MODULE 4: BASIC BIOLOGY OF WETLAND ANIMALS

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OVERVIEW

An assortment of animals inhabit wetlands, with many invertebrates, amphibians and reptiles, fishes, birds, and some mammals being wetland specialists. Wetlands provide water, food, and cover that benefits resident animals, but periodic high floods, frequent drying, and often harsh water quality (low-oxygen, acidic, saline) can stress wetland animals. Animals successful in wetlands have developed adaptations to cope with these stresses. Animal biodiversity in wetlands is particularly valued by people, from ecotourists and bird watchers who observe it, to hunters and fishers who harvest aspects of it. Animals such as alligators and beavers create or physically modify wetland environment. This activity is called ecosystem engineering and makes these animals among the most important organisms to wetland ecology. Wetlands have high biodiversity and support rich communities of wetland invertebrates, and are primary breeding habitats for most amphibians, and many migratory birds rely on wetlands during some part of their annual cycle. The interactions of animals with plants (herbivory, cutting) and each other (predation) strongly shape wetland environments and affect nutrient cycling. Human impacts on wetlands can negatively affect many animals through habitat loss, resulting in many wetland amphibians, reptiles, and birds being listed as threatened and endangered species. Thus, wetland conservation is vital to conserve many animal species.

INVERTEBRATES

Invertebrates are particularly important in wetland ecosystems. Most of the biodiversity in wetlands is found among the invertebrates, and invertebrates are the primary energetic link between plants and higher animals (such as fish and birds). Invertebrates can also be useful bioindicators of wetland habitat quality.

Common invertebrate groups in wetlands include insects (dragonflies, beetles, aquatic flies), crustaceans (shrimps, crabs, microcrustaceans), mollusks (snails, clams, oysters, mussels), annelids (earthworms, leeches), and nematodes (roundworms). To succeed, wetland invertebrates must contend with periodic drying and low-oxygen conditions (anoxia), and these processes directly influence which groups do or do not thrive. For example, stoneflies are common in streams but are rare in wetlands because their nymphs are intolerant of both drying and anoxia.

Contending with drying involves tolerance or avoidance (Figure 1). Many wetland invertebrates have stages that persist even after surface water disappears. For example, mosquitoes and some crustaceans (such as brine shrimps) have desiccation resistant propagules that persist in dry substrates for long periods, sometimes years, and when wetlands reflood, propagules hatch and a new life cycle is initiated. Many beetles and shrimps simply bury themselves in moist substrates to survive. Some crabs and crayfish dig burrows that retain a connection to subsurface water; these burrows also provide temporary refuge for other organisms. Many winged insects are adept at avoiding drying; adult females fly to newly flooded wetlands to lay eggs, and the immature stages develop rapidly so new adults emerge before wetlands dry (to fly to other wetlands).

Surviving anoxia also involves either tolerance or avoidance. Some midge larvae tolerate low oxygen conditions using features of anatomy (soft, tubular bodies that maximize surface area), physiology (ability to respire anaerobically; presence of oxygen-binding hemoglobin in haemolymph), and behavior (build U-shaped tubes where water can be circulated, quiescence). Oysters and some worms also have hemoglobin to outlast low-oxygen conditions in wetlands. Many aquatic insects do not rely on dissolved

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oxygen in the water but instead breathe air by accessing surface air with respiratory tubes (mosquito and some beetle larvae), capturing air bubbles under their wings or along their bodies (adult beetles, water bugs), or accessing oxygen sources in or surrounding plants roots. Most estuarine invertebrates can respire during both dry and wet periods.

Invertebrates in tidal wetlands must also contend with changing salinity and wave and tide action. In most estuaries, water salinities change constantly over daily tidal cycles. To survive, estuarine invertebrates must either tolerate or respond quickly to drastic changes in these environmental conditions.

Behaviors of invertebrates in wetlands can be divided into instinctive behaviors related to their physiological functions (feeding, molting, reproduction), and responses to environmental factors (light, water flow, substrate, dissolved oxygen, salinity, temperature). Nematodes are the most diverse and abundant invertebrates in many wetlands. This broad group of species can exploit variation in wetland habitats using a wide array of feeding strategies, including algal-feeding, herbivory, bacterivory, fungivory, carnivory, and omnivory, and can detect environmental changes using chemoreceptors (called amphids). To grow, arthropods periodically molt; molting has the added benefit of shedding external parasites and permits regeneration of damaged limbs.

Some aquatic beetles and bugs, called cyclic colonizers, migrate back and forth between temporary water wetlands and permanent water aquatic habitats. They take advantage of the temporary wetlands as food-rich and predator-free habitats for their progeny, while avoiding wetland dry periods by taking refuge in permanent water bodies. Many estuarine invertebrates reside in the substrate during the day (often in burrows), where they are protected from desiccation and predators and can conserve energy, and then emerge and become active at night.

Two major ecological transitions shape invertebrate communities in freshwater wetlands: 1) a permanence transition, and 2) a predator (fish) transition (Figure 1). If a wetland dries, resident invertebrates must tolerate or avoid desiccation and develop rapidly before surface water disappears; organisms lacking these abilities do not survive. Typical residents of temporary waters include mosquitoes, fairy shrimps, water fleas, water beetles, and water bugs. Permanent water wetlands can support these same taxa, but also other taxa poorly adapted for drying, such as snails, mayflies, and dragonflies. However, permanent waters can support fish, some species of which visually target larger, active invertebrates as prey and may reduce their abundances. Invertebrates coexisting with fish tend to be small, cryptic (camouflaged), and sedentary, such as midges and worms. Thus, temporary wetlands are dominated by fast-developing invertebrates adapted for drying; permanent wetlands with fish are dominated by small, sedentary, slow-developing invertebrates that can avoid predation; and permanent wetlands without fish are dominated by large, active invertebrates (Figure 1; see Wellborn et al. 1996).

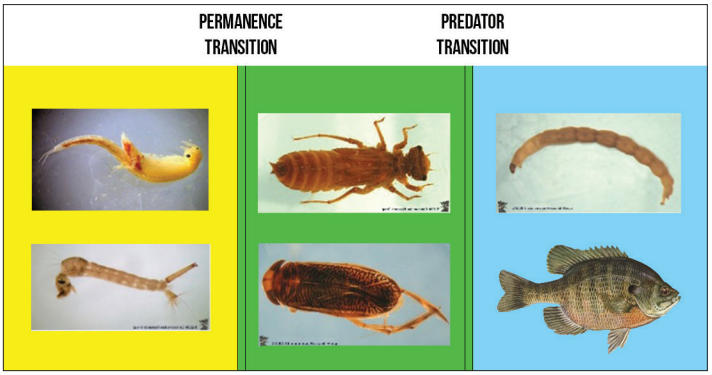

Figure 1. Key controls on wetland invertebrate assemblages: the permanence transition between temporary (yellow) and permanent (green, blue) waters and the predator transition between fish-bearing (blue) and fishless (green) permanent waters (adapted from Wellborn et al. 1996).

Invertebrates of freshwater wetlands are, however, notoriously difficult to predict with respect to abundances, distributions, and habitat associations (Batzer 2013). Most freshwater wetlands are highly variable in space and time and evolutionary and life histories of wetland invertebrates are adapted to this variability. Many wetland invertebrates are generalists adapted for environmental variation, coping with a range of hydrological and water quality conditions and consuming a range of foods (detritus, algae, other invertebrates). Conditions that develop in freshwater wetlands in any given year may be unknowable, and evolutionary strategies may develop that result in high

production in good years and high mortality in poor years.

Estuarine and tidal wetlands have been affected by tides for eons, leading to the gradual adaptation of invertebrates to environmental fluctuations (Jones and Candy 1981). The density and biomass of invertebrates are influenced by multiple factors (Levin and Talley 2002): organic detritus deposition controls nematode communities; temperature and silicate content controls polychaetes and echinoderms; salinity, dissolved oxygen and pH control mollusks; and inorganic nitrogen and phosphate control crustaceans. Polychaete worms grow best in muddy habitats with small grain sizes (Oyenekan 1986). Bivalves are burrowers and prefer habitats with sandy and clay substrates (Holland and Dean 1977). Salinity gradients act as physiological barriers to both saline marine species and freshwater species (Liu and He 2007). In general, estuarine invertebrate diversity increases with increased salinity. On the other hand, invertebrate densities tend to decrease with increased tidal levels, with burrowing species being most affected. Crabs of tidal flats follow zonal distributions along tidal gradients (Lee and Koh 1994).

More detail on invertebrate adaptations of invertebrates for wetland conditions can be found in Peterson (1991), Mendelssohn et al. (2014) and Batzer and Boix (2016). Lists of invertebrates common in freshwater and tidal wetlands can be found in Online Appendix 1 (https://www.sws.org/education-modules-wetland-science/).

AMPHIBIANS AND REPTILES

The word amphibian is derived from the Greek amphibios, which means living both in water and on land. Most amphibians are closely tied to water for reproduction because their eggs are surrounded by a gelatinous capsule and are susceptible to desiccation. However, amphibian species range from being fully aquatic to truly amphibious (semiaquatic) and they occur in lotic (flowing water), lentic (still water), and ephemeral systems (relatively short-lived or quick-drying), and some even live an entirely terrestrial existence. Amphibians are grouped into three orders including the caecilians, Anura frogs, and the Urodela salamanders, which combined are estimated to include >8400 species (Womack et al. 2022). They occur globally and inhabit freshwater, brackish, and even saltwater wetland systems from sea-level to mountain areas.

Amphibians display an array of reproductive adaptations for persisting across a gradient of wetland conditions. For example, species that breed in permanent water where large predators like fish are present may lay eggs singly or may have cryptically patterned larvae to avoid detection by predators. For species that breed in seasonally inundated wetlands, eggs may be laid on the moist substrate and hatch only after the wetland begins to fill, thus minimizing risk of predation. For other species using ephemeral wetlands, larval development to metamorphosis can be extremely rapid, allowing fully formed juveniles to exit before a wetland dries. Other species are not dependent on aquatic systems at all, with eggs developing to fully formed terrestrial juveniles on moist substrate, foam nests, or in small pools of water that collect in plants. A few species protect their eggs from desiccation by brooding eggs in special pouches in the oral cavity or on their backs, enveloped under a protective layer of skin (like the Pipa toads from Surinam).

With some exceptions, most amphibians have a biphasic life history with aquatic larvae that metamorphose to a juvenile stage (Figure 2a-b). Caecilians, which are earthworm-like in appearance with blunt heads for burrowing (Figure 2c), reproduce either through direct development to an adult form or have an aquatic larval stage. Larval caecilians and salamanders are morphologically similar to adults, whereas frogs produce free-swimming larvae (tadpoles) that undergo metamorphosis and transform into semi-aquatic or terrestrial frogs (see Online Appendix 2: https://www.sws.org/education-modules-wetland-science/). Many salamanders have a free-swimming larval stage, with external gills and a tail fin, and transform into terrestrial juveniles. However, some species (e.g., mole salamanders and striped newts) can attain sexual maturity and breed while in the aquatic larval life form with external gills and a tail fin, a phenomenon called paedomorphosis (see Online Appendix 2: https://www.sws.org/education-modules-wetland-science/). This allows salamanders to capitalize on opportunities to breed when water is available, rather than undergo

risky migrations through the terrestrial environment. Fully aquatic salamander taxa (e.g., *Siren*, *Amphiuma*) retain external gills and an aquatic larval morphology as adults.

Amphibians are an important component of wetland food webs, as both primary and secondary consumers, and as prey. Tadpoles filter particulate matter from the water column and may also use tooth-like keratinized mouth parts to scrape periphyton and algae from submerged macrophytes. Tadpoles undergo radical changes during metamorphosis, where larval mouth parts are replaced by jaws, teeth, and often a tongue, and the long-coiled intestine of herbivorous tadpoles becomes the shortened gut of a carnivorous frog. Salamanders are carnivorous as both larvae and adults and can be apex predators in some wetland systems (Urban 2013). Several salamander species develop a broad-headed morphotype that becomes cannibalistic under conditions of high density (Hoffman and Pfennig 1999). Both frogs and salamanders with aquatic larvae and terrestrial juvenile and adult stages transport nutrients across ecosystem boundaries (Atkinson et al. 2021, Smith et al. 2019, Bashinskiy et al. 2023). Amphibians can occur in high abundance during breeding migrations or as juveniles emerging from wetlands. Although the movement of individuals can be considerable, studies documenting the magnitude of nutrient fluxes via amphibians are generally lacking.

Amphibians are less common in saline wetlands (where they tend to suffer from dehydration) than in freshwater ones, but they are not entirely absent (Hopkins and Brodie 2015). More than 100 amphibian species are adapted to exploit coastal and inland saline habitats. The list includes representatives from 1 of the 10 caecilian families (10%), 5 of the 9 caudate families (56%), and 22 of the 56 anuran families (39%). Two anurans, the crab-eating frog and the European green toad, are among the most salt-tolerant species.

Figure 2a. Adult and larva of the ornate chorus frog. (Photo: Gabe Miller)

Figure 2b. Adult and larva of the eastern tiger salamander. (Photo: Amanda Subalusky)

Figure 2c. Adult caecilian. (Photo: Kevin Stohlgren)

Reptiles (turtles and terrapins, lizards, snakes) are common in many saline and freshwater wetlands, and are particularly diverse in habitats occurring in warmer climates (tropics, sub-tropics). They can be the top predators in wetlands, with crocodilians (crocodiles, alligators, caiman; Figure 3), snapping turtles and some snakes feeding on an assortment of other vertebrates (amphibians, fish, birds, mammals, other reptiles). The thick skin of reptiles makes them more resistant than amphibians to saline conditions, and reptiles (most notably crocodilians) can be important components of saline wetland food webs. Given the predatory nature of so many reptilian species, it is important to exercise caution around them; however, most species will ignore you unless disturbed. American alligators (Figure 3) in wetlands of the southeastern United States (such as the Everglades, https://www.nps.gov/ever/learn/nature/alligator.htm) can shape their environments by creating wallows, nests, and trails, which are exploited by many other plants and animals, an example of ecosystem engineering. Because alligators are both important engineers and predators, they and other large relatives are key species to the ecology of the wetlands where they reside (Somaweera et al. 2020).

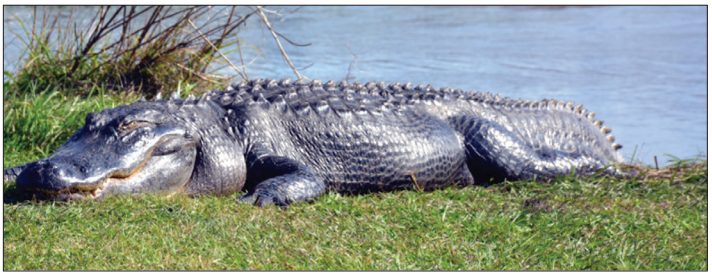

Figure 3. American alligator. (Photo: Jonathan Freedman, U.S. Geological Survey)

More details on amphibian and reptile diversity and their adaptations for wetland conditions can be found in Hopkins and Brodie (2015), Stebbins and Cohen (2021), and Zug (1993). A list of the taxonomic names of organisms listed in this subsection is available in Online Appendix 3 (https://www.sws.org/education-modules-wetland-science/).

WETLAND FISHES

An assortment of fishes resides in wetlands (Batzer et al. 2014). Some migrate between deeper waterbodies, such as rivers, lakes or oceans, and adjacent wetlands. Others reside full-time in wetlands. Those species living in wetlands year-round tend to be small-bodied forms, such as killifishes, sticklebacks, mosquitofish, gobies or other diminutive species. Small immatures of larger fishes may use wetlands as nursery habitat, to hatch and grow, before migrating to deeper waters as adults. Often coastal wetlands form part of a mosaic of neighboring nursery habitats, which may also include seagrass, mudflats, and oyster reefs (Lefcheck et al. 2019). The ecology of many marine fisheries is highly dependent on coastal wetlands. Tidal coastal wetlands, such as mangroves and salt marshes, provide foraging and refuge opportunities for larvae and juveniles of species that are fished commercially or recreationally as adults, such as mullets (Figure 4), bream, and spot. Tidal coastal wetlands also provide foraging and refuge habitat for small fishes (and invertebrates) consumed as prey by the adult fisheries species.

Compared to lakes, rivers, and oceans, however, the number of fish species permanently residing in wetlands tends to be small, due to the harsh environmental conditions. Only a few fishes can tolerate habitat drying, and during drying events the majority of wetland fishes either migrate to deeper waters or perish from desiccation. The smallest species can persist during dry periods in small residual pockets of water, such as crab/crayfish burrows or tree rot holes. Some of the killifishes can survive drying and hatch from eggs or revive when wetlands reflood (much as invertebrates do; see above). Interesting exceptions to this rule include the living fossil lungfishes; these air-breathing fish can not only move across grasslands in search of a new wet pond, but they can also endure regular periods of drought by digging into the mud and covering themselves with mucus that prevents dehydration. Due to periodic drying or isolation, many depressional wetlands are either completely fishless, or support only one or two species (such as mosquitofish, sticklebacks) (Zimmer et al. 2002).

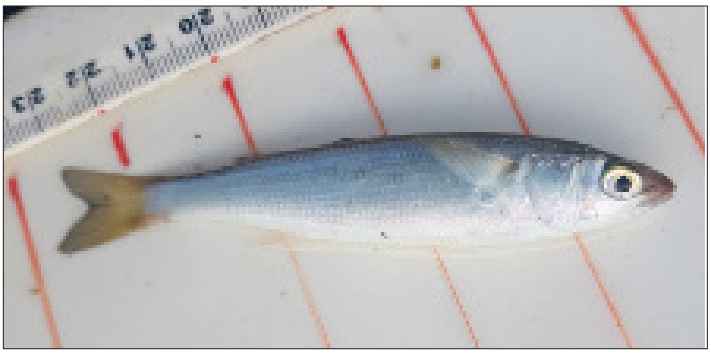

Figure 4. A juvenile mullet, a common saltmarsh fish. (Photo: Violet Harrison-Day)

Besides habitat drying, another major constraint on fishes in wetlands is a lack of oxygen in the water. Respiration with gills requires sufficient dissolved oxygen levels to be effective, and only a few fish species can tolerate hypoxia. Some fishes (such as carp) will gulp air to survive temporary periods of oxygen stress. Salinity is another important constraint on some fishes, especially in salt marsh, mangrove, or estuarine habitats. Fishes in brackish (moderately saline) water tend to either have a connection to the adjacent saltwater habitat or alternatively to the adjacent freshwater habitat, but rarely both. Fish productivity in brackish waters can, however, be very high because of these connections, and because of the abundant invertebrate food resources found in estuaries. Some fishes (such as some hardyheads) have wide salinity tolerances and survive easily in wetlands subject to changing salinities. Other fishes (such as eels and salmon) occupy saline and brackish wetlands as transitory visitors when moving between marine and freshwater environments during different life stages. Finally, acidity is another water quality constraint on

fishes, and highly acidic (low pH) peatlands tend to support only a few fish taxa. Acid conditions impair some physiological processes in fishes (Mendelssohn et al. 2014).

Historically, many coastal wetlands were converted from saline or brackish marshes to freshwater wetlands. Changes to salinity and other aquatic conditions in these wetlands led to a transition from salt tolerant to freshwater fish assemblages. Interest in returning tidal flows to impounded and levied coastal wetlands (for fisheries and other ecosystem service benefits) is growing, however, and many are being restored, allowing saline-tolerant wetland fishes to return (Raposa and Talley 2012). The restoration process requires careful planning, taking into consideration the site-specific habitat characteristics, conditions, and fish species currently and previously present.

The presence or absence of fishes is considered one of the major controls on other wetland animals. Large fishes may be the top aquatic predators in wetlands, and as visual predators tend to target some of the larger, more-active prey animals. Many amphibians (tadpoles, salamanders) and large, active-swimming invertebrates (water bugs, beetles) do poorly in the presence of fish predators, and the overall structure of animal communities in many freshwater wetlands is determined by fishes (Wellborn et al. 1996; see Figure 1). Fish predation may indirectly promote algal growth by reducing the numbers of invertebrate grazers. In tidal wetlands, shallow vegetated habitat can provide important refuge for small fishes (juveniles and small bodied adults) that are avoiding predation by large fishes. Different fishes can occupy tidal habitats at different times and water depths, balancing the benefits of refuge (and foraging opportunities) with the risks of stranding, adverse water conditions, and the energetic costs of travelling with or against the tide (Rountree and Able 2007). Fish themselves are primary food items for many wetland birds and mammals. For example, wading birds such as herons, egrets, and storks target fish prey in shallow waters, and thus find wetlands to be critical foraging habitats (Batzer et al. 2014). Similarly, American mink, North American river otter, and brown bear rely on fish found in wetland ecosystems.

In addition to predation, fishes can exert other ecological influences. Bioturbation of substrates by carp can affect wetland water clarity and water quality (Batzer et al. 2014). Excretion by fishes can fertilize wetland waters, affecting algal growth.

Many freshwater wetlands are naturally fishless, and the introduction of fishes into these habitats can be ecologically damaging. Zimmer et al. (2002) found that fathead minnows can exert important ecological controls on invertebrates and amphibians in natural prairie potholes of north central North America, and introductions of these fish into otherwise fishless potholes (to commercially rear them as baitfish) is a concern. The mosquitofish is native to the southeastern United States, but the species has been actively introduced to many other places in an effort to control mosquitoes. Thus, the mosquitofish is now the most wide-spread freshwater fish in the world and can have unintended negative effects on native species (Pyke 2008).

Introduced plant species can also affect wetland habitat conditions for fishes. Rapidly spreading salt marsh grasses such as cordgrass (*Spartina* spp.) were introduced in many parts of the world to help stabilize shorelines and have become major invaders of native wetland habitats. Changes to habitat structure and conditions resulting from vegetation change may affect nursery habitat quality, prey type and availability, and accessibility of the habitat for fishes.

A list of the taxonomic names of organisms listed in this subsection is available in Online Appendix 3 (https://www.sws.org/education-modules-wetland-science/).

WETLAND BIRDS

Many birds rely on wetlands for some portion of their annual cycle; thus, conservation and management of wetlands is critical to bird conservation. Approximately 138 species of birds in the United States are considered obligate wetland species, meaning that their survival and reproduction is entirely dependent on resources provided by wetlands; these include ducks, geese, swans, cranes, herons, rails, plovers, sandpipers, grebes, storks, and various passerines, such as some blackbirds and sparrows. An even larger group of birds are facultative wetland species and use wetlands for certain critical life-history events, such as foraging, roosting, nesting, and brood rearing (e.g., many passerines, owls, and hawks). Although many bird species are declining,

waterbirds in general, and ducks in particular, have increased 18 percent and 34 percent, respectively, in North America since 1970 (North American Bird Conservation Initiative, U.S. Committee 2017).

Birds that depend heavily on wetlands have many adaptations to exploit wetland resources (Table 1). Most species are migratory, primarily because of the transient nature of wetlands and the resources they provide. In many regions, some of the most productive wetlands for birds have temporary or seasonal water regimes, meaning they only contain water for a few weeks or months. These wetlands provide abundant invertebrates and seeds that offer forage for birds when inundated. Due to the variable hydrologic conditions, birds must not only be able to exploit wetland foods when there is water but also be able to relocate or otherwise adapt during dry periods. In a similar fashion, where winters are cold and wetlands freeze, birds have evolved a mostly north-south pattern of seasonal movements in the spring and autumn.

Anatomy and Morphology
Leg placement for easier swimming and diving
Bone and lung modifications for light weight and oxygen intake at altitude
Eye adaptations for underwater vision to aid foraging
Flight (wing) adaptations for diving or taking off from water
Webbed and lobed feet for swimming and diving
Long legs for wading to improve foraging efficiency
Bill and beak specializations for filtering, grasping, digging
Oil glands for water resistance
Countercurrent heat exchange to warm legs and feet in wet and cold conditions
Behavioral
Water-responsive behaviors, such as preening, drying
Specific foraging strategies, such as dabbling, tipping-up, diving
Seasonally variable social behaviors, gregariousness vs. spacing and aggression
Energetic efficiencies, use of thermal cover for roosting
In some cases, diet plasticity in response to wetland availability
Predation avoidance strategies, hiding, safety in numbers
Unique foraging behaviors, including kleptoparasitism

Table 1. Some avian adaptations to wetland habitats (adapted from Weller 1999). More information on adaptations of birds to wetlands may be found in Weller (1981) and Baldassarre (2014).

Once a waterbird arrives at a wetland and determines that conditions are adequate to settle on that site (e.g., Johnson 1980), it must be able to exploit available resources to meet various life-history needs. To this end, evolution has shaped many adaptations to exploit specific wetland resources while avoiding competition and depredation (Table 1). Most wetland birds eat plant material (e.g., seeds), invertebrates, or both and these foods exist in wetlands at varying water depths and sediment types. Duck bill morphology provides an excellent example of phenotypes that evolved to forage efficiently and promote niche partitioning (evolved strategies by which species can coexist when there is competition for resources), thereby minimizing competition. Specifically, bill lamellae, which are comb-like structures that line the upper and lower bills of ducks, vary considerably among duck species, and relate directly to the foraging niche they occupy. Ducks that mostly feed in shallow water are called dabbling ducks. For example, the northern shoveler has a scoop-like bill with fine, dense lamellae that allows them to efficiently strain invertebrates from shallow water (Figure 5). In contrast, some ducks such as canvasbacks can dive and have bills with thick, less dense lamellae that help them forage in deeper water and dense sediments for hard-shelled invertebrates (e.g., fingernail clams) or the roots and tubers of submersed aquatic plants. Intermediate examples include the wood duck, which eats plant seeds and invertebrates and has a shorter bill with less-dense lamellae and prominent bill nails to aid in grabbing submerged acorns or plant bulbs. Finally, mergansers eat almost exclusively animal matter; their bill resembles a set of needle-nose pliers with a sharp hook for grasping fish, crayfish, or other aquatic organisms. Their teeth-like lamellae aid in retaining prey even though ducks do not chew their food.

Body shapes, eye positions, and foot and leg morphologies also help birds exploit wetlands (Table 1). Bitterns, egrets, and herons have long legs that allow them to hunt for prey in water of various depths, and long necks that enable a top-down view of aquatic prey that reduces surface glare. They also possess sharp,

knife- or spear-like bills for impaling or grabbing fish, amphibians, and larger invertebrates. Their eyes are placed on the side of their head to promote peripheral vision for detecting threats yet are far enough forward to offer some binocular vision important to predators that stalk their prey.

Because birds are often prey themselves, their morphologies balance the needs of foraging and vigilance (i.e., predator avoidance). Northern shovelers and Eurasian green-winged teal typically filter feed with their eyes above the water surface; lateral eye placement allows peripheral vision of 220°, so they can see in front, above, and behind while feeding (Guillemain et al. 2002). In contrast, Eurasian wigeon have eye placement that puts the bill in front of the field of vision, restricting its field of view and causing a slight blind spot behind the head (Guillemain et al. 2002). A tradeoff for improved forward vision requires them to spend more time with their head up scanning for predators, reducing total foraging time.

Variation in leg length and bill size among shorebirds allows them to all forage in the same wetlands for the same prey species with minimal competition. The curlew, American oystercatcher, and sanderling may occur at the same sites, but each targets different size-classes of clam prey (Myers et al. 1980; Zwarts and Wanink 1984). Different shore birds have evolved different foraging strategies, such as visually pecking (e.g., willet, killdeer) versus feeding tactilely (e.g., Pectoral sandpiper), which allows for coexistence with less competitive overlap (Rojas et al. 1999; Thomas et al. 2006). Visual feeders run a short distance, quickly stop and watch for movement from prey which they grab from the surface when spotted. In contrast, long-billed shorebirds probe deep into mud substrates to feel and capture prey not visible from the surface. Despite being unable to see their prey, some shorebirds have finely tuned sensory mechanoreceptors in their bill tips that help them identify vibrations of buried invertebrates (Gerritsen and Meijboom 1986; Piersma et al. 1998).

Bird abundance and species composition in wetlands are driven primarily by: 1) hydrologic regime; 2) heterogeneity of avian habitat features (mixtures of water and plants); and 3) geographic location. In general, wetlands with fluctuating water levels are more productive ecosystems due to increased nutrient cycling, vegetation regeneration, and abundant macro-invertebrates (Harris and Marshall 1963; Niemuth et al. 2014). More stable wetlands, however, serve as refugia when water levels are low (Mattsson et al. 2012). Depressional wetlands experience periodic drawdown and reflooding, which strongly influence their avian communities. Northern pintails in North America, for example, vary the latitude at which they breed depending on how wet or dry wetlands are when they arrive in spring (Figure 5). During periods of drought, they may migrate further north while readily settling into southern areas in times of deluge (Mattsson et al. 2012). However, periodic drawdown and reflooding of wetlands is critical to maintaining productivity and the most diverse avian communities are typically found after wetlands reflood (Fredrickson and Taylor 1982; Taft et al. 2002; Farley et al. 2022).

The most important factor influencing abundance and diversity of wetland birds is the relative availability of multiple habitat types at local (i.e., within wetland and immediate watershed) and landscape extents. Due to niche partitioning, each bird species thrives in slightly different conditions (see above). Thus, avian diversity typically increases as heterogeneity of wetland resources (e.g., cover, forage) increases (Figure 5). Wetlands with interspersed submergent and emergent aquatic vegetation that approximate a 50:50 cover to water ratio (i.e., a hemi-marsh; Weller and Spatcher 1965; Masto et al. 2022) generally support the greatest abundance and diversity of wetland birds (Smith et al. 2004). Bird use is driven more by the structure and cover patterns within a wetland than the actual species composition of plants (Fairbairn and Dinsmore 2001). Copious emergent vegetation can support multiple vegetation zones and, therefore, greater habitat and bird diversity (Stewart and Kantrud 1971). At the landscape extent the greatest avian diversity is usually supported by a high density of wetlands (Webb et al. 2010; Fairbairn and Dinsmore 2001) that encompass all stages of the wetland cycle, offer greater wetland area, and an assortment of cover types and water depths, which each fill the requirements for foraging, loafing, or roosting habitats for individual species. To sustain wetland birds, conserving wetland complexes at local and landscape scales is an important consideration.

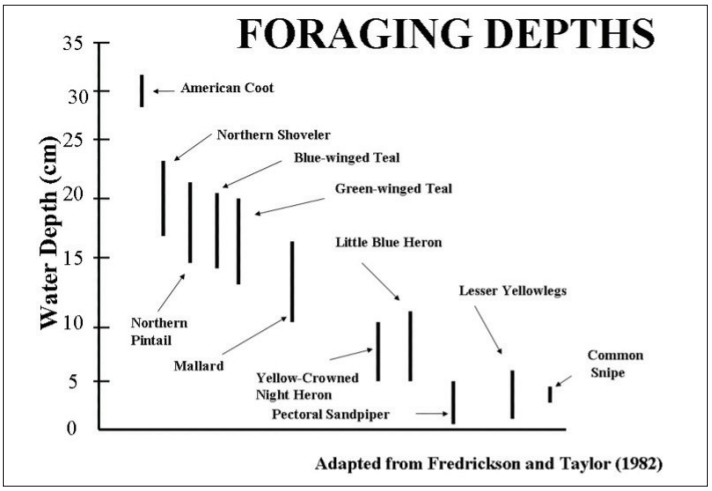

Figure 5. Relationship of some wetland-dependent bird species to variation in water depth.

Wetlands in many regions are considered endangered ecosystems due to climate and land-use pressures driving habitat fragmentation, degradation, and loss. Conversion of wetlands to agriculture has been a primary driver of wetland loss. In North America, king rail, sora, Virginia rail, and least bittern are notable wetland-dependent species that forage in areas of wetlands with emergent vegetation and high-stem densities that have been negatively impacted by human development (Rahlin et al. 2022); these species populations are estimated to have declined by ~25% since 1970 (Bolenbaugh et al. 2012). For most wetland-dependent birds, habitat loss in breeding areas may result in reduced population sizes or in the forcing of birds to less-suitable habitats where reproduction and survival may be lower (Stewart 1996). Because so many bird species use wetlands for food, shelter, and/or breeding (Kroodsma 1979), these ecosystems need protection to prevent species loss and ensure healthy populations into the future.

A list of the taxonomic names of organisms listed in this subsection is available in Online Appendix 3 (https://www.sws.org/education-modules-wetland-science/).

WETLAND MAMMALS

Of the 6,399 recognized extant mammal species (Burgin et al. 2018), approximately 4,000 have evolved to exploit wetland habitats and depend on wetland resources to meet at least some life-history needs (Vaughan et al. 2013). As with other terrestrial taxa, there is a gradient in the dependence of individual species on wetland resources, with some species being entirely dependent on wetlands (e.g., muskrats, capybaras, and beavers). Many other species of mammals are facultative wetland species and may thrive in wetland habitats but are not totally dependent on them for survival and reproduction and may persist where wetlands are scarce (e.g., raccoon). Finally, many species of mammals do not explicitly associate with wetlands but benefit from the resources they provide when available (e.g., white-tailed deer, American black bears). This gradient in wetland dependence is reflected in mammalian species morphology and behaviors.

Mammals play important roles in wetland ecosystems. As consumers, mammals may eat invertebrates, plants, birds, fish, and even other mammals, all of which may be abundant in and near wetlands (Dertien et al. 2020). These feeding activities add nutrients to wetlands, may cultivate the soil, and can influence vegetation patterns and abundance (May 2001). Mammals that transfer nutrients between aquatic and terrestrial systems are deemed ecotone specialists (Johnston 2017; Tischler et al. 2022). For example, brown bears feed extensively on salmon and move nutrients from the river to adjacent floodplain and upland areas. Similarly, bats feed on aerial insects with aquatic life stages, connecting the aquatic and terrestrial realms. Conversely, beavers fell trees and those terrestrially sourced resources increase the nutrient content of wetlands as well as provide underwater structure for aquatic species.

Some mammals hold the special distinction of being able to alter or create wetland habitats. The best-known example is the North American beaver, which creates extensive networks of aquatic areas through their works, such as building dams and developing canals. These activities can create new wetlands that not only benefit the beavers themselves, but a host of other species and ecosystem services (Johnston 2017). The muskrat, although a much smaller rodent than beavers, can also alter wetlands through their foraging patterns (Bomske and Ahlers 2021). Muskrats create heterogeneity in vegetation structure in marshy wetlands and can create open water areas that are used by a variety of taxa. An even smaller rodent, the North American water vole, acts as an ecosystem engineer via its burrowing activities which enhance diversity of riparian vegetation (Bryce et al. 2013).

The activities of large mammals may actually alter waterways themselves. Hippopotamuses can wear down deep channels and expand wetlands to surrounding areas. Elephants can similarly build water channels as they move between isolated ponds and rivers, and their tracks can eventually link distinct wetlands. Asian elephants divert monsoon rains directly into rivers (Sidle and Ziegler 2010). The wallows of American bison and peccaries in the Neotropics create ephemeral wetlands that are used by frogs (Gerlanc and Kaufman 2003; Beck et al. 2010).

Because wetland ecosystems are threatened throughout the world, some mammals have also experienced significant population declines due to losses of critical wetland habitats. One of the best-known and charismatic examples is the Florida panther, which was on the brink of extinction for many years. Results of GPS tracking research have shown these animals tend to spend their days in and around wetlands, particularly cypress swamps, and move into grasslands at night (Onorato et al. 2011). Their diet reflects their tendency to use wetlands, including items such as waterfowl and alligators (McBride and McBride 2010). In recent decades, the population of Florida panthers has increased due to significant conservation actions and genetic management, but human development in southern Florida continues to put pressure on this iconic species. In South America, the aquatic rat is an endangered rodent endemic to Ecuador and Colombia. Although little is known about this species, it is semi-aquatic and relies on arthropods and other insects that are abundant in wetlands. It appears the species has a small native range, which makes it especially vulnerable to disturbances to aquatic habitats, such as pollution or wetland loss. Therefore, conservation efforts for this species may consider protection of critical habitats within its narrow areas of distribution. As with the other aforementioned taxa, many wetland habitats that mammals rely on are threatened by loss or degradation. These species evolved to exploit the seasonally abundant resources that wetlands provide. In addition to efforts to restore and protect aquatic ecosystems everywhere they are under threat, management is beginning to re-embrace wetland reliant mammals as important parts of aquatic ecosystems. For example, ranchers in some areas of the Western U.S. now support increased North American beaver abundances and the natural infrastructure they provide, such as ponded water that cattle may use (e.g., https://www.beefmagazine.com/policy/beaver-power-provides-year-long-water-to-idaho-ranch). Such attitudes towards aquatic species may help preserve wetlands systems while taking advantage of the ecosystem services they can provide.

A list of the taxonomic names of organisms listed in this subsection is available in Online Appendix 3 (https://www.sws.org/education-modules-wetland-science/).

Figure 6. A North American beaver. (Photo: Courtesy of Kansas State University Research and Extension Service)

DISCLAIMER

Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Link to Supplemental Online Appendices: https://www.sws.org/education-modules-wetland-science/

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MODULE 5: WETLAND COMMUNITY ASSEMBLY

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OVERVIEW

Wetland habitats are occupied by species that can tolerate flooded and—in the case of coastal wetlands—salty soils (Figure 1). Relatively few species can tolerate these conditions, but species with the right adaptations can be very abundant in wetland habitats. Wetlands vary in how stressful the conditions are, and plant and animal biomass varies correspondingly, from almost zero to extremely high. Within a wetland, plants and animals are often arranged in "zones" along a gradient of physical stress, with the best competitors occupying the least stressful habitats and excluding all others. In turn, the species that are best able to tolerate stress, but are poor competitors, occupy the most stressful habitats. In contrast to the negative effects of competition, the presence of stress-tolerant plants and animals may reduce the level of physical stress in the habitat and benefit other species, a process called "facilitation." In addition, wetland species are negatively affected by consumers. Animals that eat plants may strongly reduce plant biomass, the abundance of these "herbivores" may be reduced by predators, and organisms on all trophic levels may be affected by parasites. Most wetlands vary over time in how "wet" they are, and this variation creates constantly changing abiotic conditions that affect all these organisms and their interactions. Wetland organisms are also affected by a variety of disturbances such as floating mats of dead vegetation, sediment deposited by floating ice, and fire. These and other disturbances reduce competition and create opportunities for species that would otherwise be excluded from the habitat. Due to global change, individual wetlands will transform over time as climate and water inputs vary. At the same time, humans directly affect wetlands by increasing nutrient supplies, removing predators, and filling or draining wetlands. All these factors—abiotic stress, species interactions, disturbance, global change, and human impacts—vary geographically, meaning that an understanding of a particular wetland requires an understanding of its geographic context.

Figure 1. Diverse plant community in a Netherlands salt marsh. (Photo: Steve Pennings)