an increase in biomass of *S. americanus* and a decrease in *S. patens* when protected from nutria, despite no change in community biomass after three years of treatment. This shift in dominance was exaggerated, and plant species richness declined when soil nutrients were amended, suggesting an important interaction between herbivory and soil nutrient availability. Ambient herbivory levels in these studies were not as high as those that generate eat-outs, but

these results suggest that moderate nutria activity can affect the structure of these plant communities, particularly when soil nutrient availability is increased, such as after sediment additions to help restore marshes.

A more recent study site has been established in the Turtle Cove Experimental Marsh near Southeastern Louisiana University's Turtle Cove Environmental Research Station to quantify the effects of multiple disturbance treatments, multiple fertility treatments, and the interactions between them, replicated within and outside of 40 × 60-meter mammalian enclosures (McFalls 2004; Geho, Campbell, and Keddy 2007). The oligohaline marsh was dominated by three species: *S. americanus* (39.0 percent), *Polygonum punctatum* (18.9 percent), and *Sagittaria lancifolia* (7.4 percent). Four ranked disturbance treatments were applied: no disturbance (control), prescribed fire, a single vegetation removal treatment, and a multiple vegetation removal treatment. The ranked fertility treatments were designed to simulate factors that affect production in Louisiana's rapidly submerging coastal zone: no fertility enhancement (control), sediment addition, fertilizer addition, and a sediment + fertilizer addition.

Similar to the studies already described, areas protected from nutria had more (1.4 times) vegetation than areas open to herbivory as measured using biomass collected after two years of experimental treatments (McFalls 2004). Biomass steadily decreased with increased disturbance level when nutria were allowed to graze, while this effect was hard to detect in areas protected from nutria herbivory. Fertility and herbivory interacted so that biomass did not appear to increase with increasing fertility unless herbivores were excluded and significant disturbance such as fire or multiple herbicide applications occurred (fig. 7.7). Apparently, nutria had the greatest impact on biomass if another disturbance was already present; that is, they tended to amplify effects of disturbance. The likely mechanism is a preference for newly growing vegetation, a common phenomenon in herbivores (White 1993). Although fire occurs in Louisiana marshes and is a management tool applied to selected marshes (O'Neil 1949; Nyman and Chabreck 1995), the short-term results of this experiment indicate that plants regenerating after fire are particularly attractive to nutria, especially if there is enhanced fertility.

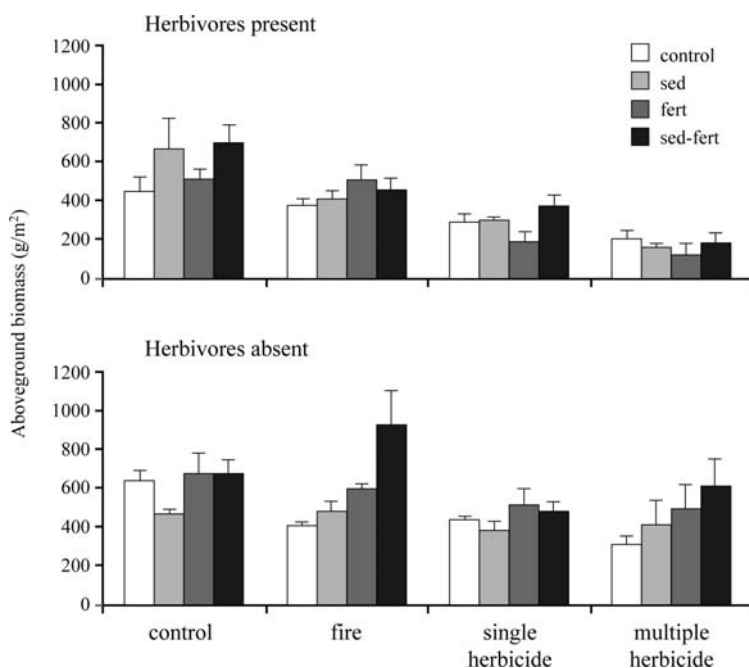


FIGURE 7.7 The effects of nutria on vegetation receiving different fertility and disturbance treatments (mean + 1 SE, $n = 96$, pooled into the error term). The bottom panel shows patterns in three fenced enclosures, while the top shows patterns in the three paired open areas. The fertility treatments are control, sediment, fertilizer, and sediment + fertilizer. The disturbance treatments are control, fire, and single and multiple herbicide application. Adapted from McFalls 2004.

In summary, the short-term results of work at Turtle Cove in addition to the published studies reviewed earlier suggest that nutria have at least two additional indirect effects on marsh restoration. They may dampen treatments designed to increase production, while they may amplify treatments that increase disturbance. The *damping effect* may be caused by conversion of plant biomass to nutria biomass. Many biologists advocate increasing nutrient inputs to coastal wetlands (e.g., freshwater diversions, sewage effluent) without considering the possibility that this may simply trigger the growth of nutria. The *accelerating effect* may be caused by nutria preferring plants with higher nutrient levels produced by new shoots after local disturbances. In this case, initial disturbances from storms or fire may attract nutria, which will prevent regeneration and expand disturbed patches, thereby accelerating the loss of marshes. While these results are drawn from only the first two years of the experiment (McFalls 2004), they illustrate the potential for increased predation on nutria to control a wide array of marsh processes.

THE DIET OF ALLIGATORS

Alligators are well-known generalist predators in wetlands. Determining diet from stomach content is always difficult, since the input of prey will vary with habitat, season, and predator size, while volume and digestibility differs among prey species (e.g., fish and turtles). In a recent review, Gabrey (2005) summarized the literature reporting alligator stomach contents. In the 1940s and 1950s, alligators in Louisiana were primarily consuming fish, crustaceans, and muskrats. Nutria were not detected in alligator stomachs until 1961 after their introduction to Louisiana in the 1940s (Valentine et al. 1972). In subsequent studies, nutria comprised a significant portion of the adult alligator diet throughout coastal Louisiana (fig. 7.8), while muskrats declined in importance (Wolfe, Bradshaw, and Chabreck 1987).



FIGURE 7.8 Dead nutria recovered from an alligator's stomach. Photo courtesy of Steven W. Gabrey, Northwestern State University, Natchitoches, Louisiana.

Juvenile alligators (less than 1.2 meters or 6 feet long) feed primarily on fish, insects, and crustaceans (Platt, Brantley, and Hastings 1990; Wolfe et al. 1987, reviewed in Gabrey 2005). Blue crabs (*Callinectes sapidus*) can account for 70 percent of prey biomass in brackish marshes (Eley et al. 1992), but crawfish can dominate prey in fresher areas (Platt et al. 1990). As alligators grow larger, they include vertebrates in their diets, such as deer (*Odocoileus virginianus*) and other terrestrial mammals (e.g., Shoop and Ruckdeschel 1990). In coastal Louisiana, mammalian prey of adult alligators (greater than 1.2 meters) are dominated by nutria and muskrats (Wolfe et al. 1987).

Differences in importance of various components of alligator diets have been correlated with habitat as well as predator size. For example, crustaceans including crabs are more important than nutria for large alligators in saline habitats (reviewed in Gabrey 2005, fig. 2). This suggests another potential trophic cascade in saline marshes: alligators may consume blue crabs that are important predators of snails, known to alter salt marsh vegetation (Silliman and Bertness 2002). Differences in prey composition for alligators likely reflect the habitat preference of nutria for brackish and fresh marshes, rather than a shift in alligator consumption patterns. Mammals have not been found to be important components of alligator diets in the Florida Everglades, probably because

mammal abundance is low (nutria and muskrats do not occur there).

In a recent examination of 553 adult alligator stomachs collected from 2002 to 2004 in five parishes in coastal Louisiana, Gabrey (2005) found that approximately 31 percent of alligators had nutria present in their stomachs, while muskrats were found only in approximately 3 percent. Measured as frequency of alligators in which the prey item was found, crustaceans (about 64 percent) and fish (about 51 percent) were more frequently encountered than mammals (about 36 percent). When prey weight was examined, mean weight of mammals was the largest of the prey categories, but variation was too high for statistical analyses to be conducted (Gabrey 2005). Confirming earlier studies of the influence of habitat on alligator diet, alligators from an intermediate marsh had a much higher frequency of crab prey than those in fresh marshes. Also, alligators from western parishes tended to have consumed more turtles than those from eastern parishes where turtles are less common. Thus, this recent study supports earlier research suggesting the importance of nutria as prey for large alligators, but also the idea of alligators as opportunistic foragers, with their diet reflecting the prey available in a particular area.

Other linkages undoubtedly occur in the diet of alligators—Gunderson and Loftus (1993) provide food web diagrams illustrating the breadth of freshwater prey consumed by alligators in the Everglades. Quantitative simulations of such food webs show that alligators can have major impacts through indirect linkages to lower trophic levels (Bondavalli and Ulanowicz 1999). McIlhenny (1935) noted that reduced alligator numbers coincided with reduced game fish abundance and attributed this to the release of garfish from alligator predation in freshwater systems in Louisiana. The stomach content data from Louisiana illustrate that the food webs may in fact be dominated by a few strong interactions (*sensu* Paine 1980)—invertebrates being favored by smaller alligators and nutria by larger alligators (Gabrey 2005).

HISTORICAL EVIDENCE OF CHANGES IN ALLIGATORS, MUSKRATS, AND NUTRIA

There are no systematically collected data, but descriptions indicate that alligator populations in Louisiana declined precipitously between 1850 and 1960 (fig. 7.9). McIlhenny (1935), who was a keen naturalist, reported that alligators “fairly swarmed” prior to harvest that began in the 1880s; they remained common until 1900 but were exterminated from many areas of Louisiana by 1935. Initially, only alligators more than 2.4 meters were harvested; but by the 1930s, as the larger alligators disappeared, every alligator that could be captured was harvested (McIlhenny 1935). In the late 1950s, alligator populations in Louisiana remained low because of illegal overharvest (fueled by a demand for skins from small individuals), and alligators as small as 0.6 meter were illegally taken (Joanen and McNease 1987). All trapping was suspended in 1962 (Joanen and McNease 1987), and poaching was virtually eliminated in parts of southwest Louisiana by the early 1960s (Tarver, Linscombe, and Kinler 1987). Alligator populations recovered enough that by 1972 there was an experimental harvest of 1,337 animals in southwest Louisiana (Tarver et al. 1987). Alligator numbers continued to increase; by 1981, the harvest was statewide, and 15,534 hides were taken (Joanen et al. 1984). Data collected by LDWF beginning in 1970 document a relatively steady increase in nests counted throughout Louisiana’s coastal zone (fig. 7.10), with a dip in 2006 attributed to combined detrimental effects of drought and hurricanes in 2005. Nesting quickly recovered in 2007, however, to one of the highest counts on record. Clearly the suspension of hunting and subsequent hunting practices are not affecting recruitment of new individuals into the population. However, larger alligators still are preferentially harvested (Taylor and Neil 1984), making it highly probable that mean size is well below that of the 1850s, and estimates of adult population size are lacking.



FIGURE 7.9 Overhunting between 1850 and 1960 caused a dramatic decline in alligator populations. It is likely that current population densities, and current alligator sizes, are still well below those encountered. "Alligator shooting in the swamps bordering on the Mississippi River, Louisiana." Reproduced with permission, Corbis, New York.

Commercial trapping of muskrats began between 1900 and 1910 (O'Neil 1949). O'Neil (1949) concluded from descriptions by early Europeans and interviews with elderly trappers living in the 1940s that the muskrat had been rare in Louisiana coastal marshes prior to the late 1800s, and it had spread westward from the eastern part of the state in the late 1800s. Such increases coincided spatially and temporally with alligator declines reported by McIlhenny (1935). O'Neil reported that muskrat trapping increased as accessible alligators were eliminated and the coastal marshes were burned to make it easier to reach alligators in their holes. Arthur (1928) reported that many people believed that muskrat numbers increased as alligators were reduced but that author did not wholly subscribe to that theory alone. By the 1940s, "the general picture of the better

marshes in every coastal parish is one of 'eaten-out' marsh due to overpopulation of muskrats" (O'Neil 1949, 70), and in the 1950s, muskrat populations in coastal Louisiana were described as "fantastic" (St. Amant 1959). Nutria were introduced into Louisiana in the 1940s (Lowery 1974; Bernard 2002) and quickly established viable populations. It is thus difficult to separate effects of nutria from those of muskrats after that decade, although trapping data suggest nutria increased in numbers as muskrats declined, perhaps because of competitive exclusion in their overlapping preferred habitat.

The increase in muskrats and nutria as alligators declined is well documented but circumstantial. For example, eat-outs became rarer in the 1970s and 1980s at the same time the alligator population increased statewide (Joannen et al. 1984). There are alternative or at least

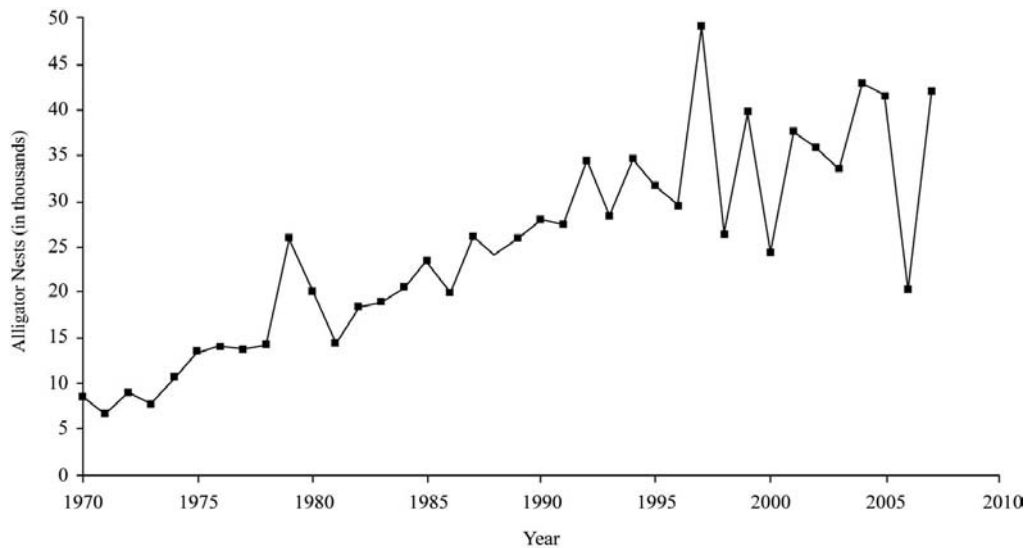


FIGURE 7.10 Annual alligator nest counts throughout coastal Louisiana show a general increase with time. Data from Louisiana Department of Wildlife and Fisheries.

overlapping hypotheses that might explain such a pattern. For example, in addition to directly reducing alligator numbers, alligator hunters also increased the fire frequency in coastal marshes. Herbivore numbers may have subsequently increased in brackish marshes because the preferred food, *S. americanus*, is more abundant in the year following a fire than in subsequent years (Nyman and Chabreck 1995). Also, changes in habitat due to road building, oil and gas exploration, draining marshes for pasture, and management practices aimed at wintering waterfowl and muskrats all occurred at the time when alligators were declining and nutria and muskrats were increasing in the 1950s and 1960s.

BOTTOM-UP AND TOP-DOWN CONTROL

The concept of the trophic cascade is part of a larger ecological issue—the recognition that there are two possible extremes in the way in which plants (and therefore coastal marshes in particular) are controlled in food webs: bottom-up and top-down. Bottom-up hypotheses assume that systems are regulated by nutrient availability from below. They assume that all organisms live under harsh conditions where

there are shortages of resources (plant parts of sufficient quality, prey that are hard to catch), even if these resources seem superficially to be abundant (Sinclair et al. 2000). White (1993) presents an enormous number of examples where nutrients in general, and nitrogen in particular, appear to limit animal populations. In contrast, the top-down view consists of a set of hypotheses about how predators might control the abundance of species lower in the food web. The key issue, from the perspective of this chapter, is the possibility of top-down control, rarely considered in wetlands (Keddy 2000), which may occur along with some degree of bottom-up regulation. For example, Carpenter and Kitchell (1988) note that lake ecosystems can simultaneously exhibit elements of “bottom-up control” through physical factors such as nutrients as well as “top-down control” through biotic interactions such as competition and predation.

The current paradigm in coastal management is almost entirely bottom-up: rivers deposit sediments, sediments allow plants to grow, and then the plants are converted into useful products that are harvested. There are several reasons why this perspective predominates. First, there is undoubtedly a geological component to the creation of wetlands

(e.g., Boyd and Penland 1988), and a certain bottom-up logic is unavoidable: without sediments, there can be no plants. Second, the scientists who study coastal processes are inevitably compartmentalized into subdisciplines based on their training and expertise. For example, plant physiologists study the links between plant growth and sediment characteristics, and rarely interact with those who study predators, while those who study nutria and alligators often have little to do with the botanists. Hence, few look up or down more than one link in the food web. Third, those who look at the entire system have in many cases adopted Odum's view of energy flow, a view that is inherently bottom-up. Fourth, alligators, like wolves, receive bad press and are seen often as merely an annoyance. Fifth, alligators are seen as an important economic resource and one that should not be restricted given current increasing population estimates. All of these reasons have contributed to the bottom-up focus: sediments make plants, and plants make wildlife. However, some land managers in Louisiana do not harvest all the alligators allowed them by the current system, because they suspect that maintaining many large alligators will reduce nutria and muskrat damage (D. Richard, Stream Wetland Services, LLC, and D. Nuth, National Parks Service, personal communication).

SIMULATION OF POTENTIAL EFFECTS OF ALLIGATOR PREDATION ON NUTRIA POPULATIONS

To examine the alligator trophic cascade hypothesis using a modeling approach, we added alligator predation to a previously published nutria population dynamics model (Carter, Foote, and Johnson-Randall 1999). The nutria model was composed of three interacting submodels: a nutria population model, an annual model of aboveground plant biomass, and a marsh surface area model. Marsh loss was controlled by plant biomass: if biomass was above a critical threshold, no area loss occurred. Below this threshold, marsh area loss increased as plant

biomass decreased. As nutria populations increased, herbivory reduced biomass, and marsh loss increased. The original model had a strong seasonal component: nutria populations that appeared sustainable in the summer on a given area of marsh caused marsh loss during the winter months, when plant biomass naturally decreased.

The first step in adding a predation component to the model was to modify the published nutria model so that it used a specified numerical carrying capacity instead of a biomass-based carrying capacity. The function of alligator predation was then added to the model as a fixed number of alligators eating a fixed number of nutria per week (determined by sensitivity analysis based on published predation rates; see later discussion). Alligators were assumed to consume nutria for thirty-one weeks per year, thereby simulating seasonal predation patterns. This population model was then allowed to run until dynamic stability near the specified carrying capacity was achieved. In this investigation, "control" was achieved when a nutria population was eliminated within ten years after the start of predation. Alligator population sizes that did not control nutria populations generally reduced mean nutria population size, which would likely have positive consequences for marsh plants. Later we will focus on the more demanding criterion of alligator population sizes that eliminated nutria. Important model assumptions were that alligator predation was strictly additive to "natural" mortality, predation was independent of nutria population density, all alligators fed on all age classes of nutria, and alligator predation was not spatially explicit.

To eliminate a nutria population over a ten-year period, the required ratio of alligators to nutria was 0.012 at carrying capacities of five hundred and above. That is, six alligators could eliminate a population consisting of five hundred nutria. As the carrying capacity decreased below five hundred, the ratio of alligator to nutria needed for control increased slightly. This increase was an artifact of alligator and nutria numbers approaching each other in magnitude,

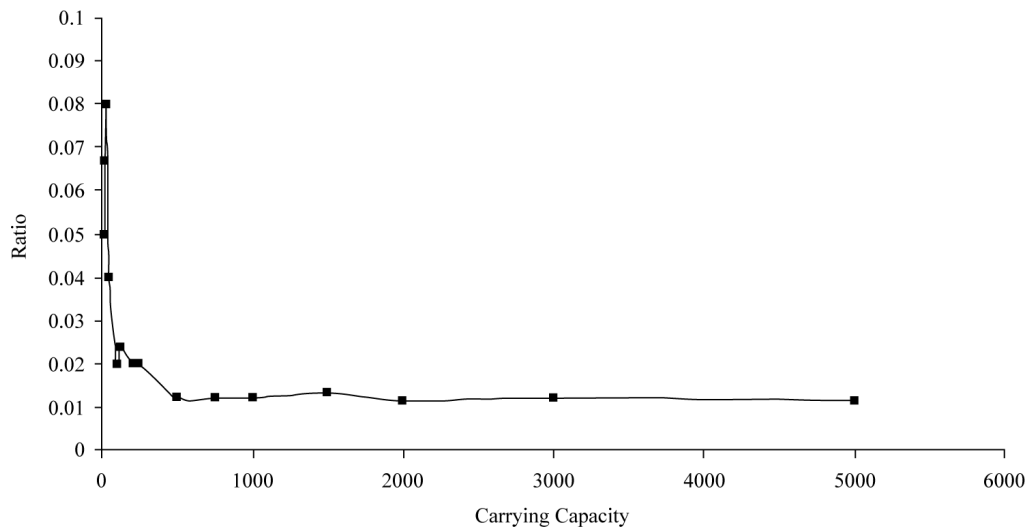


FIGURE 7.11 Ratio of alligators to carrying capacity of nutria needed for control of nutria populations as a function of nutria carrying capacity. Above a nutria carrying capacity of five hundred, the ratio of alligators to nutria is approximately constant at 0.012. The ratio varies at lower carrying capacities because the nutria and alligator numbers are close in magnitude. Weekly alligator predation rate was constant at one for seven months of predation per year.

but the ratio was never higher than 0.067 (fig. 7.11). This result suggests that the larger nutria populations that may occur in especially fertile habitats should be no more difficult to control than those that may occur in less fertile habitats.

According to an examination of alligator stomachs by Wolfe et al. (1987), weekly nutria predation rates range from around 0.08 for

smaller adult animals to 1.0 for alligators over three meters in total length. We therefore explored the possible effects of changing predation rates from the low of 0.08 per week to the high of 1.0 per week (fig. 7.12). In our model, the ratio of alligators to nutria needed to eliminate the nutria population increased by an order of magnitude as the predation rate declined by

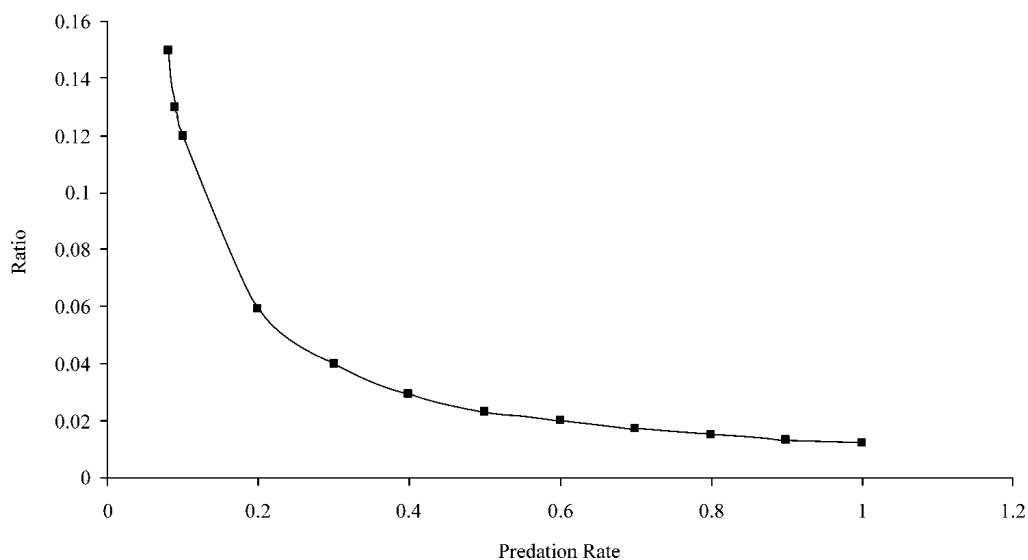


FIGURE 7.12 Ratio of alligators to carrying capacity of nutria needed for control of nutria populations as a function of predation rate (number of nutria consumed per week). Nutria carrying capacity was constant at one thousand, and duration of predation was seven months per year.

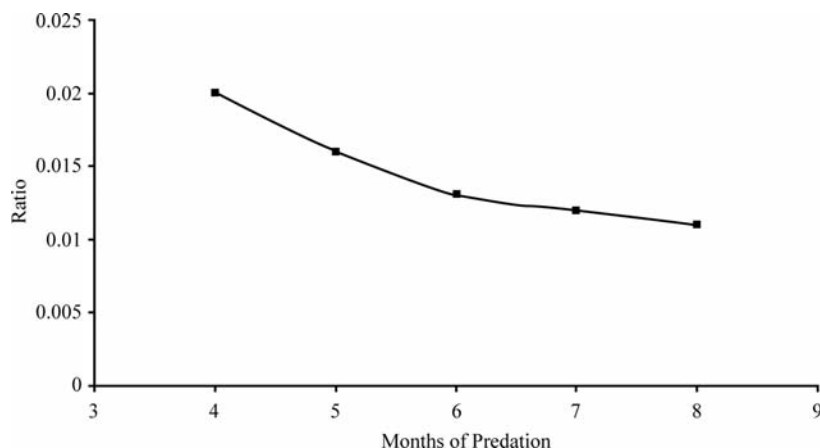


FIGURE 7.13 Ratio of alligators to carrying capacity of nutria needed for control of nutria populations as a function of the number of months of predation. Nutria carrying capacity was constant at one thousand, and weekly predation rate was one nutria per alligator.

an order of magnitude. For example, a nutria population stabilized around 1,000 could be eliminated by 12 larger alligators with a predation rate of 1 (each alligator eating one nutria per week), or by 120 smaller alligators with a predation rate of 0.1 (each alligator eating one nutria every ten weeks). Thus, one alligator over three meters in length has the effective kill rate of ten small alligators.

The ratio of alligators to nutria needed for nutria elimination changed only slightly with the number of months per year that alligators fed (fig. 7.13). For a carrying capacity of one thousand and a predation rate of one per week, the ratio ranged from about 0.01 for eight months of predation to 0.02 at four months of predation. Thus, the number of alligators needed for effective control will likely decrease in climates with longer activity seasons and will vary locally with year to year variation in the weather.

Because of the assumptions outlined here, the model may overestimate the impact of alligators on nutria populations, especially for the smaller alligators. Additionally, density-dependent predation rates in nature may result in the nutria population being reduced rather than eliminated. Therefore, this model should not be used to estimate the number of alligators needed to control a given nutria population.

On the other hand, as a conceptual model, it does demonstrate that (1) a relatively small alligator: nutria ratio can control nutria populations and preserve plant biomass, (2) larger alligators (with higher predation rates) will have a disproportionate effect on nutria population dynamics than smaller animals, and (3) regions with longer alligator activity periods should have more effective control of nutria populations at a given alligator:nutria ratio. Finally, although our goal in this exercise was to predict conditions for the outright elimination of nutria populations, lower alligator population levels or lower predation rates could still effectively reduce the population size of nutria, which could still translate into significant benefits on marsh vegetation.

THE NEED FOR FIELD EXPERIMENTS TO TEST THE ALLIGATOR TROPHIC CASCADE HYPOTHESIS

Although some historical trends and natural history observations are consistent with the alligator trophic cascade hypothesis, definitively making these correlations is currently impossible for several reasons. The biggest difficulty is estimating nutria population size and density. Wildlife managers and others have been

attempting to adequately sample the populations for years. Mark–recapture studies have been unsuccessful, as nutria once marked are rarely recovered. Although the state of Louisiana maintains data on nutria trapping, no adequate data exist for nutria population sizes or densities, and trapping data may not be strongly correlated with population parameters. Comparable data for alligator populations are also missing. This may be even more problematic because alligator size and age are correlated with prey choice, and therefore the number of adult alligators (not just the number of individuals) must be known to examine correlations with herbivore population dynamics. Finally, data on plants, nutria, and alligators are not being collected simultaneously using standard protocols that can be compared across sites and regions.

In addition, historical data are sketchy, particularly from the period when alligators may have been most common. Muskrats in particular have dramatic population fluctuations, tending to reduce confidence in historic reconstructions. Even if correlative trends exist, they do not demonstrate cause and effect, because many other human activities such as logging, trapping, commercial fishing, and coastal development might be implicated in contributing to such patterns.

Areas along the coast exhibit wide variations in alligator and nutria densities (as determined by qualitative observations), creating patterns that are difficult to interpret. In Terrebonne Parish, an area of primarily freshwater marsh, alligator nest densities are the highest that have been documented along the coast, approximately one nest every thirty-five to forty acres (N. Kinler, LDWF, personal communication). Consequently, this parish has one of the highest regulated harvest rates of one alligator from every sixty acres. This is simultaneously an area of great nutria damage and high nutria harvest; approximately 50 percent of the nutria-caused marsh damage in 2007 was in this parish, while in the 2006–2007 trapping season, almost one

hundred thousand nutria were harvested (CWPPRA 2008). In 2002, 13 percent of alligators from this parish had nutria in their stomachs, while 37 percent did in 2004 (Gabrey 2005). There were concurrent increases in crayfish and insect frequencies and decreases in crab frequencies. These data suggest that when habitat conditions are right, both nutria and alligators can flourish, but many questions remain. The high harvest rates (one alligator per sixty acres), for example, may indicate that all but the smallest alligators were removed. In our experience, alligator hunters know the exact locations where the few remaining large alligators live, and they explicitly plan to remove them, leaving ever larger numbers of juveniles. The idea that there are still vast unknown areas of swamp where large alligators can hide is, in our experience, a misunderstanding of how familiar trappers are with local wetlands and how accessible most marshes are to trapping. A further complication is the mobility of nutria. Once nutria have damaged an area, they tend to move to new areas for food. With human harvesting of both nutria and alligators in the parish, both animal populations may be being maintained at levels that allow marsh damage to continue. It remains to be seen what would happen if alligators were not harvested in an area such as this.

An appropriate test of the alligator trophic cascade hypothesis would involve manipulation of alligator densities (and possibly size classes) in properly randomized experiments. Owing to the size of alligators, the difficulty of constructing fences in large wetlands, the need for proper replication, and the long duration required for differences to become large enough to be detectable, such experiments require multidisciplinary collaboration among scientists with expertise in sediments, vegetation, and animals. Therefore, we present two different approaches to testing this hypothesis in new field efforts.

First, ongoing manipulations of alligator numbers that are in progress could be paired and analyzed. Pairs of wetlands along the Gulf Coast having similar habitat, but differing in

presence or absence of alligator harvest, or pairs of wetlands known to already differ in alligator density for other reasons, such as past management regimes, could be compared. In each pair of sites, data would be needed on densities of herbivores (particularly, but not exclusively, nutria and muskrat) as well as alligators. Alligator nest density data are available for most coastal regions of Louisiana, but the relationship between nest numbers and densities of adult alligators (and particularly large alligators) is not well understood. Obtaining adult densities and size distributions would be crucial for an adequate test of this hypothesis. Data should simultaneously be collected for biomass and species composition of plants. Ideally, sites that had been trapped or not trapped for at least five years would be paired because it may take many years to reach an alligator density in which large males presumably control recruitment of juveniles. Or pairs of sites could be selected, and then trapping could be imposed on half of them; this would, however, increase the expense and require a longer period of time to answer the question.

A second approach would be to compare sites differing in rates of wetland loss. Similar areas currently experiencing high rates of wetland loss could be paired with those that are not, and nutria and alligator densities could be compared. This approach might be hampered by the rapid changes in vegetation composition that occur during rapid loss, potentially making it difficult to pick comparable pairs of sites. But again, without systematically collecting the data, we do not know if areas where marsh damage has not yet occurred are being protected from nutria by predation.

Additional approaches involving herbivore enclosures and manipulation of alligator densities are ideal but logistically much less tractable.

MANAGEMENT IMPLICATIONS

The most important management implication of the alligator trophic cascade hypothesis is the possible existence of another tool for slow-

ing marsh loss from herbivore damage: reducing alligator harvest wherever nutria damage is documented. Harvested alligators could be regulated for size to ensure that large alligators capable of eating nutria remain in the population, or alligators could be harvested in proportion to their availability. Perhaps guidelines similar to those used in managed fisheries could be established, such as harvesting intermediate-sized alligators to ensure larger animals with higher predation rates were able to persist and better control the nutria population. Our modeling exercise suggests that controlling for alligator size in a harvest would indeed have a dramatic effect on nutria populations. Needless to say, this is a difficult decision to propose for wetland managers in a state like Louisiana, where the wild alligator harvest can be worth \$9 million annually to local trappers and processors (LFAAC 2004). In addition, the public is generally fearful of alligators and may not be sympathetic to allowing large animals to increase in number.

Given the available data on alligator population size and diet, the severity of current damage from herbivores to coastal wetlands, and the large scale and long duration of the appropriate experiments, we suggest that a collaborative venture is needed to test the alligator trophic cascade hypothesis. In the interim, wetland managers should consider the cautious strategy of allowing for increased density and increased size of alligators in coastal wetlands where nutria and muskrat damage have been documented. As current coastal restoration plans are being evaluated and modified following the 2005 hurricanes (Committee on the Restoration and Protection of Coastal Louisiana 2006), management plans need to incorporate the potential role of alligators in indirectly controlling marsh damage and, perhaps more importantly now, in subsequently affecting restoration efforts. Initial evidence suggests alligators and nutria did not suffer severe mortality from the storms (fig. 7.10; LDWF 2008); therefore, the possibility for this trophic cascade still exists and may become more important given the land loss

caused by the hurricanes and the restoration efforts to come.

Acknowledgments. Steven Gabrey generously shared his unpublished report of alligator stomach contents with us and provided us with constructive comments on a draft of this chapter. We thank Len Bahr, Jeff Bounty, and Paul Kemp for helpful discussions; Mark Bertness for comments on an early draft; and the anonymous reviewers for their suggestions. Additional insight into nutria and alligator populations was provided by several staff members at the Louisiana Department of Wildlife and Fisheries, including Noel Kinler.

REFERENCES

- Abraham, K. F., and C. J. Keddy. 2005. The Hudson Bay Lowland. Pages 118–148 in L. H. Fraser, and P. A. Keddy (eds.), 2005. *The World's Largest Wetlands: Ecology and Conservation*. Cambridge: Cambridge University Press.
- Arthur, S. C. 1928. *The Fur Animals of Louisiana*. Bulletin No. 18. New Orleans: Department of Conservation, State of Louisiana.
- Barras, J. A., P. E. Bourgeois, and L. R. Handley. 1994. *Land Loss Rates in Coastal Louisiana 1956–90*. National Biological Survey, National Wetlands Research Center Open File Report 94-01. Lafayette, LA: National Wetlands Research Center.
- Bartram, W. 1791. *Travels through North & South Carolina, Georgia, East & West Florida, the Cherokee Country, the Extensive Territories of the Muscogulges, or Creek Confederacy, and the Country of the Chactaws; Containing an Account of the Soil and Natural Productions of Those Regions, Together with Observations on the Manners of the Indians*. Philadelphia: James & Johnson. Electronic version: Documenting the American South, University of North Carolina at Chapel Hill, 2001.
- Bernard, S. K. 2002. M'sieu Ned's rat? Reconsidering the origin of nutria in Louisiana: The E. A. McIlhenny Collection, Avery Island, Louisiana. *Louisiana History* 20: 281–293.
- Boesch, D. F., M. N. Josselyn, A. J. Mehta, J. T. Morris, W. K. Nuttle, C. A. Simenstad, and D. P. J. Swift. 1994. Scientific assessment of coastal wetland loss, restoration and management in Louisiana. *Journal of Coastal Research*, Special Issue No. 20.
- Bondavalli, C., and R. E. Ulanowicz. 1998. Unexpected effects of predators upon their prey: The case of the American alligator. *Ecosystems* 2: 49–63.
- Borer, E. T., E. W. Seabloom, J. B. Shurin, K. E. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2005. What determines the strength of a trophic cascade? *Ecology* 86: 528–537.
- Boyd, R., and S. Penland. 1988. A geomorphologic model for Mississippi River Delta evolution. *Transactions—Gulf Coast Association of Geological Societies* 38: 443–452.
- Bricker-Urso, S., S. W. Nixon, J. K. Cochran, D. J. Hirschberg, and C. Hunt. 1989. Accretion rates and sediment accumulation in Rhode Island salt marshes. *Estuaries* 12: 300–317.
- Callaway, J. C., R. D. DeLaune, and W. H. Patrick Jr. 1997. Sediment accretion rates from four coastal wetlands along the Gulf of Mexico. *Journal of Coastal Research* 13: 181–191.
- Carpenter, S. R., and J. F. Kitchell. 1988. Consumer control of lake productivity. *BioScience* 38: 764–769.
- Carter, J., A. L. Foote, and L. A. Johnson-Randall. 1999. Modeling the effects of nutria (*Myocastor coypus*) on wetland loss. *Wetlands* 19: 209–218.
- Carter, J., and B. P. Leonard. 2002. A review of the literature on the worldwide distribution, spread of, and efforts to eradicate the coypu (*Myocastor coypus*). *Wildlife Society Bulletin* 30: 162–175.
- Coastal Wetland Planning, Protection, and Restoration Act Task Force. 2008. Coastwide nutria control program (LA-03b) fact sheet. <http://www.lacoast.gov/projects/list.asp>.
- Committee on the Restoration and Protection of Coastal Louisiana. 2006. *Drawing Louisiana's New Map: Addressing Land Loss in Coastal Louisiana*. Ocean Studies Board, National Research Council. Washington, DC: National Academies Press.
- Craighead, F. C. 1968. The role of the alligator in shaping plant communities and maintaining wildlife in the southern Everglades. *Florida Naturalist* 41: 2–74.
- Day, J. W., and P. H. Templet. 1989. Consequences of sea level rise: Implications from the Mississippi Delta. *Coastal Management* 17: 241–257.
- Dundee, H. A., and D. A. Rossman. 1989. *The Amphibians and Reptiles of Louisiana*. Baton Rouge: Louisiana State University Press.
- Elsley, R. M., L. McNease, T. Joanen, and N. Kinler. 1992. Food habits of native and farm-released juvenile alligators. *Proceeding of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 46: 57–66.
- Evers, D. E., C. E. Sasser, J. G. Gosselink, D. A. Fuller, and J. M. Visser. 1998. The impact of vertebrate

- herbivores on wetland vegetation in Atchafalaya Bay, Louisiana. *Estuaries* 21: 1–13.
- Fahrenthold, D. A. 2004. Blackwater refuge now nutria-free. *Washington Post*, November 17, p. B1.
- Ford, M. A., and J. B. Grace. 1998a. Effects of vertebrate herbivores on soil processes, plant biomass, litter accumulation, and soil elevation changes in a coastal marsh. *Journal of Ecology* 86: 974–982.
- . 1998b. The interactive effects of fire and herbivory on a coastal marsh in Louisiana. *Wetlands* 18: 1–8.
- Fuller, D. A., C. E. Sasser, W. B. Johnson, and J. G. Gosselink. 1985. The effects of herbivory on vegetation in Atchafalaya Bay, Louisiana. *Wetlands* 4: 105–114.
- Gabrey, S. W. 2005. Impacts of the nutria removal program on the diet of American alligators (*Alligator mississippiensis*) in south Louisiana. Report to Louisiana Department of Wildlife and Fisheries, New Orleans.
- Geho, E. M., D. Campbell, and P. A. Keddy. 2007. Quantifying ecological filters: The relative impact of herbivory, neighbours, and sediment on an oligohaline marsh. *Oikos* 116: 1006–1016.
- Gosselink, J. G., R. Hatton, and C. S. Hopkinson. 1984. Relationship of organic carbon and mineral content to bulk density in Louisiana marsh soils. *Soil Science* 137: 177–180.
- Gough, L., and J. B. Grace. 1998a. Effects of flooding, salinity, and herbivory on coastal plant communities, Louisiana, United States. *Oecologia* 117: 527–535.
- . 1998b. Herbivore effects on plant species density at varying productivity levels. *Ecology* 79: 1586–1594.
- Grace, J. B., and M. A. Ford. 1996. The potential impact of herbivores on the susceptibility of the marsh plant *Sagittaria lancifolia* to saltwater intrusion in coastal wetlands. *Estuaries* 19: 13–20.
- Gunderson, L. H., and W. F. Loftus. 1993. The everglades. Pages 199–255 in W. H. Martin, S. G. Boyce, and A. C. Echternacht (eds.), *Biodiversity of the Southeastern United States: Lowland Terrestrial Communities*. New York: Wiley.
- Jeffries, R. L., and R. F. Rockwell. 2002. Foraging geese, vegetation loss and soil degradation in an Arctic salt marsh. *Applied Vegetation Science* 5: 7–16.
- Joanen, T., and L. McNease. 1987. The management of alligators in Louisiana, USA. Pages 33–42 in G. J. W. Webb, S. C. Manolis, and P. J. Whitehead (eds.), *Wildlife Management: Crocodiles and Alligators*. Chipping Norton, Australia: Surrey Teatty.
- Joanen, T., L. McNease, G. Perry, D. Richard, and D. Taylor. 1984. Louisiana's alligator management program. *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* 38: 210–211.
- Keddy, P. A. 2000. *Wetland Ecology: Principles and Conservation*. Cambridge: Cambridge University Press.
- Keddy, P. A., D. Campbell, T. McFalls, G. P. Shaffer, R. Moreau, C. Dranguet, and R. Heleniak. 2007. The wetlands of lakes Pontchartrain and Maurepas: Past, present and future. *Environmental Reviews* 15: 43–77.
- Louisiana Department of Wildlife and Fisheries. 2008. *Nutria: Wetland Damage*. New Orleans: Author. <http://www.nutria.com/site4.php>.
- Louisiana Fur and Alligator Advisory Council. 2004. *2003–2004 Annual Report*. Shreveport: Author. <http://www.alligatorfur.com>.
- Loveless, C. M. 1959. A study of the vegetation in the Florida everglades. *Ecology* 40: 1–9.
- Lowery, G. H. 1974. *The Mammals of Louisiana and Its Adjacent Waters*. Baton Rouge: Louisiana State University Press.
- Lynch, J. J., T. O'Neil, and D. W. Lay. 1947. Management and significance of damage by geese and muskrats to Gulf Coast marshes. *Journal of Wildlife Management* 11: 50–76.
- McCaffrey, R. J., and J. Thomson. 1980. A record of the accumulation of sediment and trace metals in a Connecticut salt marsh. *Advances in Geophysics* 22: 165–236.
- McFalls, T. 2004. Effects of disturbance and fertility upon the vegetation of a Louisiana coastal marsh. Unpublished master's thesis, Southeastern Louisiana University, Hammond.
- McGinnis, T. E., III. 1997. Shoreline movement and soil strength in a Louisiana coastal marsh. Unpublished master's thesis, University of Southwestern Louisiana, Lafayette.
- McIlhenny, E. A. 1935. *The Alligator's Life History*. Boston: Christopher. Republished by the Society for the Study of Amphibians and Reptiles, miscellaneous publications, Facsimile Reprints in Herpetology, 1976.
- Myers, R. S., G. P. Shaffer, and D. W. Llewellyn. 1995. Bald cypress (*Taxodium distichum* (L.) Rich.) restoration in southeastern Louisiana: The relative effects of herbivory, flooding, competition and macronutrients. *Wetlands* 15: 141–148.
- Nyman, J. A., and R. H. Chabreck. 1995. Fire in coastal marshes: History and recent concerns. Pages 135–141 in S. I. Cerulean and R. T. Engstrom (eds.), *Proceedings of the Nineteenth Tall Timbers Fire Ecology Conference—Fire in Wetlands: A Management Perspective*. Tallahassee, FL: Tall Timbers Research.

- Nyman, J. A., R. D. DeLaune, H. H. Roberts, and W. H. Patrick Jr. 1993. Relationship between vegetation and soil formation in a rapidly submerging coastal marsh. *Marine Ecology Progress Series* 96: 269–279.
- O'Neil, T. 1949. *The Muskrat in the Louisiana Coastal Marshes*. New Orleans: Federal Aid Section—Fish and Game Division, Louisiana Department of Wildlife and Fisheries.
- Paine, R. T. 1980. Food webs: Linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* 49: 667–685.
- Palmer, M. L., and F. J. Mazzotti. 2004. Structure of Everglades alligator holes. *Wetlands* 24:115–122.
- Patuxent Wildlife Research Center. 1999. South American nutria destroy marshes. PWRRC Fact Sheet 1999–01. <http://www.pwrc.usgs.gov/resshow/nutria.htm>.
- Penland, S., and K. E. Ramsey. 1990. Relative sea-level rise in Louisiana and the Gulf of Mexico: 1908–1988. *Journal of Coastal Research* 6: 323–342.
- Platt, S. G., C. G. Brantley, and R. W. Hastings. 1990. Food habits of juvenile American alligators in the upper Lake Ponchartrain Estuary. *Northeast Gulf Science* 11: 123–130.
- Reyes, E., M. L. White, J. F. Martin, G. P. Kemp, J. W. Day, and V. Aravamuthan. 2000. Landscape modeling of coastal habitat change in the Mississippi Delta. *Ecology* 81: 2331–2349.
- Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: The primacy of trait-mediated indirect interactions. *Ecology Letters* 7: 153–163.
- Shoop, C. R., and C. A. Ruckdeschel. 1990. Alligators as predators on terrestrial mammals. *American Midland Naturalist* 124: 407–412.
- Silliman, B. R., and M. D. Bertness. 2002. A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Sciences of the USA* 99: 10500–10505.
- Sinclair, A. R. E., C. J. Krebs, J. M. Fryxell, R. Turkington, S. Boutin, R. Boonstra, P. Secombe-Hett, P. Lundberg, and L. Oksanen. 2000. Testing hypotheses of trophic level interactions: A boreal forest ecosystem. *Oikos* 89: 313–328.
- St. Amant, L. S. 1959. *Louisiana Wildlife Inventory and Management Plan*. New Orleans: Pittman-Robertson Section—Fish and Game Division, Louisiana Wild Life and Fisheries Commission.
- Tarver, J., G. Linscombe, and N. Kinler. 1987. *Fur Animals, Alligator, and the Fur Industry in Louisiana*. Baton Rouge: Fur and Refuge Division, Louisiana Department of Wildlife and Fisheries.
- Taylor, D., and W. Neal. 1984. Management implications of size-class frequency distributions in Louisiana alligator populations. *Wildlife Society Bulletin* 12: 312–319.
- Teller, J. T., and L. H. Thorleifson. 1983. The Lake Agassiz–Lake Superior connection. Pages 261–290 in J. T. Teller and L. Clayton (eds.), *Glacial Lake Agassiz*. Geological Association of Canada Special Paper 26. St. John's, Newfoundland: Geological Association of Canada.
- Turner, R. E. 1997. Wetland loss in the northern Gulf of Mexico: Multiple working hypotheses. *Estuaries* 20: 1–13.
- U.S. Geological Survey. 2000. *Nutria, Eating Louisiana's Coast*. USGS FS-020-00, updated April 20, 2001. Washington, DC: Author.
- . 2005. *USGS Reports New Wetland Loss from Hurricane Katrina in Southeastern Louisiana*. Washington, DC: Author. <http://www.usgs.gov/newsroom/article.asp?ID=997>.
- Valentine, J. M., J. R. Walther, K. M. McCartney, and L. M. Ivey. 1972. Alligator diets on the Sabine National Wildlife Refuge. *Journal of Wildlife Management* 36: 809–815.
- White, T. C. R. 1993. *The Inadequate Environment: Nitrogen and the Abundance of Animals*. Berlin: Springer.
- Wolfe, J. L., D. K. Bradshaw, and R. H. Chabreck. 1987. Alligator feeding habits: New data and a review. *Northeast Gulf Science* 9: 1–8.