6 Herbivory

Many kinds of animals eat plants, so it might be reasonable to expect animals to have a significant effect on wetlands. Yet when we visit wetlands, we find that many are green and covered in plants, which could mean that herbivores are relatively unimportant. So just what is the story?

In general, we will see that plants are actually rather well defended from animals. There are two particular ways by which this occurs. First, the plants may have chemical defenses that deter herbivores from eating the plant, or interfere with their ability to digest the plants. Further, many plants have such low nutrient levels in their tissues that they provide a very poor food source and are thereby avoided.

We shall also see that there is evidence that predators may keep the populations of herbivores from becoming large enough to remove the plants from wetlands. The absence of natural predators may, in fact, be what has caused those exceptional cases where herbivores have turned the marsh into mud flats.

Herbivory interacts with other factors. Some processes add biological material to wetlands, and other processes remove it. The former include photosynthesis, growth, and reproduction; the latter include fire, decomposition, and herbivory. Processes that remove biomass are generally considered to be disturbances (Chapter 4). Disturbances can be considered either abiotic (flooding, fire, ice scour, landslides) or biotic (herbivory, burrowing, trampling). In some ways these disturbances are similar; in other ways they are different. They are similar in that standing crop is temporarily reduced, and light penetration is increased; they are different in that herbivory has the potential to be far more selective than other disturbances.

6.1 Some herbivores have large impacts on wetlands

Overall, there are only a few known cases where animals remove most of the vegetation and turn the wetland into mud. We shall begin with these few obvious examples. In many other cases, the effects of animals are much less obvious. The animals are apparently removing certain kinds of plants preferentially, but not affecting the dominant ones.

6.1.1 Effects of muskrats on freshwater wetlands

Small mammals such as muskrats have long been studied because of their importance to the fur industry. Fritzell (1989) and Murkin (1989) have reviewed some aspects of muskrat grazing in prairie wetlands, while O'Neil (1949) and Lowery (1974) have described their impacts on coastal wetlands. Muskrats not only consume large amounts of fresh plant material, but the amount of cattail destroyed and not consumed may be two to three times that. Around their lodges, muskrats may remove 75% of the above-ground standing crop in areas 4–5 m in diameter. In his classic book on muskrats, O'Neil describes how "The marsh is denuded of all vegetation by a complete eat-out and the peaty floor is usually broken to a depth of as much as

20 inches" (p. 70). Small fenced areas called exclosures (Figure 6.1) illustrate how completely the plants can be removed by grazing animals.

By destroying patches of vegetation, muskrats can greatly influence the composition of wetlands. When muskrats destroy mature vegetation, the marsh plants can regenerate from buried seeds, or from buried fragments of rhizome. Cycles in muskrat populations are therefore somewhat like cycles of rainfall, in that both drive changes in plant composition (Figure 4.13). Together, they control the composition of many small wetlands.

Grazing can also interact with fire. Smith and Kadlec (1985a) found that grazing intensity was particularly high in burned areas, where it ranged from 48% for *Typha* to 9% for *Scirpus maritimus*. It may be that plants shoots that are newly emerging after a burn have higher nutrient levels in their tissues. Burning has been used historically to manage marshes for muskrat production (O'Neil 1949); however, it should not be used as a tool without clear objectives and awareness of the potential impacts on other wetland species. In coastal marshes, peat production may be necessary to adjust to rising sea levels. In other wetlands, such as the Everglades (recall Section 4.3.2), fires that

FIGURE 6.1 Sometimes grazing animals, such as nutria, can almost eliminate wetlands plants – as illustrated by this experimental fenced plot (exclosure) in a Louisiana marsh. (Courtesy Louisiana Department of Wildlife and Fisheries.) (See also color plate.)

burn peat can change the wetland from wet prairie or marsh to shallow water.

6.1.2 Effects of snow geese on boreal salt marshes

The effects of foraging by lesser snow geese on coastal wetlands have also been extensively studied (e.g. Jefferies 1988a; Bazely and Jefferies 1989; Belanger and Bedard 1994). There is growing evidence of serious impacts – of the approximately 55 000 ha of salt marsh along the coasts of Hudson Bay and James Bay, one-third is considered "destroyed" and another third "nearly devastated" with the geese now moving to feed on the remaining third (Abraham and Keddy 2005). The impacts of goose feeding can even be seen on satellite photographs (Figure 6.2) There are several reasons why goose populations have increased to this level, including increased food during migration, and reduced hunting pressure.

Exclosure experiments allow scientists to measure the severity of grazing. In one set of small experimental plots (Table 6.1) Jefferies (1988a) found that effects depend upon the type of feeding activity,

grazing on above-ground tissues only, or grubbing, which includes consuming rhizomes as well. Grazed plots were nearly identical to control plots; in contrast, grubbing for rhizomes significantly reduced the number of shoots of both graminoid and dicotyledonous species.

The geese can have an effect on long-term vegetation changes along the coast. Typically, low marsh consists of *Puccinellia–Carex* swards, which slowly change to *Calamagrostis–Festuca* swards as elevation increases from isostatic uplift. Geese can delay this process by heavy grazing, but when small exclosures (0.5 × 0.5 m) were built, the normal succession occurred and there was eventual dominance by *Calamagrostis deschampsoides* and *Festuca rubra* (Hik *et al.* 1992).

6.1.3 Effects of nutria on marshes

The nutria or coypu (*Myocastor coypus*) is a large (up to 10 kg) South American rodent that has been introduced to both North America and Europe. Typical of the problems in wetland terminology, this animal is called coypu in the European literature (Moss 1983, 1984) and nutria in the American

Table 6.1 **Effects of herbivory (grazing and grubbing) by geese on wetlands along the coast of Hudson Bay – small-scale details for Figure 6.2. The data give the total number of shoots of graminoid plants and dicotyledonous plants in plots on intertidal flats (plots were 10 × 10 cm, n = 10, SE in parentheses)**

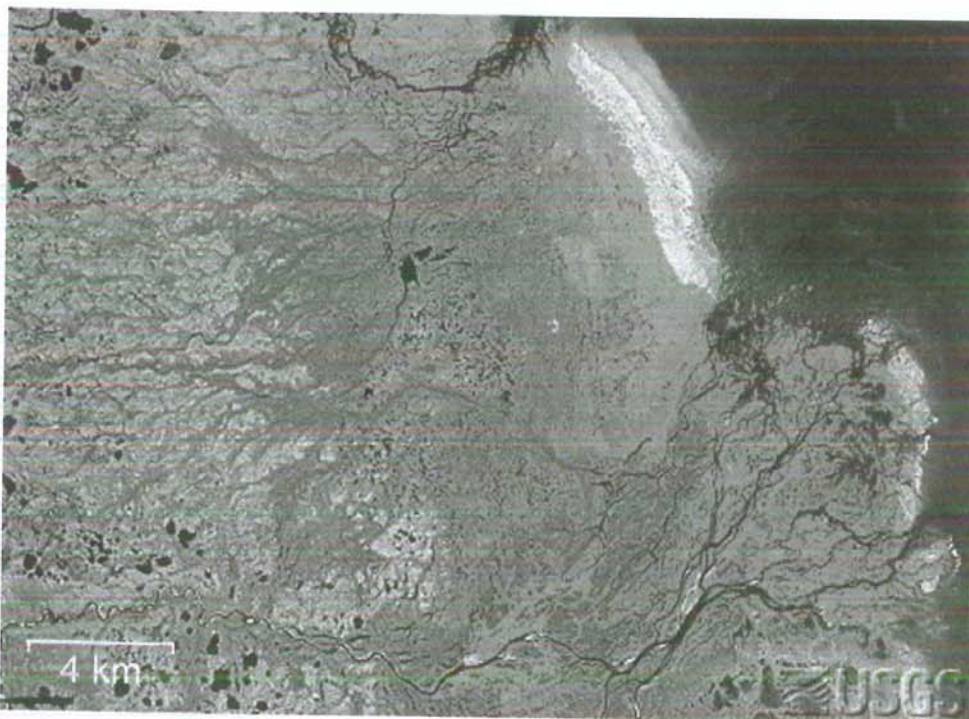|	Graminoid plants		Dicotyledonous plants	
	June	August	June	August
Ungrubbed plots				
Grazed plots	45.5 (5.0)	45.0 (7.5)	4.0 (2.0)	4.8 (1.8)
Exclosed plots	45.5 (5.0)	45.8 (7.8)	4.0 (2.0)	4.1 (1.7)
Grubbed plots	7.0 (1.0)	15.0 (5.2)	2.2 (0.7)	1.0 (0.8)

Source: From Jefferies (1988a).

FIGURE 6.2 Geese are grazing coastal wetlands along the shore of Hudson Bay so intensely that some areas of marsh have been converted to mud flats, as shown in this July 18 satellite image of the Knife River delta in Manitoba, Canada. The mud flats are indicated by the bright strip of land. (U.S. Geological Survey 1996.) (See also color plate.)

(Atwood 1950; Lowery 1974). Whichever name you use, Lowery (1974, p. 29) describes them as "huge, ungainly, stupid looking rodents" that have a devastating impact upon native vegetation.

In England, nutria were introduced to fur farms about 1929. Of course, some escaped, and then multiplied to an estimated 200 000 animals by the 1960s. Moss (1984) observes that coypus "are extremely destructive grazers, uprooting reed and other swamp [marsh] plants to eat the rhizomes," and attributes the loss of fringing reed marshes to herbivory by *M. coypus*.

In North America, fur farmers similarly introduced nutria in the 1930s. Again they escaped, and by the 1950s there were an estimated 20 million of these rodents "chewing away at the foundations of our wetlands" (Lowery 1974, p. 30). At the same time the number of muskrats declined.

Table 6.2 **The effects of grazing by *Myocastor coypus* on deltaic wetlands as illustrated by four 40 × 50 m exclosures and paired control areas**

Species	I Exclosure	I Control	II Exclosure	II Control	III Exclosure	III Control	IV Exclosure	IV Control
Amaranthus tamariscina	–	–	–	–	16	–	–	–
Alternanthera philoxeroides	12	–	–	–	14	–	6	–
Justicia ovata	27	19	31	11	62	40	24	35
Leersia oryzoides	2	–	3	–	51	7	87	27
Paspalum distichum	–	–	–	–	3	3	5	–
Polygonum punctatum	14	1	2	–	52	1	33	12
Sagittaria latifolia	95	1	128	–	82	59	73	22
Sagittaria platyphylla	18	1	11	–	18	4	52	5
Scirpus americanus	–	–	–	–	4	1	9	–
Scirpus validus	1	–	–	–	5	–	6	2
Spartina alterniflora	–	–	–	–	1	–	6	–
Typha domingensis	9	–	–	–	–	–	–	–
Total cover	178	22	175	11	308	115	301	103
Total species	8	4	5	1	11	7	10	6

Note: Numbers are cover value sums for 30 plots.
Source: Shaffer *et al.* (1992).

Fenced exclosure experiments have been used to study the impacts of nutria – Figure 6.1 shows the impacts of nutria. But what are the details? Table 6.2 shows that, relative to controls, exclosure plots had much higher cover and more plant species. Plants that were preferred food of *M. coypus* (e.g. *Sagittaria platyphylla*, *S. latifolia*) dominated exclosures, while species presumably less preferred (*Justicia ovata*, *Leersia oryzoides*) dominated the control sites.

Grazing can also change the distribution of species. Although *S. latifolia* is a relatively flood-tolerant species, it was restricted to higher elevations, which Shaffer *et al.* (1992) attribute to the grazing by *M. coypus* at lower elevations. Shipley *et al.* (1991b) similarly found that damage (in this case from muskrats) to emergents such as *Acorus calamus* was much greater at lower elevations in riverine marshes. More recent work in Louisiana by Taylor and Grace (1995), using smaller exclosures, showed that the biomass of dominant plant species

such as *Panicum virgatum*, *Spartina patens*, and *S. alterniflora* increased if *M. coypus* was excluded, but they were unable to detect changes in the number of species.

The secondary effects of herbivory may be even more dramatic. We have seen three examples now of herbivores that not only eat foliage, but actually dig up and destroy rhizomes. Plants can replace damaged leaves from below ground, but once the rhizomes are destroyed, the plant dies. Moreover, the positive effects of the rhizomes on stabilizing the wetland soil are lost. Once the plants are damaged or gone, the productivity declines, and so there is less accumulation of peat. Hence, grazing animals can actually change the rate at which wetlands respond to sedimentation and changes in sea level. Even partial defoliation can be harmful, since shoots transport oxygen to rhizomes (Section 1.4). Hence, grazing can increase the sensitivity of plants to other environmental factors, particularly flooding.

6.2   Wildlife diets document which animals eat which plants

It has long been observed by naturalists that animals feed on wetland plants. Most of us will have seen one or more examples: a beaver lodge made of willow trees, a muskrat house made of *Typha* and *Sparganium*, a moose munching on water lilies at sunset, or a duck feeding on *Potamogeton*. Wildlife biologists have investigated this in two principal ways: they have observed feeding by wild animals, and they have studied feces to reconstruct diets. They have then tabulated the biological utilization of wetland plants for the use of managers. To illustrate, Table 6.3 shows the kinds of plants consumed by snapping turtles (like the one on the

cover), while Table 6.4 shows plants consumed by waterbirds. Let us consider four other examples in more depth.

Table 6.4 Plant species identified in the gizzards of 1102 birds of 15 species of waterfowl in 58 locations in the eastern United States and Canada (abundance was measured by volumetric percentage)

Scientific name	Common name	Abundance
Potamogeton spp.	pondweeds	13.29
Polygonum spp.	smartweeds	6.69
Zizania aquatica	wild rice	5.10
Scirpus spp.	bulrushes	4.90
Najas flexilis	northern naiad	4.32
Lemna, Spirodela, etc.	duckweeds	2.97
Vallisneria spiralis	wild celery	2.49
Leersia, chiefly L. *oryzoides*	cutgrass	2.02
Setaria spp.	bristlegrasses	1.62
Echinochloa, chiefly E. *crusgalli*	wild millet	1.59
Sparganium spp.	bur-reeds	1.33
Carex spp.	sedges	1.21
Sagittaria spp.	arrowheads	1.00
Brasenia schreberi	watershield	0.95
Nymphaea spp.	water lilies	0.77
Ceratophyllum demersum	coontail	0.77
Bidens spp.	beggar's ticks	0.65
Cyperus spp.	sedges	0.57
Pontederia cordata	pickerel weed	0.48
Zea mays	corn	2.30
Fagopyrum esculentum	buckwheat	1.40
Sorghum vulgare	sorghum	0.51
Algae (microscopic)	algae	0.87
Characeae	algae	1.87
Miscellaneous		14.69
Total		74.36
Invertebrates		25.64

Source: Adapted from Crowder and Bristow (1988).

Table 6.3 The contents of the stomachs of 22 snapping turtles

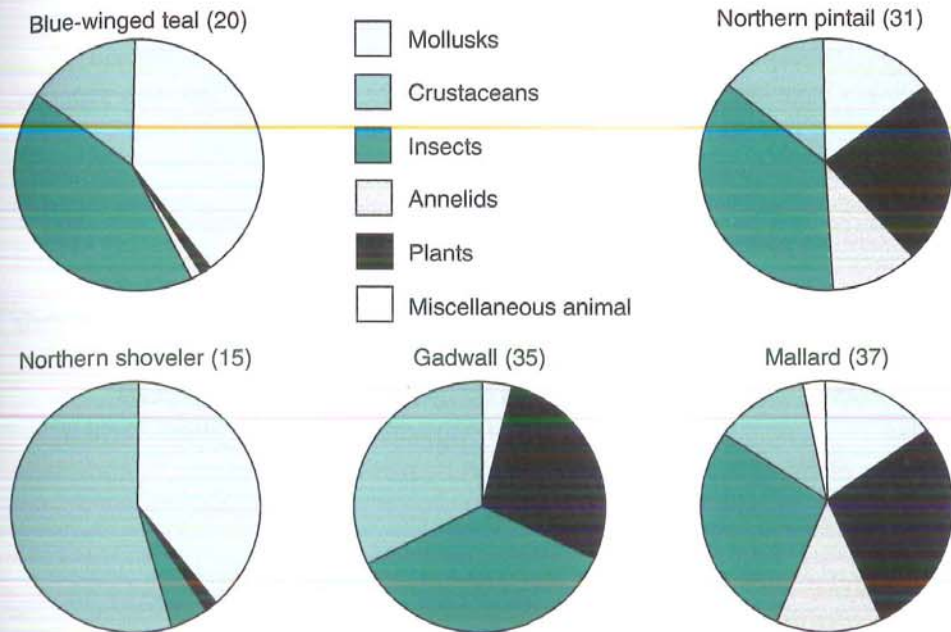| Food item	Number of stomachs	Percent of samples
Plants		
Potamogeton sp.	15	68.2
Algae	8	36.4
Polygonum sp.	6	27.3
Lemna sp.	4	18.2
Other	9	40.9
Fish		
Carp (*Cyprinus carpio*)	16	72.8
Pike (*Esox lucius*)	6	27.3
Bass (*Micropterus* sp.)	4	18.2
Perch (*Perca flavescens*)	4	18.2
Mollusks		
Snail (*Physa, Planorbula, Gyraulus*)	21	95.4
Other	4	18.2
Insects	11	50.0
Birds	5	22.7
Turtles	1	4.5

Source: From Hammer (1969).

FIGURE 6.3 Plants can make up a significant proportion of the diet of waterfowl. (From van der Valk and Davis 1978.)

Waterbirds consume both plants and invertebrates. Egg-laying females and young tend to emphasize invertebrates in their diets, presumably because of the higher food quality of animal protein. Even so, Figure 6.3 shows that some species such as the northern pintail and gadwall consume plants directly as one-fourth of their diet, while Table 6.4 shows the importance of plants in waterbird diets as a whole. Most such studies focus on the food quality of plants for waterfowl, however. Whether the waterbirds, in turn, affect the plants is much less explored.

Many fish are also dependent upon wetland plants. A striking example is the fish that feed upon fruits and seeds in floodplain forests (Goulding 1980). The Amazon basin has some of the largest areas of flooded forest in the world – some 70 000 km². Some trees are flooded to depths of 15 meters and for up to 10 months of the year. Plant germination and growth appear to be restricted to the few months when the floodplain is drained. Up to 3000 species of fish may inhabit this region. Of the more than 1300 described

to date, about 80% are either catfishes or characins (Figures 2.5d, 9.1). The latter group has radiated extensively in the Amazon lowlands, and includes carnivores, frugivores, detritivores, and planktivores. Goulding closes by suggesting that this is very important for human welfare too – some 75% of the commercial catch may originate in flooded forests.

Perhaps the most remarkable conclusion, however, is that most animals eat not the plants themselves, but rather feed on other animals that feed on decaying plants. Study after study over the past 50 years has demonstrated the same startling result: a vast majority of plant biomass goes directly into the decomposer food web, where it is processed by small invertebrates and microorganisms. This generalization ranges from arid tropical grasslands (Desmukh 1986) to temperate salt marshes (Adam 1990), although aquatic algae are an apparent exception (Cyr and Pace 1993). Further, fire often removes a substantial portion of biomass not consumed by decomposers; in tall grass areas like

the Serengeti plains, more than half of the plant biomass is burned (Desmukh 1986). Therefore, while it is easy for us to observe plants that have been grazed by animals, we should remember that scenes like Figures 6.1 and 6.2 are rare – overall, grazing animals process less than 10% of the biomass in the vegetation. The rest decays and then supports a decay-based food web.

6.3   Impacts of some other herbivores on wetlands

Having dealt with some of the most extreme examples in Section 6.1, let us now move on to explore some of the more typical examples of herbivory that occur in wetlands.

6.3.1 Snails in salt marshes

The periwinkle snail (*Littoraria irrorata*) often feeds on salt marsh cordgrass (*Spartina alterniflora*). Snail densities can reach hundreds per square meter. To measure effects of snail grazing, Silliman and Zieman (2001) constructed 1-m^2 cages in a Virginia salt marsh, and created three levels of snail density: zero, ambient, and three times ambient. They also manipulated fertility by adding nitrogen as ammonium chloride. Figure 6.4 shows that as snail density increased from left to right, the production of cordgrass fells from 274 to 97 g/m^2. When nitrogen was added, the snail removal had an ever greater effect, cordgrass growth falling from 1490 to 281 g/m^2. The reduction in growth was not just the result of tissue being consumed by the snails. It appears that the rasping by the snail radulae causes and maintains wounds, leading to the death of stems and leaves, and thereby suppressing plant growth. Hence, the effect of snails is not only grazing, but defoliation and diversion of plant tissue to the detritus food web. Silliman and Zieman suggest that this effect of snails be called "top down control."

What controls the abundance of snails in natural marshes? Snails are eaten by predators including crabs and turtles – a topic to which we return in Section 6.6.2. Snails are also thought to have important impacts on freshwater wetlands, and their impacts on aquatic plants may in turn be controlled by fish that eat snails (Brönmark 1985, 1990; Carpenter and Lodge 1986; Sheldon 1987, 1990).

6.3.2 Large mammals in African grasslands

Large herbivores like the hippopotamus affect wetlands by grazing, and by excavating depressions
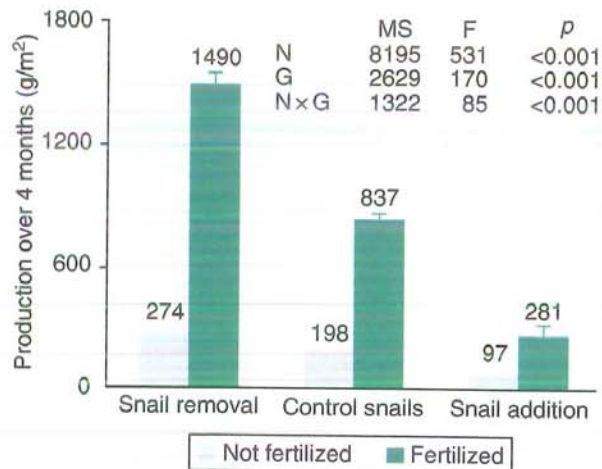

FIGURE 6.4 Snail grazing has significant impacts on salt marsh cordgrass (*Spartina alterniflora*). Note that the middle histogram was the control containing the naturally occurring snail populations. When fertilizer was added (dark histograms), plant production increased, but the negative effects of grazing remained. Both main effects and the interaction term are significant, $p < 0.001$. (After Silliman and Zieman 2001.)

1 Matetite reed
   Phragmites sp.
2 Hippopotamus
   Hippopotamus amphibius
3 Hammerhead stork
   Scopus umbretta
4 Black crake
   Limnocorax flavirostra
5 Sitatunga
   Tragelaphus spekki
6 Swamp worm
   Alma emini
7 Saddlebilled stork
   Ephippiorhynchus
   senegalensis
8 Water cabbage
   Pistia stratiotes
9 Water lily
   Nymphaea sp.
10 Bichir
   Polypterus sp.
11 Catfish
   Malapterurus sp.

12 Lily trotter
   Actophilornis africana
13 African spoonbill
   Platalea alba
14 Papyrus
   Cyperus papyrus
15 Malachite kingfisher
   Corythornis cristata
16 Herald snake
   Crotaphopeltis
   hotamboeia
17 Shoebill
   Balaeniceps rex
18 Squacco heron
   Ardeola ralloides
19 Snail
   Biomphalaria sudanica
20 Marsh mongoose
   Atilax paludinosus
21 Lungfish
   Protopterus aethiopicus

FIGURE 6.5 Large herbivores remain important in African wetlands, and their impacts affect many other wetland species. (From Dugan 2005.) (See also color plate.)

(Figure 6.5). There are, however, many other herbivores that use wetlands only seasonally. It is easy for us to focus on only those herbivores that are permanent residents of wetlands. To keep a broader perspective, let us consider the temporary use of wetlands by large African mammals (Western 1975; Sinclair and Fryxell 1985). Recall (Chapter 1) that many of the large ungulates on the African plains graze in wetlands during the dry season, and then use the surrounding grasslands in the wet season.

As consequence, each vegetation type receives a period free from herbivory, and as well, by using the combined productivity of this range of habitats, many more animals can be supported (Sinclair and Fryxell 1985). The ungulate populations in Africa are large and diverse; for example, Sinclair (1983) points out that one family, the Bovidae (in the order Artiodactyla), containing the buffalo and antelope, has as many species (78) as the most diverse rodent family, the Muridae. Some of these

bovids are adapted to wetlands, such as the kob and lechwe. Ungulates, as a whole, have four main habitats: forest, savanna, desert, and wetland (Sinclair 1983); and the wetlands range from forested swamp to *Papyrus* marshes to seasonally flooded wetlands (Thompson and Hamilton 1983; Howard-Williams and Thompson 1985; Denny 1993a, b). Most large mammals use these wetlands at some time of year (Table 6.5), and distance from water is a good predictor of biomass of herbivores (Figure 6.6), but the shortage of water has placed constant selective pressure upon herbivores. There have been two main evolutionary responses. Independence from water requires a shift from herbivory on grasses to browsing upon shrubs; browsers are less dependent upon water and wetlands. Further, reproduction is timed to coincide with the rainy season when the habitat is as productive as possible; this is found in species such the elephant, white rhinoceros, zebra, hippopotamus, warthog, buffalo, giraffe, and kudu. The importance of seasonal surges in production is illustrated by an exception to the above rule (Sinclair 1983). "Lechwe live on riverine floodplains that are seasonally flooded ... Optimum food conditions occur when water is at the lowest level exposing the greatest area of floodplain, and it is then that the peak of births occur." Such studies should remind us that many animals that are not normally considered "wetland" animals may benefit from the wetlands in a landscape.

6.3.3 Slugs and sheep in peatlands

In contrast to the African plains, the peatlands of the British Isles have vast herds of slugs and sheep. Overall, there are more than 1 million ha of moorland in Britain (Miller and Watson 1983). The principal habitat gradients are soil moisture, soil nutrient supply, and sheep grazing intensity. These areas have been extensively modified by humans. The original oak forests were cleared during Roman and medieval times, and eventually replaced by scrub and grassland following the use of the mountains for

grazing. The density of the main vertebrate herbivores is estimated as 50 sheep, 65 red grouse, 10 red deer, and 16 mountain hare per km^2 in the highlands of Scotland. Even so, less than 10% of the primary production of *Calluna vulgaris* (heather) is actually consumed by herbivores (Miller and Watson 1983).

Consider the example of moorland in Snowdonia, northern Wales. Here there is a mosaic of vegetation types including grassland, *Eriophorum* mire, and heath (Perkins 1978). Slug species such as *Agriolimax reticulatus* and *Arion intermedius* can reach densities exceeding 10/m^2. They consume approximately 1 g/m^2 per month (Lutman 1978). Sheep are the dominant vertebrate herbivore, with densities from 5 to 19 animals per hectare (Brasher and Perkins 1978). The sheep show a preference for grassland areas (*Agrostis–Festuca* swards) and reject sedges, rushes, and herbs, many of which are typical of wetter sites. Red grouse are often studied because of their hunting value. They feed primarily upon *C. vulgaris* shoots, but eat only a negligible proportion of the primary production on their territories (Miller and Watson 1978). The principal effects of grouse arise from the human practice of burning moorlands to improve the habitat for grouse hunting. This changes plant species composition, stimulating the growth of *Calluna* in particular, and may have deleterious effects upon the development of wet blanket bog (Rawes and Heal 1978). Further, the burning leads to volatilization of nitrogen and leaching of potassium from the remaining ash (Miller and Watson 1983).

An exclosure experiment in the Pennines, northern England, showed that after 7 years of excluding sheep, biomass increased by 50%, and the number of plant species declined from 93 to 67 (Rawes and Heal 1978). These patterns typified drier areas; grazing on the blanket bog itself is so low that the sheep appear to have "little noticeable effect." Comparison with a bog that was grazed continually for many years suggests that grazing reduces the shrub *C. vulgaris* and increases *Eriophorum vaginatum*.

Table 6.5 Seasonal habitat changes in the large herbivores of the Rukwa Valley, Tanzania; habitats used for the greatest duration are italicized

Animal species	Jan	Feb	Mar	April	May	June	July	Aug	Sept	Oct	Nov	Dec
								Time of year				
Elephant	Acacia and escarpment woodlands						*Floodplain*				Woodlands	
Buffalo	*Woodlands – Lakeshore and delta grasslands*						*Floodplain*				Woodlands	
Hippopotamus	*Fringe river and delta grasslands*			Wander widely along drainage							*River fringe*	
Puku				Delta and lakeshore grassland all year								
Topi	Perimeter grassland			*Lakeshore and delta grassland*			Vossia pasture			Acacia woodland		
Zebra	Acacia woodland		Perimeter grassland		Acacia parkland		*Floodplain grassland*			Acacia woodland		
Bohor Reedbuck				*Floodplain grassland*								
Eland	Dry perimeter plains				*Delta grasslands and Vossia pasture*					Acacia woodland		
Giraffe and Impala					Acacia grassland							
Warthog					Acacia grassland and forest edge							
Waterbuck, Duiker, Baushbuck, and Steinbuck							Woodlands					

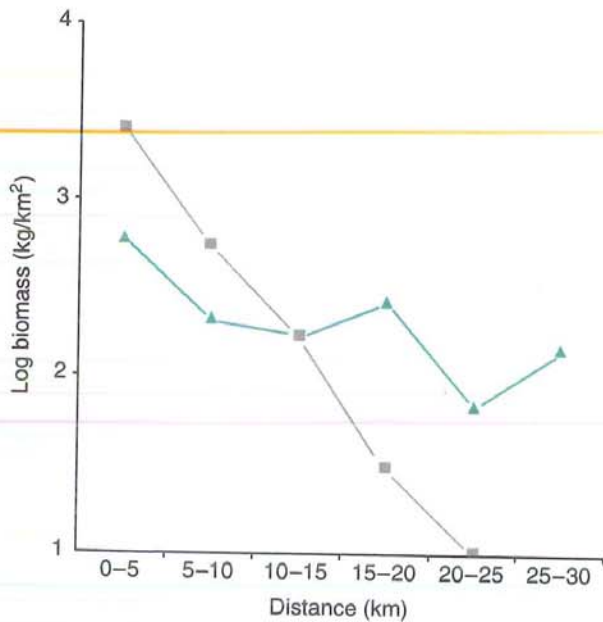*Source:* After Vesey-FitzGerald (1960).

FIGURE 6.6 The biomass of herbivores varies with distance from water during the dry season in Kenya. Water-independent browsers (triangles) are less affected than water-dependent grazers (squares). (From Western 1975, in Sinclair 1983.)

6.3.4 Rhinoceros in tropical floodplains

Although large herbivores like rhinoceros are becoming rare, their potential impacts upon vegetation need to be considered, if only because their effects will be lost if the species becomes extinct. We may think of rhinoceros as representing some of the large numbers of enormous animals that once occurred in our landscapes, but which were killed off by aboriginal hunters (Section 6.4.4).

Asian lowland forests contain several large herbivores including the Asiatic elephant, greater one-horned rhinoceros, and Javan rhinoceros. Tree diversity is relatively low, but large browser biomass is almost as high as the highest values reported from Africa (Dinerstein 1992). More than 300 of the greater one-horned rhinoceros (*Rhinoceros unicornis*) occur in Royal Chitwan National Park in Nepal. Two tree species are dominant, *Litsea monopetala* (Lauraceae) and *Mallotus philippinensis*

(Euphorbiaceae). All of the understory *Litsea* showed signs of moderate to heavy browsing and trampling by rhinoceros. Exclosure experiments showed that *Litsea* growth was enhanced when it was free from browsing for 3 years.

Rhinoceros also distribute the seeds of floodplain trees such as *Trewia nudiflora*, which produces a hard green fruit. Dung piles in floodplain grasslands appear to be important colonization sites. Thirty-seven other plant species have been recorded from rhinoceros latrines and the flora as a whole includes 77 fleshy-fruited species that are dispersed by vertebrates (Dinerstein 1991). At the time of these studies, the rhinoceros population was recovering from heavy poaching, so natural population levels would be expected to have greater impact.

6.3.5 Effects of cattle on the flooding Pampa

Unlike African grasslands, Pampean grasslands in South America developed under low intensities of natural herbivores (Facelli *et al.* 1989). Cattle and horses were introduced by the Spanish settlers in the 1500s, and in the mid-1800s, fences were built, so that herbivory was further intensified. As agriculture replaced ranching, natural grasslands were ploughed, except for areas subjected to regular flooding, the flooding Pampa. Such trends are similar to those found in the Pantanal (see conclusion, Chapter 1) and the North American prairies. The Pampas of Argentina cover some 750 000 km^2; the main wetland area is in the Salado basin, a flat area approximately 60 000 km^2 with mild winters and warm summers. Facelli *et al.* (1989) compared a 1-ha plot that had been grazed steadily at a stocking rate of roughly one head per 2 ha with a 1-ha plot from which cattle had been excluded for 9 years. Grazing had major effects on species composition. The ungrazed site had cover that was 95% monocotyledons, particularly large tussock grasses; *Paspalum dilatatum* and *Stipa bavioensis* dominated. The tall grasses form a dense canopy which probably shades out shorter species.
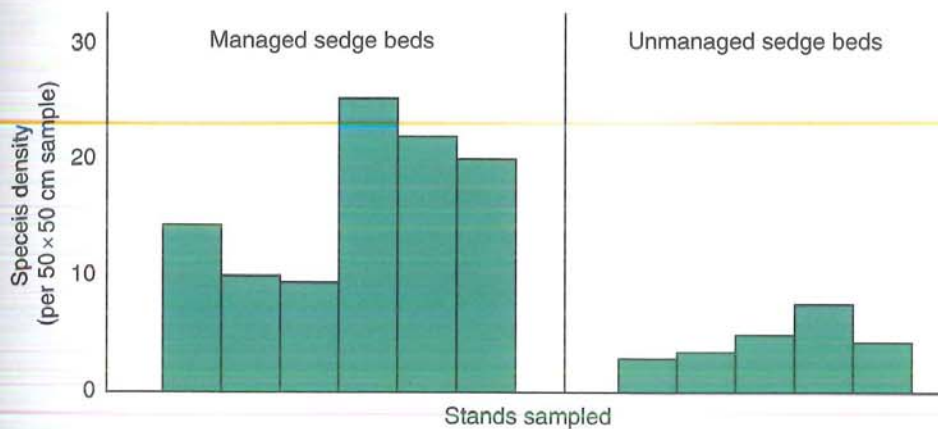
FIGURE 6.7 Mowing by humans can change the number of plant species (as measured by species density) in English sedge beds. (After Wheeler and Giller 1982.)

In contrast, the grazed community was almost 60% dicotyledonous species, many of which were exotic, such as *Mentha pullegium*.

6.3.6 Humans as herbivores: mowing

Humans sometimes harvest wetland vegetation to feed livestock, to gather thatching for roofs, or even to construct boats. Although such activities are often considered quaint by urban scientists, they are considered important in Europe, for example, because mowing and the product – thatched roofs – are needed to maintain traditional landscapes. Mowing as traditionally practiced often increases the number of plant species found in wetlands. Managed sedge beds (composed largely of *Cladium mariscus*) had lower biomass, less litter, and more species than unmanaged beds (Figure 6.7). As well, bryophytes were largely restricted to managed beds. The effects of mowing on reed beds (composed largely of *Phragmites communis*) were much less noticeable. Mowing and grazing are not necessarily equivalent – in European salt marshes, grazed areas had more more species than mowed areas (Figure 6.8).

When traditional mowing ceases, changes occur. In wet meadows along the Oste valley in northwestern Germany, the cessation of mowing allowed valued marsh marigold meadows (e.g. *Caltha*

palustris, Senecio aquaticus) to develop into stands of reeds and tall forbs (e.g. *Glyceria maxima, Phalaris arundinacea, Urtica dioica*). These latter species produce dense shade and thick accumulations of litter, which reduce diversity in plant communities. Overall, the number of plant species declined from ca. 30 species to ca. 10 species (Müller *et al.* 1992). Mowing twice a year restored typical plant diversity within 3–5 years. The wet grasslands scattered along slow-flowing rivers in Belgium also have a history of mowing (Dumortier *et al.* 1996). Mowing effects were measured in an experiment that varied the timing (one of 6 months, June to November) and number of harvests (one or two harvests, July and October). Overall 63 plant species were recorded. Harvesting once or twice increased the number of plant species, while the number declined with time in the unmowed control plots. Different mowing times likely select for different species composition. The most important plant traits for predicting responses to mowing appear to be germination characteristics and the degree of rhizome production. Rhizomatous species are most damaged by midsummer harvesting, since summer is when their shoots would normally translocate energy back to roots and rhizomes; consequently, rhizomatous plants are favored by late fall harvesting.

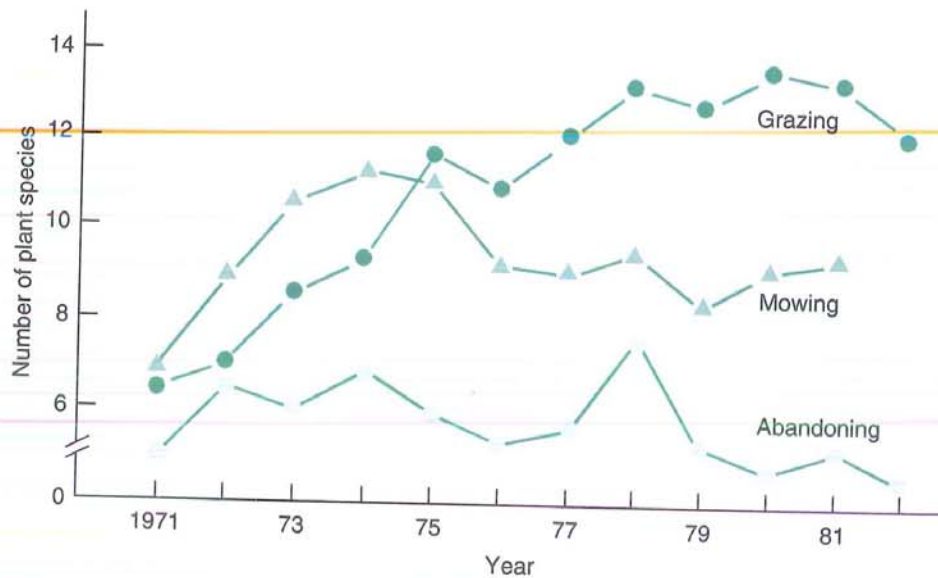Although many other landscapes such as North American wet meadows do not have a long tradition

FIGURE 6.8 Species richness plotted against time in European salt marshes with three contrasting types of management ($n = 5$, 2×2 m^2 quadrats). (After Bakker 1985.)

of mowing, the increasing dominance of wetlands by large clonal plants such as *Phragmites australis* and *Phalaris arundinacea* is becoming more of a management problem (Keddy 1990a; Kercher *et al.* 2004; Zedler and Kercher 2004). (Of course, historians will remind us that removing "marsh hay" from wetlands was a time-honored tradition in early European settlement of North America.) On one hand, we could argue that there are some valuable lessons to be learned from wetland management in Europe, and a remarkable lack of respect of the literature on this topic is found in many North American articles.

On the other hand, before we start using mowing elsewhere, it is essential to appreciate that many of the wetlands in western Europe have been produced by, or at least shaped by, mowing or grazing, for hundreds if not thousands of years. Their problems arise when traditional gazing and mowing regimes cease. Other vegetation types, however, may not have a history of mowing or herbivory, particularly the infertile peatlands and alluvial wetlands in less populated regions of the Earth. The floras in such regions may be stress tolerators (*sensu* Grime 1977, 1979) and mowing or herbivory could have negative effects upon them.

6.4   Plants have defenses to protect them against herbivores

In order to protect themselves against the impacts of herbivores, plants have evolved many different tactics for defense. In this section we will cover some of the common strategies employed by wetland plants.

6.4.1 Morphological defenses

Spines, thorns, and prickles deter herbivores (e.g. Crawley 1983; Marquis 1991; Raven *et al.* 1992).

If many such plants were present in wetlands, it would be relatively convincing evidence that herbivores are important in wetlands. Yet, in spite of the many plants that bear large spines, few occur in wetlands. Figure 6.9 shows a few selected examples of devices thought to protect wetland plants from herbivores.

Where anti-herbivore traits are present, evidence suggests that herbivory is less important under water than above it. *Pontederia cordata*, which is shown on
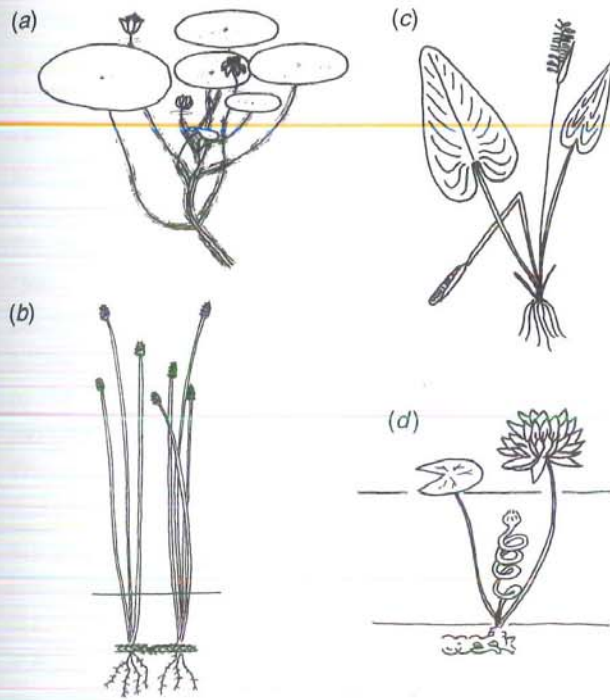
FIGURE 6.9 Some traits that confer resistance to herbivory: (a) gelatinous coating on stems and foliage (*Brasenia schreberi*; from Hellquist and Crow 1984), (b) buried rhizomes (*Eleocharis palustris*), (c) peduncle that bends to submerge fruits (*Pontederia cordata*), (d) peduncle that coils to pull fruits into the water (*Nymphaea odorata*).

the cover of this book, has showy flower stalks, but once the flowers are pollinated, the stem bends to hide the stalk under the water (Figure 6.9c). Similarly, *Nymphaea odorata* has conspicuous flowers on the surface of many northern lakes and slow-moving rivers, but once the flowers are pollinated, the peduncles coil like a spring, pulling the fruits down to the bottom of the lake (Figure 6.9d).

6.4.2 Chemical defenses

Chemical traits are less visible than morphological ones, but may be equally important in deterring herbivory. While some plant compounds have obvious roles to play in photosynthesis, growth, and reproduction, others do not. These latter secondary

metabolites were once thought to be just waste products. It has now become clear that many of these compounds play active and important roles in defending plants against herbivores (Marquis 1991). There are three main groups of anti-herbivore compounds: terpenes, phenolics, and nitrogen-containing secondary products (e.g. Taiz and Zeiger 1991). There is only limited information on anti-herbivore defense compounds in wetland plants in standard references such as Rosenthal and Berenbaum (1991). This could be a consequence of either one of two causes: the actual rarity of defense compounds in wetlands (a phenomenon of real ecological interest) or the lack of study of wetland plants by chemists (a phenomenon of interest only to those who study the behavior and sociology of scientists). There are passing references to glucosinolates (Louda and Mole 1991), coumarins (Berenbaum 1991), and possibly iridoid glycosides (Bowers 1991) in protecting wetland plants from herbivorous invertebrates. Coumarins have been found in more than 70 plant families, and these include important wetland families such as the Cupressaceae, Araceae, Cyperaceae, Poaceae, and Juncaceae (Berenbaum 1991).

In contrast with these sources, McClure (1970) documents a prominent role for secondary metabolites in aquatic plants. Going from wet to dry, he found that flavonoids are predominant in free-floating species, phenols and flavonoids are found in submerged and emergent taxa, and alkaloids predominate among rooted floating-leaved species (e.g. the Nymphaeaceae). In contrast, terpenoids are apparently more common in plants of waterlogged soils and seasonally flooded areas (e.g. Cyperaceae, Poaceae, Acanthaceae). Ostrofsky and Zettler (1986) examined 15 species of aquatic plants including *Cabomba caroliniana*, *Vallisneria americana*, and nine species of *Potamogeton* to assay for alkaloids, finding between 0.13 and 0.56 mg/g dry weight, values that are "low, but certainly within a range which is pharmacologically active, and consistent with a potential role as herbivore deterrents." The actual kind of alkaloid varied greatly among
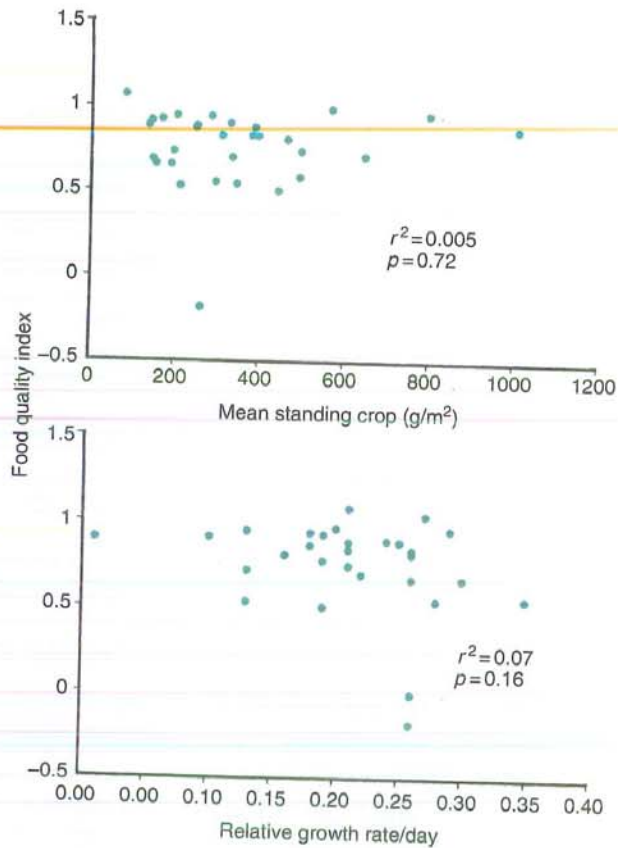
FIGURE 6.10 The food quality of 30 kinds of wetland plants is correlated neither with the biomass of the habitat (top) nor with the relative growth rate of the species (bottom). (After McCanny et al. 1990.)

to reduce impacts of herbivores, and whether the production of defense compounds varies among habitats. McCanny et al. (1990) evaluated the anti-herbivore defenses in 42 wetland plant species, and then tested whether anti-herbivore defenses were increased in infertile habitats where the costs of grazing to plants should be greater (Coley 1983). First they extracted secondary metabolites from the test plants, and added them into the diet of an insect herbivore. The larvae showed reductions in growth of up to 50%, thereby showing some evidence of anti-herbivore compounds. There was no difference in toxicity of forbs and graminoids. The food quality index (as measured by the performance of the insect herbivore) was then plotted against the fertility of the habitat typical of each plant species. There was no relationship between the food quality index and soil fertility, plant biomass (Figure 6.10, top), or plant relative growth rates (Figure 6.10, bottom).

In conclusion, while there is some evidence that morphological traits or secondary plant metabolites play a role in defense against herbivores, the evidence is far from conclusive. The study of effects of grazing upon existing communities requires evidence outside the comparative realm.

6.4.3 Nitrogen content is the key to understanding food quality

Nitrogen is thought to be the most important factor determining food value of plants (Lodge 1991; White 1993). We have also already seen that nitrogen content of aquatic plants is frequently well below 5% (Table 3.1), and Lodge (1991) shows that emergent, floating, and submersed macrophytes, as well as algae, all have similar nitrogen contents, usually of 2% to 3% (with extremes from 1% to at least 5%). These are very low values for supporting grazing animals. Hence, it may be that the strongest defense wetland plants have against herbivores is the low quality of the food they provide.

To illustrate the importance of nitrogen content to herbivores tissues, White (1993) describes attempts

species, with the *Potamogeton* species being no more similar to each other than to other genera. Gopal and Goel (1993) list other examples such as fatty acids, allomones, mustard oils, and steroids, but in general the role of such secondary metabolites is still poorly documented and even more poorly understood. The compounds may provide defense against herbivores, but there may be other functions such as antimicrobial activity and allelopathic interactions with competing neighbors including planktonic algae.

Simply screening for the presence of possible defense compounds in wetland plants, while helpful, still leaves important unanswered questions. We need to know whether these compounds are actually able

to control *Salvinia molesta*, an aquatic fern from Brazil which has become a serious weed in many tropical regions. Initial attempts to import and establish insects from Brazil to control it in Australia and Papua New Guinea had variable success; at concentrations of nitrogen of 1% or less dry weight, the imported pyralid moth could not establish. "However, increasing the level of nitrogen in the fern to only 1.3% dry weight by simply adding urea fertilizer to the water can cause an to explosive increase in the abundance of the moth and severe damage to the plants" (p. 77). The species of weevil introduced from Brazil to Australia to combat *Salvinia* was also limited by nitrogen availability. In contrast, when Lodge (1991) studied herbivory preferences of the crayfish *Orconectes rusticus* among 14 submersed macrophytes, he found clear preferences for certain species, but he was unable to detect statistically significant differences in nitrogen content among the plants.

Simple comparisons of plant tissue may conceal real differences in nitrogen content if herbivores are consuming only selected tissues. In general, herbivores show a preference for reproductive structures, particularly seeds, and newly growing shoots. We have already noted above that muskrats are attracted to feed on new shoots in burned areas. Sinclair (1983) and White (1993) have described many examples of herbivores preferentially selecting new growth. Beavers not only favor certain species, as we shall see below, but they consume mainly the young bark and cambium, which has much higher nutrient content than the actual wood. White adds the example of green turtles (*Chelonia mydas*), marine herbivores that feed on the aquatic vascular plant called seagrass (*Thalassia testudinum*). These turtles maintain areas of cropped seagrass and feed upon the flush growth in the cropped area, ignoring adjacent stands of tall seagrass. Beavers can be seen doing the same – once some larger trees have been felled, the new saplings that regenerate can provide a steady source of younger and more edible trees.
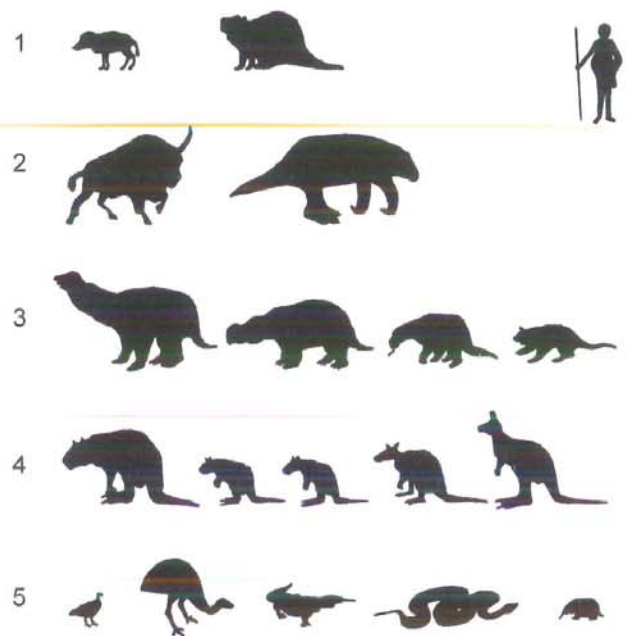

FIGURE 6.11 Some examples of the megafaunas that became extinct at the time humans arrived in North America (top) and Australia (bottom). North America: 1, *Platygonus, Castoroides*; 2, *Bison latifrons, Nothrotheriops*. Australia: 3, *Diprotodon optatum, Zygomaturus trilobus, Euowenia grata, Thylacoleo carnifex*; 4, *Procoptodon goliah, Sthenurus maddocki, Sthenurus atlas, Protemnodon brehus, Macropus ferragus*; 5, *Progura gallinacea, Genyornis newtoni, Megalania prisca, Wonambi naracoortensis, Zaglossus ramsayi*. A human is shown for scale. (Adapted from Martin and Klein 1984.)

6.4.4 Herbivores of the past: missing pieces

There is a further complication. As we try to put the puzzle of herbivory together, we find there are important missing pieces. The presence of anti-herbivore defenses tells us that herbivores affected evolution, but it in no way demonstrates the active occurrence of herbivory in present-day communities. This point is by no means trivial or pedantic. We know that, in relatively recent times, only about 10 000 years BP, both North America and Australia lost entire megafaunas (Figure 6.11). It has been argued that many plants possess adaptations to dispersal by large mammals that are now extinct

(Janzen and Martin 1982). It seems equally plausible that plants could have adaptations to protect themselves from herbivores that no longer play a role in determining wetland community structure. Further into the past, in the late Mesozoic, we also find herbivorous dinosaurs, and some of these are thought to have been semi-aquatic. The effects of herbivory on wetlands may thus extend back hundreds of millions of years.

Take, for example, the giant beaver (Kurtén and Anderson 1980; Parmalee and Graham 2002). This species reminds us that near the end of the last ice age, North American wetlands had beavers the size of black bears felling trees, while herds of millions of bison, horses, and camels waded through wetlands. Only Africa remains (Figure 6.5) to illustrate how many other parts of the world might have been. Elsewhere, near the end of the last ice age, a majority of these animals became extinct. The precise cause is still argued, but it is most likely the result of over-hunting by newly arrived predators – human beings.

Bones of *Castoroides ohioensis* have been found from Florida to Alaska, although the largest concentrations are south of the Great Lakes, hence the name. The giant beaver could have weighed 200 kg (compared to 30 kg for a modern beaver). Their teeth were up to 15 cm long. Experts disagree whether the giant beaver felled trees; some authorities suggest that the animal likely fed more like a modern muskrat. However, one Ohio fossil site appeared to have a lodge constructed from saplings about 7.5 cm in diameter. And a relatively well-preserved beaver pond, locked in permafrost on Ellesmere Island in the Canadian Arctic, has gnawed sticks. Perhaps the early painting of the animal (Figure 6.12) was correct after all.

The great beaver is here to make a point. Reading a book like the *Pleistocene Mammals of North America* (Kurtén and Anderson 1980) one is struck by the recurrence of two themes: wetland habitats and extinct species. An entirely haphazard selection of important fossil sites include former "shallow vegetation-choked water" in Texas (p. 35), "ponds or stream channels" in California (p. 53), and "pond
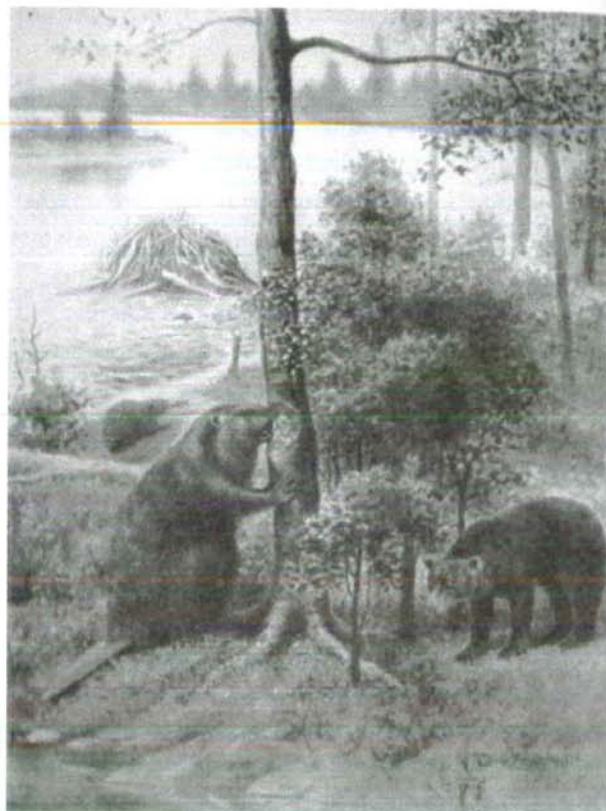

FIGURE 6.12 Giant beavers (*Castoroides ohioensis*), up to 2.5 m long and weighing 60–100 kg, were once widespread in North America, but became extinct after the last ice age. Note the black bear for scale. (Painting by O. M. Highley, from Tinkle 1939.)

and marsh habitat" in Florida (p. 57). Of course, there were many other habitats, including caves and grasslands, but the large number of fossil sites that were once wetlands matters to those of us who study wetlands. And the wetland fauna – now vanished – including glyptodonts (a creature that looked like a turtle but was a mammal), the giant beaver mentioned above, megathere ground sloths (some weighing more than 3 tons), equine horses and zebras, and giant tortoises (*Geochelone* spp.). The bones of these species are mixed with familiar species that we find in wetlands today – including marsh rice rats, muskrats, beavers, and moose. One is left with the disturbing impression that not only has the fauna changed, but key processes such as herbivory and disturbance may now be a mere shadow of their former extent and intensity.

So, let us end with a series of questions raised by such missing species. We concluded that herbivores can occasionally destroy their food supply, as in the case of the muskrat "eat-outs" described by O'Neil (1949). We also concluded that such events appear to be infrequent. (And, in any case, it is decomposers that process a majority of the plant material in wetlands.)

Now to the questions. Are such "eat-outs" a natural consequence of population dynamics of herbivores? Are they just a natural part of the vegetation cycle of wetlands, as in Figure 4.13? Or should we view them as something dysfunctional? Perhaps eat-outs are evidence of a missing predator that once controlled the herbivore. Does, say, the absence of large alligators, or absence of timber wolves, allow more eat-outs than in the past? Or is the reverse true, were eat-outs actually more common, even typical, back when North America had more big herbivores? Are most wetlands now in a state that by historical standards would be under-grazed? Were there other species that depended upon disturbance from large herbivores? If so, are they in decline or even extinct from lack of habitat? Perhaps the effects of introduced grazers, like nutria in Louisiana, actually produce the sort of heavily grazed wetlands that may have been common in the past. Should we also suggest that it was normal to have streams and rivers blocked not only by many more beaver dams, but by larger dams built by larger beavers?

Not all scientific questions have easy answers, so I leave you to think about what, if anything, examples such as the extinct giant beaver tell us about the significance of grazing in wetlands today.
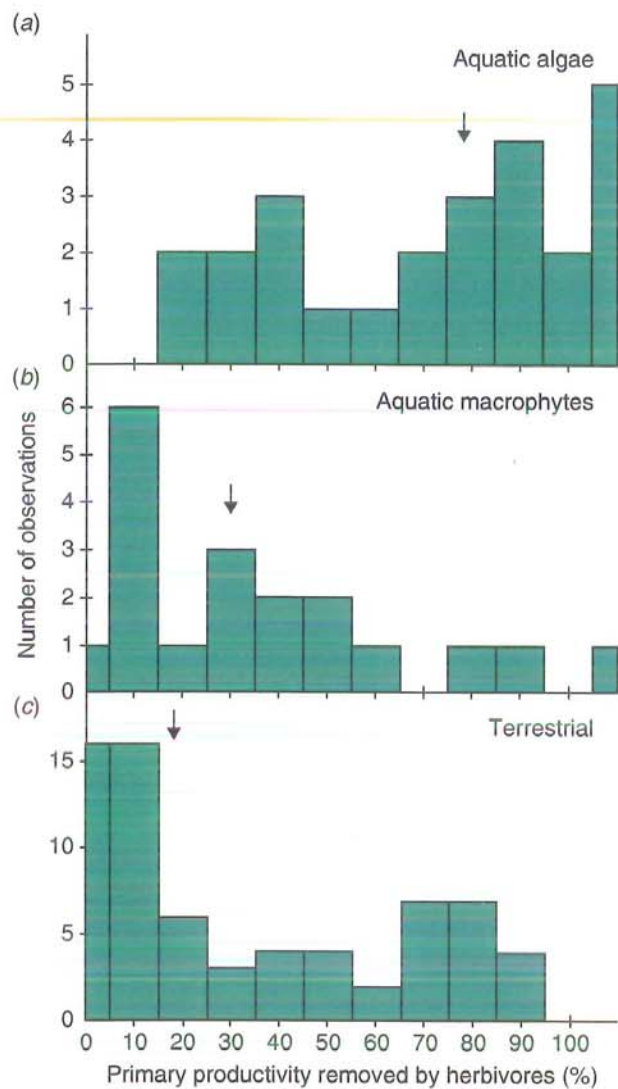

FIGURE 6.13 Frequency distributions of the proportion of annual net primary productivity removed by herbivores for (a) aquatic algae (phytoplankton, $n = 17$, and reef periphyton, $n = 8$); (b) submerged ($n = 5$) and emergent ($n = 14$) vascular plants; and (c) terrestrial plants ($n = 67$). Arrows indicate median values (aquatic algae, 79%; aquatic macrophytes, 30%; terrestrial plants, 18%). (From Cyr and Pace 1993.)

6.5 General patterns in herbivory

One of the most fundamental properties of grazing is the proportion of the primary productivity that is consumed. This proportion can be considered a measure of the "importance" of herbivory in a particular habitat. Cyr and Pace (1993) compiled estimates of this property for a wide array of aquatic and terrestrial habitats: the producers were phytoplankton ($n = 17$), reef periphyton ($n = 8$), submerged macrophytes ($n = 5$), emergent macrophytes ($n = 14$), and terrestrial plants ($n = 67$). Figure 6.13 shows the importance of

herbivory when these are lumped into three groups: aquatic algae, aquatic macrophytes, and terrestrial plants. A striking result from this figure is that aquatic macrophytes are much more like terrestrial plants than aquatic algae. This echoes earlier themes in fertility, where we were challenged to decide whether wetland plants were limited by phosphorus (as with algae) or by nitrogen (as with many terrestrial plants), finding that both phosphorus and nitrogen could be important depending upon the type of wetland. The median proportion of productivity removed by herbivores of aquatic macrophytes is some 30% (compared to 79% for algae and 18% for terrestrial plants). Plotting the rate of removal by herbivores against primary productivity (Figure 6.14, top) gives a linear relationship with a slope not different from 1, suggesting herbivores remove the same proportion of primary productivity across a wide range of fertility levels. The top of Figure 6.14 also shows that consumption rates are apparently an order of magnitude lower in macrophytes (triangles) than algae (circles).

In the rest of their analyses, Cyr and Pace regrettably combine algae and macrophytes into one "aquatic" category for comparisons with terrestrial plants. However, certain general conclusions about herbivores in wetlands can be extracted. Figure 6.14 (bottom) plots the biomass of herbivores against net primary productivity in all habitats. The two triangles at the upper left are submerged macrophyte beds where herbivore biomass was strikingly high. (The circle at the lower left is a terrestrial tundra site.) Excluding the two outlying triangles, herbivore biomass increases significantly with productivity, and, also excluding the outlying circle, there is no significant difference between the lines for aquatic and terrestrial habitats. Therefore, for a given level of net primary productivity, herbivores reach similar average biomass in aquatic and terrestrial ecosystems. Important questions about wetlands remain unanswered, and Figure 6.13 suggests that much could be learned by treating wetlands as a
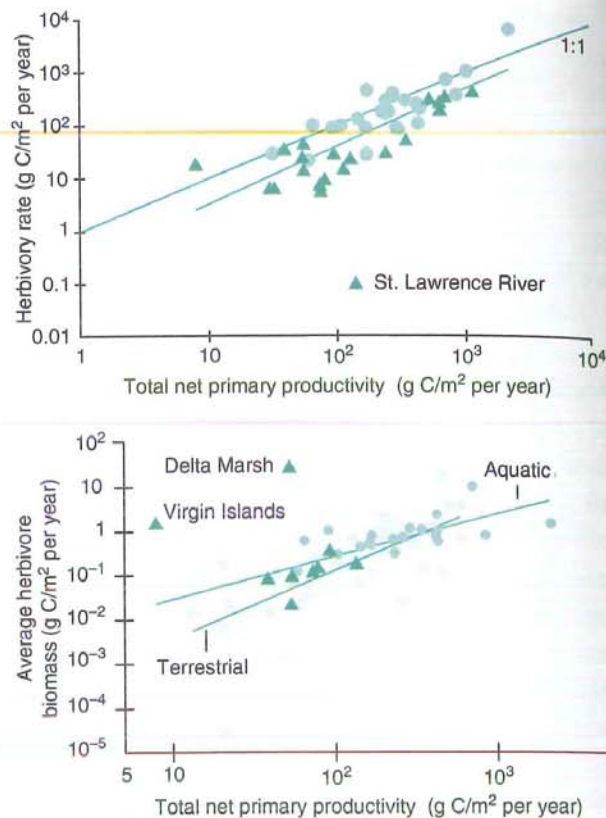

FIGURE 6.14 Rate of grazing (top) and herbivore biomass production (bottom) both increase with net primary productivity (algae, dark circles; macrophytes, triangles; terrestrial, light circles). (From Cyr and Pace 1993.)

separate category in future work of this sort. This criticism aside, Cyr and Pace have provided an important introduction to the study of herbivory in wetlands.

Lodge (1991) reviewed some 25 experiments that measured herbivory in wetlands, covering examples from invertebrates grazing upon submersed macrophytes to mammals and birds grazing upon emergent macrophytes (see also Brinson et al. 1981). Herbivore impact, estimated by the difference in biomass between grazed and ungrazed plots, ranged from 0% to 100%, with many values in the 30% to 60% range. He concludes that many herbivores can therefore have a substantial effect upon macrophytes.

6.6 Three pieces of relevant theory

In this chapter we have looked at a number of examples of herbivory and plant defense; now we will think about some of the theoretical models that underlie the impacts of herbivory.

6.6.1 Selective grazing can increase or decrease diversity

Herbivores can either increase or decrease plant diversity. In this chapter, we have seen examples of both. It is important that you have a general understanding of why it can go either way. One key issue is how selective the herbivore is. There are good biological reasons for expecting very selective herbivory, for the animal to prefer certain plants and certain tissues because of higher palatability or higher nutrient content.

Beavers (*Castor canadensis*) are a good example. One can walk through the forest and easily see both the stumps of the trees that they ate, and the remaining trees that they left. Hence, beaver diets have inspired a good bit of study. Typically, one counts and measures all the trees eaten and samples the trees left (Table 6.6). One can then measure whether the beavers preferred certain species or sizes by using different measures of electivity. In one example from Massachusetts, for example, Jenkins (1975) concluded:

They preferred trees of certain genera, they preferred trees of certain diameters and their diameter preferences varied with genus. Specifically, the Blue Heron Cove beavers favored birch, selected against pine, and cut about the same proportion of oak and maple at each site as were available at that site.

Hence, at that site, beaver were shifting the forest from birch to pine. Preferences changed within and among years (Jenkins 1979) and with distance from water (Jenkins 1980). Overall, beaver diets depended upon the selection of trees available to them, the size of those trees, and the time of year.

Now imagine the following circumstances. Picture a plant community, say a forest, having a mixture of species, some common and some uncommon. Now introduce a herbivore. What will happen? The answer is that we don't know unless we specify the feeding habits of the herbivore. Consider two extremes.

- At one extreme, the herbivore feeds upon the rarer species in the landscape. In this case, adding herbivores will actually reduce diversity.
- At the other extreme, the herbivore feeds solely upon the common species and avoids the uncommon species. In this case, adding herbivores will increase diversity.

Of course, the herbivore, if it had no preferences, would feed on the species in direct proportion to their occurrence in nature. In this case, the effects would be small, and largely determined by the species' relative degrees of resistance to the damage of

Table 6.6 The trees eaten (yes) or not eaten (no) by beaver in three size classes at one site in a tract of forest surrounding a beaver pond in Massachusetts

Diameter (cm)	Birch (*Betula*)		Maple (*Acer*)		Oak (*Quercus*)		Pine (*Pinus*)	
	yes	no	yes	no	yes	no	yes	no
2.5–6.2	0	0	10	4	0	0	0	1
6.3–11.3	11	7	0	9	1	2	0	1
>11.3	11	14	0	12	1	7	0	5

Source: From Jenkins (1975).

herbivory. Yodzis (1986) provides a mathematical exploration of these situations. Such investigations illustrate that the effects of introducing exotic herbivores, or reintroducing extirpated herbivores, may be difficult to predict.

Returning to the beavers in Table 6.6, by favoring birch in their diet, they were selectively removing it from the landscape. There are many consequences.

Diversity From the perspective of the forest and landscape, birch was the most common species, and pine was less common. In this plot, beavers would tend to increase tree diversity by removing the commonest species selectively. If we applied specific measures of diversity to these plots, we could quantify just how much diversity changed.

Composition In addition to changing diversity, beavers were shifting the forest composition toward conifers. On my own property, the valleys are filled with conifers – pine, spruce, fir, and cedar, along with freshly cut hardwood stumps – suggesting that the beavers are continuing to remove the deciduous trees and leaving the conifers, thereby creating conifer-dominated woodlands.

Other effects There are other secondary effects, since the type of breeding birds and number of forest floor plants will likely change with the tree species, particularly the dominance of conifers. This is a reminder that when beavers are called "ecosystem engineers," they are not only making wetlands, but are changing the forests around the pond.

Beavers also illustrate – with trees – how mowing can change herbaceous vegetation. In one sense, mowing can be thought of as simulating a relatively unselective herbivore. Mowing actually is somewhat selective – it tends to preferentially remove larger species with dense canopies, thereby allowing smaller species such as rosette forms to persist. Hence, as we have seen in European wet meadows, it is generally found that mowing increases biological diversity.

6.6.2 Bottom–up or top–down? The overlooked potential for biological control of herbivores

There is one other issue about herbivores that demands careful thought. There are two very different ways of thinking about plants and herbivores, and it is by no means clear which view is correct. I have written this chapter in a way that sidesteps the problem because of the uncertainties. But this does not mean you can ignore the topic, because it may have important implications for managing wetlands. From one perspective, call it the **top–down** view, the composition of wetlands is controlled by species at the top of food webs, that is by predators, who control herbivores, and hence control vegetation. From another perspective, called the **bottom–up** view, the composition of wetlands is largely driven by plant–environment interactions, and herbivores and predators merely feed on surplus material. Both are possible (e.g. Hunter and Price 1992; Power 1992). To offer one specific example, do plants determine the abundance of alligators (bottom–up) or do alligators determine the abundance of plants (top–down) (Figure 6.15)?

At the very least, we can be certain that there is some bottom–up control, for the very simple reason that, without plants, the consumers disappear (Hunter and Price 1992). It is therefore quite reasonable to start off with the assumption that the vegetation in wetlands controls wildlife, both through habitat and food. But, as for the second issue, whether the consumers also influence or control the producers, this turns out to be much less clear-cut. Resurrecting Hairston *et al.* (1960) we can naively observe that most wetlands are green – since the plants are not eradicated by herbivores, something else must be controlling herbivore abundance. So far, it seems plausible. But then, as White (1993) argues, a good deal of this green matter has such low nitrogen content that it hardly qualifies as food anyway, and the growing literature on secondary metabolites (Rosenthal and Berenbaum 1991) suggests that much
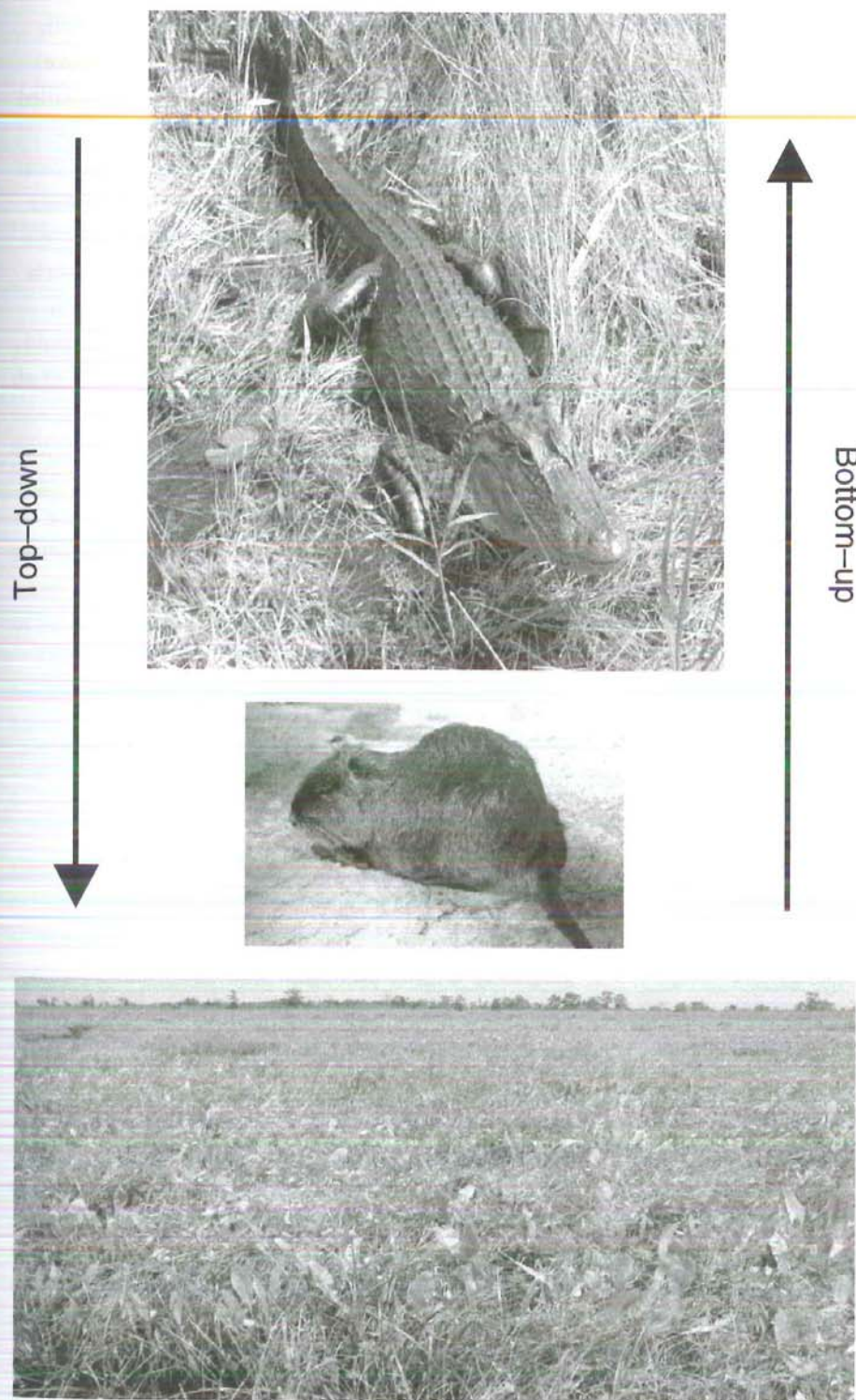
FIGURE 6.15 Does the amount of vegetation control the abundance of nutria, and hence the number of alligators? Or does the number of alligators control the abundance of nutria, and hence the amount of vegetation? The first is termed bottom–up control, and the second is termed top–down control. It is by no means clear which is the correct view, or whether both are happening simultaneously. (See also color plate.)

visually apparent green food is well protected from herbivores. Therefore, the issue of whether herbivores control the abundance of plants, and the composition of wetlands, is open for evaluation.

Second, apparently clear-cut dichotomies like this, while attractive, often turn out to be misleading (Dayton 1979; Mayr 1982; Keddy 1989a). It is possible that both operate simultaneously, that neither operates except for rare exceptions, or that other factors such as habitat productivity (Oksanen 1990), habitat heterogeneity (Hunter and Price 1992), or omnivory (Power 1992) may override the apparent dichotomy.

You should be aware that there could be even more possibilities, three at least, and the kind of grazing system found depends upon the primary productivity of a site, including the supply of soil resources to plants (Oksanen *et al.* 1981). According to this model, herbivore pressure should be most severe in relatively unproductive environments. As primary productivity increases, the impact of herbivory should decline because the growing abundance of the herbivores allows predators to survive and regulate herbivore populations. In very productive systems, herbivory again becomes important owing to the occurrence of predators upon the predators, which releases the herbivores from regulation. (Oksanen *et al.* 1981) present a model, building upon work by Fretwell (1977) that shows how such transitions in herbivore-plant relationships might occur, and they present some data that are qualitatively consistent with these kinds of changes. There are, in fact, many possible complex feedbacks, such as animals increasing the rates of nitrogen cycling, fertilizing plants with their waste products, and even altering competition between plants and soil microbes for nitrogen (McNaughton *et al.* 1988). Hence, generalizations about interactions between herbivores and plants, while highly desirable, await further experimental testing of such models.

Does it matter? Let us illustrate two cases where it might. First, we have the example in Figure 6.4 where grazing by snails may control the amount of vegetation in coastal marshes. Where these salt marshes are declining, it is possible that the snails are causing the decline – and that the snails have increased in abundance because humans have killed the crabs that would normally control the snails (Silliman and Zieman 2001). Similarly, there is clear evidence that nutria are causing enormous damage to coastal wetlands (Figure 6.1). But alligators are a major predator on nutria, and it may be that nutria damage is increasing because humans have been preferentially killing the large alligators that would otherwise control the nutria populations (Keddy *et al.* 2009). Hence, while the issue of top–down or bottom–up might appear to be theoretical, those who ignore the possibility of top–down control may be blinding themselves to important possibilities for biological control of herbivores. Perhaps areas where coastal marshes are declining need more crabs and more alligators.

6.6.3 Simple models show how populations can both grow and crash

The effects of grazing upon vegetation, and the response of herbivores to vegetation, can both be explored with simple mathematical models. One of the simplest models adapts the logistic equation, which is widely used by ecologists to describe the growth of animal populations (Wilson and Bossert 1971). The logistic model assumes that, when there are few organisms and abundant resources, growth is (almost) exponential, but that, as population size increases, and resources become scarce, the population growth slows and reaches a level known as the carrying capacity, K. This can be used equally to describe plant populations (Noy-Meir 1975; Starfield and Bleloch 1991) as:

$$\frac{\mathrm{d}P}{\mathrm{d}t} = gP\frac{(K - P)}{K}$$

where P is the amount of plant material (e.g. biomass/unit area), g is the growth rate, and K is the maximum amount of plant material that a unit area can support. Another way of thinking about this that is more similar to familiar animal population models is to
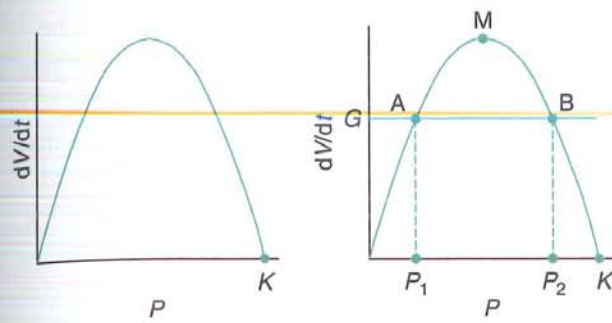
FIGURE 6.16 A simple model for herbivore–plant interactions. The vegetation growth rate dP/dt is plotted against plant biomass P for the logistic model: (left) no grazing and (right) constant grazing pressure G. (After Starfield and Bleloch 1991.)

consider P to be the number of plant cells and K the carrying capacity of plant cells for a particular area of landscape.

To explore the behavior of vegetation without herbivores, we can plot growth rate (dP/dt) against biomass (P), which produces an inverted parabola (Figure 6.16, left). The growth rate of the population of plant cells therefore at first increases as more and more cells are available for photosynthesis, and then slowly declines as the resources available to each cell become restricted. The botanical logic behind this seems to make sense: when plant biomass is low, each new cell will improve the photosynthetic capacity of the vegetation, but as biomass increases, more and more cells will be needed to provide structural support for photosynthetic cells, and others will be shaded so that photosynthesis is below the maximum potential. If we compare short turf, for example, with young forest, the number of plant cells allocated to support tissues (trunks, branches, and stems) becomes a considerable proportion of the biomass in a forest. Further, the lower leaves on the trees are shaded by the upper leaves. Yet another way to think of this is the compounding effects of competition for resources such as light and nutrients; growth ceases when resources become severely constrained. In any case, when the mean photosynthetic yield of all cells just balances their mean respiratory demands, growth will come to

a halt; the level K on the horizontal axis will have been reached. Halfway between 0 and K the growth rate is at a maximum. This is the familiar pattern of logistic growth; the novelty lies solely in applying it to plant biomass. The level of biomass K will depend upon environmental factors such as flood duration, growing season and soil fertility. In the absence of herbivores, all vegetation will tend toward point K.

Now, add in a constant grazing pressure from a herbivore. Assuming that the herbivores remove a fixed amount of biomass per unit time, designated G, the equation becomes:

$$\frac{dP}{dt} = gP\frac{(K-P)}{K} - G.$$

Since the grazing rate is set to be independent of biomass, we can plot G as a horizontal line across the parabolic model of plant growth (Figure 6.16, right). There is no need to solve the differential equation to learn a good deal about the behavior of such a herbivory system; a good deal can be deduced simply from the structure of the equations and the resulting graph (Starfield and Bleloch 1991). Returning to the growth of vegetation, it is apparent that the growth rate is positive only between points A and B, where the growth parabola lies above the herbivory rate, and biomass therefore accumulates. On either side of this range, the herbivory rate exceeds the growth rate. At points A and B, growth just matches herbivory.

The next step is to examine stability by considering what kinds of changes might occur through a period of time. Let's consider point B, where the corresponding amount of plant biomass is indicated as P_2. If growing conditions improve, pushing the amount of biomass to the right, the growth rate will fall below the herbivory rate, and the vegetation will decline back to level P_2. If, on the other hand, drought or flooding were to reduce biomass below P_2, then simultaneously, the difference between the herbivory rate and the growth rate increases, so that biomass accumulates, pushing the system back toward

point P_2. Since the system returns to point B when it is lightly perturbed, this is called a stable equilibrium point.

Point A, in contrast, is unstable, because the same procedure shows that, if the system is perturbed, it slides even further away from point A. If it is perturbed to the left of P_1, say, by a drought, then growth rates fall further and further below the herbivory rate until the plants disappear; the system slides to the bottom left and collapses. Conversely, if there is a surge of growth above P_1, then the vegetation temporarily escapes from herbivory, and continues to move to the right, because as biomass increases, the difference between herbivory rate and growth rate increases as well. Eventually the entire system slides over to point P_2. In this simple system, then, the only stable point is one where plant biomass is P_2. Over a broad range of biomass levels, this model herbivory system will return to this point after perturbation.

These dynamics can be deduced slowly from the structure of the equations. If, further, the growth rate of plants were actually measured to establish the maximum growth rate (point M), then one can see that if the herbivory rate were increased above this level M (equivalent to sliding the horizontal line above the parabola) the animals would graze faster than the vegetation grew, which is an unstable situation.

Other models could be used to describe herbivore–plant interactions, by, for example, allowing for growth rates to fluctuate in response to rainfall or flooding, or using a different model for plant growth (Starfield and Bleloch 1991). Others have addressed the interactions between plants competing for light (Givnish 1982) and their responses to added herbivory pressure (Oksanen 1990). If grazing pressure is not constant, but varies with plant biomass, then a variety of outcomes is possible, depending upon the functional responses of the herbivore (Yodzis 1989).

CONCLUSION

The food quality of plant species for herbivores is determined by their nitrogen content, nitrogen being a limiting factor for plant and animal growth (Chapter 3). To reduce biomass loss, plants may be equipped with morphological (gelatinous tissue coating, buried rhizomes, peduncle movement to immerse fruits) or chemical (terpenes, phenolics, and nitrogen-containing secondary products) defenses to deter herbivores. Herbivores can either increase or decrease plant diversity, depending on the intensity of grazing and the species consumed.

To what extent are grazing animals, just like flooding or fire, able to control the composition and functions of wetland communities? When you look out across a vast green wetland you may think the effects of herbivores are small; when you look at mud flats with small vegetated cages (Figure 6.1), you may think the effects of herbivores are enormous. Overall, it seems that properly designed exclosure experiments are too few and far between to draw any firm conclusions. The evidence to date suggests that in most cases herbivores are far less important than flooding, fertility, or competition are in creating the types of wetland communities we see. In general, it appears that the plants in wetlands determine the abundance of the herbivores (bottom–up control) rather than vice versa (top–down control). But, there may be important exceptions, such as snails,

beavers, and snow geese. Wetland ecologists thus face two tasks in their future work: the first to determine what generalizations about herbivores are possible, and the second is to discover the noteworthy exceptions.

Since some kinds of herbivores are increasing in abundance – from nutria and snow geese (which we have discussed here) to white-tailed deer and carp (which you will have to read about on your own) – it is likely that the impacts of grazing upon wetlands will be a topic you will often have to consider.