Heitmeyer, M.E., R.J. Cooper, J.G. Dickson, and B. D. Leopold. 2005. Ecological relationships of warmblooded vertebrates in bottomland hardwood ecosystems. Pages 281-306 in Ecology and Management of Bottomland Hardwood Systems: The State of Our understanding. L.H. Fredrickson, S.L. King, and R.M. Kaminski, editors. University of Missouri-Columbia. Gaylord Memorial Laboratory Special publication No. 10. Puxico.

Ecology and Management of Bottomland Hardwood Systems:
The State of Our Understanding

Publishers: University of Missouri-Columbia, Gaylord Memorial Laboratory Special Publication No. 10
Mississippi State University, Forest and Wildlife Research Center, Publication WF-212

Acknowledgements: Redactory and copy editing by Sandy Clark

Ilustrations and photos courtesy of: Forest History Society, Durham, NC, Wylie C. Barrow, Jr. for cover photo and use of photos by James T. Tanner, Frank Nelson, Karen Kyle, U. S. Fish & Wildlife Service

Editors: L. H. Fredrickson, S. L. King, and R. M. Kaminski

Production/design: Karen Kyle

Citation:
2005. Ecology and Management of Bottomland Hardwood Systems: The State of Our Understanding. L. H. Fredrickson, S. L. King and R. M. Kaminski, editors. University of Missouri-Columbia. Gaylord Memorial Laboratory Special Publication No. 10. Puxico.

Gaylord Memorial Laboratory Special Publication No. 10
University of Missouri-Columbia
Rt. 1 Box 185, Puxico, MO 63960
573-222-3531 • email: gaylord1@starband.net

ECOLOGICAL RELATIONSHIPS OF WARMBLOODED VERTEBRATES IN BOTTOMLAND HARDWOOD ECOSYSTEMS

MICKEY E. HEITMEYER, [1] Gaylord Memorial Laboratory, The School of Natural Resources, University of Missouri-Columbia, Puxico, MO 63960.
ROBERT J. COOPER, School of Forest Resources, The University of Georgia, Athens, GA 30602.
JAMES G. DICKSON, School of Forestry, Louisiana Tech University, Ruston, LA 71272.
BRUCE D. LEOPOLD, Department of Wildlife and Fisheries, PO Box 9690, Mississippi State University, Mississippi State, MS 39762.

Abstract: Bottomland hardwood forest (BLH) in the southeastern United States supports rich associations of warmblooded vertebrate species (birds and mammals) that have striking adaptations to diverse and dynamic resources. Here, we describe avian and mammalian species that commonly occur in BLH and summarize community structure of the system and challenges for conservation. Species richness of mammal communities in BLH is comparable to, or exceeds, that found in nearby habitats, such as upland forests and grasslands. The greatest paucity of mammalian species is among small ground-dwelling species, especially Rodentia, whose populations often are ravaged by floods. Bird communities in BLH are especially rich and more species use BLH than most other ecosystems in North America. Bird species are distributed horizontally across hydrologic gradients and vertically across tree and shrub layers. Most common mammal and bird species in BLH are omnivores, have diverse diets within a trophic level (similar positions on the food chain), or are present only during pulses of specific food availability. Seasonal omnivory is common for most species that stay for extended periods. Many species capitalize on major system events, such as floods to secure new, previously unavailable, or concentrated prey. Many species also are highly mobile and relatively long-lived. Food chains in BLH often are long, complex, and ultimately based on detrital decomposition. Populations of most BLH species apparently are limited by "bottom-up" seasonal and annual variation in primary and secondary production and not by "top-down" predation. The integrity of BLH systems depends on large contiguous and interconnected areas of floodplain forest that are heterogeneous, seasonally inundated (usually by floods), and receive regular inputs of nutrients and sediments. Conservation of functional communities of mammals and birds in BLH must address: 1) continued loss and fragmentation of remaining BLH patches, 2) alterations in local and regional hydrology, 3) maintenance of multi-trophic food webs and nutrient flow, and 4) changes in bottom-up species relationships and population dynamics. Compared to other ecosystems, bird and mammal communities in BLH remain relatively intact and diverse today. High retention of species, despite considerable destruction and degradation, may be the result of basic adaptations of most species to be responsive and resilient to seasonal and spatial dynamics of resources. Species that have been extirpated typically are those that are food and habitat specialists, large higher order predators, ground dwellers, or are area sensitive. Despite biologic richness of BLH systems, many species have relatively high amplitude population dynamics caused by major episodic events, especially flooding. Clearly, more information is needed on which seasonal resources are most critical to species using BLH, how widely population levels can swing before imbalances or crashes occur, and potential impacts of system changes and loss on the diverse and complex species and predator/prey relationships.

Key words: Biodiversity, birds, bottomland hardwood forest, carnivores, food webs, mammals, raptors, songbirds, waterbirds.

BLH is among the most productive and dynamic wetland ecosystem in North America. These lowland forest areas support high biodiversity of plants and animals that are adapted to diverse and dynamic hydrology and resources. Locally, BLH supports 2-5 times more species and individuals than adjacent habitats such as upland forests (Brinson et al. 1981, Harris et al. 1984). Birds and mammals are the highest trophic-ordered and most conspicuous vertebrates that inhabit BLH. Understanding how these warmblooded vertebrates interact with BLH resources and each other potentially offers insight into how ecosystems in general are structured, how species have evolved in complex and dynamic environments, and how conservation strategies can be designed to restore and sustain functional BLH communities.

In this paper we describe the warmblooded vertebrates that commonly occur in BLH in the southeastern USA. In a somewhat modified "community ecology" approach, we attempt to identify patterns that characterize natural assemblages of species, understand causes of these patterns, and determine

[1] Email address: gaylord4@starband.net

how consistent ecological relationships are among taxa. This approach to understanding warmblooded vertebrate communities rests on the belief that current patterns are the consequences of past or ongoing ecological processes. Consequently, we begin with a discussion of how the BLH ecosystem is structured and its regulating processes. Then, we describe the species that use BLH including brief aspects of their life histories. Finally, we summarize the community structure of the system and challenges for conservation of birds and mammals.

HOW DOES THE SYSTEM WORK?

Structure and Climate

Most BLH occurs in floodplains of rivers and streams in the southeastern USA. Historically these forests occupied several million hectares; the largest area was approximately 10 million ha within the Mississippi Alluvial Valley (MAV); (MacDonald et al. 1979). BLH typically was contiguous along floodplain corridors and patch sizes were large (e.g., several million hectares connected in the MAV). Geomorphology and associated soils and surface topography of BLH floodplains represent historically active fluvial environments (Hupp et al. 2005). These landscapes are composed of heterogeneous networks of meander belts, valley trains, alluvial fans, backswamps, natural levees, point-bar accretions, abandoned channels and courses, crevasse splays, and tributary fill (Saucier 1994). Even small differences in elevation greatly affect depth, duration, and extent of flooding.

Vegetation in BLH is dominated by woody species that are arrayed along elevation and flooding gradients relative to their tolerance of soil saturation and inundation (e.g., Bedinger 1979, Conner and Sharitz 2005). "Zones" or "bands" of similar species groups occur commonly along these elevation gradients. However, the interspersion of plant species and zones of associated species usually are very heterogenous in locations that have multiple and complex formative processes and geomorphic histories. Consequently, inclusions of species dominant in 1 community type (e.g., baldcypress, *Taxodium distichum*) often are present within another community type (e.g., intermediate elevations dominated by red oaks [*Quercus* spp.] and sweetgum [*Liquidambar styraciflua*]).

Low elevations in BLH, such as abandoned channels and courses, are flooded for extended periods each year, and sometimes over several years. These low areas support relatively water tolerant plants, including buttonbush (*Cephalanthus occidentalis*), baldcypress, water tupelo (*Nyssa aquatica*), and many aquatic plants. Higher elevations, such as point-bar ridges and natural levees, are flooded irregularly within or among years. These high sites support plant species that are transitional from upland to bottomland such as hickories (*Carya* spp.); cherrybark oak (*Q. pagoda*); post oak (*Q. stellata*); and numerous shrubs, grasses, and sedges. In addition to horizontal zones of plant species across elevational gradients, the diversity of plants and their structure also creates vertical layers of plant type, height, and complexity. Vines or lianas especially are more abundant in BLH than in upland forests.

Location and composition of plant species in floodplains change when flood events alter stream courses, local topography, and water regimes. Sedimentation and scouring from floods often eliminate conditions that supported 1 plant community and replace it with another. In addition to regular changes in fluvial environments, extreme natural disturbance events (e.g., flood, drought, fire, and tornados) occur regularly in BLH and cause mortality and redistribution of tree species locally and sometimes over broad areas. Data from several subtropical forests, and relatively undisturbed BLH sites in the USA, suggest that about 3-5% of historic BLH areas were in tree-gaps at any given time (Hartshorn 1980, Uhl and Murphy 1981, Heitmeyer et al. 1989, King and Antrobus 2001). These gaps are caused by death or windthrow of 1 or more trees and become temporary open habitats within the forest. Individual gaps are short-lived, however, because they quickly become colonized by herbaceous plants, shrubs, and tree seedlings.

The climate of BLH in North America is warm temperate tending toward subtropical. Most areas typically receive 100-150 cm of rain annually; most rainfall occurs from late winter to early summer. Summers are hot and dry, with average temperatures exceeding 30°C and rainfall below 5 cm/month in July and August. Winter temperatures generally are mild, especially in the southern USA. At northern extremes of BLH, ice often is present for 1-2 months each winter and moderate snowfall occurs.

Hydrology

Seasonal and long-term dynamics of surface flooding and soil saturation are primary ecological

processes governing structure, functions, and values of BLH. Almost all BLH habitats are flooded for at least some portion of most years (Fredrickson 1979, Wharton et al. 1982, Heitmeyer et al. 1989, Hupp et al. 2005). Timing, depth, duration, extent, and source of flood water vary among locations in floodplains depending on elevation, geomorphic setting, proximity to rivers and streams, and underlying aquifers. Lower elevation sites typically are flooded for extended periods, whereas higher elevations may be flooded only a few days or be completely dry in some years (Fig. 1).

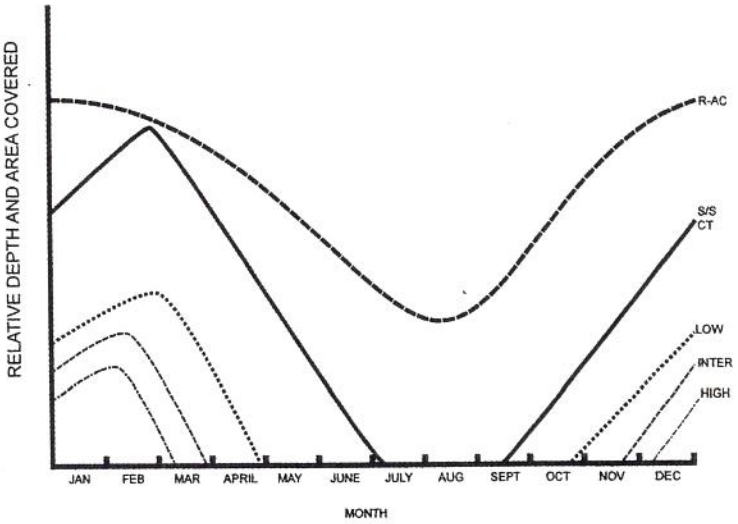

Figure 1. Relative annual flooding dynamics of habitat types in bottomland hardwood forests (after Heitmeyer et al. 1989). LOW: low elevations dominated by overcup oak; INTER: forest zones at intermediate elevations usually containing significant amounts of Nuttall, willow, or pin oak, sweetgum, and green ash; HIGH: high elevations near transition zones with upland forests and containing water oak, cherrybark oak, sugarberry, and hickory; S/S-CT: low elevations containing shrub/scrub and/or baldcypress and water tupelo; R-AC: rivers and abandoned channels.

Waters inundate BLH from a variety of sources including on-site rainfall and puddling in depressions, head- and backwater flooding from local and regional rivers and streams, and recharges from groundwater flows, especially alluvial aquifers. The source of flood water determines timing and extent of flooding, nutrient inflow and export, and site productivity (Hupp et al. 2005). Annual flooding is dynamic seasonally and among years. Precipitation and runoff typically are greatest in late winter and spring in BLH regions; consequently, most flooding occurs at this time (Fig. 1). Bottomland forests typically dry during late summer and early fall, although high precipitation and flood events occasionally can occur during every month of the year. Periodic extended drying is important in this system to recycle nutrients and stimulate decomposition processes, allow germination of plants especially trees, and maintain physiological functions of less water tolerant vegetation.

Long-term streamflow data from gages on major rivers in the southeastern USA indicate that extensive winter and spring floods in BLH regions are episodic. For example, 10 of 17 major rivers in the MAV flooded >5 days in winter 1961-62, but none flooded the following winter 1962-63 (Heitmeyer 2005). These same rivers had large areas of their floodplains flooded an average of ca. 4 years/decade during 1939-99. Generally, large rivers such as the Mississippi and Arkansas flood less frequently (<1 year/decade) than small rivers such as the Hatchie, Boeuf, and Obion (>7 years/decade). Interestingly, high flooding periodicity (and conversely low flow drought periods) occurs at 7-9 year intervals for many BLH locations.

When flows in major rivers are very high, almost all BLH habitats in floodplains are inundated, often quite deeply. Even short duration floods can quickly inundate several thousand hectares of BLH (e.g., U.S. Army Corps of Engineers 1970). During large precipitation events headwater floods can inundate extensive areas of BLH within a few hours. Typically, however, inundation and drainage of BLH during flood events are gradual and often prolonged because of the relatively flat topography, dense vegetation, labyrinth of streams within floodplains, and relative proximity to major river channels. This pattern of flooding produced widespread slow sheetflow of flood water across floodplains.

Nutrient Flow and Food Webs

Annual primary production and aboveground biomass of BLH are among the greatest of any ecosystem in North America (Rodin and Bazilevich 1967, Brinson 1990). High production is sustained because of high fertility of alluvial soils, a nearly subtropical climate, fluctuating water levels, and regular sediment and nutrient inflows. Secondary productivity also is high in BLH and is sustained primarily by a large detrital base created by annual leaf and other litter inputs from woody and herbaceous vegetation (Batema et al. 2005). Decomposition rates are relatively rapid in BLH, and nutrients and organic material are recycled quickly and transported over

wide areas by flood waters and animals (Johnson and Bell 1976).

The diverse vegetation composition, vertical and horizontal heterogeneity, and seasonal pulses of resources create many potential foods and niches for animals in BLH (Fredrickson 1978, Harris and Gosselink 1990, Junk et al. 1989). BLH trees produce large crops of hard and soft mast including acorns, drupes, and samaras (Table 1). Understory species produce abundant seeds and browse. Herbaceous ground cover, especially in tree gaps, produces seeds, tubers, rootlets, and stems. Aquatic plants are very dense in permanently flooded sites. Invertebrate communities in BLH include rich compositions of arboreal insects associated with canopy and subcanopy layers of trees and detrital communities composed mainly of grazers and shredders such as crustaceans and snails (Batema et al. 2005).

Primary and secondary production are highly seasonal in BLH and vary among years in relation to dynamics of climate, flooding, and nutrient availability. As an example, acorn production in BLH may vary 10-fold among years. Secondary production and detrital invertebrate populations depend on seasonal timing and duration of flooding that control decomposition rates. Collectively, system dynamics, especially hydrology, make large quantities of nutrients available to consumers but during relatively short seasonal and annual pulses.

The heterogeneity of BLH systems causes complex food webs (Wharton et al. 1982). Diverse communities of animals use BLH resources, and the habitat breadth of species typically is broader than in most other ecosystems. Most animals in BLH rely on multiple food sources during the year, or they are present only during seasons when specific resources (e.g., detrital invertebrates, arboreal insects, acorns, etc.) are present. Omnivory is the most common foraging strategy among species. Furthermore, the most abundant species are mobile and capable of using foods and habitats over wide areas. This mobility causes nutrient flow to be distributed widely through the system

Table 1. Types and relative abundance[a] of foods available and consumed by mammals and birds in bottomland hardwood forests.

	Habitat Type[b]						
Food type	Low forest	Intermediate forest	High forest	Scrub/ shrub	Slough/ oxbow	River	Herbaceous wetland
Plant foods							
Acorns		++	+++				
Seeds	+	+	++	++	+		+++
Samaras	+++	+++	++	+	+		
Roots/tubers	+	+	+	+	+		++
Aquatic plants	+			++	+++	+++	+
Browse	+	+++	+++	+			++
Animal foods							
Worms	++	++	+++	+	+		+
Snails	+++	+++	+++	++	++	+	+++
Crustaceans	+++	+++	+++	+++	++	++	+
Clams	++	++	+++	++	++	+	
Spiders	++	++	+++	++	+	+	++
Aquatic insects	++	+	+	++	+++	+++	+++
Arboreal insects	+++	+++	+++	++	+	+	
Fish	+			+	++	+++	
Small mammals	+	++	+++	+	+		+
Bird eggs/young	++	+++	+++	++	+		+
Amphibians/reptiles	++	++	+	++	++	++	+

[a] Relative abundance: +++ large, ++ medium, + small numbers and biomass (compiled from Fredrickson 1978, Wharton et al. 1982, Heitmeyer et al. 1989, and Fredrickson and Batema 1993).
[b] Low, intermediate and high forests refer to relative elevation and depth and duration of flooding in BLH (see text); scrub/shrub are low elevation sites dominated by shrubs, such as buttonbush; herbaceous wetland includes tree gaps and other open areas dominated by emergent vegetation.

(at least when patches historically were large and highly connected).

WHO LIVES THERE?

Mammals

Species richness of mammal communities in BLH is comparable or greater than other nearby habitats, such as upland forests and grasslands. For example, in the Grand Prairie Region of Arkansas, 37 mammal species use BLH habitats, whereas 31 species use upland forests, 24 species use slash, 22 species use remnant savanna, and 16 species use small remnant patches of prairie grassland (Heitmeyer et al. 2000). Despite selective pressures that mammals face from regular and extensive flooding in BLH habitats (especially ground-dwelling species), relatively more niches are available in BLH than in other habitats because of the multi-layered vertical structure (trees in BLH compared to shrubs and grasses in prairies) and aquatic media (wetlands compared to upland forests). The greatest paucity of mammalian species richness in BLH compared to other habitats is in small ground-dwelling species, especially Rodentia, whose populations often are ravaged by floods.

Insectivora.—Only 3 shrews, the southeastern shrew (*Sorex longirostris*), short-tailed shrew (*Blarina brevicauda*), and least shrew (*Cryptotis parva*), and the eastern mole (*Scalopus aquaticus*) commonly occur in BLH habitats (Lowery 1974, Sealander and Heidt 1990). None of these species is very abundant, however, and they typically occur only at higher elevations, in tree gaps, and at the transitional zone between bottomlands and uplands. The short-tailed shrew is the most common insectivore in BLH; nevertheless, it is relatively rare compared to its abundance in upland and grassland habitats.

Shrews and eastern moles generally avoid highly flood prone areas in BLH. Where present, shrews and moles favor grassy vegetation and sandy loam soils; heavy clays are avoided (Lowery 1974). Consequently, distribution is mostly restricted to higher ridges and natural levees. Shrew nests often are above ground in rotten or hollow fallen logs or immediately under tree stumps in tree gaps. Shrew and mole populations in BLH probably fluctuate greatly among years and likely become devastated in lower elevations during prolonged flood events.

As the taxonomic designation implies, most of the diet of shrews and the eastern mole is insects and other invertebrates. In BLH, diets of shrews apparently are more diversified than in uplands and contain significant mixtures of insects, snails, worms, small vertebrates, nuts, berries, and seeds (Sealander and Heidt 1990). Short-tailed shrews have the most diverse diet and commonly prey on frogs, salamanders, and some small mice. Shrews are consumed, in turn, by several carnivores especially weasel, skunk (*Mephitis* spp.), fox, bobcat (*Lynx rufus*), and owls.

Chiroptera.—Twenty species of bats are present in the southeastern USA and 11 of these commonly use BLH (Harvey et al. 1999). Two species, hoary bat (*Lasiurus cinereus*) and silver-haired bat (*Lasionycteris noctivagans*), are migratory and typically only occur in BLH during winter. In contrast, Indiana bats (*Myotis sodalis*) and some Brazilian free-tailed bats (*Tadarida brasiliensis*) migrate to BLH during summer but winter elsewhere. Evening bats (*Nycticeius humeralis*) use BLH mostly for breeding and during migration to southern wintering locations, but at least a few evening bats also winter in BLH (Baker and Ward 1967). The other 6 species-southeastern myotis (*Myotis austroriparius*), eastern pipistrelle (*Pipistrellus subflavus*), big brown bat (*Eptesicus fuscus*), red bat (*Lasiurus borealis*), seminole bat (*Lasiurus seminolus*), and Rafinesque's big-eared bat (*Plecotus rafinesquii*) all breed in BLH and are present most, if not all, of the year. A few other species, such as little brown bat (*Myotis lucifugus*) and gray bat (*Myotis grisescens*), occasionally are found in BLH but mostly they occur in upland forests near BLH areas. Interestingly, only 2 of the common bats in BLH are of the same genera. Relative population sizes of bats in BLH regions are unknown, but common species apparently are abundant, albeit declining (Harvey and Saugey 2001). Populations of Indiana bat (which are primarily in northern BLH areas) and southeastern myotis have declined significantly from former levels and now are listed as species of concern (Harvey and Saugey 2001).

Most of the bats found in BLH primarily are tree dwellers although several species commonly hibernate in caves on bluffs and uplands near floodplains. Some species, such as Indiana bat, use caves for most activities, but forage extensively along streams and sloughs in BLH (e.g., LaVal et al. 1977). Tree-dwelling bats apparently are most common in older-aged BLH stands. These older stands typically have greater structural diversity, more cavities, hollow boles, and exfoliating bark that are used for roosting and hibernacula. These

stands also have a richer and more abundant supply of arboreal insects than younger stands. Insects comprise most of the diet of bats in BLH, and diverse insect prey are abundant in canopy and subcanopy layers along riparian corridors and over standing water. Additionally, many insects and invertebrates are present near, or at the top, of detrital layers. Consequently, many potential niches are available for bats and the number of species that use BLH habitats is greater than the number present in most other North American ecosystems.

Bats are relatively long-lived and apparently develop traditions for use of specific sites, including individual trees in BLH regions. Preferred sites usually are large mature trees that have cavities or hollow areas. Baldcypress and water tupelo are especially important for bats, because they often have large openings in the bole.

Bats adjust to seasonal flooding and dynamics of food in BLH in several ways. First, bats are very mobile and forage over wide areas and in many BLH habitat types. Some species, such as Indiana bat, migrate to BLH during summer to take advantage of peaks of arboreal insects. Competition between bats and other insectivores, such as songbirds, probably is low during summer because of the great abundance of insects. Most bats in BLH breed in fall immediately following summer peaks of insect foods. They also store relatively large nutrient reserves in fall that fuel migration and sustain individuals during hibernation. Young are born in spring when seasonal populations of arboreal insects are greatest. Most bat species that winter in BLH hibernate high in hollow parts of mature trees or in caves near BLH floodplains. These sites allow bats to escape floods and reduce energy needs in winter when insect foods are scarce. Species such as red bat that winter in BLH, but generally do not hibernate, reduce activity, probably rely on stored nutrient reserves for much of their daily energy needs, and forage mostly in high elevation areas. Numbers of bats in BLH probably are related to annual variation in food supplies; predation on bats is low and mostly restricted to a few snakes, raccoons (*Procyon lotor*), and owls.

Lagomorpha.—Two rabbits, eastern cottontail (*Sylvilagus floridanus*) and swamp rabbit (*Sylvilagus aquaticus*), occur in BLH habitats, but only the swamp rabbit is truly a BLH inhabitant (Lowery 1974). Cottontails are mostly present in higher elevation fringes of BLH areas where open areas adjoin, or are in small patches within bottomlands. Swamp rabbits largely replace cottontails in BLH habitats. Swamp rabbits are present throughout BLH, but are most associated with tree gaps, slash areas, and relatively open new growth areas that have considerable grasses and sedges.

Swamp rabbits are one of the few true herbivores in BLH systems. They consume a variety of plants especially grasses, sedges, and new growth of giant cane (*Arundinaria gigantea* [hence the nickname "canecutter" for swamp rabbits]) that are present in tree gaps and other semi-open areas. Swamp rabbits regularly use fallen logs for loafing and often build nests in hollow fallen trees. Swamp rabbits have high reproductive rates, and breeding seasons extend from January through summer depending on flooding conditions. They are capable swimmers and readily climb to low levels of trees and shrubs. During floods, swamp rabbits climb trees, use fallen (and sometimes floating) logs, and move to high ridges and natural levees.

Little is known about population densities of swamp rabbits across their range. It is doubtful that numbers ever were very high because of their strong affinity with small scattered tree gaps and open areas within BLH; tree gaps probably only covered 3-5% of BLH areas during presettlement times. Swamp rabbits depend on periodic disturbances such as wind storms, fire, and extreme flooding to create their favored open habitats, yet these disturbances cause dynamic and disjunct populations of rabbits. Furthermore, populations that use newly created openings may quickly decline and become redistributed as trees regenerate in open areas. Where cane invades open areas, it usually persists for extended periods (e.g., 2-3 decades), prolongs tree regeneration, and consequently sustains open conditions, food supplies, and greater swamp rabbit numbers for longer periods than in other BLH areas.

Rodentia.—The order Rodentia is the largest mammalian order in the world, yet rodent species and numbers are relatively low in BLH systems (Burt and Grossenheider 1976). Only 14 rodent species are common in BLH habitats (Schwartz and Schwartz 1959, Lowery 1974, Sealander and Heidt 1990, Dickson 2001). Rodents in BLH are: 1) largely arboreal, 2) aquatic associated and excellent swimmers, and/or 3) exist at the upland margins of BLH. Arboreal species include 3 squirrels, the southern flying squirrel (*Glaucomys volans*), gray squirrel (*Sciurus carolinensis*), and fox squirrel (*Sciurus niger*), and one mouse, the golden mouse (*Ochrotomys nuttalli*). The white-footed mouse (*Peromyscus leucopus*) and cotton mouse (*P. gossypinus*) also are excellent climbers, often nesting in

trees and shrubs, and regularly using trees when BLH areas are flooded. Aquatic species include beaver (*Castor canadensis*), muskrat (*Ondatra zibethicus*), and, since the 1940s, the exotic nutria (*Myocastor coypus*); (Lowery 1974). The marsh rice rat (*Oryzomys palustris*), hispid cotton rat (*Sigmodon hispidus*), and southern bog lemming (*Synaptomys cooperi*) all are excellent swimmers and readily move to higher elevations when floods occur (Stafford and Stout 1983). The fulvous harvest mouse (*Reithrodonotomys fulvescens*), woodland vole (*Microtus pinetorum*), and wood rat (*Neotoma floridana*) are common on edges of BLH and they frequent higher elevational ridges and natural levees to escape floods. Generally, all small rodents are more common on higher elevational point-bar ridges than in lower frequently flooded backswamp areas (McComb and Noble 1979).

Almost all rodents in BLH have relatively diverse diets and use different foods seasonally. For example, mice consume various nuts, seeds, and numerous invertebrates. Mice are prolific breeders and, although populations apparently fluctuate greatly in BLH, they are resilient to normal flood, fire, and wind disturbance (Blair 1939, Sheppe and Osbourne 1971). Fringe species, such as wood rat, woodland vole, and fulvous harvest mouse, probably are most susceptible to extended flooding. Many of the common species nest in trees or on or in fallen logs. Nests of some mice, such as cotton mouse, may not be high above ground, but raising nests even a few inches may be enough to avoid inundation during local flood events. The fulvous harvest mouse also regularly builds nests in abandoned bird nests. The golden mouse is remarkably arboreal in all activities.

Squirrels consume a variety of plant materials, insects, and occasionally bird eggs and nestlings from the ground and within trees. They store large quantities of food for winter, when they are largely confined to trees because of ground flooding. Numbers of squirrels vary with annual abundance of food caused by dynamics of climate and flooding. During years with poor mast crops, overwinter survival of squirrels is low and subsequent populations often decline markedly or disperse considerable distances to better locations. Some populations of squirrels in BLH areas are almost migratory; they move to lower elevations during dry periods of summer and early fall and then to higher elevational ridges and margins during winter and early spring (Sealander and Heidt 1990).

Beaver, muskrat, and nutria are among the most aquatic mammals in BLH. They primarily use low elevational BLH and drainages that are flooded for most if not all of the year. Beaver are capable of manipulating their habitats to create and maintain flooded areas and withstand drought periods. They also are very mobile and can escape severe flood and drought. Beaver, muskrat, and nutria often survive severe drought by bank-dwelling and consuming roots of woody and herbaceous vegetation. Reproductive rates of beaver and muskrat are high, and life spans, especially of beaver, are long compared to other rodents. Populations of both species often are dynamic and probably are related to flooding and drying cycles in BLH. Beavers are almost entirely herbivorous but muskrats have a diverse diet that includes bulbs, stems, roots, and leaves of aquatic vegetation and animal foods, such as crayfish, frogs, clams, and carrion (Jones and Leopold 2001).

Carnivora and Marsupialia.—A diverse array of furbearer species use BLH habitats. Five species are strictly carnivorous and include 1 felid the bobcat and 4 mustelids, including river otter (*Lutra canadensis*), longtailed weasel (*Mustela frenata*), mink (*Mustela vision*), and striped skunk (*Mephitis mephitis*), although the skunk is primarily insectivorous. Other furbearers have varying degrees of omnivory and include 1 marsupial, the Virginia opossum (*Didelphis virginiana*), 1 procyonid, the raccoon (*Procyon lotor*), 2 canids, gray fox (*Urocyon cinereroargenteus*) and coyote (*Canis latrans*), and 1 ursid, Louisiana black bear (*Ursus americanus luteolus*). Three other species, cougar (*Puma concolor*), gray wolf (*Canis lupus*), and red wolf (*Canis rufus*) have been extirpated from BLH systems except for small residual populations of Florida panther and red wolf.

The most abundant furbearer species in BLH habitats are omnivorous and use aquatic and arboreal resources. Breeding sites of most species are either aquatic-oriented or in trees. Mink and longtailed weasel are the rarest species in BLH and seldom are found far from aquatic systems (Hall 1951). River otters also depend mostly on rivers, ditches, and canals and forage on fish, clams, and crustaceans. The most abundant species is the raccoon which regularly uses all BLH types. Bobcats are the largest remaining carnivorous furbearer, with local extinction of cougars and wolves. Coyotes are recent inhabitants to BLH; they were relatively rare in this system before the

1970s (Hill et al. 1987). In general, all furbearer species are widely distributed in BLH.

Furbearers occupy most available niches in BLH systems. High productivity in BLH provides high densities of food resources (plants, mice, insects, etc.), yet dynamic flooding deters species from becoming too specialized. Where it exists, specialization (i.e., strict carnivory) occurs for only a few species. For example, carnivory by bobcat is possible because of abundant and diverse foods including rodents, lagomorphs, and sciurids. The confounding factor for carnivores is winter-spring flooding which may temporarily reduce availability of prey and cause individuals to die, disperse, curtail, or reduce reproductive output. Generally, prey populations rebound quickly after floods, and they typically recolonize sites and restore preflood densities through increased reproduction rates (Blair 1939). The river otter, another strict carnivore, is less impacted by flooding because fish populations are not diminished during floods. However, fish are greatly dispersed during floods and may be less available to otters at that time. Consequently, densities of bobcat and otter are less than densities of omnivorous species in BLH.

Omnivorous furbearers readily shift diets in response to changing conditions and seasonal abundances of animal and plant material. The raccoon, for example, is very adapted for arboreal and hydric environments and can exploit foods in both water and trees and escape direct effects of flooding by eating different foods and becoming inactive in tree dens during high water. Likewise, black bear use both ground and tree resources, and they use den sites high (≥60 feet) in mature BLH stands (Oli et al. 1997). The opossum readily consumes carrion, enhancing its ability to survive stressful periods. Coyotes also are omnivorous and resilient species.

Predominance of omnivory and diverse food use cause complex and interrelated food webs among furbearers in BLH systems. For example, over 10 major food groups are used by raccoons including hard and soft mast, vegetation, crustaceans, reptiles and amphibians, invertebrates, earthworms, birds, mammals, fish, and mollusks (Chamberlain and Leopold 2001). Consequently, the potential for furbearers to significantly impact any single group of prey species is unlikely. Also, many prey are widespread and numerous and act as buffers for other types. Raccoons and skunks can significantly impact ground-nesting species such as birds, shorebirds, and turtles in local BLH areas (Guthery and Beasom 1977). Generally, however, density of skunks is low and precludes significant impacts. In general, prey of carnivores in BLH are bottom-up limited by food made available by natural system dynamics (flooding) and disturbances (fire) and not by top-down predation of carnivores. Also, carnivores are not "keystone" species in BLH like they are in prairie and montane ecosystems. This is especially true now that top carnivores, such as cougar and wolf, are extirpated from BLH.

Populations of furbearers in BLH are subject to specific zoonoses, such as distemper, rabies, and sarcoptic mange. Raccoon, grey fox, and skunk are especially sensitive to distemper (Davidson and Nettles 1988). Although distemper can vary in intensity, it may reach epizootic tendencies every 5-10 years in which case a large percentage of local populations may be impacted. When intrinsic self-regulating mechanisms weaken (perhaps following extended flooding), populations of these furbearers may be severely impacted by distemper (Leopold and Chamberlain 2001). This is important because the raccoon is the most abundant furbearer in BLH and has the greatest potential to impact prey species. In contrast, zoonoses have less effect on bobcat, otter, and weasel and their densities rarely reach high levels that enable diseases to spread widely and thus limit populations. Larger species, such as bear, cougar, and wolves are (were) "area-sensitive" in BLH. They need(ed) relatively large home ranges to provide them access to dry sites during extreme flood events, diverse prey among seasons, and alternate prey when populations of individual prey species were low (White et al. 2000). These species have declined or were extirpated as BLH areas have become smaller and more fragmented.

Artiodactyla.—The only hoofed mammal present in BLH habitats is the white-tailed deer (*Odocoileus virginianus*), although elk (*Cervus canadensis)* and bison (*Bison bison)* historically were present in nearby habitats and probably occasionally used edges of BLH. Artiodactyla are large highly mobile animals, and they range over wide areas during their life cycles. While numbers of white-tailed deer typically are most abundant in borders or edges of BLH stands, they use most BLH habitat types during some time of the year (Newsom 1984). The nonsedentary habits of deer allow them to move throughout BLH systems in response to seasonal and annual dynamics of food, changes in predator populations, and flooding and drying events.

Deer have a diverse diet in BLH habitats and primarily feed on leaves, twigs, and fruits of trees

and shrubs and foliage of herbaceous and woody plants. They also consume seeds, fungi, mosses, lichens, and grasses. Acorns are a very important seasonal food for deer and provide nutrient reserves for reproductive events and extended cold or flood periods. Dynamics of acorn production can influence reproductive performance and population dynamics of deer in some forest systems (Rogers et al. 1990), and this also may be true in BLH. Extreme flooding during winter and spring also can reduce important understory plants and can limit or move local populations of deer.

It is uncertain if deer populations in BLH historically were so dense that they significantly impacted, or limited, preferred plant distribution and growth through herbivory. Even though relatively dense deer populations occurred in local areas, floods regularly caused deer to move to higher areas where competition for foods was greater and they were more susceptible to predation from large carnivores, such as cougar and wolf, as well as native people and European settlers. Deer densities in BLH may be greater today than historically, and abiotic factors that regulated populations such as extensive floods are greatly reduced in many areas. Consequently, current deer populations may potentially impact tree reproduction, shrub communities, and even nesting structure and habitat of some birds in local areas (e.g., DeCalesta 1994, Jones et al. 1997). Also, it is uncertain if predation ever limited deer numbers in BLH, because large carnivores were not greatly abundant and their numbers were influenced by seasonal and annual dynamics of numerous prey. Furthermore, deer are not keystone species in BLH systems, as they may be in southeastern upland forests (Miller 2001), in that they do not regulate plant composition, growth, and distribution or numbers of their primary predators.

Birds

Bird communities in BLH are diverse. Published accounts of birds in BLH differ in the number of species listed depending on how authors have defined BLH habitats and what geographical region is included. Smith et al. (1993) listed 200 bird species that occur in the MAV, largely in BLH, which is >85% of 236 species of birds listed in eastern North America. Frentress (1986) and USFWS (1984) recorded 273 species that use BLH and associated habitats throughout the southeastern USA. Hamel (1992) listed 149 species associated with oak-gum-cypress forests and 163 species associated with elm-ash-cottonwood stands in the southeastern USA. Regardless of the exact count, more bird species use BLH habitats than almost any other ecosystem in North America (calculations from ranges in several field guides; e.g., National Geographic Society [1980])

Locally, bird species richness typically is greater in BLH than in adjacent upland forests (e.g., Dickson 1978a, USFWS 1984, James and Neal 1986); patterns are less clear at regional and continental scales. BLH systems generally have greater productivity and more potential foods for birds than upland and grassland systems. Bird species in BLH are distributed horizontally across hydrologic gradients and vertically across tree and shrub layers (Wakely and Roberts 1996). Data from Breeding Bird Censuses (BBC) indicate the number of bird territories is greater in BLH than in upland forests from the same region (Table 2). Territory densities reported by Twedt et al. (1999) for several BLH sites also are very close to those found in Table 2. Nonetheless, some upland sites approach or exceed BLH sites in bird abundance (Lowe 1995, 1996).

Species richness (indicated by BBC data) during the breeding season tends to be similar among BLH and upland forests. However, it is important to note that aquatic species such as waterfowl and wading birds, usually are not recorded in BBC surveys because their home ranges cover areas much larger than typical BBC survey plots (<20 ha). Consequently, we suspect beta diversity (species across habitat zones) is greater in BLH than in upland forests. In contrast to breeding season, winter bird communities in BLH have more birds and species than in upland forests (Table 3). This trend in winter is apparent nationwide (Lowe 1995, 1996) and regionally (e.g., in Arkansas; James and Neal 1986). Despite weaknesses in BBC data, we conclude that BLH habitats support richer bird communities than other forested ecosystems, especially in winter.

Anseriiformes.—Thirty-one of over 50 species of waterfowl in North America use BLH habitats, at least occasionally (Bellrose 1980). Large numbers of 12 species commonly use BLH habitats throughout the southeastern USA, small numbers of 11 species regularly use specific areas in BLH, and 8 species are relatively rare in BLH (Fredrickson and Heitmeyer 1988, Heitmeyer 2001). Only 2 species, wood duck (*Aix sponsa*) and hooded merganser (*Lophodytes cucullatus*), breed in BLH habitats and both are cavity nesters. Historically, small numbers

Table 2. Published data reporting mean bird densities and numbers of species in bird communities from Breeding Bird Census plots. Most studies compare communities in bottomland hardwood forests with those in upland forests.

Location	Habitat	Territories/ 40 ha	Number of species	Number of plots	Reference
LA, TX	Bottomland	412	20	3	Dickson 1978a
	Pine (sawtimber)	133	18	2	
	Pine-hardwood	143	17	1	
NW AR	Bottomland	207	19	1	James and
	Upland	149	21	1	Neal 1986
NE AR	Bottomland	129	24	1	James and
	Upland	183	22	1	Neal 1986
Central AR	Bottomland	149	25	1	James and
	Upland	85	26	1	Neal 1986
Southern AR	Bottomland	487	35	1	James and
	Upland	241	39	1	Neal 1986
Eastern USA	Bottomland	309	28	26	Various[a]
	Upland and mixed	301	26	76	
LA, MS	Bottomland uncut	330	NR[b]	14	Twedt et al.
	Bottomland cut	319	NR	6	1999

[a] Data are from Breeding Bird Census reports from 1994 and 1995 compiled by Lowe (1995, 1996).
[b] Not reported on a per plot basis.

of giant Canada geese (*Branta canadensis maxima*) and trumpeter swans (*Cygnus buccinator*) nested on stumps and other raised vegetation in larger, deeper BLH wetlands. Today, growing numbers of resident Canada geese nest in BLH, but breeding swans have been extirpated.

Large numbers of mallard (*Anas platyrhynchos*), American black duck (*A. rubripes),* gadwall (*A. strepera*), American wigeon (*A. americana*), northern pintail (*A. acuta*), American green-winged teal (*A. crecca carolinensis*), blue-winged teal (*A. discors*), northern shoveler (*A. clypeata*), ring-necked duck (*Aythya collaris*), and medium subspecies of Canada geese (e.g., *Branta canadensis interior*) use BLH habitats, including cleared bottomland areas, from fall through spring. Until recently, few lesser snow geese (*Chen caerulescens*) were present in BLH regions, but today large numbers are present in winter where BLH has been cleared and converted to agriculture, especially rice. Despite large regional numbers, however, snow geese seldom use actual BLH habitats. Small numbers of other waterfowl species, such as canvasback (*Aythya valisineria*), redhead (*Aythya americana*), lesser scaup (*Aythya affinis*), ruddy duck (*Oxyura jamaicensis*), common goldeneye (*Bucephala clangula*), bufflehead (*B. albeola*), and red-breasted merganser (*Mergus serrator*) mainly use rivers and larger open waters within BLH regions for short periods during migration.

Waterfowl have many basic adaptations to seasonal wetland resources across North America, and they occupy many niches in BLH (Heitmeyer 2001). They are large, long-lived, gregarious, highly mobile, and capable of storing large nutrient reserves. These traits allow birds to move over extensive areas and exploit seasonally available resources. Nutrient reserves also fuel migration and help meet energetic requirements during periods of low and widely dispersed food availability. Many species store large nutrient reserves while in BLH during seasonal pulses of food availability, such as when acorns and moist-soil seeds occur abundantly (Heitmeyer 1988). Species that use BLH for extended periods (wood ducks, mallards, hooded mergansers) also time key annual cycle events, such as pairing, prebasic molt of females, and egg laying to coincide with seasonal availability of select foods and flooded habitats (Fig. 2, Heitmeyer 1987, Fredrickson and Heitmeyer 1988, Bellrose and Holm 1994, Dugger et al. 1994). Waterfowl quickly respond to newly flooded areas in BLH where they find extensive areas of newly available food, cover, and undisturbed refuge (Heitmeyer 1985, Reinecke et al. 1988).

The 2 most abundant waterfowl species in BLH, mallards and wood ducks, are present for the longest periods (year round for wood ducks and early fall through spring for mallards), and are omnivores that take advantage of many food pulses such as moist-soil seeds in fall, acorns in late fall and winter, detrital macroinvertebrates in late winter and spring, and aquatic insects and samaras in spring (Drobney and Fredrickson 1979, Heitmeyer and Fredrickson 1990). Geese and swans, wigeon, gadwall, and ring-necked ducks are primarily herbivores when in BLH habitats, but these birds also consume significant amounts of invertebrates in early fall and spring. Pintail and teal consume a diverse diet of

moist-soil seeds and aquatic invertebrates while in BLH. Hooded merganser and shoveler are mostly carnivorous, although shovelers eat large amounts of seeds during fall and early winter. Few shovelers winter in BLH habitats. Although hooded mergansers breed in BLH, many individuals apparently move away from BLH areas in summer when BLH habitats are driest and primary aquatic prey such as crayfish and small fish probably are least available (Dugger et al. 1994).

Annual populations of waterfowl are dynamic across North America and reflect variation in wetland and upland habitat conditions throughout their continental ranges. Population size and annual recruitment of most species are correlated with wetness of primary breeding habitats, and at least for some species, also migration and wintering habitats. Condition (i.e., amount and type of habitat flooded, annual food production, availability of refuges) of habitats throughout the southeastern USA, especially BLH in the MAV, during winter is influenced by annual precipitation and temperature which influences local and regional distribution of species (e.g., Nichols et al. 1983), and subsequent production and survival of mallards and wood ducks (Heitmeyer and Fredrickson 1981, Kaminski and Gluesing 1987, Reinecke et al. 1987, Moser and Graber 1990, Bellrose and Holm 1994, Kelley 1997, Kennamer 2001). More mallards winter in or near BLH habitats in the MAV than any other location in the world, and the entire population of midcontinent mallards in the USA may be periodically affected by winter habitat availability and food abundance in BLH systems (Heitmeyer and Fredrickson 1981, Kaminski and Gluesing 1987). Winter influences may occur most often when populations are high, breeding conditions are good and not constraining, and when many BLH habitats are dry or flooded late (see Reinecke et al. 1988, Raveling and Heitmeyer 1989). In dry winters in BLH, food is less available, inter- and intra-specific competition is heightened, and body mass of individual females is reduced (Heitmeyer 1988). General correlates between mallard and wood duck populations and annual habitat conditions in BLH may be exacerbated today, because BLH habitats have been greatly destroyed and fragmented.

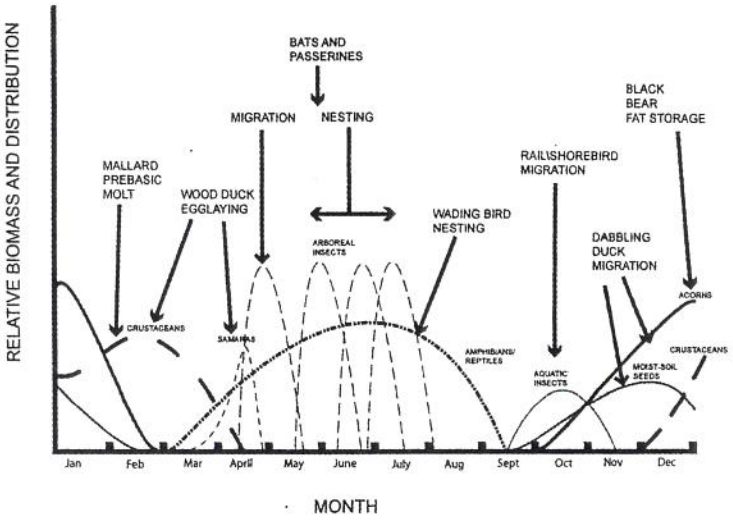

Figure 2. Examples of seasonal pulses of food types in bottomland hardwood forests and key annual cycle events of some species that coincide with these pulses.

Charadriiformes and Gruiformes.—Approximately 331 species of shorebirds, gulls, and their allies (Charadriiformes) and 209 species of marsh birds, such as rails, coots, and cranes (Gruiformes) are present worldwide (Gill 1990), but only 31 species of shore-

Table 3. Published data reporting mean bird densities and numbers of species in bird communities from Winter Bird Population Study plots. Most studies compare bird communities in bottomland hardwood forests with those in upland forests.

Location	Habitat	Birds/ 40 ha	Number of species	Number of plots	Reference
NW AR	Bottomland	176	23	1	James and
	Upland	35	16	1	Neal 1986
NE AR	Bottomland	218	34	1	James and
	Upland	83	25	1	Neal 1986
Central AR	Bottomland	447	28	1	James and
	Upland	72	19	1	Neal 1986
Southern AR	Bottomland	559	47	1	James and
	Upland	150	33	1	Neal 1986
Eastern USA	Bottomland	211	24	9	Various[a]
	Upland and mixed	122	18	26	

[a] Data are from Winter Bird Population Study plots from 1994 and 1995 compiled by Lowe (1995, 1996).

birds, 6 gulls and terns, 7 rails and gallinules, and the American woodcock (*Scolopax minor*) commonly use BLH habitats. This relative paucity of shore and marsh birds in BLH is not surprising because most of these species prefer: 1) open water (e.g., gulls, terns), 2) herbaceous marshes (e.g., rails, snipe), or 3) ephemeral shallow mud flats and sandbars (e.g., sandpipers). These habitat types historically comprised only 5-10% of BLH landscapes and often were temporally (e.g., mudflats along margins of oxbows) and spatially dispersed.

Most shore and marsh bird species use BLH habitats only during migration, staying for relatively short periods. More shorebirds are present in late summer and early fall than during spring in BLH. Peak migrations through the region coincide with declining water levels and exposed mud flats in lower elevational open areas in mid- late summer and early fall. Water levels in BLH in spring typically are high and few mudflats are exposed. Medium and large, and short- and intermediate-distance, shorebird species are most common in BLH; relatively few small and long-distance migrants stop in BLH (Skagen et al. 1999). These larger species that move short distances between migration stopover sites probably do not depend on predictable site-specific resources to meet energy demands of migration, and they may be better able to use spatially and temporally dynamic BLH habitats. Nonetheless, even these larger shorebirds have greatly reduced numbers in BLH compared to coastal, Great Plains, and Intermountain areas (Skagen et al. 1999).

Most marsh birds and woodcock use open areas and edges of BLH where herbaceous vegetation is present. Marsh species, such as rail and snipe, typically prefer larger openings in BLH that become seasonally flooded from fall through spring. Woodcock typically are found in forested areas and openings, such as tree gaps, and edges of higher elevation sites in BLH (Straw et al. 1994). Many woodcock winter in BLH, and a few birds remain to breed, especially in the southern USA. Interestingly, however, many woodcock that breed in BLH migrate north out of BLH regions in summer only to return in late fall (Causey et al. 1987, Straw et al. 1994). Breeding king rail (*Rallus elegans*), purple gallinule (*Porphyrula martinica*), and common moorhen (*Gallinula chloropus*) also may move from BLH habitats in summer to more permanent coastal and inland marshes (Helm 1994, Reid et al. 1994).

Only killdeer, least terns, and formerly black terns migrate to BLH specifically for breeding (Hayman et al. 1986, Brown et al. 2001). The killdeer is a flexible species that uses many shallow water areas that recede during spring and summer. In contrast, terns use larger rivers where sandbars used for nest sites historically were exposed, and side-channels and chutes used for foraging on small fish were shallow and narrow during summer. Rapid rises in water levels of rivers during late spring and summer greatly reduce nest success and fledgling survival (e.g., Dugger 1997), and summer floods and modern changes in seasonal flows of major rivers likely limit populations.

Only a few shore and marsh species, such as sora (*Porzana carolina*), common snipe (*Gallinago gallinago*), American coot (*Fulica americana*), killdeer, herring gull (*Larus argentatus*), woodcock, greater yellowlegs (*Tringa melanoleuca*), and lesser yellowlegs (*Tringa glavipes*) commonly winter in BLH habitats. The largest concentrations of these species occur in southern parts of BLH and, except for woodcock, total numbers are small.

Most shorebirds and marshbirds are mostly carnivorous while in BLH, the most abundant species and those present for extended periods (e.g., rails, woodcock) are omnivorous (e.g., Rundle and Sayre 1983, Straw et al. 1994). Within the last century, shallowly flooded agricultural lands (e.g., rice fields), moist-soil impoundments on lands managed for wildlife, aquaculture ponds, and irrigation reservoirs have increased habitats for shorebirds and marshbirds, probably well beyond what was historically present.

Podicipediformes, Pelecaniformes, Gaviformes.— These aquatic-associated birds are not diverse worldwide (87 species total), nor do many species use BLH habitats. The pied-billed grebe (*Podilymbus podiceps*), double-crested cormorant (*Phalacrocorax auritus*), and anhinga (*Anhinga anhinga*) are the most abundant species in BLH habitats. Small numbers of eared grebe (*Podiceps nigricollis*), horned grebe (*Podiceps auritus*), and white pelican (*Pelecanus erythrorhynchos*) also use BLH during fall and spring. Common loons (*Gavia immer*) are observed rarely on larger open wetlands such as oxbow lakes. Except for anhinga, all of these species are migrants through BLH regions and none breed there. Anhingas nest in scattered locations in very southern BLH regions, typically in low elevation sites where large baldcypress trees and permanent water occur. Here they apparently find ample supplies of fish and other prey during summer.

Habitats used by grebes, pelicans, cormorants, and loons in BLH are restricted mostly to deeper open water areas of natural lakes, abandoned channels,

rivers, and man-made ponds and lakes. Burgeoning populations of cormorants and pelicans are problematic during winter and spring migration in aquaculture areas in the MAV, especially in Mississippi and Arkansas. Pied-billed grebes use the greatest diversity of habitats including herbaceous wetlands, open waters, and BLH. All species, except for pied-billed grebes, are mostly picivorous. The pied-billed grebe consumes a wide diversity of foods including small fish, amphibians, reptiles, insects, crustaceans, seeds, and occasionally other plant parts.

Ciconiiformes.—Most (14 of 18) wading bird species found in North America use BLH habitats at least occasionally; 12 of these species breed regularly in this system. Species that are especially abundant include black-crowned night heron (*Nycticorax nycticorax*), yellow-crowned night heron (*Nycticorax violaceus*), green heron (*Butorides striatus*), little blue heron (*Egretta caerulea*), great blue heron (*Ardea herodias*), cattle egret (*Bubulcus ibis*), snowy egret (*Egretta thula*), great egret (*Casmerodius albus*), and wood stork (*Mycteria americana*). Least bittern (*Ixobrychus exilis*), American bittern (*Botaurus lentiginosus*), and glossy ibis (*Plegadis falcinellus*) also nest in a few local areas (e.g., Sutton 1967; Gibbs et al. 1992a,b; Davis and Kricher 2000). Many of these species are present in BLH only during summer breeding periods (e.g., yellow-crowned night heron), but some populations of wading bird species (e.g., little blue heron) from other breeding locations throughout North America also migrate through, or into BLH habitats during nonbreeding periods. Also, some individuals of several species (e.g., green heron, great blue heron, great egret, wood stork) use BLH habitats year-round. Consequently, patterns of use of BLH by wading birds are complex and vary inter- and intra-specifically and also seasonally and annually.

The Ciconiiformes is an ancient order, and distribution and adaptations of species are closely aligned with presence of fluctuating water levels in freshwater and marine wetland systems. Generally, species are very mobile and have complex social systems including colonial or semi-colonial nesting, diverse diets, and specific morphological adaptations (e.g., leg length, bill length and shape) to dynamic water conditions. Except for bitterns, all species that breed in BLH habitats nest in trees and shrubs, and they readily move colony sites among years in relation to changes in hydrology and prey distribution. Most species forage considerable distances from nesting locations and take advantage of seasonally available resources distributed over relatively large areas (Kushlan 1978). Some species, such as cattle egret and great blue heron, also regularly use terrestrial habitats adjacent to BLH.

Although most wading bird species have diverse diets, they tend to segregate niches and food use relative to water depth and cover type (Kushlan 1978). A few species have relatively specific diets, e.g., yellow-crowned night herons are crustacean specialists, and are more confined to habitats where these foods are available (Watts 1995). Wading bird communities typically are more diverse in tropical and semi-tropical regions than in temperate regions (Kushlan 1978). The wading bird community richness in BLH is comparable to more tropical regions presumably because of its comparable system productivity, diversity, and multiple prey types.

Diets of most wading bird species vary with seasonal availability of select prey items and many forage extensively on a wide selection of small fish, amphibians, reptiles, crayfish, small mammals, and some other birds, such as wood duck ducklings (Davis 2001). Generally, waders rely on fluctuating water levels in BLH to make prey more available. Wading birds opportunistically use rising and falling water levels. For example, rising water from flooding often moves prey, such as small fish, into high elevation shallow flats while decreasing water often concentrates prey, such as amphibians, in drying isolated pools of water.

Little is known about factors that regulate wader numbers in BLH, but likely annual variation in extent and type of flooding, climate, and regional population size influences prey availability, energetic demands, competition, and optimal nest locations. Distribution and success of nesting colonies of several species are correlated with local habitat conditions. Adult waders have relatively few predators in BLH, and colony nesting deters some predators and increases vigilance and defense of nests (Lima 1993). Winter habitat conditions also are correlated with subsequent population sizes of waders (Den Held 1981). Most wading birds that nest in BLH migrate to subtropical and tropical wetlands during winter where preferred foods probably are more available. Nonetheless, some wading birds do winter in BLH habitats and it seems possible that dry winters in BLH regions may negatively influence some local wader populations similar to influences on some waterfowl (e.g., mallards; Heitmeyer and Fredrickson 1981).

Passeriformes, Piciformes, and Cuculiformes.—About 130 species of songbirds and woodpeckers regularly use BLH habitats. Interestingly, relatively

equal numbers of songbird species (ca. 1/4 of the total) are: 1) residents, 2) migrate to BLH in summer to breed, 3) migrate to BLH to winter, or 4) use BLH only during spring and fall migration. Consequently, only about ½ of the 130 species are present at any given time. The greatest number of species occurs in spring when residents, some early breeders, and some late migrants are all present. Apparently, this temporal segregation allows many species to use this very rich, yet very seasonal, system without manifesting competition and niche overlap, especially during crunch periods (such as dry years, extended floods, cold winters, etc.). Still, the 60-70 species of songbirds and woodpeckers present, for example during the breeding season, is among the greatest of any ecosystem in North America. Most species that migrate to BLH in summer or pass through during fall and spring are neotropical migrants that winter in subtropical forests in Central and South America. All woodpeckers are year-round residents except the yellow-bellied sapsucker (*Sphyrapicus varius*) which is present only during winter.

Many common breeding songbirds in BLH are canopy dwellers and many are considered interior forest species that typically do not frequent edges of forest patches. Other common breeding species, such as northern water-thrush (*Seiurus noveboracensis*), hooded warbler (*Wilsonia citrina*), white-eyed vireo (*Vireo griseus*), and wood-thrush (*Hylocichla mustelina*), nest in shrub-level vegetation on higher BLH sites (Dickson 1978b). Species that nest or forage extensively on the ground often are less abundant and have scattered distributions. Of common breeding songbird species at White River National Wildlife Refuge (NWR), 32% are cavity nesters, 33% nest in the upper canopy of forests, 16% nest in the lower canopy, and 18% nest on or near the ground (R. J. Cooper, unpublished. data). Species strongly associated with specific plants, such as cane (e.g., Swainson's warbler, *Limnothlypis swainsonii*), or that are area-sensitive and require large contiguous patches of forest (e.g., cerulean warbler, *Dendroica cerulea*) are rare or locally and regionally extirpated (e.g., Bachman's warbler, *Vermivora bachmanii*).

A few species are mostly associated with large stands of old-growth forest (Dickson and Warren 1994), and at least 1, the ivory-billed woodpecker (*Campephilus principalis*) probably is extinct in North America. Species considered to be characteristic of either elm-ash-cottonwood or oak-gum-cypress forests include yellow-billed cuckoo (*Coccyzus americanus*), pileated woodpecker (*Dryocopus pileatus*), red-bellied woodpecker (*Melanerpes carolinus*), red-headed woodpecker (*Melanerpes erythrocephalus*);(especially in winter), Acadian flycatcher (*Empidonax virescens*), Carolina wren (*Thryothorus ludovicianus*), eastern tufted titmouse (*Baeolophus bicolor*), American robin (*Turdus migratorius*);(winter only), blue-gray gnatcatcher (*Polioptila caerulea*), prothonotary warbler (*Protonotaria citrea*), northern parula (*Parula americana*), yellow-rumped warbler (*Dendroica coronata*);(winter only), yellow-throated warbler (*Dendroica dominica*), Kentucky warbler (*Oporonis formosus*), hooded warbler (*Wilsonia citrina*), American redstart (*Setophaga ruticella*), rusty blackbird (*Euphagus carolinus*);(winter only), and white-throated sparrow (*Zonotrichia albicollis*);(winter only) (Hamel 1992).

Many of the above species are tied to specific features of BLH; for example, many are cavity nesters. Also, the yellow-billed cuckoo, a nomadic and somewhat rare species throughout much of its range, is quite abundant in BLH, probably because of abundant large prey, such as small lizards, tree frogs, and snails in addition to large arthropods (R. J. Cooper, unpublished. data). Interestingly, bird species in BLH are arrayed as much horizontally along wetness gradients (e.g., Wakely and Roberts 1996) as they are in classical vertical distributions by canopy layers in other forest types (e.g., MacArthur 1958). The combination of horizontally arrayed trees and shrubs along hydrologic gradients, coupled with the vertically arrayed multilayered shrubs and trees, have created numerous niches that BLH birds exploit.

Most songbirds in BLH are insectivorous during spring migration and the breeding season. Birds readily respond to seasonal pulses of insects and other invertebrates and most species feed opportunistically at insect hatches when they occur (e.g., Petit et al. 1990). Apparently, these super abundances of insects are so large that they can feed many bird species (see also previous discussion on bats). At other times, though, insectivorous birds feed on specific prey, as they do in upland forests. One of the most important food items for many of these birds is lepidopteran larvae, which have been termed "ecological currency" because of their importance in bird diets, especially those of nestlings (Greenberg 1995). Insectivorous birds in BLH probably are not limited by food availability during the breeding season. For example, in 6 years of monitoring over 2000 nests of BLH songbirds on the White River NWR in Arkansas, <10 nests were

abandoned while young were still in the nest (R. J. Cooper, unpublished data). Woodpeckers remain mostly insectivorous year round; however, the most abundant species, such as red-headed and red-bellied woodpeckers are omnivorous and depredate songbird nests in spring and summer. Other species, such as crows, are omnivorous year round.

Paradoxically, the very thing that makes BLH habitats so rich in species and numbers of songbirds also can limit composition of bird communities. Sites that are inundated frequently for long periods do not have an abundance of ground-nesting species, such as Kentucky warblers, except during dry years. Other species that typically nest low to the ground respond to flooding by nesting higher in the canopy. Indigo buntings (*Passerina cyanea*) at White River NWR, for example, have a mean nest height of 4.2 m, an above-average height for this species (Welch 2000).

Nest heights of many songbird species are higher in BLH than in upland forests. An obvious explanation would be that they are nesting at a normal height, but it is relative to the water level and not the ground. However, some species actually increase their nest height after floodwater recedes (Wilson and Cooper 1998). A possible explanation for increasing nest height later in the breeding season is avoidance of nest predation by placing nests in areas with more concealment after trees have fully leafed out. We believe breeding songbird populations in BLH are not limited by food, but by nest depredation, the leading cause of nest failure in most passerine species (Ricklefs 1969). A myriad of nest predators exist in BLH including raccoons, squirrels, blue jays (*Cyanocitta cristata*), fish crows (*Corvus ossifragus*) and other corvids, grackles, several woodpecker species (most notably red-bellied woodpecker), and snakes, especially rat snakes (*Elaphe spp*). Interestingly, most of the above nest predators are generalists and, perhaps except for rat snakes, they do not specifically search for bird nests but encounter and exploit them while searching for other prey or while searching a particular substrate for prey in general (Wilson and Cooper 1998, Cooper et al. 1999, Schmidt and Whelan 1999). Therefore, a bird that shifts its nest location away from a particular height, plant species, or other substrate may avoid 1 predator only to encounter another.

It is unknown what regulates numbers of migrant and wintering songbirds and woodpeckers in BLH systems. Also, the role that BLH plays in regulation of continental populations of migrant species is understood poorly. Many birds use BLH only during specific seasons, or periods of high food availability, and migrant songbirds capitalize on pulses of certain foods, such as acorn and seed rain in fall, insect hatches in spring, and lepidopteran larvae in early summer. Undoubtedly, seasonal and annual dynamics of food influence numbers and distribution of birds in the system. For example, wintering numbers of red-headed woodpeckers are correlated strongly with annual variation in acorn production in a variety of forested regions of Missouri including BLH habitats (Smith and Scarlett 1987). Likely, the degree that migrant or wintering species are affected by annual variation in food supplies depends on how food-specific the species are, how widespread pulses or "busts" of food are, energetic needs associated with specific annual events, and the presence of other foods and habitats along migration corridors. For example, neotropical migrants are very dependent on foods found in very southern BLH regions when they first make landfall after having flown hundreds of miles over the Gulf of Mexico (Moore and Kerlinger 1987, Moore et al. 1990). It is tempting to speculate that the significant loss and fragmentation of BLH has greatly affected nutritional balances and perhaps survival of many neotropical migrants in the southeastern USA. In contrast to the apparent influence of food supplies, predation on migrant and wintering songbirds probably is low and relatively unimportant in population dynamics. This is true because birds are very mobile at this time of year and predators may seek other prey (such as rodents) that are easier to obtain and more concentrated (e.g., during flood events).

Falconiformes and Strigiformes.—Sixteen raptor species commonly use BLH habitats (Hamel 1992). These species include 2 vultures; 9 kites, hawks, and eagles; 2 falcons; and 3 owls. Few raptor species are associated closely with BLH; these are the red-shouldered hawk (*Buteo lineatus*), Mississippi kite (*Ictinia mississippiensis*), American swallow-tailed kite (*Elanoides forficatus*), and barred owl (*Strix varia*). The 2 kite species are not found elsewhere in North America. Ten of the 16 species breed in BLH but only 7 are common. The remaining 6 non-breeding species primarily migrate through BLH regions to and from primary wintering sites in more southern areas.

Raptors use BLH habitats much the same way as in upland forests, principally feeding on large prey, such as rodents, snakes and other reptiles, and birds (in the case of falcons and accipiters). Because herpteofauna are so common in BLH, they are eaten by

raptors more frequently than in upland sites where large hawks and owls feed mostly on rodents. In BLH, raptors buffer seasonal and annual cycles of specific prey by being relatively non-specific and flexible in diets and habitats used. The most abundant raptors are scavengers (the vultures) or prey on a seasonally diverse diet of small birds, rodents, amphibians, and reptiles (e.g., red-shouldered hawk, Cooper's hawk [*Accipiter cooperii*], sharp-shinned hawk [*Accipiter striatus*], screech owl [*Otus asio*]). Barred owls and red-shouldered hawks also feed readily on crayfish and wood duck ducklings (Davis 2001). Mississippi kites are primarily insectivorous. Swallow-tailed kites consume mainly large arthropods, such as dragonflies and cicadas, and lesser amounts of amphibians, reptiles, small fish, and birds.

Factors that regulate raptor numbers and distribution in BLH are not entirely known. Raptors have very few natural predators (usually 1 raptor species preying on a smaller raptor) and population densities and fluctuations seem mostly related to annual dynamics of primary prey. Undoubtedly, during the mid-1900s, pesticide residues also negatively impacted these species. Both kites require large patches of BLH to sustain breeding populations (Cely and Sorrow 1990, Hunter et al. 2001). Kites appear to have the most limited range of prey among raptors in BLH and they may need large patch sizes to secure adequate numbers of preferred prey consistently throughout the year and to buffer annual and seasonal dynamics of prey availability.

Raptors consume many small birds and mammals in BLH, but comparatively, predation rates by raptors on birds and mammals are low in BLH and unlikely to control prey numbers. It is conceivable that raptors might impact some prey species, especially if they are very concentrated or already reduced by other system events (such as during extensive floods), but generally, prey populations (see previous sections on rodents and wintering and migrant passeriformes) in BLH are regulated by bottom-up processes.

Other Bird Species.—A few other bird species of several diverse orders use BLH habitats, but no order includes more than 2-3 species. The most common species include wild turkey (*Meleagris fallopavo*), northern bobwhite (*Colinus virginianus*), common nighthawk (*Chordeiles minor*), ruby-throated hummingbird (*Archilochus colubris*), belted kingfisher (*Ceryle alcyon*), chimney swift (*Chaetura pelagica*), and mourning dove (*Zenaida macroura*). Each of these species occasionally nests in BLH.

The ruby-throated hummingbird appears to be more abundant in BLH than in upland forests. BBC data (Lowe 1995, 1996) show this species to have a mean abundance of 0.2 territories/plot (s = 0.54, n = 32, with 3 additional plots listing ruby-throated hummingbirds as visitors) in upland forests. In 15 BLH sites, they had a mean abundance of 0.93 territories/plot (s = 1.35), while visiting 4 other plots. BBC data from Arkansas (James and Neal 1986) show the ruby-throated hummingbird to be about twice as abundant in the MAV as in the Coastal Plain or Interior Highlands. Reasons for increased abundance in BLH include increased abundance of flowering vines such as trumpet creeper (*Campis radicans*) and crossvine (*Bignonia capreolata*) in many forests, and the abundance of flowers in disturbed areas such as tree gaps. Like songbirds, hummingbirds are largely insectivorous during the breeding season, so the increased productivity found in BLH produce more food for hummingbirds as well.

Mourning doves and bobwhites mainly use BLH during fall and winter, and occur mostly on the edges of openings or near the upland-bottomland forest interface. Nighthawks also use mainly edges of the BLH. These higher edge areas tend to support more flowering plants sought by hummingbirds, seasonal arthropods for the crepuscular-foraging nighthawks, and less frequent summer flooding that would destroy ground nests of nighthawks. Kingfishers mainly use permanent or semi-permanent wetlands and drainages in BLH. Densities of kingfishers are low in BLH and their numbers probably are influenced by floodplain dynamics and subsequent availability of small fish and nest sites. Chimney swifts nest in hollow trees in several BLH habitat zones. They forage primarily on flying insects above standing water, as do swallows.

The ubiquitous wild turkey ranges widely through BLH habitats and consumes a wide diversity of foods. Foods of turkeys include plant (seeds, tubers, rootlets, forbs) and animal (insects, invertebrates, amphibians) material. Periodic flooding and fire can reduce availability of certain foods and also safe nest sites for turkeys. During extended flooding, nesting success of turkeys is poor in BLH and local populations can be impacted significantly. Many predators, including bobcat, coyote, raccoon, skunk, gray fox, and raptors prey on turkeys and/or their nests (Chamberlain et al. 1996, Wieme 2001).

COMMUNITY STRUCTURE AND SPECIES ADAPTATIONS

Biodiversity and Abundance

The diversity and abundance of birds and mammals in BLH systems is among the greatest of any ecosystem in North America. Relatively large numbers of taxa and species are present within a region (alpha diversity) and across habitat zones (beta diversity). High alpha biodiversity in BLH is consistent with general trends of greater diversity in ecosystems that have high productivity and structural complexity such as tropical and subtropical ecosystems (Schluter and Ricklefs 1993). Beta diversity also is high in BLH and similar to tropical systems (e.g., Tuomisto et al. 1995). Generally, diversity in BLH seems intermediate between temperate and tropical systems. BLH and tropical forests both have high primary and secondary productivity, landscape heterogeneity, many horizontal and vertical gradients and niches, strong seasonal pulses of energy flow, and large contiguous area; these features support large numbers of resident and seasonally-occurring species.

The abundance of birds and mammals in BLH reflect the high species richness of the system and their diverse adaptations to system resources (Table 4). For example, over 75% of bird species are present in BLH only during certain seasons and the timing of movements to BLH and annual events engaged in while there coincide with pulses of specific resources (mostly food) in the system (Fig. 2). Many mammal species, such as bats, also are very mobile and range widely over BLH areas to use seasonal resources (Fig. 2). Energy pulses in BLH are diverse and large, but many are short-lived (e.g., insect hatches). Consequently, many species and individuals quickly respond to the pulses and exploit the abundance with relatively little competition.

BLH contains more birds (species and individuals) than mammals and numerically is more bird-dominant than most other North American ecosystems, e.g., grasslands. This high bird:mammal

Table 4. Adaptations of mammal and bird species to heterogeneous, spatially dynamic, and seasonally available resour bottomland hardwood forests.

	Adaptation						
Taxon	Mobility	Long-lived	Omnivorous	Arboreal	Swim/wade/ dive	Seasonal occurrence	Hiber
Mammals							
Insectivora			+[a]			++	+
Chiroptera	+++	+		+++			
Lagomorpha	+			+	+		
Rodentia	++	++	++	+++[b]	+++[c]	+	
Carnivora	+++	+++	+	++	+	+	+
Marsupulia	+		+++	+++	+		
Artiodactyla	+++	++			+	+	
Birds							
Anseriformes	+++	++	+++	+	+++	+++	
Charadriiformes	+++		+		+++	+++	
Gruiformes	++	+	+		+++	+++	
Podicipediformes	++		+		+++	++	
Pelicaniformes	+++	++			+++	++	
Gaviiformes	+++	++			+++	++	
Ciconiiformes	+++	++		++	+++	+++	
Passeriformes	+++		+++	+++		+++	
Piciformes	+	+	+	+++			
Cuculiformes	+++	+	+++	+++		+	
Falconiformes	+++	+++	++	+++		++	
Strigiformes	++	++	+	+++			
Columbiformes	+++		++	++		+++	
Galliformes	++	++	+++	++	+	+	
Apodiformes	++			+++		++	
Coraciiformes	+++	+		++	++	++	

[a] Number of pluses indicates relative degree of adaptation.
[b] Squirrels, golden mouse, white-footed mouse, cotton mouse.
[c] Beaver, muskrat, rice rat, hispid cotton rat, southern bog lemming.
[d] Black bear.

species ratio in BLH is caused mostly by the great diversity of songbirds and waterbirds (>200 species) and conversely, the relative paucity (<20 species) of small ground-dwelling mammals. Among bird and mammal taxa, species that are small, relatively sedentary, and ground-dwelling (or nesting) do not fare well in BLH habitats and their numbers are low. For example, bats which are mobile and arboreal have high numbers and diversity, whereas only small numbers of a few species of the fossorial and sedentary shrews and moles are present.

Food Webs and Niches

High and diverse primary and secondary production, structural and spatial heterogeneity, and large contiguous areas create many niches in BLH, albeit many are temporal. Habitat breadth of the most common and abundant species in BLH, especially residents, is large and seasonally variable. These system attributes cause many species to be relative generalists except during seasonal or annual crunch times when species become more food and habitat specific and competition within and among species is heightened (e.g., winter). Many species (e.g., wading birds, songbirds, and bats) migrate or disperse from BLH during these crunches. Species that are the most specific in habitat or food preferences typically are rarer, in lesser abundance, and have been extirpated more easily (e.g., Bachman's warbler).

Most common species in BLH are omnivorous (e.g., raccoon), have diverse diets within a trophic level (e.g., otters), or are present only during pulses of specific foods (e.g., migrant insectivorous songbirds). Seasonal omnivory (i.e., changing foods and trophic levels among seasons) is common for most species that stay extended periods (e.g., residents, wintering species) in BLH. Some species are omnivorous throughout the year and they consume whatever they can find, secure, and digest (e.g., opossum, skunks). Omnivory helps animals to take advantage of many diverse pulses of food availability (e.g., insect emergence, acorn drop, crustacean blooms, rodent reproduction, etc.) and buffers species against seasonal and annual busts in production (e.g., acorn failure) and major system events especially extended floods or droughts. Many species capitalize on major system events to secure new, previously unavailable, or concentrated prey. For example, mallards and wood ducks move quickly to newly flooded areas at higher elevations to forage on foods including acorns, terrestrial insects, and seeds from herbaceous plants. Raptors and bobcat quickly move to higher ridges during floods to escape flooding and take advantage of concentrated small mammals. Similarly, annual and seasonal black bear movement patterns in these systems are closely linked to abundance of seasonal fruits of trees and shrubs. Small mammals disperse into low elevation sloughs and abandoned channels during droughts to eat seeds and other plant parts exposed as waters recede; breeding wading birds use these same sites to forage on concentrated fish and amphibians.

Many common warmblooded species in BLH are very mobile and relatively long-lived. High mobility enables individuals to search for, and use, resources in many different habitats and locations and also allows animals to take advantage of, or escape, major system events such as floods that drastically change prey availability, predation, and competition. By being long-lived, species such as black bear that depend on, and may be periodically limited by, BLH resources can survive years of low resource abundance. Living long generally requires species to be more generalists in habit and typically their numbers are controlled by annual variation in food supplies and not by predation (see below).

Food chains within BLH systems often are long, complex, and ultimately based on detrital decomposition (Fig. 3). The litter biomass in BLH is large, annually recharged, rapidly decomposed, and supplemented by regular inputs of nutrients and sediments from flood waters. This litter creates high diversity and production of invertebrates, amphibians, and reptiles. For example, flooded litter in low elevations supports huge populations of crustaceans ranging from zooplankton to isopods to crayfish. These crustaceans are prey for many diverse species including larval and adult fish, amphibians and reptiles, waterfowl and waders, and some mammals. First order consumers then are exploited by higher level predators and omnivores, including otter, bears, mustelids, raptors, kingfishers, and larger wading birds.

Predator-Prey Relationships

Given the complex and usually inter-trophic food webs of most BLH species, predator-prey relationships in this system also are complex and less controlling than in many other ecosystems. Most species of warmblooded vertebrates in BLH apparently are limited by bottom-up seasonal and annual variation in first order primary and secondary production (i.e., seeds, insects, etc.) and not by top-down predation. Bottom-up processes also control plant distribution and primary production (e.g., Forkner and Hunter 2000). Even small animals such as mice, whose numbers often are regulated by

high predation rates and fluctuate inversely with predator numbers in many ecosystems, operate differently in BLH where they are regulated primarily by episodic floods. Some exceptions to this generally bottom-up regulation do occur, at least periodically (e.g., woodpecker depredation of songbird nests, cowbird parasitism, bobcat predation on turkeys), but they are the exception rather than the rule. In cases where 1 animal greatly influences another, the usual problem is nest parasitism or depredation (e.g., cowbird parasitism and woodpecker depredation on songbird nests), and not direct mortality of adults. Also, phenomena such as nest predation (top-down effect) are greatly influenced by availability of alternative foods for potential nest predators (bottom-up effect). For example, if primary aquatic foods for raccoons, a major nest predator, are not available, then temporarily there may be increased nest predation (Cooper et al. 1999). This was observed for prothonotary warblers in the White River NWR (Wood 1999).

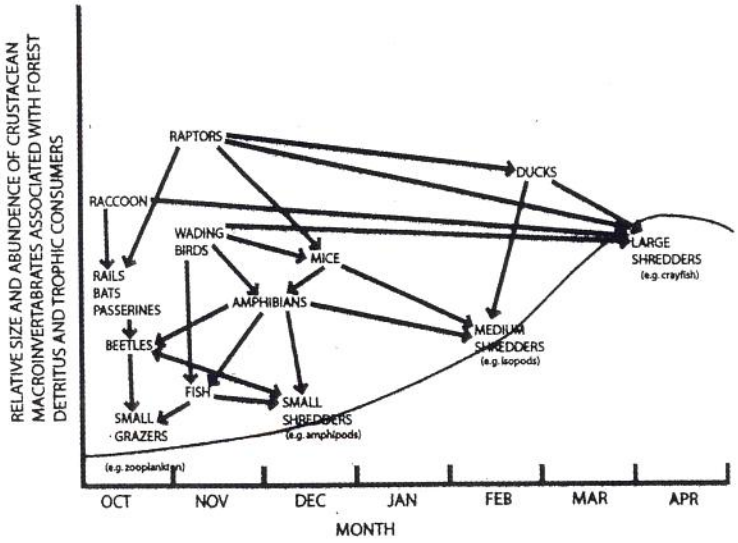

Figure 3. An example of a detrital-based food chain in bottomland hardwood forests that begins with crustaceans.

Numbers of larger predators in BLH fluctuate with major system events that create variation in prey (e.g., floods, drought, fire) or from disease outbreaks (e.g., sarcoptic mange in canids). System attributes of BLH create a diverse, but dynamic and relatively unpredictable, food base for higher-order predators. This causes predators in BLH to be mobile and to use BLH seasonally to tolerate vagaries in flooding and prey abundance. Diversity of the predator taxon in BLH is relatively high, but, interestingly, relatively few species are present in each taxon. Comparatively, there are more top-order avian than mammalian carnivores.

It is uncertain what role native peoples played in community structure in BLH systems since they first occupied the southeastern USA ca. 11,000-12,000 years ago. While populations of native people may have been abundant in BLH habitats in the last 2000 years, especially during dry seasons, they may have had only limited influence on BLH animals, with the possible exception of larger species such as deer (Hudson 1976). The large area of BLH, highly diverse and generally mobile nature of animals, extensive seasonal and annual flooding, and relatively intolerable conditions of many BLH habitats and seasons (e.g., mosquito abundance in low elevations in summer) would have mediated direct human predation on most animals. Furthermore, those species most easily captured (e.g., small mammals) had large and generally resilient populations. During the last 1000 years, native people began to clear and manipulate (e.g., burning) larger areas of BLH which may have had local impacts on some BLH species. Ironically, activities of native people may have actually benefitted a few less abundant species that were highly associated with small openings and cane such as Swainson's warbler and swamp rabbit.

CONSERVATION CONSIDERATIONS

Ecosystem and Community Integrity

The integrity of BLH systems depends on large contiguous and interconnected areas of floodplain forests that are heterogeneous, seasonally inundated (usually by floods), and receive regular inputs of nutrients and sediments. These characteristics and processes sustain the high primary productivity; large detrital bases and secondary production; and diversity of resources, niches, and species of homeothermic vertebrates in BLH. Paradoxically, the very system features that sustain productivity also challenge species because of: 1) highly dynamic, often punctuated, and periodically extreme flooding and drought; 2) heterogeneous, often widely dispersed, and unpredictable spatial availability of resources; and 3) strong seasonal pulses of energy flow. The common species in BLH have fundamental adaptations to these dynamics that allow them to sustain populations (Table 4).

Conservation of functional communities of homeothermic vertebrates in BLH must address the following contemporary issues: 1) continued loss and fragmentation, and forestry practices, of remaining

BLH patches; 2) alterations in local and regional hydrology; 3) maintenance of multi-trophic food webs and nutrient flow; and 4) changes in bottom-up species relationships and population dynamics.

First, large patches and regional areas of BLH are needed to sustain biodiversity and abundance of mammals and birds over time. Landscapes that have large amounts of BLH usually retain more functional hydrology, complete complements and heterogeneity of vegetation communities, and regional connectivity. Unfortunately, over 80% of BLH habitats in the USA have been destroyed, and remaining patches are highly fragmented (Twedt and Loesch 1999). Highly fragmented BLH patches have fewer, less diverse, and more widely dispersed resources than larger contiguous patches. Those species that require, and are adapted to, many different seasonal resources may have to move more often and over wider areas to obtain resources, and thereby, they become more susceptible to seasonal or annual reductions in resources, especially food.

Some species (e.g., swallow-tailed kite) require large BLH patches to sustain viable populations. Most other species in BLH do not necessarily require large individual forest patches, but they do depend on extensive areas of BLH within a region to meet annual cycle needs. The amount and distribution of regional BLH needed by a species depend on the amount and type of resources provided in individual patches, the range capability of the species, and nutritional requirements of various annual cycle events and movement between patches. Furthermore, large regional areas of BLH with connected corridors are needed to allow safe movement between patches, dispersal from source areas, and genetic interchange among subpopulations within a metapopulation. This is especially important for smaller sedentary species. Conservation initiatives that seek to reforest and reconnect patches will be valuable but much information is needed on ultimate effects on populations and species related to patch size, location, composition, and proximity to refuges and foods.

All animals require at least some escape from disturbance and predation. If refuges are not available or are limited, species and populations will move from an area or have altered energy balances, reproductive success, and survival. Few true refuges exist in BLH that have relatively intact and complete complements of BLH habitats and resources. Also, with few exceptions, such as White River NWR most tracts are small, frequently used and disturbed, and are relative islands in form and function. Information is badly needed on the values of refuges in relation to their size, location, types of resources provided, and proximity to other refuges and foods.

Most remaining patches of BLH have been heavily cut-over since presettlement times and age class and composition of tree species are changed significantly (Conner and Sharitz 2004). If these changes and continued short-rotation harvests continue over broad areas, the types, amounts, timing, and location of nutrients and energy flow in BLH also will change and affect basic productivity and food webs in BLH systems. Obviously, more rapid turnover reduces old-growth stands and impacts species that rely on these areas such as kites, songbirds, and black bear (Wigley and Roberts 1994, Wigley and Lancia 1988).

Functional floodplain hydrology ultimately controls vegetation composition and primary and secondary production in BLH. It also creates seasonal pulses of nutrient flow and food resources. Ultimately, these natural pulses, especially floods, have been a key evolutionary factor influencing organismal adaptations and strategies for colonizing and exploiting BLH resources. The timing of seasonal pulses of energy (or devastating events such as floods) is critical in BLH because animals in the system have evolved timing of annual events to coincide generally with these pulses (or absence thereof). The consequences of even modest changes in timing of events can be devastating to birds and mammals. For example, altered flood hydrology that creates extended spring floods may destroy annual production of most ground-nesting species, or plant food supplies for herbivores. Conversely, delayed flooding in late fall and early winter will delay and decrease detrital invertebrate populations in late winter and spring that are critical for important functions of many species such as prebasic molt of mallards, egg-laying in night herons and hooded mergansers, embryo development in raccoons, and storage of nutrient reserves needed by hibernating black bear.

Unfortunately, almost all remaining patches of BLH have altered hydrology. Modifications to hydrological components of BLH landscapes have site-specific and regional impacts. Many modifications are seemingly minor (e.g., construction of a road through a BLH patch), but are insidious changes that ultimately affect water regimes, vegetation composition, and nutrient flows in the system. Relatively little is known about total cumulative impacts of direct (e.g., drainage ditches) and indirect (e.g., agri-

cultural water use in upstream watersheds) changes in hydrology on animals in BLH.

Most food webs of homeothermic vertebrates in BLH are complex and very inter-trophic. Energy flow in and out of the system is marked because of basic system processes (e.g., flooding) and because so many species use BLH only seasonally during specific energy pulses. Changes to BLH that alter timing and availability of diverse foods will significantly alter food webs and nutrient flow and have the potential to significantly change many system elements. For example, when forests become fragmented and drier, small rodent populations increase greatly causing reduced survival of newly germinated tree seedlings and changes to detrital bases which have ripple-effects throughout most food chains in the system. Few keystone species exist in BLH, yet many species are very important simply because of the trophic level they inhabit and their numbers. These include bats, passerines, mallards and wood ducks, raccoons, and red-shouldered hawks. If changes to BLH alter the relative importance of single species or species composition, the bottom-up nature of the system may be jeopardized.

Population Viability

Although population levels of some homeothermic vertebrate species in BLH are greatly reduced from presettlement times, relatively few species are extinct or have been extirpated from this system. Compared to other ecosystems, the warmblooded vertebrate community remains relatively intact and diverse today (e.g., Hunter et al. 2001). Apparently, the high retention of species in the system, despite considerable habitat destruction and degradation, is the result of basic adaptations of most species that use BLH to be responsive and resilient to seasonal and spatial dynamics of resources. Species that are extirpated (cougar, red wolf, Bachman's warbler), extinct (Carolina parakeet, passenger pigeon, ivory-billed woodpecker), or have low potentially imperiled populations (e.g., swallow-tailed kites, Cerulean warbler, Swainson's warbler, black bear) typically are those that are food or habitat specialists, large higher order predators, ground dwellers, and/or area sensitive. We doubt that any of these species ever had high populations in BLH because they either occupied the very top level of food chains, or habitats and areas they required were scarce and highly dynamic (e.g., tree gaps and giant cane used by Swainson's warbler).

Despite the richness of BLH systems, many species (e.g., mice, muskrat, wading birds, waterfowl) that use these habitats have relatively high amplitude population dynamics caused by major episodic events, especially flooding. For these species, there may be crucial points in the low ebbs of population swings that can cause significant reduction (and perhaps even extirpation) in species occurrence, at least locally. "Thresholds" of these points are not known, but may be most critical for resident species that rely solely on BLH resources. However, some seasonal visitors to BLH systems, especially those that winter there (e.g., mallards), also may be periodically limited by annual system dynamics. Clearly, more information is needed on which seasonal resources are most critical to species using BLH, how widely population levels can swing before imbalances or crashes occur, and potential impacts of system changes and loss on the diverse and complex species and predator/prey relationships.

ACKNOWLEDGMENTS

This paper benefitted from helpful reviews by P. R. Covington, L. H. Fredrickson, R.B. Hamilton, R. M. Kaminski, S. L. King, and S. Lor. M. K. Clark assisted with initial planning of the manuscript and presentation at the Bottomland Hardwood Symposium. Support for authors was provided by their respective institutions. Heitmeyer's participation in this work was funded through the University of Missouri Center for Agroforestry under cooperative agreements AG-02100251 with the USDA ARS Dale Bumpers Small Farms Research Center, Booneville, AR. and C R 826704-01-0 with the US EPA. The results presented are the sole responsibility of the P.I. and/or MU and may not represent the policies or positions of the ARS or EPA. B. Schuster helped prepare figures and S. Clark and K. Kyle assisted with final preparation of the manuscript.

LITERATURE CITED

Baker, R. J. and C. M. Ward. 1967. Distribution of bats in southeastern Arkansas. Journal of Mammalogy 48:130-132.

Batema, D. L., R. M. Kaminski and P. A. Magee. 2005. Wetland invertebrate communities and management of hardwood bottomlands in the Mississippi Alluvial Valley. Pages 173-190 *in* L. H. Fredrickson, S.A. King, and R.M. Kaminski, eds. Ecology and Management of Bottomland Hardwood Systems: The State of our

Understanding. University of Missouri-Columbia. Gaylord Memorial Laboratory Special Publication No. 10, Puxico.

Bedinger, M. S. 1979. Relation between forest species and flooding. Pages 427-435 *in* P. E. Greeson, J. R. Clark and J. E. Clark, eds. Wetland functions and values: the state of our understanding. American Water Resources Association, Minneapolis, MN.

Bellrose, F. C. 1980. Ducks, geese and swans of North America, 3rd ed. Stackpole Books, Harrisburg, PA. 540pp.

Bellrose, F. C. and D. J. Holm. 1994. Ecology and management of the wood duck. Stackpole Books, Harrisburg, PA 540pp.

Blair, W. F. 1939. Some observed effects of stream-valley flooding on mammalian populations in eastern Oklahoma. Journal of Mammalogy 20:304-306

Brinson, M. M. 1990. Riverine forests. Pages 87-141 *in* A. E. Lugo, M. M. Brinson and S. L. Brown, eds., Forested wetlands, Volume 15. Ecosystems of the world. Elsevier Science Publishers B.V., Amsterdam, The Netherlands.

Brinson, M. M., B. L. Swift, R. C. Plantico and J. S. Barclay. 1981. Riparian ecosystems: their ecology and status. U.S. Fish and Wildlife Service, Biological Services Program, FWS/OBS-81/17, Washington, DC. 151pp.

Brown, S., C. Hickey, B. Harrington and R. Gill, eds. 2001. The U.S. shorebird conservation plan, 2nd ed. Manomet Center for Conservation Sciences, Manomet, MA.

Burt, W. H. and R. P. Grossenheider. 1976. A field guide to the mammals, 3rd ed. Houghton Mifflin Company, Boston, MA. 289pp.

Causey, M. K., M. K. Hudson and T. P. Mack. 1987. Breeding activity of American woodcock in Alabama as related to temperature. Proceedings of Southeastern Association Fish and Wildlife Agencies 41:373-377.

Cely, J. E. and J. A. Sorrow. 1990. The American swallow-tailed kite in South Carolina. South Carolina Wildlife and Marine Resources Department 1, Charleston. 160pp.

Chamberlain, M. J., D. A. Miller, B. D. Leopold and G. A. Hurst. 1996. Predation rates on wild turkey hens in a hardwood bottomland forest and a mixed forest in Mississippi. Proceedings Annual Conference Southeastern Association of Fish and Wildlife Agencies 50:428-435.

Chamberlain, M. J. and B. D. Leopold. 2001. Omnivorous furbearers. Pages 278-292 *in* J. G. Dickson, ed., Wildlife of southern forests: habitat and management. Hancock House Publishers, Blaine, WA.

Conner, W. H. and R. C. Sharitz. 2005. Forest communities of bottomlands. Pages 93-120 *in* L. H. Fredrickson, S.A. King, and R.M. Kaminski, eds. Ecology and Management of Bottomland Hardwood Systems: The State of our Understanding. University of Missouri-Columbia. Gaylord Memorial Laboratory Special Publication No. 10, Puxico.

Cooper, R. J., R. R. Wilson, G. D. Zenitsky, S. J. Mullin, J. A. DeCecco, M. R. Marshal, D. J. Wolf and L. Y. Porama. 1999. Does nonrandom nest placement imply nonrandom nest predation? - a reply. Condor 101:920-923.

Davidson, W. R. and V. F. Nettles. 1988. Field manual of wildlife diseases in the southeastern United States. Southeastern Cooperative Disease Study, University of Georgia, Athens. 309pp.

Davis, J. B. 2001. Survival, recruitment, and management of box-nesting populations of wood ducks in Mississippi and Alabama. PhD Dissertation, Mississippi State University, Mississippi. 185pp.

Davis, W. E. and J. Kricher. 2000. Glossy ibis. *In* A. Poole and F. Gill, eds. Birds of North America 595., The Birds of North America, Inc., Philadelphia, PA.

DeCalesta, D. S. 1994. Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. Journal of Wildlife Management 58:711-718.

Den Held, J. J. 1981. Population changes in the purple heron in relation to drought in the wintering area. Ardea 69:185-191.

Dickson, J. G. 1978a. Forest bird communities of the bottomland hardwoods. Pages 66-75 *in* R. M. DeGraaf, ed., Management of southern forests for nongame birds. General Technical Report SE-14, U.S. Department of Agriculture Forest Service, Southeastern Forest Experiment Station, Asheville, NC.

Dickson, J. G. 1978b. Seasonal bird populations in a south central Louisiana bottomland hardwood forest. Journal of Wildlife Management 42:875-883.

Dickson, J. G. 2001. Terrestrial small mammals. Pages 350-358 *in* J. G. Dickson, ed., Wildlife of southern forests: habitat and management. Hancock House Publishers, Blaine, WA.

Dickson, J. G. and M. L. Warren, Jr. 1994. Wildlife and fish communities of eastern riparian forests. Pages 1-31 *in* Riparian ecosystems in the humid U.S.: functions, values, and management. National Association of Conservation Districts, Washington, DC.

Drobney, R. D. and L. H. Fredrickson. 1979. Food selection by wood ducks in relation to breeding status. Journal of Wildlife Management 43:109-120.

Dugger, K. M. 1997. Foraging ecology and reproductive success of least terns nesting on the Lower

Mississippi River. PhD Dissertation, University of Missouri, Columbia. 137pp.

Dugger, B. D., K. M. Dugger and L. H. Fredrickson. 1994. Hooded merganser. *In* A. Poole and F. Gill, eds., Birds of North America 98. Academy of Natural Sciences of Philadelphia, Philadelphia, PA.

Forkner, R. E. and M. D. Hunter. 2000. What goes up must come down? Nutrient addition and predation pressure on oak herbivores. Ecology 81:1588-1600.

Fredrickson, L. H. 1978. Lowland hardwood wetlands: current status and habitat values for wildlife. Pages 296-306 *in* P. E. Greeson, J. R. Clark and J. E. Clark, eds., Wetland functions and values: the state of our understanding. American Water Resources Association, Minneapolis, MN.

Fredrickson, L. H. 1979. Floral and faunal changes in lowland hardwood forests in Missouri resulting from channelization, drainage, and impoundment. FWS/OBS-78/91, U.S. Department of the Interior, Fish and Wildlife Service, Washington DC. 130pp.

Fredrickson, L. H. and M. E. Heitmeyer. 1988. Waterfowl use of forested wetlands of the southern United States: an overview. Pages 307-323 *in* M. W. Weller, eds., Waterfowl in winter. University of Minnesota Press, Minneapolis.

Fredrickson, L. H. and D. L. Batema. 1993. Greentree reservoir handbook. Gaylord Memorial Laboratory Wetland Mangement Series 1. University of Missouri, Puxico. 88pp.

Frentress, C. D. 1986. Wildlife of bottomlands: species and status. Pages 37-57 *in* C. A. McMahan and R. G. Frye, eds., Bottomland hardwoods in Texas. Texas Parks and Wildlife Department, Austin.

Gibbs, J. P., S. Melvin and F. A. Reid. 1992a. American bittern. *In* A. Poole, P. Stettenheim, and F. Gill, eds., The birds of North America 18. The Academy of Natural Sciences, Washington, DC.

Gibbs, J. P., F. A. Reid and S. Melvin. 1992b. Least bittern. *In* A. Poole, P. Stettenheim, and F. Gilll, eds. The birds of North America 17. The Academy of Natural Sciences, Washington, DC.

Gill, F. B. 1990. Ornithology. W. H. Freeman and Company, New York. 660pp.

Greenberg, R. 1995. Insectivorous migratory birds in tropical ecosystems: the breeding currency hypothesis. Journal of Avian Biology 26:260-264.

Guthery, F. S. and S. L. Beasom. 1977. Responses of game and non-game wildlife to predator control in south Texas. Journal of Range Management 30:404-409.

Hall, E. R. 1951. American weasels. University of Kansas Publication, Museum of Natural History 4:1-466.

Hamel, P. B. 1992. The land manager's guide to the birds of the south. The Nature Conservancy, Chapel Hill, NC. 367pp.

Harris, L. D. and J. G. Gosselink. 1990. Cumulative impacts of bottomland hardwood conversion on hydrology, water quality, and terrestrial wildlife. Pages 259-322 *in* J. G. Gosselink, L. C. Lee and T. A. Muir, eds., Ecological processes and cumulative impacts: illustrated by bottomland hardwood wetland ecosystems. Lewis Publications Inc., Chelsea, MI.

Harris, L. D., R. Sullivan and L. Badger. 1984. Bottomland hardwoods: valuable, vanishing, vulnerable. Institute of Food and Agricultural Sciences, University of Florida, Gainesville.

Hartshorn, G. S. 1980. Neotropical forest dynamics. Biotrophica (Suppl.) 12:23-30.

Harvey, M. J., J. S. Altenbach and T. L. Best. 1999. Bats of the United States. Arkansas Game and Fish Commission, Little Rock. 64pp.

Harvey, M. J. and D. A. Saugey. 2001. Bats. Pages 359-371 *in* J. G. Dickson, ed., Wildlife of southern forests: habitat and management. Hancock House Publishers, Blaine, WA.

Hayman, P., J. Marchant and T. Prater. 1986. Shorebirds: an identification guide to the waders of the world. Houghton Mifflin Company, Boston, MA. 412pp.

Heitmeyer, M. E. 1985. Wintering strategies of female mallards in relation to dynamics of lowland hardwood wetlands in the upper Mississippi Delta. PhD Dissertation, University of Missouri, Columbia. 378pp.

Heitmeyer, M. E. 1987. The prebasic moult and basic plumage of female mallards (*Anas platyrhynchos*). Canadian Journal of Zoology 65:2248-2261.

Heitmeyer, M. E. 1988. Body composition of female mallards in winter in relation to annual cycle events. Condor 90:669-680.

Heitmeyer, M. E. 2001. Waterfowl. Pages 209-223 *in* J. G. Dickson, ed., Wildlife of southern forests: habitat and management. Hancock House Publishers, Blaine, WA.

Heitmeyer, M. E. 2005. The importance of winter floods to mallards in the Mississippi Alluvial Valley. Journal of Wildlife Management. 69: (in press).

Heitmeyer, M. E. and L.H. Fredrickson. 1981. Do wetland conditions in the Mississippi Delta hardwoods influence mallard recruitment? Transactions of the North American Wildlife and Natural Resources Conference 46:44-57.

Heitmeyer, M. E. and L. H. Fredrickson. 1990. Fatty acid composition of wintering female mallards in relation to nutrient use. Journal of Wildlife Management 54:54-61.

Heitmeyer, M. E., L. H. Fredrickson and G. F. Krause. 1989. Water and habitat dynamics of the Mingo Swamp in southeastern Missouri. U.S. Fish and Wildlife Service, Fish and Wildlife Research 6. 26pp.

Heitmeyer, M. E., L. H. Fredrickson and S. L. King. 2000. An evaluation of ecosystem restoration options for the Grand Prairie region of Arkansas. Gaylord Memorial Laboratory Special Publication for U.S. Army Corps of Engineers, Memphis District, University of Missouri, Puxico. 72pp.

Helm, R. N. 1994. Purple gallinule. Pages 159-165 *in* T. C. Tacha and C. E. Braun, eds., Migratory shore and upland game bird management in North America. International Association of Fish and Wildlife Agencies, Washington, DC.

Hill, E. P., P. W. Summer and J.B. Wooding. 1987. Human influences on range expansion of coyotes in the southeast. Wildlife Society Bulletin 15:521-524.

Hudson, C. 1976. The southeastern Indians. University of Tennessee Press, Knoxville. 573pp.

Hunter, W. C., D. N. Pashley, J. G. Dickson and P. B. Hamel. 2001. Bird communities of southern forests. Pages 322-349 *in* J. G. Dickson, ed., Wildlife of southern forests: habitat and management. Hancock House Publishers, Blaine, WA.

Hupp, C. R., M. R. Walbridge and B. G. Lockaby. 2005. Fluvial geomorphic processes, water quality, and nutrients of bottomland hardwood systems. Pages 37-56 *in* L. H. Fredrickson, S.A. King, and R.M. Kaminski, eds. Ecology and Management of Bottomland Hardwood Systems: The State of our Understanding. University of Missouri-Columbia. Gaylord Memorial Laboratory Special Publication No. 10, Puxico.

James, D. A. and J. C. Neal. 1986. Arkansas birds: their distribution and status. University of Arkansas Press, Fayetteville. 402pp.

Johnson, F. L. and D. T. Bell. 1976. Plant biomass and net primary production along a flood-frequency gradient in the streamside forest. Castanea 41:156-165.

Jones, J. C., H. A. Jacobson and D. H. Arner. 1997. Plant community characteristics within an 18-year old deer exclosure in southern Mississippi. Proceedings Annual Conference Southeastern Association Fish and Wildlife Agencies 51:250-258.

Jones, J. and B. D. Leopold. 2001. Herbivorous furbearers. Pages 293-308 *in* J. G. Dickson, ed., Wildlife of southern forests: habitat and management. Hancock House Publishers, Blaine, WA.

Junk, W. J., P. B. Bayley and R. E. Sparks. 1989. The flood pulse concept in river-floodplain systems. Canadian Special Publication of Fisheries and Aquatic Sciences 106:110-127.

Kaminski, R. M. and E. A. Gluesing. 1987. Density- and habitat-related recruitment in mallards. Journal of Wildlife Management 51:141-148.

Kelley, J. R. Jr. 1997. Wood duck population monitoring initiative: final report. Atlantic Flyway Council, Mississippi Flyway Council, and U.S. Fish and Wildlife Service Administrative Report, Laurel, MD.

Kennamer, R. A. 2001. Relating climatological patterns to wetland conditions and wood duck production in the southeastern Atlantic Coastal Plain. Wildlife Society Bulletin 29:1193-1205.

King, S. L. and T. J. Antrobus. 2001. Canopy disturbance patterns in a bottomland hardwood forest in northeast Arkansas, USA. Wetlands 21:543-553.

Kushlan, J. A. 1978. Feeding ecology of wading birds. Pages 249-297 *in* A. Sprunt, J. C. Ogden and S. Winckler, eds., Wading birds. National Audubon Society Research Report 7. National Audubon Society, New York.

LaVal, R. K., R. L. Clawson, M. L. LaVal and W. Caire. 1977. Foraging behavior and nocturnal activity pattens of Missouri bats, with special emphasis on the endangered species *Myotis grisescens* and *Myotis sodalis*. Journal of Mammalogy 58:592-599.

Leopold, B. D. and M. J. Chamberlain. 2001. Carnivorous furbearers. Pages 248-277 *in* J. G. Dickson, ed., Wildlife of southern forests: habitat and management. Hancock House Publishers, Blaine, WA.

Lima, S. L. 1993. Ecological and evolutionary perspectives on escape from predatory attack: a survey of North American birds. Wilson Bulletin 105:1-47.

Lowe, J. D. (Compiler). 1995. Resident bird counts. Journal of Field Ornithology Supplement 66.

Lowe, J. D. (Compiler). 1996. Resident bird counts. Journal of Field Ornithology Supplement 67.

Lowery Jr., G. H. 1974. The mammals of Louisiana and its adjacent waters. Louisiana State University Press, Baton Rouge. 565pp.

MacArthur, R. H. 1958. Population ecology of some warblers in northeastern coniferous forests. Ecology 39:599-619.

MacDonald, P. O., W. E. Frayer and J. K. Clauser. 1979. Documentation, chronology and future projections of bottomland hardwood habitat losses in the lower Mississippi alluvial plain, Vol. I. U.S. Fish and Wildlife Service, Washington, DC. 133pp.

McComb, W. C. and R. E. Noble. 1979. Small mammal and bird use of some unmanaged and managed forest stands in the Mid-south. Proceedings Annual Conference Southeastern Association Fish and Wildlife Agencies 34:482-491.

Miller, K. V. 2001. White-tailed deer. Pages 95-107 *in* J. G. Dickson, ed., Wildlife of southern forests: habitat and management. Hancock House Publishers, Blaine, WA.

Moore, F. R. and P. Kerlinger. 1987. Stopover and fat deposition by North American wood-warblers (Parulinae) following spring migration over the Gulf of Mexico. Oecologia 74:47-54.

Moore, F. R., P. Kerlinger and T. R. Simons. 1990. Stopover on a Gulf Coast barrier island by spring trans-Gulf migrants. Wilson Bulletin 102:487-500.

Moser, T. J. and D. A. Graber. 1990. Stream brood surveys as indicators of wood duck production. Pages 205-208 *in* L. H. Fredrickson, G. V. Burger, S. P. Havera, D. A. Graber, R. E. Kirby and T. S. Taylor, eds., Proceedings of the 1988 North American wood duck symposium. 20-22 February 1988, St. Louis, MO.

National Geographic Society. 1980. Field guide to the birds of North America. National Geographic Society, Washington, DC. 464pp.

Newson, J. D. 1984. Coastal Plain. Pages 367-380 *in* L. K. Halls, ed., White-tailed deer ecology and management. Stackpole Books, Harrisburg, PA.

Nichols, J. D., K. J. Reinecke and J.E. Hines. 1983. Factors affecting the distribution of mallards wintering in the Mississippi Alluvial Valley. Auk 100:932-946.

Oli, M. K., H. A. Jacobson and B. D. Leopold. 1997. Denning ecology of black bears in the White River National Wildlife Refuge, Arkansas. Journal of Wildlife Management 61:700-706.

Petit, L. J., D. R. Petit, K. E. Petit and W. J. Fleming. 1990. Intersexual and temporal variation in foraging ecology of prothonotary warblers during the breeding season. Auk 107:133-145.

Raveling, D. G. and M. E. Heitmeyer. 1989. Relationships of population size and recruitment of pintails to habitat conditions and harvest. Journal of Wildlife Management 53:1088-1103.

Reid, F. A., B. Meanley and L. H. Fredrickson. 1994. King rail. Pages 181-193 *in* T. C. Tacha and C. E. Braun, eds., Migratory shore and upland game bird management in North America. International Association of Fish and Wildlife Agencies, Washington, DC.

Reinecke, K. J., C. W. Shaiffer and D. Delnicki. 1987. Winter survival of female mallards in the lower Mississippi Valley. Transactions of the North American Wildlife and Natural Resources Conference 52:258-263.

Reinecke, K. J., R. C. Barkley and C. K. Baxter. 1988. Potential effects of changing water conditions on mallards wintering in the Mississippi Alluvial Valley. Pages 325-337 *in* M. W. Weller, ed., Waterfowl in winter. University of Minnesota Press, Minneapolis.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contribution to Zoology 9: 1-48.

Rodin, L. E. and N. I. Bazilevich. 1967. Production and mineral cycling in terrestrial vegetation. Oliver and Boyd, London, UK.

Rogers, M. E., L. K. Halls and J. G. Dickson. 1990. Deer habitat in the Ozark forests of Arkansas. Research Paper SO-259, U.S. Department of Agriculture Forest Service 17pp.

Rundle, W. D. and M. W. Sayre. 1983. Feeding ecology of migrant soras in southeastern Missouri. Journal of Wildlife Management 47:1153-1159.

Saucier, R. T. 1994. Geomorphology and quaternary geological history of the lower Mississippi Valley, Vols I and II. U.S. Army Corps of Engineers Waterways Experiment Station, U.S. Department of the Army, Vicksburg, MS.

Schluter, D. and R. E. Ricklefs. 1993. Species diversity, an introduction to the problem. Pages 1-10 *in* R. E. Ricklefs and D. Schluter, eds., Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Illinois.

Schmidt, K. A. and C. J. Whelan. 1999. Nest placement and mortality: is nest predation a random event in space and time? Condor 101:916-920.

Schwartz, C. W. and E. R. Schwartz. 1959. The wild mammals of Missouri. University of Missouri Press and Missouri Conservation Commission, Columbia. 341pp.

Sealander, J. A. and G. A. Heidt. 1990. Arkansas mammals: their natural history, classification, and distribution. University of Arkansas Press, Fayetteville. 308pp.

Sheppe, W. and T. Osbourne. 1971. Patterns of use of a flood plain by Zambian mammals. Ecological Monographs 41:179-205.

Skagen, S. K., P. B. Sharpe, R. G. Waltermire and M. B. Dillon. 1999. Biogeographical profiles of shorebird migration in midcontinental North America. Biological Science Report USGS/BRD/BSR--2000-003, U.S. Government Printing Office, Denver, CO. 167pp.

Smith, K. G. and T. Scarlett. 1987. Mast production and winter populations of red-headed woodpeckers and blue jays. Journal of Wildlife Management 51:459-467.

Smith, W. P., P. B. Hamel and R. P. Ford. 1993. Mississippi Alluvial Valley forest conversion: implication for eastern North American avifauna. Proceedings

Annual Conference Southeastern Association Fish and Wildlife Agencies 47:460-469.'

Stafford, S. R. and I. J. Stout. 1983. Dispersal of the cotton rat, *Sigmodon hispidus*. Journal of Mammalogy 64:210-215.

Straw, J. A., D. G. Krementz, M. W. Olinde and G. F. Sepik. 1994. Woodcock. Pages 97-114 *in* T. C. Tacha and C. E. Braun, eds., Migratory shore and upland game bird management in North America. International Association of Fish and Wildlife Agencies, Washington, DC.

Sutton, G. M. 1967. Oklahoma birds. University of Oklahoma Press, Norman. 674pp.

Tuomisto, H., K. Ruokolainen, R. Kalliola, A. Linna, W. Danjoy , and Z. Rodriguez. 1995. Dissecting Amazonian biodiversity. Science 269:63-66.

Twedt, D. J. and C. R. Loesch. 1999. Forest area and distribution in the Mississippi alluvial valley: implications for breeding bird conservation. Journal of Biogeography 26: 1215-1224.

Twedt, D. J., R. R. Wilson, J. L. Henne-Kerr and R. B. Hamilton. 1999. Impact of forest type and management strategy on avian densities in the Mississippi Alluvial Valley, USA. Forest Ecology and Management 123:261-274.

Uhl, C. and P. G. Murphy. 1981. Composition, structure, and regeneration of a terra firme forest in the Amazon Basin of Venezuela. Tropical Ecology 22:219-237.

U. S. Army Corps of Engineers. 1970. Floodplain information, Bayou Meto and tributaries, Jacksonville, Arkansas. U.S. Army Corps of Engineers, Vicksburg District, Mississippi. 35pp.

U.S. Fish and Wildlife Service (USFWS). 1984. Texas bottomland preservation program: category 3. U.S. Department of the Interior, Fish and Wildlife Service, Albuquerque, NM. 378pp.

Wakely, J. S. and T. H. Roberts. 1996. Bird distributions and forest zonation in a bottomland hardwood wetland. Wetlands 16:296-308.

Watts, B. D. 1995. Yellow-crowned night heron. *In* A. Poole and F. Gill, eds., Birds of North America 161. Academy of Natural Sciences of Philadelphia, Pennsylvania.

Welch, D. J. W. 2000. The effect of uneven-aged silviculture on the breeding ecology of the indigo bunting (*Passerina cyanea*) in a bottomland hardwood forest. MS Thesis, University of Georgia, Athens.

Wharton, C. H., W. M. Kitchens, E. C. Pendleton and T. W. Sipe. 1982. The ecology of bottomland hardwood swamps of the southeast: a community profile. FWS/OBS-81/37, U.S. Fish and Wildlife Service, Biological Services Program, Washington, DC. 133pp.

White, T. H. Jr., J. L. Bowman, B. D. Leopold, H. A. Jacobson, W. P. Smith, and F. J. Vilella. 2000. Influence of Mississippi Alluvial Valley rivers on black bear movement and dispersal: implications for Louisiana black bear recovery. Biological Conservation 95:323-331.

Wieme, B. J. 2001. Juvenile survival, cause-specific mortality, and selected harvest trends of male eastern wild turkeys in Mississippi. MS Thesis, Mississippi State University, Mississippi. 50pp.

Wigley, T. B. and T. H. Roberts. 1994. A review of wildlife changes in southern bottomland hardwoods due to forest management practices. Wetlands 14: 41-48.

Wigley, T. B. and R. A. Lancia. 1998. Wildlife communities. Pages 205-236 *in* M. G. Messina and W. H. Conner, eds., Southern forested wetlands: ecology and management. Lewis Publishers, New York.

Wilson, R. R. and R. J. Cooper. 1998. Acadian flycatcher nest placement: does placement influence reproductive success? Condor 100:673-679.

Wood, L. A. 1999. Short-term effects of timber management on prothonotary warbler (*Protonotaria citrea*) breeding biology. MS Thesis, University of Georgia, Athens.