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William J. Platt
University of Iowa

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WILLIAM J. PLATT[1]

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SYNOPSIS: The vertebrates in communities comprising a habitat with unpredictable water levels (the Coralville Reservior) were compared to those present in communities comprising a habitat without severely fluctuating water levels (Cone Marsh). From data on the species of vertebrates and their relative abundance, it was determined that extensive ecosystem simplification had occurred in communities along the Coralville Reservior. The major characteristics of this simplification were the following: 1) several species with similar modes of feeding were present at Cone Marsh but only species with generalized food habits were present along the Coralville Reservoir; 2) species at the top of food chains often were very rare or absent in communities along the Coralville Reservoir flood plain, and 3) food chains that were dominant at Cone Marsh often were less important on the Coralville Reservoir flood plain. On these characteristics is based the following hypothesis of ecosystem simplification: 1) a massive trophic simplification and reduction in the number of species present; 2) alterations in the trophic structure so that major food chains are different; 3) the replacement of specialized species by more generalized species capable of adapting to the environmental stresses imposed; and 4) severe reductions in, or elimination of, top trophic levels, which eliminates a mechanism for binding together communities in the same habitat.

INDEX DESCRIPTORS: Vertebrates, Community Ecology, Ecosystem Simplification, Coralville Reservoir in Iowa, Cone Marsh in Iowa.

The effects of human activities upon habitats and the ecosystems within them often are difficult to assess until after considerable alterations already have occurred. The construction of the Coralville Reservoir on the Iowa River has drastically altered the habitat, converting a river flood plain into a large impoundment with highly fluctuating water levels. The types of ecosystems now present are marshes with intermittent forests, open meadows and fields, and temporary ponds along the border of the reservoir. The vertebrate fauna of these ecosystems was studied to determine which species were present, and how the vertebrate communities were organized. To obtain a standard for comparison, a marsh with relatively stable water levels also was studied. The objectives of this study were to compare the vertebrate species present in the different ecosystems comprising the two habitats and to describe the structure of the vertebrate communities within the different ecosystems. Hypotheses based on these data concern changes in the structure of vertebrate communities affected by unpredictable water levels.

MATERIALS AND METHODS

For the past three years, the vertebrate zoology class at The University of Iowa has conducted surveys of two areas in eastern Iowa. The Coralville Reservoir west of U.S. Highway 218 in Johnson County has large and unpredictable fluctuations in the water levels. Numerous ponds, creeks, meadows, and forests are present in this area. Cone Marsh drains into the Iowa River just north of Columbus Junction in Louisa County, Iowa. It was selected for comparison with the Coralville Reservoir because of similar physical features, similar ecosystems, and stable water levels.

Surveys of the vertebrate fauna were taken during early fall of 1970 and 1972 and late spring of 1971 and 1972. I visited each area during the summer of 1970. Surveys of the fish species present were made by seining and electroshocking. Amphibians and reptiles were collected by handcapturing and by seining. Mammals were trapped, observed, or signs were noted. Birds were observed in the field. All species collected were identified using Blair, et al. (1957) or Harlan and Speaker (1959). Observations of species or signs of species were identified using field guides (Peterson, 1947; Burt and Grossenheider, 1952). From the collections and observations, the relative abundance of different species in the two areas was determined. Food habits of the various species were accepted as reported in the literature. These data were used to determine the trophic structure of the communities studied.

RESULTS

Vertebrate species present in the Coralville Reservoir and Cone Marsh habitats are presented in Table 1. A summary of numbers of vertebrate species in each class collected in the two habitats is given in Table 2. There are more species in each class at Cone Marsh. Since the habitats are quite similar in many respects, the different kinds of species present in different ecosystems in each habitat were examined more closely. From data on food habits, food webs of the communities in both habitats were constructed. The habitats were divided into four communities. These were designated as: aquatic, semiaquatic (marsh), open fields and meadows, and flood plain forests. Depending upon where they were observed or collected, species were assigned to at least one of these communities. Although these community divisions were somewhat arbitrary, they permitted direct comparisons to be made.

Simplified food webs for aquatic communities in the Coralville Reservoir flood plain region are presented in Figure 1. Similar food webs for aquatic communities at Cone Marsh are presented in Figure 2. The arrows denote directions of energy flow within the various food webs. Species with sim-

[1] Department of Zoology, The University of Iowa, Iowa City, Iowa 52242.

ilar food habits are grouped together. Three distinct units were present in both habitats. These were:

1) creeks flowing into the marsh or into the reservoir impoundment;
2) ponds along the border of the marsh or reservoir impoundment, and the marsh or littoral region of the reservoir;
3) the creek draining the marsh or the main channel of the Iowa River (i.e., drainage areas).

The food webs of the semiaquatic or marsh communities are presented in Figures 3 and 4. For purposes of keeping the food web diagrams relatively simple the fish were grouped together as a single component. Thus the illustrated trophic structure is that of tetrapod vertebrates.

The food webs for open meadows and fields, presented in Figures 5 and 6, were constructed for species of vertebrates restricted to or spending considerable time in those habitats. Open-meadow and field communities for the Coralville Reservoir were divided into two categories, those that were flooded frequently (at least annually), and those that were flooded infrequently or not at all.

Figures 7 and 8 illustrate food webs of flood plain forests along the Coralville Reservoir and the creek draining Cone Marsh. These forests were periodically flooded in both areas.

TABLE 1. SPECIES OF VERTEBRATES COLLECTED ALONG THE CORALVILLE RESERVOIR FLOOD PLAIN (CRF) AND AT CONE MARSH (CM).

Class Teleostomi
- Order Lepisosteiformes
  - Lepisosteidae
    - *Lepisosteus platostomus* (CM)
- Order Amiiformes
  - Amiidae
    - *Amia calva* (CM)
- Order Clupeiformes
  - Clupeidae
    - *Dorosoma cepedianum* (CM)
- Order Salmoniformes
  - Esocidae
    - *Esox lucius* (CRF*, CM)
- Order Cypriniformes
  - Catastomidae
    - *Catastomus commersoni* (CM)
    - *Ictiobus cyprinellus* (CRF*, CM)
    - *Carpoides forbesi* (CM)
    - *Carpoides carpio* (CM)
    - *Carpoides cyprinus* (CRF*)
    - *Moxostoma aureolum* (CRF*)
  - Cyprinidae
    - *Semotilus atromaculatus* (CRF, CM)
    - *Notemigonus chrysoleucas* (CM)
    - *Cyprinus carpio* (CRF, CM)
    - *Pimephales promelas* (CRF, CM)
    - *Notropis dorsalis* (CRF, CM)
    - *Notropis atherinoides* (CRF*, CM)
    - *Notropis cornutus* (CM)
  - Ictaluridae (Siluriformes)
    - *Ictalurus melas* (CRF, CM)
    - *Ictalurus natalis* (CM)
    - *Ictalurus punctatus* (CRF*, CM)
    - *Noturus flavus* (CM)
    - *Pylodictis olivaris* (CRF*)
- Order Perciformes
  - Serranidae
    - *Roccus chrysops* (CRF*, CM)
  - Centrarchidae
    - *Lepomis macrochirus* (CRF, CM)
    - *Lepomis cyanellus* (CRF, CM)
    - *Lepomis gibbosus* (CM)
    - *Lepomis humilis* (CM)
    - *Micropterus salmoides* (CRF*, CM)
    - *Pomoxis annularis* (CRF, CM)
    - *Pomoxis nigromaculatus* (CRF, CM)
    - *Chaenobryttus coronarius* (CM)
  - Scianidae
    - *Aplodinotus grunniens* (CM)
  - Percidae
    - *Stizostedion vitreum* (CRF*, CM)
    - *Stizostedion canadense* (CM)

Class Amphibia
- Order Anura
  - Bufonidae
    - *Bufo americanus* (CRF, CM)
  - Hylidae
    - *Hyla versicolor* (CRF, CM)
    - *Acris crepitans* (CM)
    - *Pseudacris streckeri* (CRF, CM)
  - Ranidae
    - *Rana pipiens* (CRF, CM)
    - *Rana palustris* (CRF)
    - *Rana clamitans* (CRF, CM)
    - *Rana catesbeiana* (CRF, CM)
- Order Urodela
  - Ambystomidae
    - *Ambystoma tigrinum* (CRF, CM)
  - Proteidae
    - *Necturus maculosus* (CM)

Class Reptilia
- Order Chelonia
  - Chelydridae
    - *Chelydra serpentina* (CRF, CM)
  - Emydidae
    - *Chrysemys picta* (CM)
    - *Pseudemys scripta* (CM)
    - *Emys blandingi* (CRF, CM)
    - *Terrepene carolina* (CM)
  - Kinosternidae
    - *Sternotherus odoratus* (CM)
    - *Kinosternon flavescens* (CM)
  - Trionychidae
    - *Trionyx spinifer* (CM)
- Order Squamata
  - Colubridae
    - *Natrix sipedon* (CRF, CM)
    - *Storeria dekayi* (CRF, CM)
    - *Thamnophis sirtalis* (CRF, CM)
    - *Thamnophis radix* (CM)
    - *Elaphe vulpina* (CM)
    - *Pituophis melanoleucas* (CRF, CM)
    - *Coluber constrictor* (CRF, CM)
    - *Heterodon platyrhinos* (CM)
    - *Lampropeltis getulus* (CM)
    - *Opheodrys vernalis* (CM)

* Indicates species that are found in Iowa River main channels, and not usually found on the flood plain regions.

Crotalidae
Sistrurus catenatus (CM)
Class Aves*
Order Podocipitiformes
Pied-bill grebe (CRF, CM)
Order Gruiformes
American coot (CRF, CM); sora rail (CRF, CM)
Order Ciconiiformes
great-blue heron (CRF, CM); green heron (CM); American egret (CRF, CM)
Order Charadriiformes
Killdeer (CRF, CM); Wilson's snipe (CRF, CM); woodcock (CRF, CM)
Order Anseriformes
blue-winged teal (CRF, CM); pintail (CRF, CM); mallard (CRF, CM); wood duck (CRF, CM)
Order Galliformes
pheasant (CRF, CM); quail (CRF)
Order Falconiformes
marsh hawk (CM); sparrow hawk (CM); red-tailed hawk (CM); turkey vulture (CRF, CM); osprey (CRF)
Order Strigiformes
great-horned owl (CM); barred owl (CRF, CM)
Order Columbiformes
mourning dove (CRF, CM)
Order Piciformes
red-headed woodpecker (CRF, CM); flicker (CRF, CM); downy woodpecker (CRF)
Order Caprimulgiformes
night hawk (CRF, CM)
Order Apodiformes
chimney swift (CRF, CM); ruby-throated hummingbird (CRF, CM)
Order Coraciiformes
belted kingfisher (CM)
Order Passeriformes
barn swallow (CRF); rough winged swallow (CM); bank swallow (CRF, CM); common crow (CRF, CM); bluejay (CM); short billed marsh wren (CM); brown thrasher (CRF, CM); American robin (CRF, CM); yellow warbler (CRF, CM); red winged blackbird (CRF, CM); purple grackle (CRF, CM); Eastern meadowlark (CRF, CM); cardinal (CM); blackcapped chickadee (CM); American goldfinch (CRF, CM); white-breasted nuthatch (CM); Eastern bluebird (CRF, CM); Baltimore oriole (CM); indigo bunting (CM); red-eyed towhee (CM); sparrows (CRF, CM)
Class Mammalia
Order Marsupialia
Didelphidae
Didelphis marsupialis (CRF, CM)
Order Insectivora
Soricidae
Cryptotis parva (CM)
Sorex cinereus (CM)
Blarina brevicauda (CRF, CM)
Talpidae
Scalopus aquaticus (CRF, CM)
Order Chiroptera
Vespertiliontidae
Myotis lucifugus (CRF, CM)
Lasiurus borealis (CM)
Eptesicus fuscus (CRF, CM)
Order Rodentia
Sciuridae
Sciurus niger (CRF, CM)
Spermophilus tridecemlineatus (CRF, CM)
Spermophilus franklini (CM)
Marmota monax (CM)
Geomyidae
Geomys bursarius (CRF, CM)
Cricetidae
Reithrodontomys megalotis (CM)
Microtus pennsylvanicus (CRF, CM)
Peromyscus leucopus (CRF, CM)
Peromyscus maniculatus (CRF, CM)
Ondatra zibethicus (CRF, CM)
Zapodidae
Zapus hudsonicus (CM)
Castoridae
Castor canadensis (CRF, CM)
Order Lagomorpha
Leporidae
Sylvilagus floridanus (CRF, CM)
Order Carnivora
Canidae
Vulpes fulva (CRF, CM)
Canis latrans (CM)
Procyonidae
Procyon lotor (CRF, CM)
Mustelidae
Mustela erminea (CM)
Mustela frenata (CM)
Mustela vison (CRF, CM)
Mephitis mephitis (CRF, CM)
Spilogale putorius (CM)
Taxidea taxus (CM)
Order Artiodactyla
Cervidae
Dama virginiana (CRF, CM)

* List is incomplete and does not include migratory species present only briefly.

TABLE 2. COMPARISON OF THE NUMBER OF VERTEBRATE SPECIES COLLECTED AT THE CORALVILLE RESERVOIR AND CONE MARSH.

Class	Coralville Reservoir Flood Plain	Cone Marsh
Teleostomi	18 (9)[1]	31
Amphibia	8	9
Reptilia	7	18
Aves	36	46
Mammalia	19	30
Total	88 (78)	134

[1] Nine species of fish were collected in shallow water along the Coralville Reservoir flood plain. An additional nine species (Table 1) also were collected from the river channel, but were not present in the littoral habitat studied.

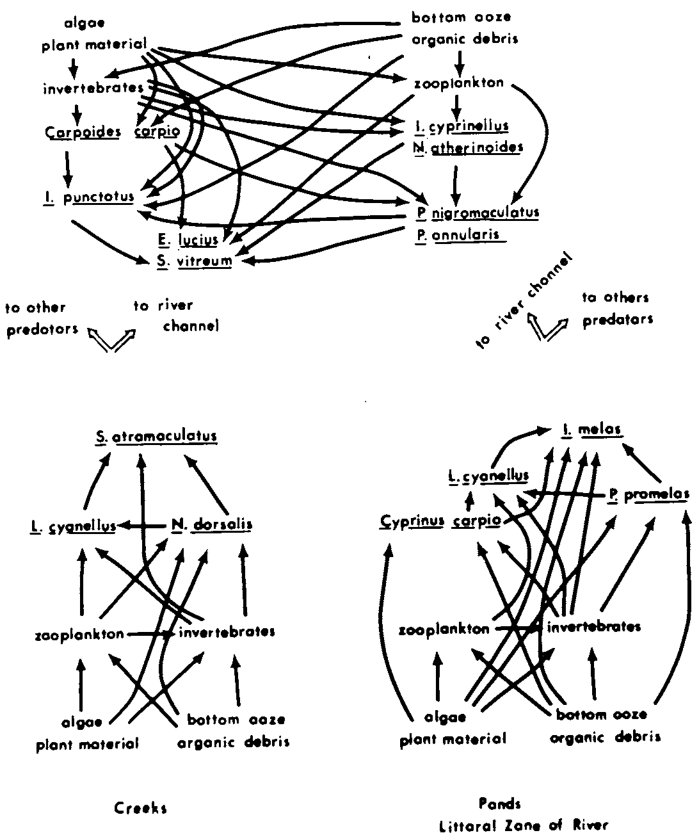

Figure 1. Food web of aquatic ecosystems on the Coralville Reservoir flood plain.

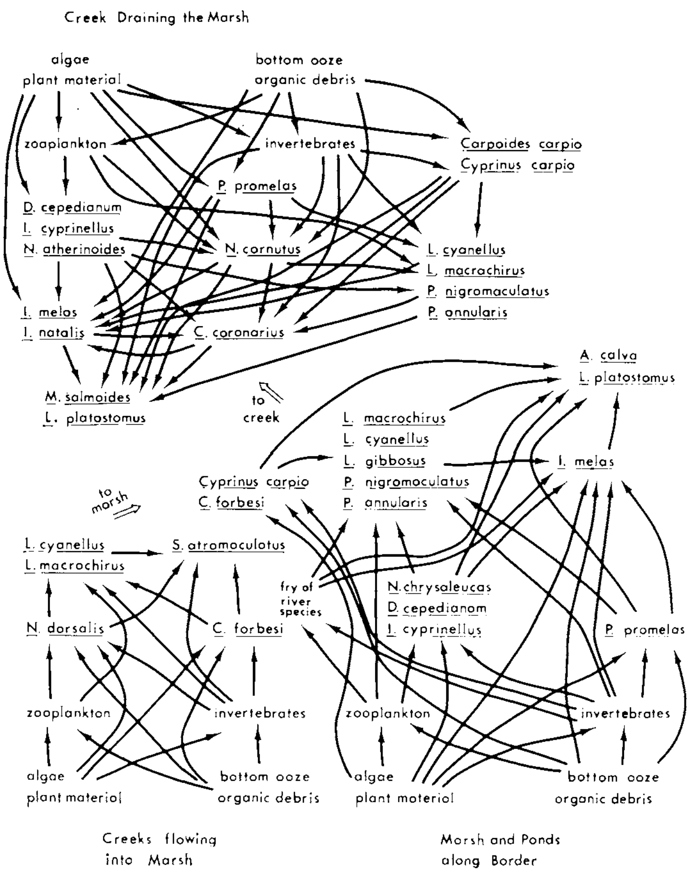

Figure 2. Food webs of aquatic ecosystems at Cone Marsh.

DISCUSSION

All of the communities along the Coralville Reservoir flood plain contained fewer species than similar communities at Cone Marsh. Also, fewer species with similar feeding habits in each community were present in the Coralville Reservoir habitat. Examination of the food habits of similar species of vertebrates in different communities provided important information regarding differences between vertebrate communities in the two habitats. Comparisons of some of these species are presented below. Others not discussed followed similar patterns.

Aquatic Communities

Consideration of the food habits of several groups of fish having different modes of feeding provided information relating to the differences between the aquatic communities in the two habitats.

In Cone Marsh, three species of fish (*Carpoides forbesi, Carpoides carpio,* and *Cyprinus carpio*) were bottom feeders. Only carp, *Cyprinus carpio,* were present on the flood plain in the Coralville Reservoir, although river carpsuckers, *Carpoides carpio,* were abundant in deeper water. Buccholz (1957) found the food habits of river carpsuckers to include various algae and bottom-dwelling invertebrates, primarily Diptera larvae. Carp in lakes feed primarily upon organic and plant debris and various bottom-dwelling invertebrates, such as Diptera and small benthic crustacea (Berner, 1951; Moen, 1953). Carp thus are more generalized feeders than carpsuckers. Decreases in water quality in reservoirs have been correlated with decreases in the diversity of benthic invertebrates (Ransom and Dorris, 1972). Sedimentation of the Coralville Reservoir (Mitzner and McDonald, 1969) undoubtedly has reduced the density of benthic invertebrate populations because of the silt layers on the bottom (Ellis, 1936). Such a reduction in both the amounts and kinds of food available in shallower water probably has resulted in the elimination of certain bottom-feeding fish in aquatic communities along the Coralville Reservoir. Carp are able to inhabit littoral regions of the flood plain and temporary ponds since they have very generalized food habits.

Two minnows, *Notropis dorsalis* and *Pimephales promelas,* were abundant in the Coralville Reservoir habitat. Griswold (1963) found that *N. dorsalis* in Clear Lake, Iowa, fed primarily upon Diptera (Chironomids) and algae. Starrett (1950) found that *N. dorsalis* in the Des Moines River, Iowa, fed primarily upon insect larvae and nymphs, but that the bottom ooze was ingested in considerable amounts in the summer and fall. As a generalized bottom-feeding minnow, *N. dorsalis* is well-suited for life in the silted streams along the Coralville Reservoir flood plain. *Pimephales promelas* feeds almost exclusively upon bottom ooze (Starrett, 1950), although it will take algae and small insects (Coyle, 1930; Keast, 1966; Konefes and Bachmann, 1970). It is found in

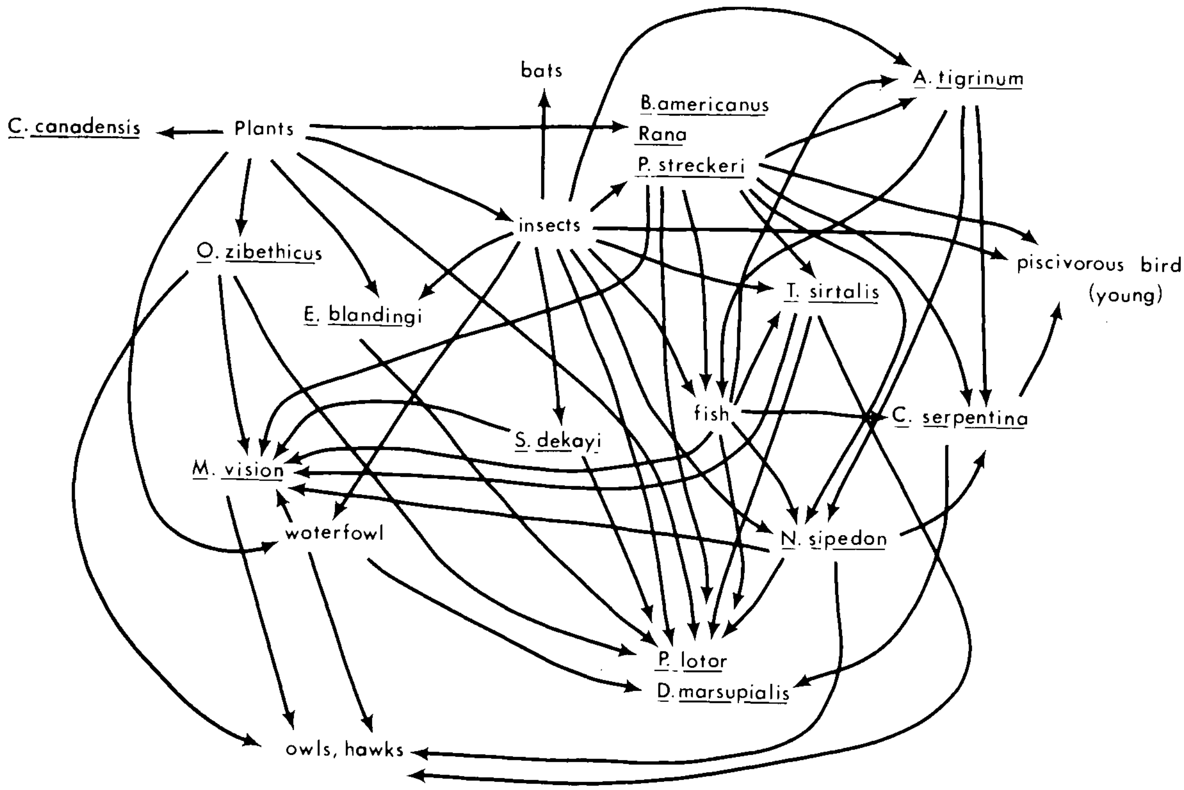

Figure 3. Semi-aquatic food web involving tetrapod vertebrates on the Coralville Reservoir flood plain.

shallow ponds and backwaters of the reservoir that contain abundant organic debris.

At Cone Marsh, *Pimephales promelas* and *Notemigonus chrysoleucas* were common in the shallow marshy areas. *N. dorsalis* was found in shallow sand streams emptying into the marsh. *Notropis cornutus* and *N. atherinoides* were found in the deeper water of the stream draining the marsh. The diets of *N. chrysoleucas* (Griswold, 1963; Hubbs and Cooper, 1936), *N. atherinoides* (Ewers, 1933; Forbes and Richardson, 1920), and *N. cornutus* (Starrett, 1950; Griswold, 1963; Fee, 1965; Keast, 1966) are more restricted than those of *N. dorsalis* or *P. promelas.* The absence of benthic insects and submerged vegetation, and noticeable fluctuations in the zooplankton are possible reasons for the absence of these three species of minnows in the littoral region of the reservoir flood plain.

Of the fish that feed mostly upon invertebrates only *Lepomis cyanellus,* the green sunfish, was abundant in the littoral aquatic communities of the Coralville Reservoir habitat. This species was collected most frequently in the deeper pools of silted creeks and occasionally in ponds. The green sunfish has a larger mouth than the bluegill, *L. macrochirus.* Although its diet usually consists of insects (Mullan and Applegate, 1970; Etnier, 1971), food items taken are more diverse than those taken by other sunfish (Minckley, 1963; Cross, 1951, from Carlander, 1972; Mullan and Applegate, 1968). The green sunfish is tolerant of turbid water; silt turbidity does not affect the feeding behavior of this species (Heimstra, *et al.,* 1969). Because of its diet breadth and the ability to adapt to turbid water, the green sunfish may be considered the generalist of the sunfish group. It seems to be capable of adapting to fluctuating water levels. However, the fish may be small and stunted, as were most of the green sunfish collected along the Coralville Reservoir flood plain.

The few bluegills (*L. macrochirus*) collected in pools of creeks along the Coralville Reservoir also were small and stunted. Data on the food habits and growth rates of *L. macrochirus* in reservoirs are considerable. Growth rates of bluegills in new impoundments are rapid, but are much slower after the reservoirs have been in existence for several years (Eschmeyer, 1948; Lane, 1954). Reduced growth rates in older reservoirs have been attributed in part to water fluctuations that delay spawning and eliminate the insect food supply (Eschmeyer, 1948; Lane, 1954). The diet of the bluegill changes as the fish increase in size. Small fish feed upon zooplankton, whereas larger fish feed primarily upon benthic invertebrates (Hall, *et al.,* 1970; Minckley, 1963; Seaburg and Moyle, 1964; Mullan and Applegate, 1968, 1970; Etnier, 1971).

Two species of sunfish, *Lepomis gibbosus* and *L. humilis,* were collected at Cone Marsh, but not along the Coralville Reservoir flood plain. *Lepomis humilis* is a small species that feeds upon insects (Kutkuhn, 1955). *Lepomis gibbosus* feeds upon insects, crustaceans, and molluscs (Seaburg and Moyle, 1964; Etnier, 1971). Both species have more re-

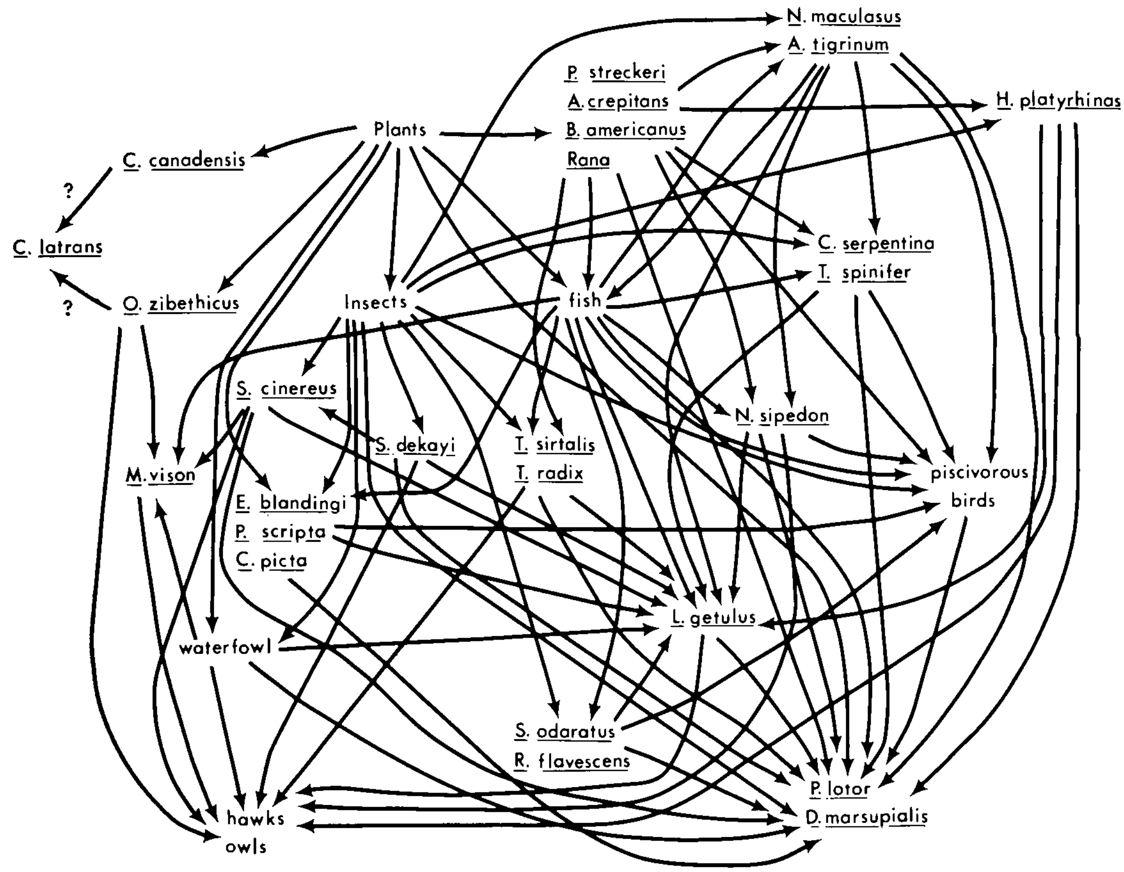

Figure 4. Semi-aquatic food web involving tetrapod vertebrates at Cone Marsh.

stricted diets than *L. macrochirus* or *L. cyanellus*.

Neither *Pomoxis annularis* or *P. nigromaculatus* were abundant in the littoral regions of the Coralville Reservoir flood plain, although they were more common in deeper water. These species differ from the sunfish in their food habits. They tend to feed more frequently upon Cladocerans, Copepods, Ostracods, and small fish than insects (Kutkuhn, 1955, 1958; Marcy, 1954; Hoopes, 1960; Neal, 1961; Keast, 1965, 1968a, 1968b; Mathur and Robbins, 1971; Mathur, 1972; Costa and Cummins, 1972).

Bullheads (*Ictalurus melas*) were common in both habitats. Food habits of the black bullhead shift with season and age (Welker, 1962). Planktonic invertebrates such as Cladocerans are important food sources in early summer. Plant material also is taken in the summer. A shift to larger invertebrates, especially Diptera, occurs later in the summer. Fish, especially fry, also are taken at this time. *I. melas* is extremely abundant in the shallow waters of the Coralville Reservoir; presumably such a generalist type of fish is well adapted for such unstable habitats. *I. punctatus* and *Pylodictis olivaris* are not found in littoral areas, but are present in deeper water. These species have less generalized food habits than *I. melas* (Bailey and Harrison, 1948; Price, 1963; Jearld and Brown, 1971; Harlan and Speaker, 1969).

Ictiobus cyprinellus, buffalo, and *Dorosoma cepedianum*, gizzard shad, are filter-feeding species (Moen, 1954; Kutkuhn, 1957; Price, 1963). Although common in the Iowa River below Iowa City, they were not collected from the Coralville Reservoir flood plain. Buffalo are common in the deeper channels of the reservoir, however. At Cone Marsh, *Dorosoma* is found most often in the shallow waters of the marsh and the backwaters of the creeks. *Ictiobus* is found in deeper water, the main creek channels, and deeper ponds. Food items taken by buffalo include phytoplankton, planktonic crustaceans, and occasionally insects, primarily Diptera (Moen, 1954). The absence of *Ictiobus* in the flood plain regions of the Coralville Reservoir might result from the absence or the unavailability of suitable plankton populations. Mitzner and McDonald (1969) have shown that the density of plankton in the Coralville Reservoir is similar to that below the dam. Since both *Dorosoma* and *Ictiobus* are found below the dam, the plankton density in the reservoir is sufficient to support both species. At high water levels in the spring and fall, blue-green algae blooms occur in shallow water. Although blue-green algae are a potential food source for *Ictiobus*, rapid growth of the algae populations may deplete the oxygen supply. Thus this food reservoir may not be utilized by buffalo if a lack of oxygen prevents them from

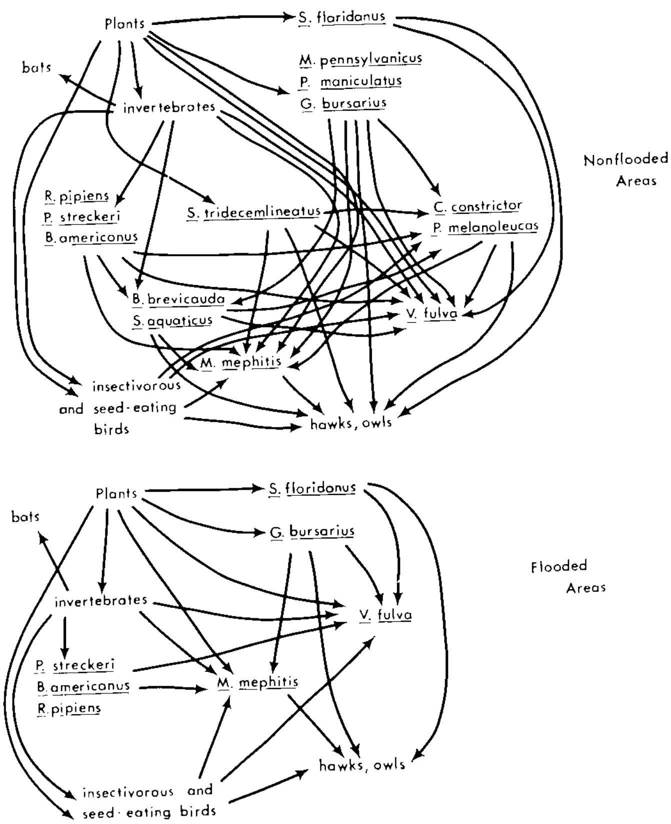

Figure 5. Food webs of flooded and nonflooded open meadows and fields on the Coralville Reservoir flood plain.

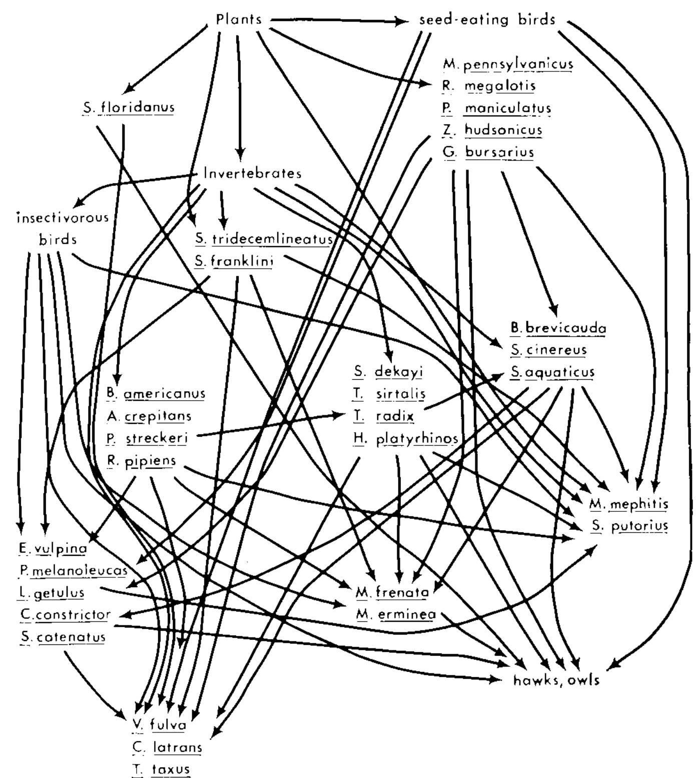

Figure 6. Food web of open meadows and fields at Cone Marsh.

entering shallow water.

The absence of shad from littoral regions of the reservoir has important implications for predatory species of fish. *Dorosoma* is a major forage fish for larger piscivorous predators (Kutkuhn, 1958). Its absence from shallow regions of the Coralville Reservoir means that predatory fish might have a reduced supply of food available to them. Thus the larger predatory fish may be restricted to deeper water by the absence of suitable prey in shallow water.

Three piscivorous fish, *Lepisosteus platostomus, Amia calva,* and *Micropterus salmoides,* were abundant in Cone Marsh and the creek draining the marsh. Both gar and bowfin can survive anoxic conditions because they can breathe air. Thus they are well adapted for life in a highly productive marsh. Bass were present in the stream, which does not become anoxic. *Chaenobryttus coronarius,* the warmouth, also was present in the streams, although it was not abundant. Larimore (1957) found that food habits of the warmouth overlapped with large mouth bass, but that there were differences in the sites in which the two species fed. The presence of all these predators at Cone Marsh obviously means that there are sufficient prey to sustain an additional trophic level. More important, the prey are present in sufficient densities and are diverse enough to support more than one species of predator. The total biomass of fish taken in ponds along the Coralville Reservoir was considerable. However, the prey biomass available to predators fluctuates both seasonally and annually. Some predation upon fish in the littoral regions of the Coralville Reservoir undoubtedly occurs during times of high water when predatory fish from the main river channel can move into shallower water. However, at these times, prey are dispersed and vulnerability of the prey is decreased.

The presence of piscivorous predators results in greater diversity of prey species than in the absence of predators (Hall, *et al.,* 1970; Brooks and Dodson, 1965). When predators are present the species composition of prey trophic levels is shifted towards smaller, more specialized prey species. It seems likely that the absence of predatory fish in the littoral regions of the Coralville Reservoir may be a very important factor in the increasing dominance of rough fish over smaller, more specialized sunfish and other such species in these areas (c.f. Mitzner, 1970). In addition, faster growth rates and a better physical condition of prey species such as bluegill have been obtained in aquatic systems with predators present (Wilford and Ward, 1968).

A number of fish collected at Cone Marsh in the spring were species that had immigrated for reproduction. These species, such as *Esox lucius, Roccus chrysops, Stizostedion vitreum,* and *Aplodinotus grunniens,* spawn in shallow water with submerged vegetation (Harlan and Speaker, 1969). The fry thus are part of the marsh fish community until they migrate into deeper water. Stable water levels and submerged vegetation are critical for successful spawning and fry survival. Likewise the presence of abundant zooplankton for fry is crucial (Smith and Moyle, 1945). The absence of a

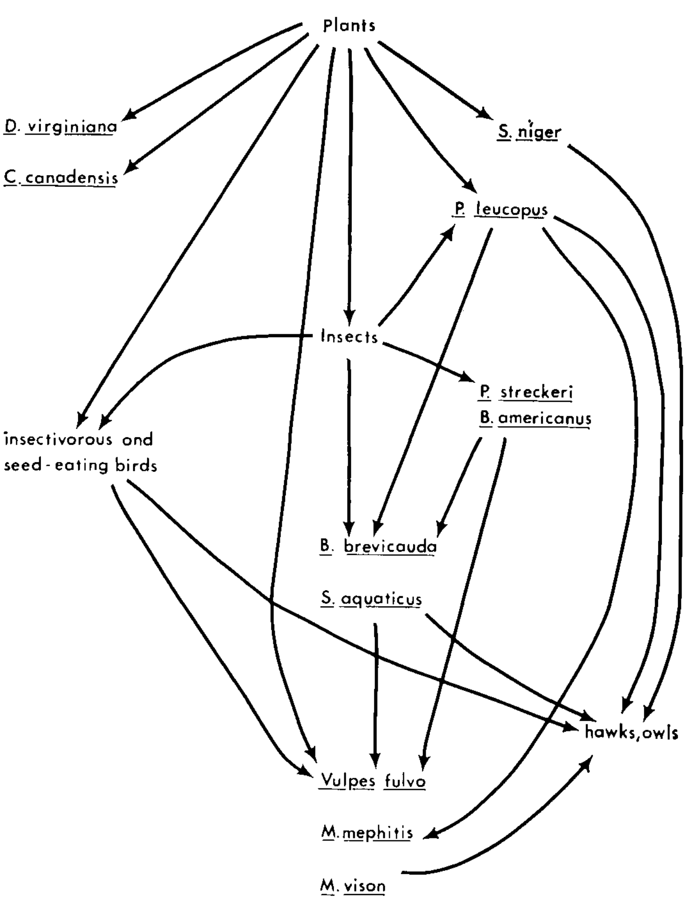

Figure 7. Food web of flood plain forests on the Coralville Reservoir flood plain.

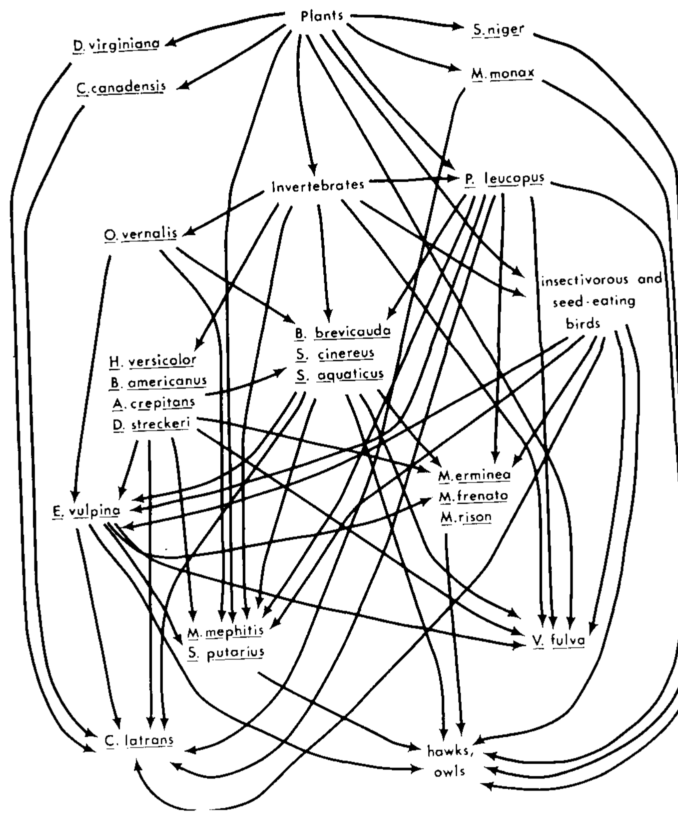

Figure 8. Food web of flood plain forests at Cone Marsh.

stable littoral zone at the reservoir probably has reduced the reproductive success of these species, since the shifting substrate cannot be successfully utilized for spawning by many fish (Ellis, 1936). The absence of suitable breeding areas for game fish must in great part account for high densities of carp and buffalo in the reservoir. These two species are most successful at spawning in water with a shifting mud bottom (Harlan and Speaker, 1969).

Terrestrial Communities

Tetrapod vertebrates, especially predators, generally were found in more than one community. Comparisons of vertebrates in the two habitats thus were made for similar taxonomic groupings.

Amphibians in general are adapted for conditions in which at least temporary bodies of water are present. In the case of frogs and toads, the tadpole stage is herbivorous-detritivorous; therefore, habitats with considerable organic debris are likely to contain such species. Both Coralville Reservoir and Cone Marsh contain abundant organic debris. The same species of frogs and toads generally are present in both habitats. However, a striking difference occurs in the numbers of individuals of each species. During the spring, large aggregations of *Rana pipiens, Bufo americanus,* and *Pseudacris streckeri* were noted on the Coralville Reservoir flood plain. These did not occur at Cone Marsh, although the habitat conditions were similar. In the fall, tremendous numbers of tadpoles were present in ponds on the reservoir flood plain. Very few tadpoles were observed at Cone Marsh. These differences were attributed to a lack of predatory species, especially fish, in marshes at the Coralville Reservoir.

Cone Marsh obviously has the food resources to support turtles (Table 1). *Chelydra serpentina, Kinosternon flavescens,* and *Sternotherus odoratus* all are bottom feeding turtles. *Chelydra serpentina,* the snapping turtle, is essentially omnivorous, and will take insects, fish, amphibians, and even vegetation (Lagler, 1943). *K. flavescens* and *S. odoratus* are more insectivorous than piscivorous (Strecker, 1927; Lagler, 1943). The shifting bottom of the Coralville Reservoir may have removed a major food source for such species of turtles. *Trionyx spinifer,* the spiny softshell, feeds primarily upon insects and crayfish; fish comprise only a minor portion of the diet (Lagler, 1943). The absence of the latter three species of turtles in the littoral region of the Coralville Reservoir flood plain is associated with low densities of benthic invertebrates. The only species at all common on the flood plain is the snapping turtle, which has less specialized food habits than the others.

Three species of turtles, *Chrysemys picta, Pseudemys scripta,* and *Emys blandingi* tend to be insectivorous and/or piscivorous when young, and herbivorous as adults (Carr, 1952; Clark and Gibbons, 1969). Of these only *E. blandingi,* the semi-box turtle, was found along the Coralville Reservoir flood plain. This species was collected only once, so it is not common in that area. At Cone Marsh, all three species are relatively common. The food habits of these species (Lagler, 1943; Carr, 1952) may be the reason why these species are either rare or absent from the Coralville Reservoir flood plain. Since *E. blandingi* has less restricted food habits than the other two species, taking fish in addition to crustaceans, molluscs, insects, and plants, it is not surprising that this is the species present on the reservoir flood plain.

In Cone Marsh, the muskrat (*Ondatra zibethicus*) is the most abundant mammal. Muskrat houses and feeding platforms are common. Muskrats are restricted to ponds along the periphery of the flood plain of the Coralville Reservoir, and are much less abundant. Small rodents and lagomorphs were abundant at the Coralville Reservoir only in areas not flooded annually. *Microtus pennsylvanicus, Peromyscus maniculatus, Spermophilus tridecemlineatus, Geomys bursarius,* and *Sylvilagus floridanus* were found in open fields and meadows. *Sciurus niger* and *Peromyscus leucopus* were found in wooded areas. In addition to the species listed above, four other species were found at Cone Marsh. *Spermophilus franklini, Reithrodontomys megalotis,* and *Zapus hudsonicus* were found in open areas. *Marmota monax* was found in wooded areas. The overall rodent densities, as determined from observations and trapping, were much higher at Cone Marsh than those on the flood plain of the reservoir.

Species of snakes feeding primarily upon small mammals were rarely seen on the Coralville Reservoir flood plain. *Coluber constrictor* and *Pituophis melanoleucas* each were found once at the Coralville Reservoir. In contrast, several species (*Elaphe vulpina, Pituophis melanoleucas, Coluber constrictor, Lampropeltis getulus, Sistrurus catenatus*), were relatively abundant at Cone Marsh. Most of these were found in wooded or meadow regions along the banks of the marsh. *Coluber constrictor,* the blue racer, has the most generalized diet, taking insects, amphibians, snakes, birds, and eggs in addition to small mammals (Schmidt and Davis, 1941; Conant, 1958). *Pituophis melanoleucas,* the bull snake, feeds upon small mammals, birds, ground squirrels, pocket gophers, and rabbits (Schmidt and Davis, 1941). The diets of the other three species are more specialized (Schmidt and Davis, 1941). *E. vulpina,* the fox snake, feeds upon mice, birds, and eggs. *L. getulus,* the king snake, feeds upon snakes, turtle eggs, and amphibians in addition to small mammals. *S. catenatus,* the massasauga, feeds upon amphibians and small mammals. Presumably these more specialized species cannot compete with the generalist species, the blue racer and the bull snake, in reservoir flood plain habitats. Small mammals in general are not abundant in the flood plain areas. Thus the serpentine predators, especially after flooding, may be faced with a scarcity of their major prey.

Five predatory birds (Falconiformes, Strigiformes) have been observed at Cone Marsh. Only two species have been observed at the Coralville Reservoir; one of these was the osprey, which is piscivorous. The absence of the hawks and owls reflects a relatively low density of small mammals on the flood plain of the reservoir.

Carnivorous mammals, as with the rodents, were less abundant on the Coralville Reservoir flood plain than at Cone Marsh. Bats (order Chiroptera) were not observed frequently at dusk along the Coralville Reservoir flood plain. Numerous bats, however, have been observed at dusk at Cone Marsh. This was associated with summer emergences of insects in the latter habitat. Shrews (*Sorex cinereus, Cryptotis parva, Blarina brevicauda*) and moles (*Scalopus aquaticus*) or signs of these animals commonly were observed along the water's edge at Cone Marsh. *Sorex cinereus* even was found in muskrat houses several feet from shore. These same species never were observed in areas at the Coralville Reservoir that were subjected to annual flooding. However, *B. brevicauda* and *S. aquaticus* were found further inland in areas flooded only rarely.

Four species of omnivorous mammals (or signs of these species) were observed in both habitats. Three of these (*Procyon lotor, Mephitis mephitis, Vulpes fulva*) are omnivorous species of the order Carnivora (Stuewer, 1943; Cabalka, et al., 1953; Errington, 1935, 1937; Hamilton, 1943; Rosenzweig, 1966). The fourth was the opossum, *Didelphis marsupialis.* The only strictly carnivorous species observed was the mink, *Mustela vison.* According to Errington (1943), mink have a wide diet range. They feed upon crayfish, amphibians, numerous sizes of fish, snakes, insects, birds, mice, ground squirrels, rabbits and muskrats. Thus the carnivorous mammals inhabiting the flood plain regions of the Coralville Reservoir either are omnivorous or, in the case of the mink, have a wide diet range.

At Cone Marsh, signs of these same species were observed more frequently than at the Coralville Reservoir, indicating a higher density of predators. In addition to the generalist species, five species with more specialized food habits are present at Cone Marsh. These include two weasels (*Mustela erminea, Mustela frenata*), spotted skunk (*Spilogale putorius*), badger (*Taxidea taxus*), and coyote (*Canis latrans*). Weasels feed almost exclusively upon mice and other animals of small size (Polderboer, *et al.,* 1941; Rosenzweig, 1966). Badgers feed upon ground squirrels, pocket gophers, other small mammals, and to a lesser extent insects (Hamilton, 1943; Snead and Hendrickson, 1942). The spotted skunk is more omnivorous than weasels or badgers (Crabb, 1941), but less omnivorous than the striped skunk, *M. mephitis* (Rosenzweig, 1966). Hamilton (1943), Korschgen (1957) and Fichter, *et al.* (1955) list the primary foods of the coyote as rabbits, rodents, birds, reptiles, insects and some fruit. Coyote scats from Cone Marsh contained only remains of rabbits (*Sylvilagus floridanus*). This is probably the only predator capable of taking deer, and it is possible that coyotes at Cone Marsh may prey upon young deer to some extent.

Community Structure

Comparison of the vertebrates present in ecosystems on the flood plain of the Coralville Reservoir with similar ecosystems at Cone Marsh has made possible inferences about ecosystem simplification. Major differences in the vertebrate fauna of the two habitats occurred in all communities. From these differences and general conclusions about the nature of ecosystem simplification as a result of the Coralville Reservoir impoundment, changes in the fauna of similar habitats following disturbances, such as impoundment of streams, can be predicted.

The obvious differences between the fish communities of the two areas were:

1) In Cone Marsh, a number of species with similar modes of feeding were common. These species differed in their food habits or distribution. In the Coralville Reservoir, only one species with broad food habits was common and more specialized species often were not present at all.
2) Piscivorous fish were present in aquatic communities

at Cone Marsh, but not those along the Coralville Reservoir flood plain.

The most obvious differences between the terrestrial communities at Cone Marsh and the Coralville Reservoir were:

1) Members of certain important food chains at Cone Marsh were absent or rare on the Coralville Reservoir flood plain.
2) Many predatory species that were common at Cone Marsh were rare or absent on the Coralville Reservoir flood plain.
3) Species with specialized feeding habits that were present at Cone Marsh often were not present on the Coralville Reservoir flood plain.

All three communities comprising the terrestrial segment of the Coralville Reservoir habitat differed from the corresponding community at Cone Marsh in a similar manner. The general characteristics of the ecosystem simplification were similar to those observed in the aquatic systems. The only food web directly affected by the unpredictable flooding was that of the open meadow-field ecosystems. Here a drastic trophic simplification was observed in flooded areas. The absence of small mammals on the flood plain region, similar to that observed by Blair (1939) and Hoslett (1961), resulted in a depauperate fauna. Predators were included in the food web (Figure 5). However, almost no signs or observations of predators such as skunk, fox, hawks, or owls have been made in the flooded meadows and open fields over the past three years. These predators probably forage in the annually flooded areas only rarely.

The presence of numerous predatory species of mammals at Cone Marsh reflects the abundance of prey and the presence of numerous species. In turn the presence of these predatory species ensures that prey outbreaks are less likely to occur. These checks and balances increase the stability of the ecosystem (Platt, 1972). The absence of the more specialized predators from the Coralville Reservoir flood plain region means that fewer controls are exercised upon prey species. The increases in the abundance of certain species of rough fish in aquatic ecosystems (Mitzner, 1970) can in great part be attributed to a lack of predators. Similar events may be occurring in terrestrial ecosystems, since the loss of predators has occurred in all ecosystems on the Coralville Reservoir flood plain. Furthermore, the loss of the predatory species has removed important links between ecosystems. In particular, terminal predators were usually very rare or not present at all. Thus effectively one level of control of community structure has been eliminated on the Coralville Reservoir flood plain. This has two important ramifications. First, the populations, without the control of these predators, can be expected to oscillate in density. Competitive exclusion of some prey species is likely to occur (or already has occurred). Thus a decrease in both diversity and stability is predicted to occur (or already has occurred) as a result of elimination of predators. Second, these predators cross-link communities, uniting them in functional ecological units. The destruction of these links results in each ecosystem being an independent unit. Changes in one ecosystem should affect the others, since the loss of cross-linking predators reduces the buffering capacity to counteract such interactions. In some cases, major food chains were reduced to a minor status or even were absent on the reservoir flood plain. These reductions were very noticeable in the aquatic, semi-aquatic and open meadow-field ecosystems. This, of course, means that resources utilized efficiently at Cone Marsh are utilized less efficiently or not at all on the Coralville Reservoir flood plain. Detritus may accumulate, causing a shift from autotrophic based communities to decomposer based communities. A concomitant increase in the density of less desirable generalist species capable of utilizing such resources may occur. Eutrophication also will occur. The ecosystem simplification along the Coralville Reservoir has produced vertebrate communities more typical of those in relatively early stages of succession (Valiela, 1971). This simplification is much greater than would be expected in natural flood plains. The severe reduction in faunal composition has resulted in low levels of biological organization.

Odum (1969) divides the uses of the environment into four compartments: productive (growth systems), urban-industrial (technical systems), compromise (multiple use systems), and protective (mature systems). Any long term environmental planning should consider these four major uses of land, their needed distribution, and those requirements for the optimal design of regional systems. The Coralville Reservoir obviously falls into a multiple use category. Its value as a protective ecosystem is very small. On the other hand Cone Marsh is primarily a protective ecosystem, although it has some multiple use function (for hunting and fishing recreation). The most general conclusion that can be made regarding the Coralville Reservoir impoundment is that such multiple use systems can not serve a protective role. The capability of the reservoir flood plain ecosystems to buffer environmental perturbations is small compared to more complex ecosystems like Cone Marsh. Moreover, the reduced protective capacity does not apply only to aquatic ecosystems; the observed environmental degradation is present also in the terrestrial ecosystems. Therefore prediction of the major characteristics of the ecological simplification resulting from impoundment applies to all ecosystems in the vicinity of the fluctuating water levels, not just to the aquatic ecosystems. These characteristics are:

1) a massive trophic simplification,
2) severe reduction in or removal of, the top trophic levels,
3) alterations in food chains, such that certain key food chains become greatly reduced in importance or are eliminated,
4) the replacement of specialized species by generalized species capable of adapting to the environmental stresses imposed, and
5) an absence of mechanisms that link ecosystems together as functional units in the habitat so affected.

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