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Descriptive Ecology of the Shenandoah Valley Sinkhole Pond System in Virginia

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INTRODUCTION

Sinkhole ponds in the Shenandoah Valley Sinkhole Pond (SVSP) system are found along the bases of western-facing slopes of the Blue Ridge Mountains in Virginia, and extend from Augusta County north to Page County, a distance of approximately 89 km. These ponds exist in colluvial and alluvial terrace deposits that consist of poorly sorted Antietam quartzite cobbles and boulders in a loosely compacted matrix of sand, silt, and clay that have been eroded from the slopes of the mountains (Duffy, 1991; Kochel, 1987; 1992; Whittecar & Duffy, 1992). These deposits can be from 100 to 500 feet thick (Hack, 1965) and lie over a thick section of relatively weak, westward-dipping carbonate limestone strata of Cambro-Ordovician age. Solution of the valley floor limestone underneath results in the formation of sinkholes; accumulated clay layers and the alluvial deposits sometimes form impermeable layers that enable the sinkholes to retain water. Age estimates for the alluvial fan deposits based on soil profiles support an early to late Pleistocene age (Whittecar & Duffy, 1992). Pollen profiles from the bottom sediments of one of the ponds (Spring Pond) indicate that the ponds have existed for over 15,000 years (Craig, 1969). Due to different hydrologies, some of the sinkhole ponds may have ground water connections, while others fill from surface runoff. The range in hydroperiod includes permanent to highly ephemeral ponds.

The SVSP system contains a unique assemblage of coastal plain and northern bog plant species and may represent relict communities of Tertiary flora (Carr, 1937, 1937-38; Gorey, 1984; Fleming & Van Alstine, 1999). Disjunct coastal plain and northern floral elements total 93 species, 27 of which are listed as endangered, threatened, or rare in Virginia (Virginia Division of Natural Heritage, 1990). The federally endangered swamp pink (*Helonias bullata*) and the federally threatened and state endangered Virginia sneezeweed (*Helenium virginicum*), an Augusta County sinkhole pond endemic, occur here. Rare animal species include the state endangered eastern tiger salamander (*Ambystoma tigrinum*), a coastal plain disjunct (Buhlmann & Hoffman, 1987; Pague & Buhlmann, 1991). The only populations of spotted turtles (*Clemmys guttata*) found west of the Blue Ridge occur in the sinkhole ponds and associated wetlands of Augusta County (Mitchell, 1994). The great diversity of dragonflies (Odonata) ranks the SVSP system as one of the most biologically significant areas in Virginia for this insect group (Roble, 1999).

Although individual sinkhole ponds are scattered north along the western flank of the Blue Ridge at Dooms, Crimora, Hairston, Deep Run, and Madison Run, the largest concentration and best protected series of ponds exists on large terrace deposits on and adjacent to the George Washington National Forest, Pedlar Ranger District, Augusta County, Virginia. All ponds addressed in this paper lie north of the Coal Road at an elevation of approximately 540 m (Fig. 1). The three groups of ponds are described in this paper as the Maple Flats, Loves Run, and Sherando Pond Complexes (Figs. 2-4). They occur in an approximately 16 km section along the base of the northern flank of the Big Levels Area (Sherando and Big Levels 7.5 minute topographic quadrangles).

Natural forest habitat on the terraces and alluvial fans surrounding these ponds consists primarily of chestnut oak (*Quercus montana*), white oak (*Q. alba*), and other hardwoods like hickory (*Carya* spp.) and red maple (*Acer rubrum*). Virginia pine (*Pinus virginiana*), shortleaf pine (*P. echinata*), and pitch pine (*P. rigida*) are interspersed on the dry, acid, and nutrient-poor soils. Stands of planted white pine (*Pinus strobus*) appear throughout the area.

Wildlife management activities have occurred on the George Washington National Forest (GWNF) since 1924. The Big Levels Game Refuge, within the GWNF, was established in 1930. During that decade, a number of botanical investigations focused on Spring Pond in the Maple Flats Pond Complex, but also reported information on other sinkhole ponds in the area (Carr, 1937; Carr 1938; Rawlinson & Carr, 1937). Between 1936 and 1941, game species including deer, bear, beaver, turkey, grouse, and quail, were stocked by the VDGIF (Schwartz and Kocka, 1999). Two ponds were created as waterfowl impoundments in the Maple Flats area adjacent to Canada Run in the 1950s (R.H. Giles, pers. comm.). Aerial photographs dated September 1937 (National Archives and Records Administration, College Park, Maryland; Fig. 6c) indicate that several small, boggy wetlands existed on the sites now occupied by those man-made ponds. Even-aged timber management began in the 1960s in the GWNF. As a result, a patchwork of clearcuts and planted pine stands, primarily consisting of white pine (*Pinus strobus*) are intermixed among 40 year-old stands of oaks and mixed hardwoods. Most of the SVSP system in the National Forest north of the Coal Road is currently designated as Management Area 16 with an emphasis on grouse management. There are two exceptions, however. The Maple Flats Pond Complex, currently placed in Management Area 4, is a candidate for designation as a U.S. Forest Service Research Natural Area, and the Loves Run Pond Complex is designated as a Special Interest Area (Smith, 1991). The area south of the Coal Road to the top of Big Levels was designated a Special Interest Area by the U.S. Forest Service in 1993.

In this paper, we present an individual descriptive account of each sinkhole pond within three pond complexes of the SVSP system. Our aim is to provide a brief overview of the physical and biological characteristics of all the natural ponds and examine this system in a landscape context. Variation in hydroperiod causes each pond to be unique in its species assemblage and is thus responsible for the significant biodiversity of each pond complex. Our findings demonstrate that in order to protect the integrity of the fauna and flora, the collective assemblage of ponds needs to be addressed in conservation and management planning.

Sinkhole Pond Accounts

The ponds we describe here are categorized into one of three major pond complexes: 1) Maple Flats (Ponds 1-19, including Spring Pond, Horseshoe Swamp, Elusive Pond, Kennedy Mountain Meadows, and the man-made ponds on Canada Run; Fig. 2, Plates 1-5); 2) Loves Run (Ponds 20-31; Fig. 3, Plates 6-7); and 3) Sherando (Ponds 32-36; Fig. 4, Plate 8). We compiled summaries of each pond from the historic literature, aerial photographs from 1937, 1979, and 1985, our own field notes, Virginia Division of Natural Heritage (DNH) files, Buhlmann (1987), and Buhlmann & Mitchell (1988). In creating Figures 2-4, we used aerial photographs to modify and correct errors in pond locations, sizes, and shapes depicted on the Sherando and Big Levels USGS 7.5 minute topographic quadrangles currently available. A few unlabeled ponds appear on our figures but are not discussed because no information on them was available. Each pond narrative is presented in the same general format: shape and size, structural description, surrounding habitat, pond vegetation, noteworthy flora, known hydrology, fauna (amphibians, reptiles, invertebrates, fish), ownership (if other than USFS), threats, and all names used by other researchers to describe the pond. All ponds are illustrated with photographs in Plates 1-8.

Number and dates of site visits varied for each pond. We use observations from these visits to describe the hydroperiod of each pond, where possible. Descriptors include 1) permanent; 2) rarely dry completely, but fluctuate; 3) dry infrequently; 4) highly ephemeral (usually fill each year, but have short hydroperiods); 5) rarely fill at all; and 6) changing (those whose hydroperiod may be changing over time).

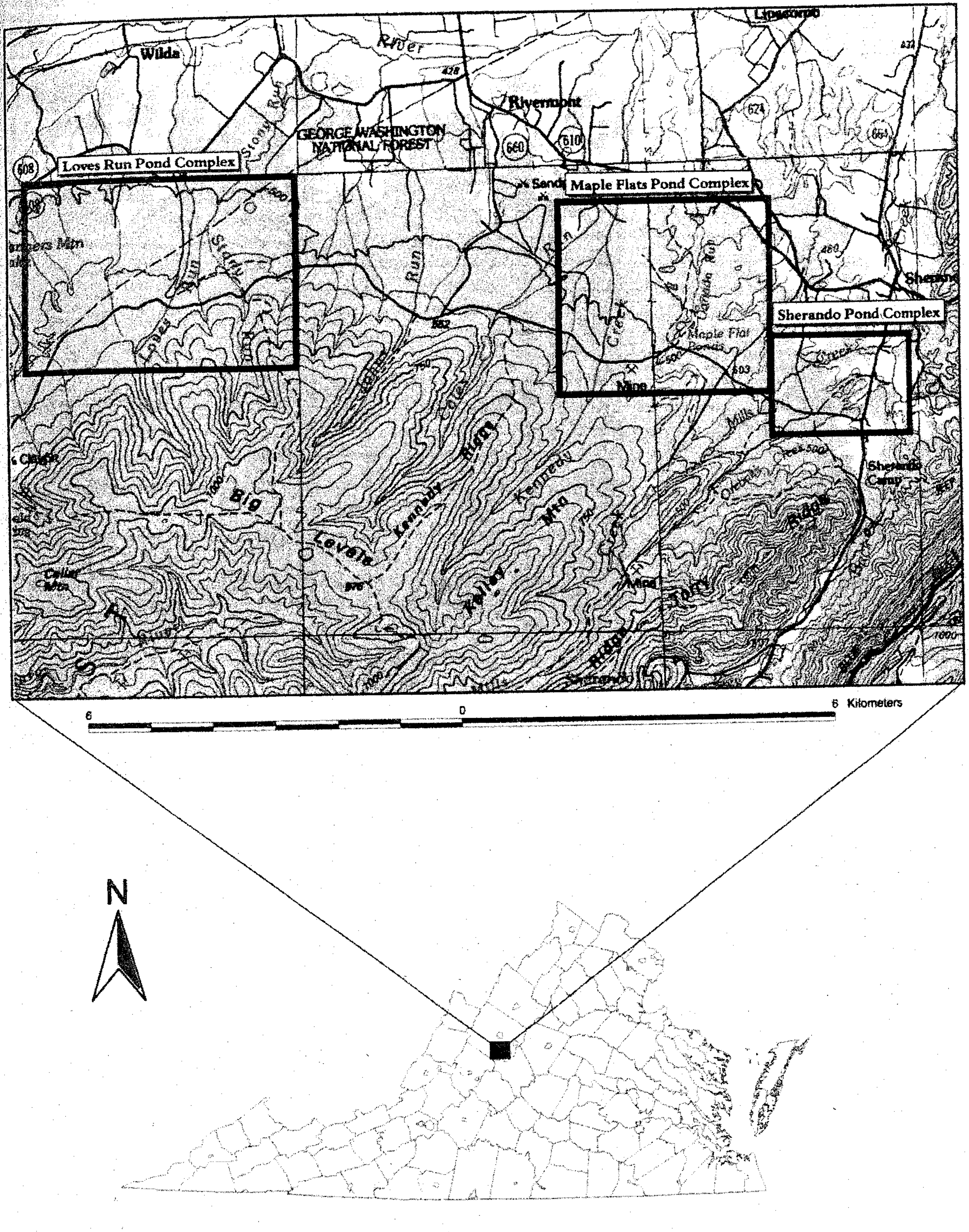


Fig. 1. Map depicting the three sinkhole pond complexes (Loves Run, Maple Flats, and Sherando) in the Shenandoah Valley Sinkhole Pond System, Augusta County, Virginia.

Maple Flats Pond Complex

The Maple Flats Pond Complex has been the focus of scientific investigations since the 1930s. Based on aerial photographs, forest habitat is known to have surrounded all of these ponds in September 1937 (Fig. 6c) when much of the surrounding Augusta County landscape was agricultural. Most of the ponds in this complex are located on U.S. Forest Service land, although significant ponds in private ownership are immediately adjacent to federal lands and are ecologically part of the complex (Fig. 1, 2, 6b). Most research and management discussions have focused on the Maple Flats complex. Twenty-two natural sinkhole ponds are described below. Two other man-made ponds also occur in the complex. We include them to provide a complete overview of the ponds in the complex and because they influence the fauna of the area.

Pond 1 (Plate 1)

Pond 1 is irregularly-shaped, measures approximately 30 x 34 m, and is 0.3 m deep when full. The pond is surrounded by an oak-hickory forest that provides a closed canopy. The bottom of Pond 1 has a decaying leaf substrate without *Sphagnum* or other aquatic vegetation. Pond 1 rarely fills and when it does, maintains water for short periods of time. It was observed filled in February 1994 and January 1998, and partially filled in March and July 1995 and February 1996. Pond 1 was dry (moist substrate) on 26 May 1987 when other ponds that rarely fill (see Ponds 3 and 14) contained some water. Successful metamorphosis of amphibian larvae from this pond has never been observed in any year from 1987-1998. Piles of dirt had been bulldozed into this pond sometime in the past and a large boulder blocks an access trail into the pond.

Pond 2 (Plate 1)

Pond 2 is oval-shaped, measures approximately 41 x 62 m, and is about 2.5-3.0 m deep when full. Trees surround the edge of the basin, but none are found within. Several large oak stumps occur within the pond near the edges. The pond has an open canopy. It is bordered to the east and south by an oak-hickory forest and to the north and west by a 1980 clearcut that was planted in white pine. When dry, the pond bottom is bare dirt and cobble with mats of *Sphagnum*, as well as some brush. When full, the surface is usually free of floating vegetation and the water is clear. A patch of grasses occurs inside the pond edge on the north side. Pond 2 is a highly ephemeral pond that sometimes fills in January (1992, 1998) or February (1994), but sometimes as early as October (1996) and occasionally not until March (1989). Pond 2 usually dries by June (1987, 1988, 1990, 1995). In July 1995, Pond 2 refilled completely after heavy rains, only to dry again by September of the same year.

The amphibian faunal assemblage consists of species that require seasonal ponds for breeding (Mitchell & Buhlmann, 1999). Annual juvenile recruitment is highly variable among species and among years and is directly related to hydroperiod. Depending on the time of filling and drying, dynamics among amphibian species vary among years (Mitchell & Buhlmann, 1999). For example, during dry autumns, female marbled salamanders (*Ambystoma opacum*) will deposit eggs under logs midway between the pond bottom and edge. The eggs hatch and larvae begin growing shortly after they are inundated by early-winter pond filling. Under these conditions, larval salamanders can attain a snout-vent-length (SVL) of 19-24 mm by March and are predators on the larvae of other later breeding amphibians. However, on 21 April 1989, the pond was overflowing after having been dry all winter. On this date, newly hatched marbled salamander larvae (SVL= 6-7 mm) and large aggregations of fairy shrimp (Order Eubranchiopoda) were observed. Fairy shrimp are among the most characteristic inhabitants of temporary ponds and pools (Pennak, 1978).

Pond 2 can be a "sink" habitat in some years for amphibians and a "source" habitat in others (e.g., Pulliam, 1988). By itself, Pond 2 could not maintain viable populations of the amphibian species in the area, but as part of a metapopulation of ponds, it is an important component in the Maple Flats Pond Complex. Another name for Pond 2 is Cold Pond (DNH files).

Pond 3 (Plate 1)

Pond 3 is nearly circular and measures approximately 46 x 52 m. It is relatively shallow and is less than 1.3 m deep when full. Although Pond 3 is surrounded by oak-hickory forest, it receives plenty of sunlight due to its size. The vegetation in the basin includes prairie willow (*Salix humilus* var. *tristis*), little blue stem (*Schizachyrium scoparium*), yellow wild-indigo (*Baptisia tinctoria*), and reindeer lichen (*Cladonia* sp.), all of which indicate infrequent filling. Other bottom substrate includes decaying leaves. One large pin oak (*Quercus palustris*) grows near the pond center and one shortleaf pine (*Pinus echinata*) grows inside near the edge; no other trees grow inside the basin. It has only been observed full with water two times (February 1994, March 1998) during the past 11 years. It was partially filled in May 1987, April 1994, and February 1995. It most often fills in winter and dries by early spring, but was observed with water in September 1996, possibly as a result of Hurricane Fran. Oddly, it was

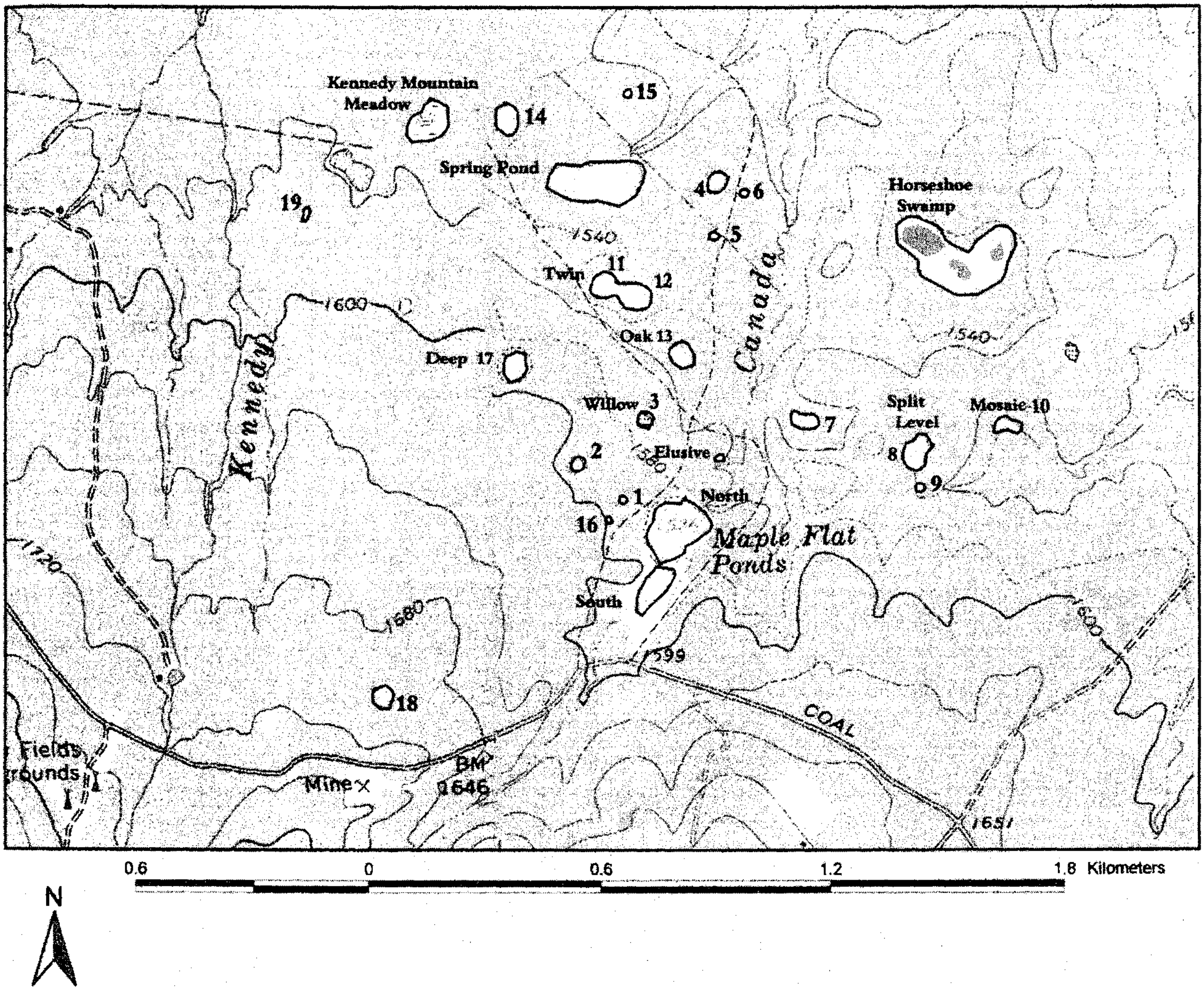


Figure 2. Maple Flats Pond Complex, Augusta County, Virginia. Each pond is numbered or named and those identifications correspond with descriptions given in the text.

completely dry on 21 April 1989 when nearby Pond 2 was overflowing.

The amphibian faunal assemblage consists of species that require seasonal ponds for breeding (Mitchell & Buhlmann, 1999). However, even in years when water was present, the hydroperiod was very short and salamander larvae (*Ambystoma* sp.) have never been observed to metamorphose successfully. Other names for Pond 3 include Dry Pond and Willow Pond (DNH files).

Pond 4 (Plate 1)

Pond 4 is oval-shaped and measures approximately 34 x 54 m. It is relatively shallow and is less than 1.2 m when full. Pond 4 is completely surrounded by a pin oak and black gum (*Nyssa sylvatica*) forest. *Sphagnum* grows throughout the pond and fallen trees are abundant in the basin. Greenbrier (*Smilax* sp.) grows around the pond edge. When the basin is full, accessing the pond edge is difficult. Little information is available about the hydrology of Pond 4. It has been observed full on 23 March 1995 and low (0.3 deep) on 14 October 1987. The pond is on private property immediately adjacent to USFS land and has been slightly impacted by dirt bikes.

Pond 5 (Plate 1)

Pond 5 is irregularly-shaped and measures approximately 26 x 27 m. It is shallow and is 1.0 m deep when full. Pond 5 is located within a former clearcut (cut in 1980). When first visited in October 1987, it was dry and filled with brush and stumps and contained some dry *Sphagnum* and bottlebrush grass (*Elymus hystrix*). When revisited on 23 March 1995 the surrounding forest consisted of 15-year-old white pine and pin oak regeneration. Pond 5 was full March 1995 and January 1997, partially full during May 1995, and dry in October 1987 and May 1997. The nearest hardwood forest is 50 m distant. Pond 5 was full on 23 March 1995 and contained numerous salamander (*Ambystoma* spp.) egg masses. Numerous metamorphic green frogs (*Rana clamitans*) were present on 4 October 1987.

Pond 6 (Plate 2)

Pond 6 is small, circular, and measures approximately 21 x 24 m. It is shallow and is 0.6 m deep when full. Pond 6 is surrounded by a mixed oak forest, including white oak (*Q. alba*), pin oak, and chestnut oak (*Q. montana*). There is one pin oak growing near the pond center. Vegetation within the pond includes some grasses, *Sphagnum*, and decaying leaves. Pond 6 was full on 5 January 1997 and dry by 28 May 1997. It was also dry on 23 March 1995. It fills infrequently. No faunal information has been collected. Pond 6 is located on private property immediately adjacent to USFS land. Between visits in 1987 and 1995, it was impacted by off-road vehicles (see Plate 2).

Pond 7 (Plate 2)

Pond 7 resembles a wooded swamp, rather than a pond. It measures 74 x 98 m and appears to be very shallow. The basin consists of a complete and thick coverage of *Sphagnum*. It has a closed canopy. Trees and greenbrier grow throughout the basin. There are no defined pond edges. Pond 7 was dry when visited on 14 October 1987.

Pond 8 (Plate 2)

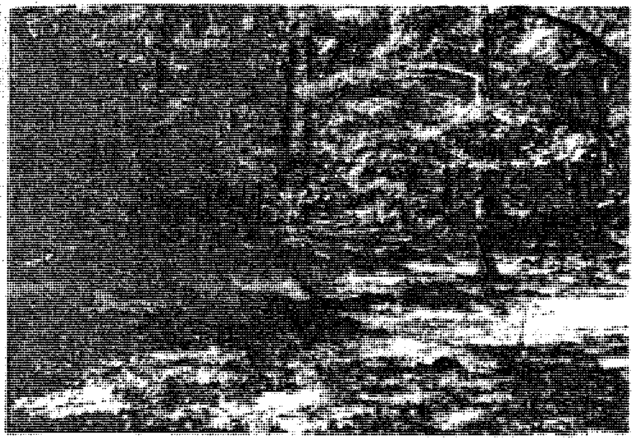
Pond 8 is a large pond that is generally elliptical with a narrow neck on the northeast side. It measures approximately 72 x 165 m. It is generally shallow and is 0.6 m deep when full. The pond is surrounded by an oak forest and has a completely open canopy. No trees grow within the large shallow basin. Pond 8 is the third largest pond in the Maple Flats complex; Spring Pond and Maple Flats Pond North are larger. The basin bottom is covered with grasses and *Sphagnum*. When full, Pond 8 is connected to Pond 9. Pond 8 was full in March 1995, but low in March 1988. Likewise, it was low in January 1992, but dry in January 1989. It contained water at least through May in 1988 and was recorded dry in September 1988 and October 1987. It was low in April 1989. Spotted salamanders (*A. maculatum*), spring peepers (*Pseudacris crucifer*), red-spotted newts (*Notophthalmus viridescens*), and snapping turtles (*Chelydra serpentina*) have been observed in Pond 8. Another name for Pond 8 is Split Level Pond (DNH files).

Pond 9 (Plate 2)

Pond 9 is a wooded swamp, approximately 27 x 32 m, and 0.6 m deep when full. It was connected to Pond 8 when water levels were high (March 1988 & March 1995) and contained some water in April 1989. It is completely shaded by surrounding forest and has a poorly defined pond edge. It contains some *Sphagnum*, but decaying leaves and brush dominate. Pond 9 is connected to Pond 10 by a small drainage. Five spotted salamander egg clusters were observed on 21 April 1989.

Pond 10 (Plate 3)

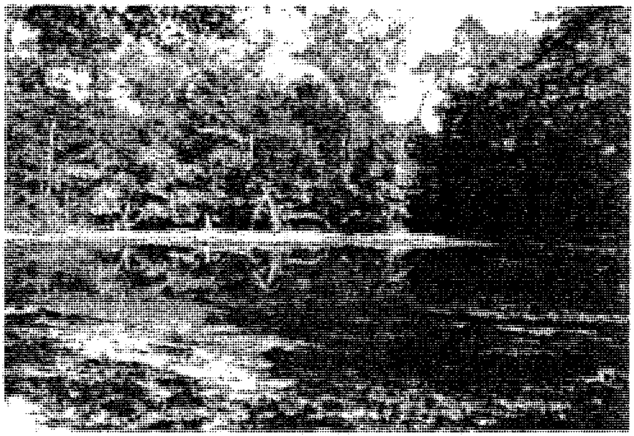
Pond 10 is approximately 35 x 72 m and is 0.6 m deep when full. It was full and thought to be relatively permanent when first visited in October 1987. Sedge clumps grew along the edges. *Sphagnum* was found throughout, and a moist grassy island was located in the pond center. The pond has an open canopy and is surrounded by mixed hardwood forest. However, Pond 10 was dry July 1988-February 1989. It was full on 21 April 1989, when spotted salamander egg clusters that appeared to have been eaten by turtles were found. Pond 10 was full in January 1992. When visited in March 1995, the drainage that flowed from Pond 10 had been impounded by beaver (*Castor canadensis*). The pond was flooded to a depth exceeding 2.0 m and the surrounding forest was flooded. A portion of the drainage towards Pond 9 was also flooded. In its current state, the habitat may not be suitable for several species of amphibians and reptiles that have been found there previously. Some turtles that were marked initially in Pond 10 in March 1988 were observed subsequently during April 1989, 2.5 km distant, in Pond 34 (Sherando



Pond 1. Photo taken 4 October 1987 from west pond edge looking east.

Pond 2. Photo taken 21 January 1988 from southeast pond edge looking northwest.

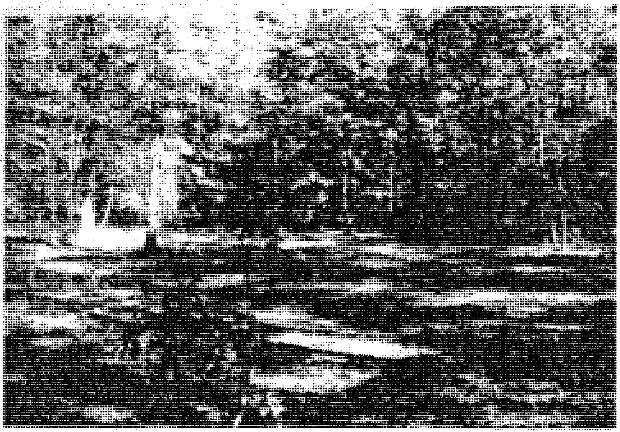
Pond 3. Photo taken 24 March 1995 from south pond edge looking north



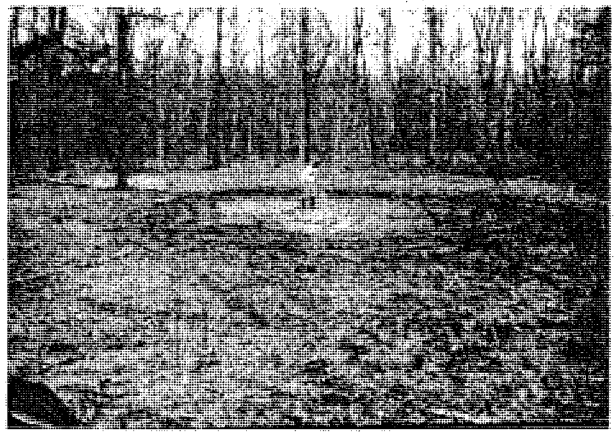
Pond 4. Photo taken 4 October 1987 from west pond edge looking east.

Pond 5. Photo taken 4 October 1987 from southeast pond edge looking northwest.

Pond 5. Photo taken 24 March 1995 from southeast pond edge looking northwest.



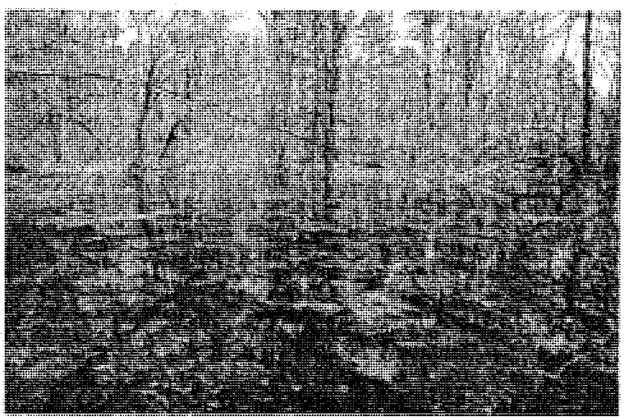
Pond 6. Photo taken 14 October 1987 from northwest pond edge looking southeast.



Pond 6. Photo taken 24 March 1995 from northwest pond edge looking southeast. Photo by JCM

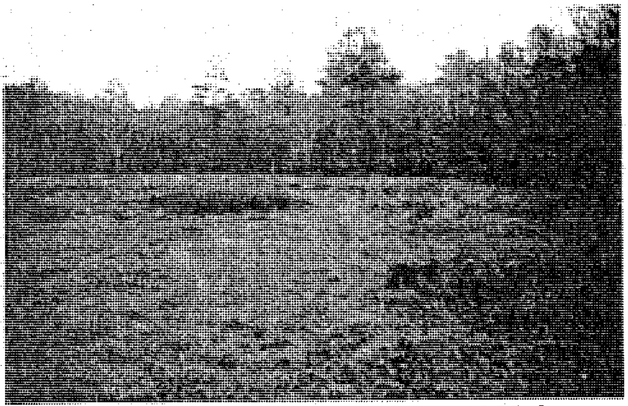
Pond 7. Photo taken 14 October 1987 from north pond edge looking south.

Pond 8. Photo taken 18 January 1989 from southwest pond edge looking northeast.

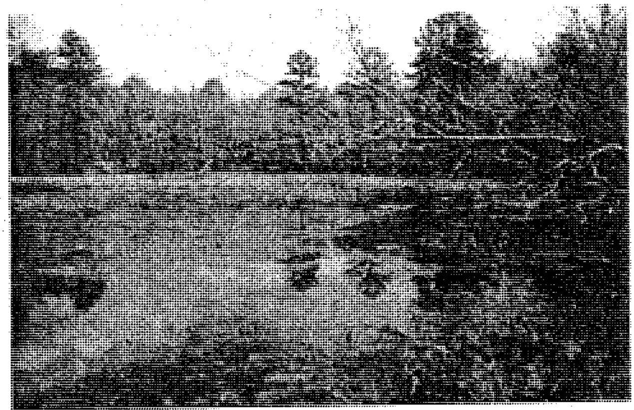


Pond 9. Photo taken 21 April 1989 from north pond edge looking south.

Horseshoe Swamp. Photo taken September 1998 by Gary Fleming.



Pond 10. Photo taken 18 January 1989 from northwest pond edge looking southeast.



Pond 10. Photo taken 21 April 1989 from northwest pond edge looking southeast.

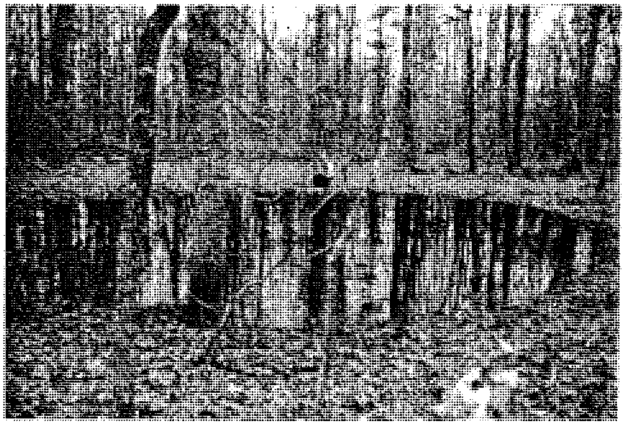
Pond 11. Photo taken 21 March 1988 from northwest pond edge looking southeast.

Pond 11. Photo taken 17 October 1998 from southeast pond edge looking northwest.

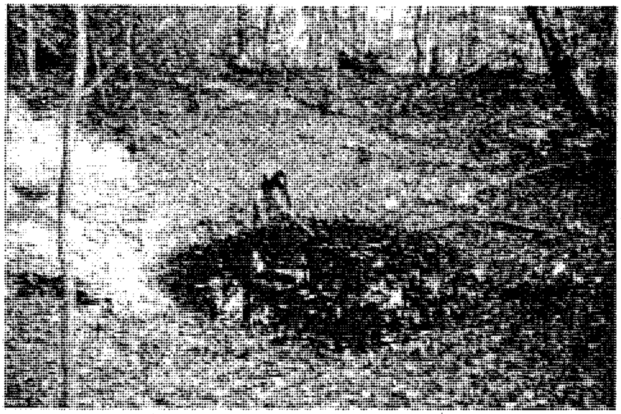
Pond 12. Photo taken January 1992 from northwest pond edge looking southeast.

Pond 13. Photo taken 18 January 1989 from west pond edge looking east.

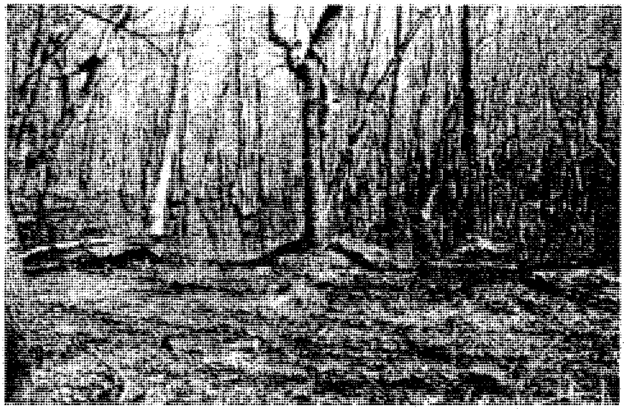
Pond 14. Photo taken 7 February 1992 from southeast pond edge looking northwest.



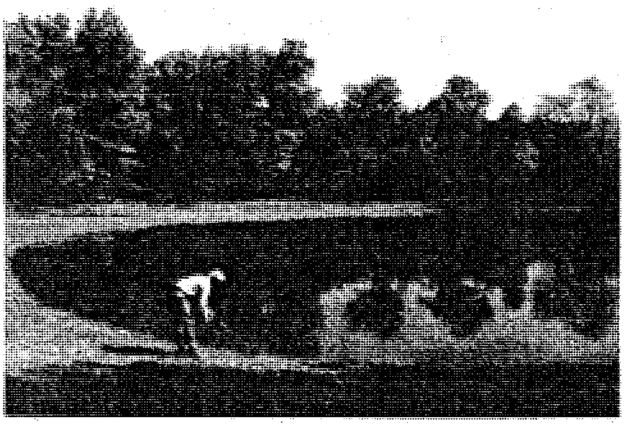
Pond 15. Photo taken 24 March 1995 from direction unknown.



Pond 16. Photo taken 4 October 1987 from west pond edge looking east.



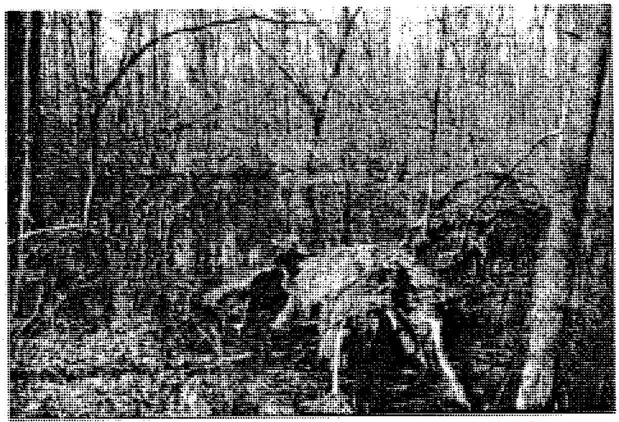
Pond 18. Photo taken 23 March 1995 from south pond edge looking north.



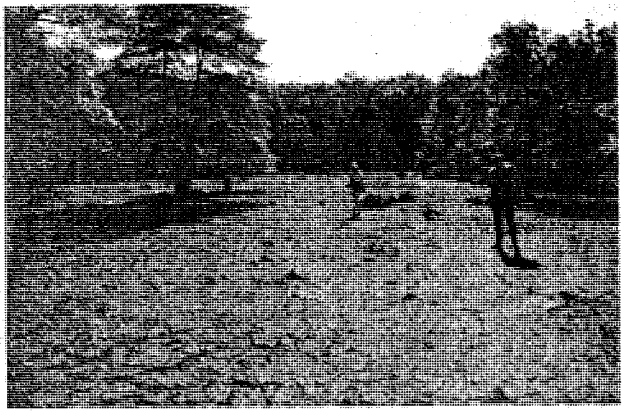
Pond 17. Photo taken 14 October 1987 from west pond edge looking east. Photo by R. Glasgow.

Pond 17. Photo taken 17 October 1998 from east pond edge looking west.

Pond 19. Photo taken 15 March 1988 from east pond edge looking west.



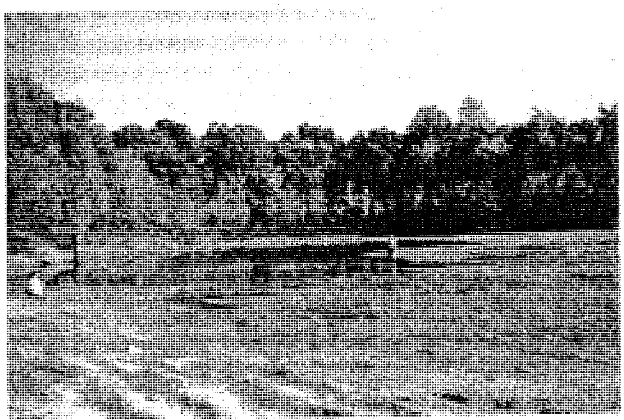
Elusive Pond. Photo taken 21 April 1989 from direction unknown.



Kennedy Mountain Meadow Pond. Photo taken 17 October 1998 from northeast pond edge looking southwest.

Spring Pond. Photo taken 26 May 1987 from south pond edge looking east.

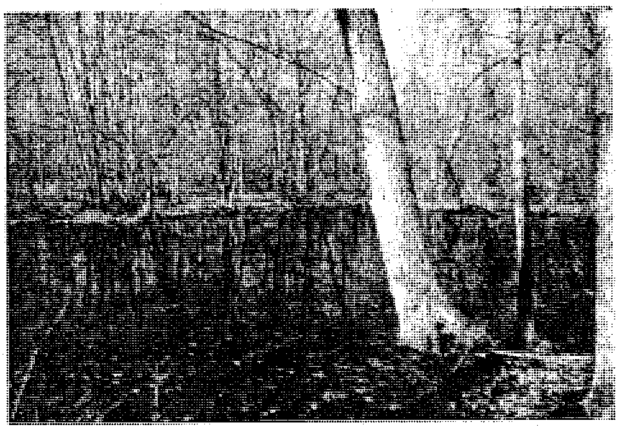
Maple Flats North Pond. Photo taken 18 January 1989 from north pond edge looking southeast.



Maple Flats North Pond. Photo taken 17 October 1998 from north pond edge looking southeast. Photo by Don Church.

Pond 20. (aka Green or Quarles Pond) Photo taken in August 1983 by Ali Wieboldt.

Pond 21. Photo taken 13 April 1988 from northeast pond edge looking southwest.

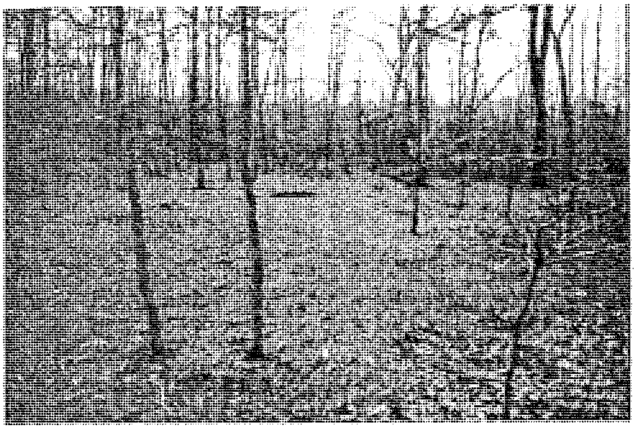


Pond 22. Photo taken 13 April 1988 from south pond edge looking north.

Pond 23. Photo taken 13 April 1988 from south pond edge looking north.

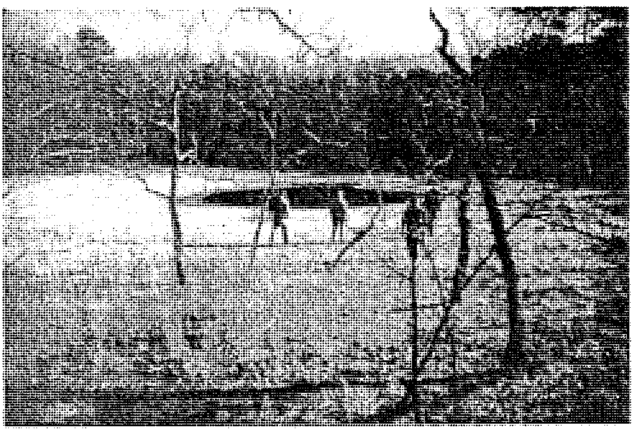
Pond 24. Photo taken 13 April 1988 from southwest pond edge looking northeast.

Pond 25. Photo taken 21 April 1989 from west pond edge looking east.

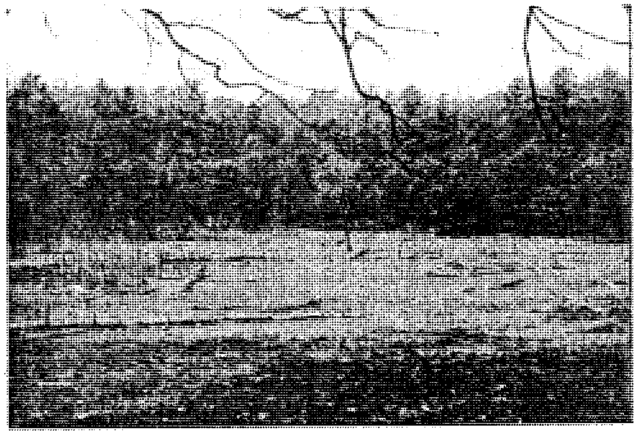


Pond 26. Photo taken 21 April 1989 from east pond edge looking west.

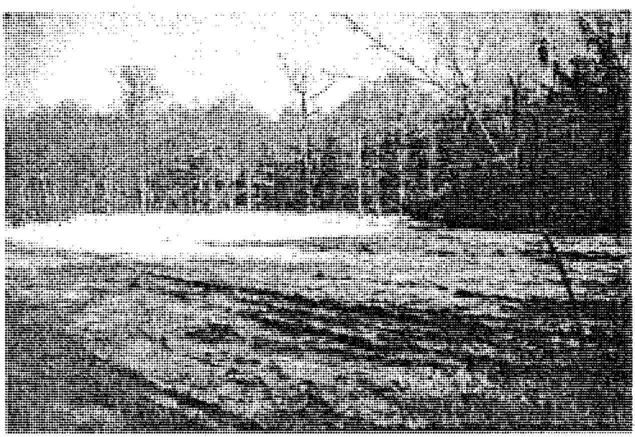
Pond 27. Photo taken 23 March 1995 from north pond edge looking south.



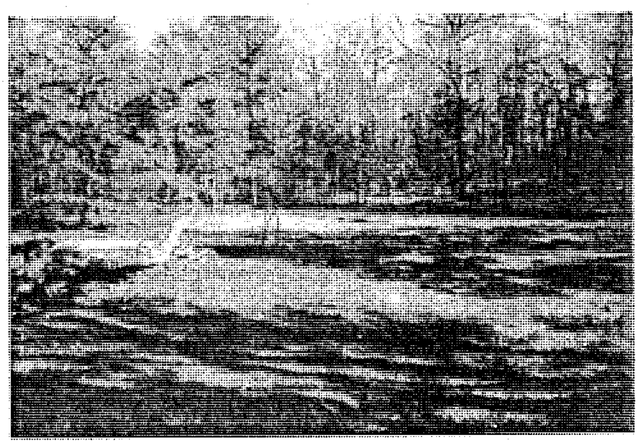
Pond 28. Photo taken 23 March 1995 from south pond edge looking north.



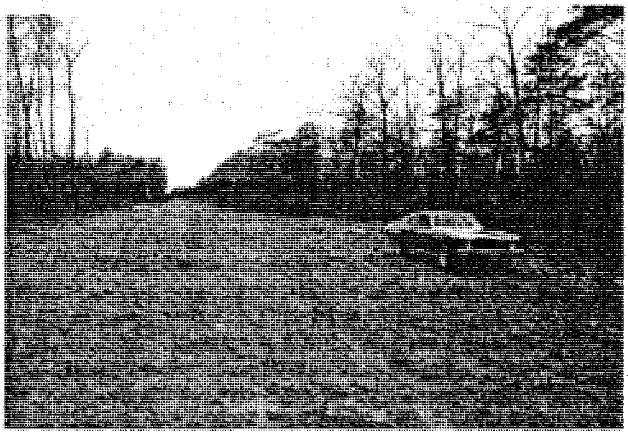
Pond 29. Photo taken 27 April 1988 from north pond edge looking south.



Pond 30. Photo taken 1 May 1988 from direction unknown.



Pond 31. Photo taken 1 May 1988 from direction unknown.

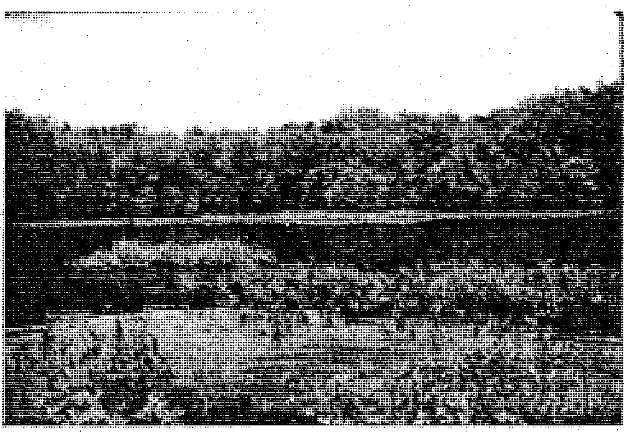


The gas right-of-way that separates ponds of the Loves Run complex, 21 April 1989.

Pond 32. Photo taken 21 April 1989 from east pond edge looking west.

Pond 33. Photo taken 21 April 1989 from northeast pond edge looking southwest.

Pond 34. Photo taken 21 April 1989 from west pond edge looking east.



Pond 35. Photo taken 18 May 1988 from west pond edge looking east.

Pond 36. Photo taken 18 May 1988 from south pond edge looking north.

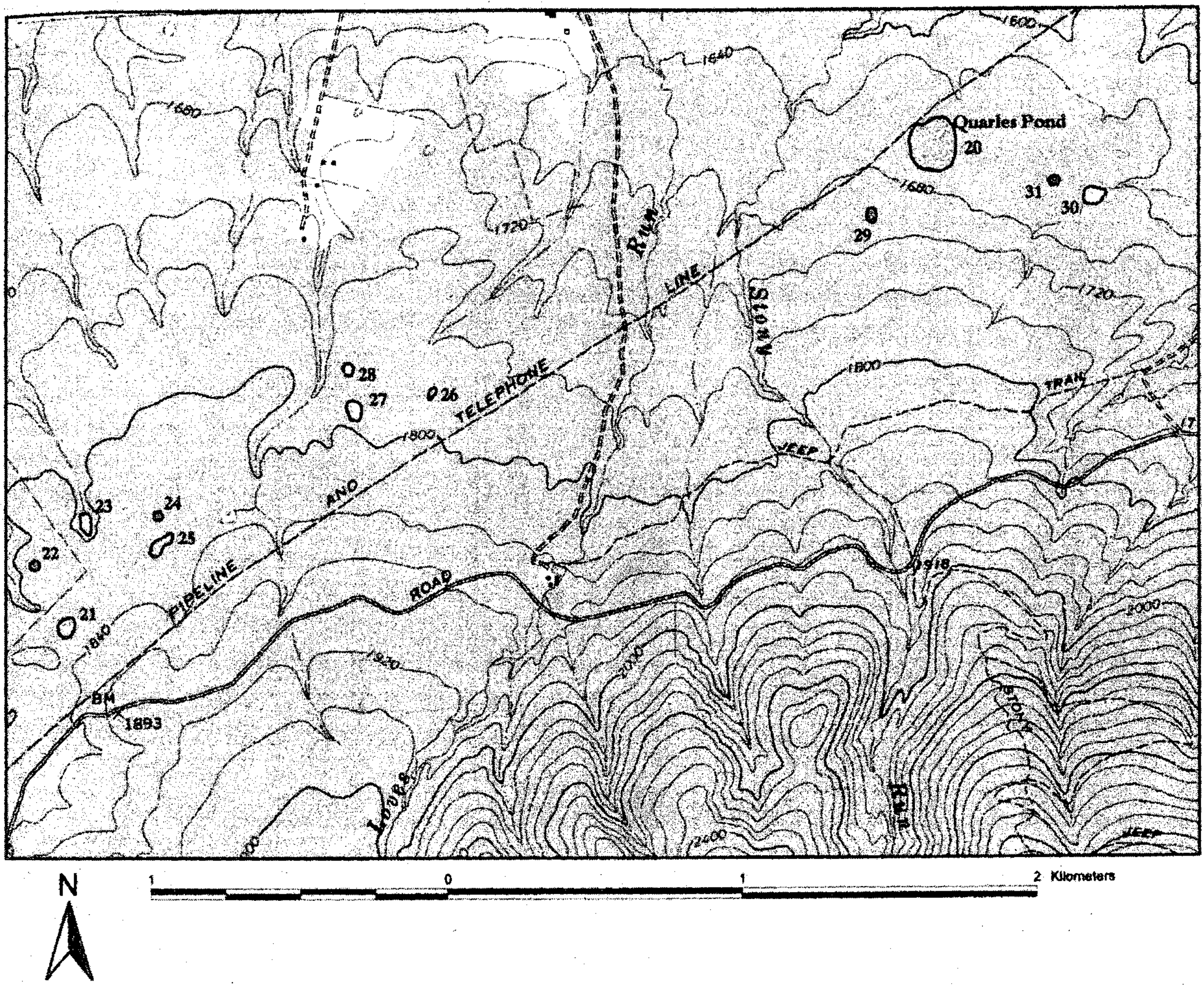


Fig. 3. Loves Run Pond Complex, Augusta County, Virginia. Each pond is numbered or named and those identifications correspond with descriptions given in the text.

Pond Complex) illustrating the need to consider conservation of the SVSP system in a metapopulation and landscape level context. Another name for Pond 10 is Mosaic Pond (DNH files).

Pond 11 (Plate 3)

Pond 11 is a circular depression approximately 53 x 66 m in size that is nearly 2.0 m deep when full. It is connected to Pond 12 when the pond is full. The two ponds together have often been referred to as Twin Pond(s). Pond 11 (Twin Pond North) is surrounded by hardwood forest but has an open canopy. No trees grow within the pond basin. This is a shallow pond with grasses growing in shallows and the rare endemic plant, Virginia sneezeweed (*Helenium virginicum*) occurring along the edges. *Sphagnum* mats are present in the deeper areas. Cobble-sized rocks are prominent on the bottom and the water is usually clear. Pond 11 dries completely only infrequently and has only been observed dry in October 1997 and 1998 since our study began in 1987. Depending on the year, Pond 11 has been observed full in most months. It has had its lowest water levels recorded in September (1992, 1994, 1997, 1998). Hundreds of dead *Rana* tadpoles were observed in a 1 m diameter depression at the pond's dry center on 17 October 1998. Although located on USFS land, 4-wheeler tracks were found in 1989. Those same ruts were still visible on the pond bottom in October 1998.

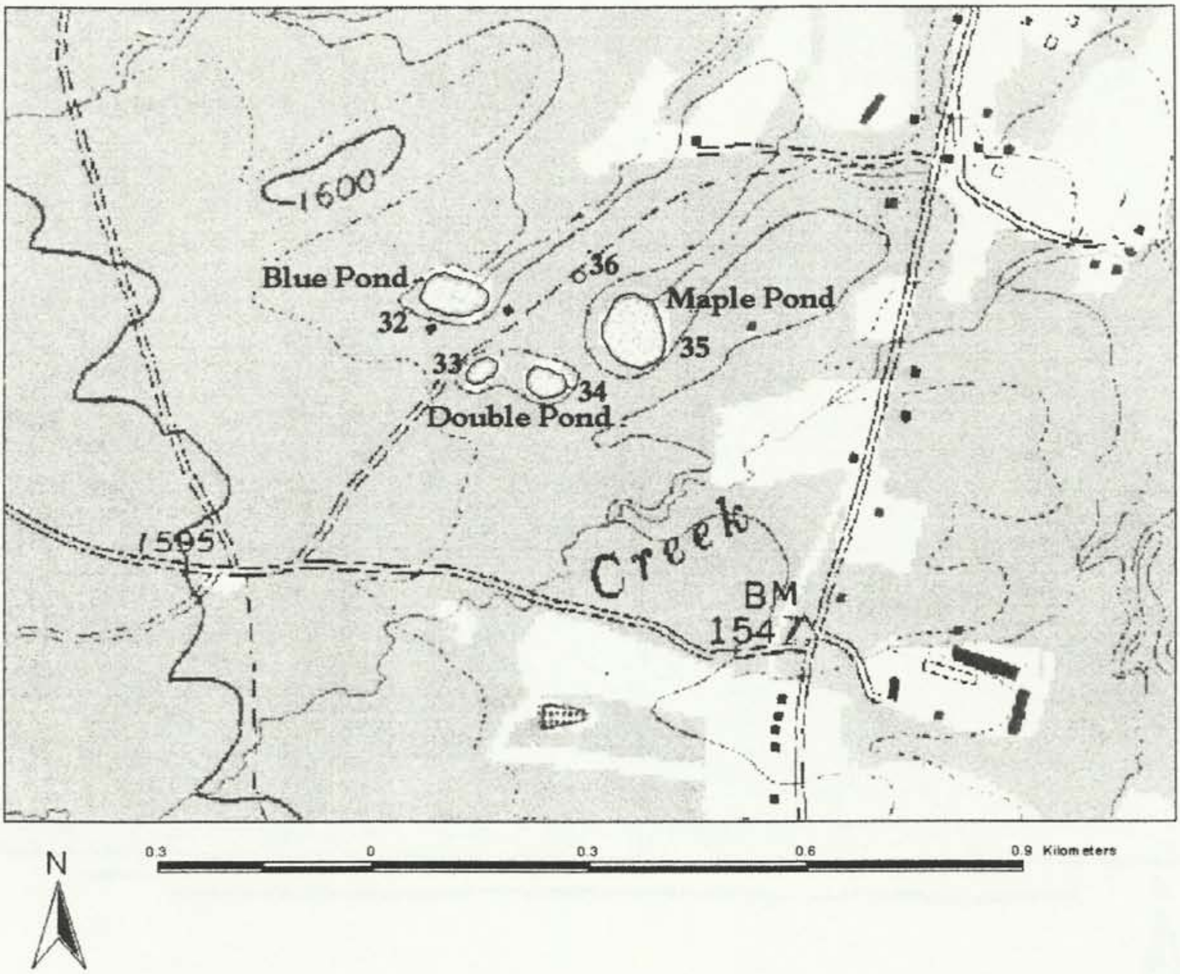


Fig. 4. Sherando Pond Complex, Augusta County, Virginia. Each pond is numbered or named and those identifications correspond with descriptions given in the text.

Pond 12 (Plate 3)

Pond 12 is a circular depression approximately 60 x 76 m and is nearly 2.0 m deep when full. It is connected to Pond 11 when the water is at its highest and has been referred to as part of the Twin Pond(s). Pond 12 (Twin Pond South) is also partially surrounded by hardwood forest but has an open canopy. The east side of this pond borders a 15-year-old clearcut that consists of white pine and pin oak. This same clearcut extends to encompass Pond 5 (see Fig. 6a). No trees grow within the pond basin. Pond 12 is a shallow pond with rare Oakes pondweed (*Potomogeton oakesianus*) occurring throughout. Cobble-sized rocks are prominent on the bottom and the water is usually clear. Pond 12 dries completely only infrequently and has only been observed dry once during October 1997, since the study began in 1987. Its hydrologic cycle seemed similar to Pond 11, but it will hold water longer by a month or so. Pond 12 contained a 50-m diameter circle of water on 17 October 1998, when other ponds that dry infrequently had dried. On several occasions, red-spotted newts have been observed under logs in dry portions of the pond basin. On 16 October 1997, Pond 12 was pumped dry by the USFS to eliminate bluegill sunfish (*Lepomis macrochirus*) that had been stocked there.

Pond 13 (Plate 3)

Pond 13, often called Oak Pond, is nearly circular, measures approximately 66 m x 72 m, and is nearly 4.0 m deep when full. The pond is surrounded by an oak-hickory forest but has an open canopy in the pond center. Large oaks surround the edge and provide partial shade on all sides. The pond has a gently sloping bottom, until it reaches the center, where there is a deep hole containing about 1 m of organic matter. The bottom of Pond 13 is covered with *Sphagnum* that often floats to the surface when the pond fills and forms large floating mats. Pond 13 fluctuates but rarely, if ever, dries completely. It has never been observed to dry completely during our study, as the center depression always retained some water. Pond 13 usually refills in either January or February. The lowest water levels have been recorded August -January. Pond 13 was near full on 21 April 1989, when Pond 2 was overflowing. Amphibian larvae have been able to metamorphose successfully from Pond 13 in all years of the study, 1987-1998. Pond 13 is probably one of the most important ponds for amphibian reproduction in the Maple Flats Pond Complex (Mitchell & Buhlmann, 1999). Frogs, such as green frogs (*Rana clamitans*) and bullfrogs (*R. catesbeiana*), that require permanent ponds can also reproduce successfully in Pond 13. Many species of odonates, giant water bugs, wood ducks, great blue and green-backed herons, and belted kingfishers have been observed.

Pond 14 (Plate 4)

Pond 14 is an elliptical pond measuring 24 x 27 m. It is < 1 m deep when full and contains little live vegetation. When full, the water is dark due to the decaying leaves in the bottom. It is partly shaded by pin oaks that grow around the edges. The surrounding habitat includes a 15-year-old clearcut planted in white pine. Pond 14 is highly seasonal and does not fill in all years. Its hydroperiod allows it to be classified behaviorally intermediate between Ponds 2 and 3. For example, it held water into June during 1987, long enough for larval salamanders to metamorphose, whereas Pond 3 dried too early in May. In February 1992, Pond 14 was partially filled, whereas Pond 3 was dry. In March 1995, the pond was partially filled; on all other visits it was dry. The pond is on USFS property but borders private land.

Pond 15 (Plate 4)

Pond 15 has been visited infrequently during this study. It is circular and measures 15 x 15 m, and is 0.6 m deep when filled. It is a small depression, surrounded by an oak forest. No vegetation other than decaying leaves was present on the clay substrate. It probably fills infrequently or has a short hydroperiod. It has been observed dry in October 1987 and partially filled in March 1995. Pond 15 is on private property adjacent USFS land and is near Spring Pond.

Pond 16 (Plate 4)

Pond 16 is a small, deep, conical pond measuring 13 x 18 m and exceeding 3.0 m in depth when full. No vegetation other than decaying leaves is present. Pond 16 is surrounded by an oak-hickory forest. The pond is most likely to be full January-March, but has been observed full in May 1992 and July 1995. It has been observed dry June-September, but begins to refill in October in some years. Recently, a large oak tree that had been growing on the inside of the sinkhole rim toppled across the basin, leading to speculation that the sinkhole might be expanding. Pond 16 was partially filled with water during Spring 1988 and never completely dried that year. On 21 June 1988, marbled salamander larvae were still present in Pond 16, although larvae of the same species had metamorphosed and left the dry basin of adjacent Pond 2. Cricket frogs (*Acris crepitans*), amphipods, and diatoms are often numerous. Bullfrogs and green frogs are often seen here. Pond 16 is also called Conical Pond (DNH files).

Pond 17 (Plate 4)

Pond 17 is a large, circular pond measuring 61 x 75 m. It is 3.0 m deep when full. The pond is bordered by a 15 year old white pine plantation on the south side and oak-hickory forest on the other three sides. The pond basin is open, and the shallower areas are covered with grasses, whereas the deepest portion of the bottom is covered with algae. The deepest section also contains a spikerush, *Eleocharis acicularis*, that is prominent when the pond is dry. It does not dry every year and its hydroperiod seems similar to Ponds 11 and 12. However, in January 1992, Pond 17, which is up slope from Ponds 11 and 12, was observed completely full when those ponds were nearly dry. The water in Pond 17 is usually very clear during winter visits, however, it was unexplainably turbid in January 1997. The pond has been observed full in the winter and spring months of most years. Even in drought years, the pond only dries in the latter part of the summer. On 12 August 1988, a small circle of water 5 m in diameter remained, but by 7 September 1988 the pond was dry. The pond was dry on 17 October 1998. Pond 17 is used by amphibians such as *Ambystoma* spp. and wood frogs (*Rana sylvatica*). The long hydroperiod of Pond 17 suggests that it is a relatively reliable source pond for recruiting metamorphosing amphibians into the adult population. Green frogs and red-spotted newts are also common. The white pine plantation that separates Pond 17 from Pond 2 may have been a barrier to amphibian dispersal when it was a clearcut, and it may still be. The effects on amphibian movements of such habitats should be evaluated. Pond 17 has been called Deep Pond (DNH files) and Clear Pond (Buhlmann & Mitchell, 1988).

Pond 18 (Plate 4)

Pond 18 is a small wooded pond with poorly defined edges that is shaded under an oak canopy. Maximum depth is 0.8 m when full. Abundant *Sphagnum* carpets the pond bottom. It is surrounded by an oak-hickory forest. Very little is known about the hydrology of Pond 18. When visited in March 1988, the pond contained water and several salamander (*Ambystoma* spp.) and wood frog egg masses were observed. It also contained some water on 23 March 1995 when more than 90 spotted salamander egg clusters were counted. Green frogs, red-spotted newts, and four-toed salamanders (*Hemidactylium scutatum*) were observed on 6 July 1998 when the pond was partially filled.

Pond 19 (Plate 5)

Pond 19 is a small shallow, elliptically-shaped pond, with a clay bottom devoid of *Sphagnum*. It was dry during visits on 15 March and 13 April 1988 and is probably < 0.6 m deep when full. A very wet spring would be needed for the pond to hold water long enough for amphibian larvae to successfully develop. In 1988, Pond 19 was proposed to be impacted by timber activities in Cut Unit 1119-2. It has not been revisited since Spring 1988, and its current condition is unknown.

Elusive Pond (Plate 5)

Elusive Pond in an irregularly-shaped, closed canopy depression. It is small and lies between Pond 13 and the man-made Maple Flats North pond. It has shrubs around the edges and a bottom covered with dead leaves. It was clear, full, and 1.0 m deep when visited on 21 April 1989. Nine spotted salamander egg clusters were observed on that date.

Horseshoe Swamp (Plate 2)

Horseshoe Swamp is a diverse wetland complex that occurs in a 10-acre, spring-fed, shallow depression that drains by a single outlet to Canada Run. It consists mostly of red maple-pitch pine dominated, seasonally-flooded swamp forest, but also includes shrub swamp and emergent wetland communities. Two open, marshy areas of approximately 1.5 acres and 0.2 acres are present. Groundwater flows into the wetland in high volumes during the winter months, but water is mostly absent in the summer and early fall. Water levels in the ponded areas range up to 1.0 m deep. The forested wetlands have a shrub layer of highbush blueberry (*Vaccinium corymbosum*), maleberry (*Lyonia ligustrina*), and swamp azalea (*Rhododendron viscosum*). *Sphagnum* occurs throughout. A portion of the community is saturated or inundated to such duration that the tree canopy thins and a shrub swamp forms, dominated by the heaths listed above. The lowest portions of Horseshoe Swamp consist of a seasonally and semi-permanently flooded herbaceous community dominated by emergent species such as Barrett's sedge (*Carex barrattii*), three-way sedge (*Dulchium arundinaceum*), Canada mannagrass (*Glyceria canadensis*), sharp-scaled mannagrass (*Glyceria acutiflora*), mild water-pepper (*Polygonum hydropiperoides*), Canada rush (*Juncus canadensis*), and buttonbush (*Cephalanthus occidentalis*). To date, only botanical investigations have been conducted; a faunal survey is needed.

Kennedy Mountain Meadows (Plate 5)

Kennedy Mountain Meadows is a large shallow pond (see Fig. 2). Carr (1937-38) described this pond as a shallow basin in the heart of the flatwoods of the Blue Ridge. The pond basin is < 1 m deep when full, pond edges are poorly defined, and small oak trees grow throughout the pond. The canopy is relatively open and the pond has a savanna-like appearance when dry. *Sphagnum* is abundant. The pond is partially surrounded by a mixed oak and pine forest and by a young stand of planted pines. The pond is on private property adjacent to Pond 14 and near Spring Pond. On 3 March 1988 it contained some water; on 21 March 1988 the depth was < 0.3 m and we counted salamander (*Ambystoma* spp.) egg clusters. On that date no marbled salamander larvae were seen, but freshwater shrimp and diatoms were collected.

When the pond was dipnetted again on 17 May 1988, no larval salamanders were found, suggesting that the pond may have dried and refilled since the previous March visit. It was dry in January 1992 and October 1998, and contained some water in March 1995. The Nature Conservancy continues to work with the landowner on the conservation of this site. An old ditch traverses the pond basin. Its effect on the hydrology is unknown. Knox (1997, 1999) studied Virginia sneezeweed (*H. virginicum*) in this pond for more than 12 years.

Spring Pond (Plate 5)

Spring Pond is one of the few permanent ponds within the Maple Flats Pond Complex. Spring Pond is a kidney-shaped depression that measures 92 x 226 m. It is approximately 1.0 m deep but has a soft, deep organic substrate. *Sphagnum* is restricted to the edges. No trees grow

Figure 5. Fragmentation of the landscape in the Sherando area of Augusta County, Virginia (circa 1979). The Maple Flats Pond Complex appears in the bottom third of the photograph. Fragmentation of the landscape and degradation of other sinkholes north of Maple Flats are evident. The Maple Flats Pond Complex represents only a remaining fraction of a once much larger complex of ponds.

in the pond basin. Golden club (*Orontium aquaticum*) covers the surface of the pond. The pond edges contain various shrubs, the rare swamp pink (*Helonias bullata*), and large-fruited cranberry (*Vaccinium macrocarpon*). Spring Pond is surrounded by hardwood forest. A small wildlife clearing is maintained adjacent to the south side of the pond.

Spring Pond maintains a relatively constant water level and is believed to be spring-fed. On 17 October 1998, the pond water level was down by 0.5 m. Spring Pond contains populations of bluegill sunfish and killifish (*Fundulus affinis*). Amphibians that prefer seasonal ponds for breeding sites, such as *Ambystoma* have not been recorded at Spring Pond. Spring Pond is the only known location for the spring salamander (*Gyrinophilus porphyriticus*) within the sinkhole pond complex and may also represent the source population for painted turtles (*Chrysemys picta*) that periodically appear in the seasonal sinkhole ponds (Mitchell & Buhlmann, 1999). Spring Pond has been referenced numerous times in the literature, and its unusual plant community was noted as early as the 1930s (Carr, 1938; Rawlinson & Carr, 1937). Spring Pond has also been called Hack Pond (Craig, 1969). Pitcher plants have been introduced here.

Maple Flats North Pond (Plate 5)

The Maple Flats North Pond is located adjacent to Canada Run in the Maple Flats Pond Complex. It is a manmade impoundment created in the 1950s for waterfowl management. The pond receives full sunlight and is approximately 135 x 150 m and 1-2 m deep when full. The water level can be controlled by a dam. The pond was reduced to a 20 x 50 m area, less than 0.25 m deep, in October 1998. It was also observed low in September 1987 and was refilling in October 1987. Bluegill sunfish and *Rana* spp. tadpoles are abundant. Spotted salamander larvae were captured in May 1987. The pond appears to have botanical characteristics of some other seasonal ponds in the area (N. Van Alstine & A. Belden, pers. comm.). Small seasonal pond or bog habitats may have been present on the site prior to construction (Fig. 6c).

Maple Flats South Pond (no photo)

The Maple Flats South Pond is fed by Canada Run that traverses the east side of the Maple Flats area. It is a man-made impoundment that was created in the 1950s for waterfowl management. The pond recieves full sunlight. It is approximately 51 x 102 m and at least 2.0 m deep when full. The water level can be controlled by a dam and has always been full when visited. Populations of cricket frogs, green frogs, and red-spotted newts inhabit this pond. Bluegill sunfish and *Rana* tadpoles are abundant. It is the only potential source for invasion of non-indigenous fishes into the sinkhole ponds of the area.

LOVES RUN POND COMPLEX

The Loves Run Pond Complex is located approximately 7.0-11.5 km west of the Maple Flats Pond Complex (Fig. 3). Only one sinkhole pond, called Grassy Pond, and containing Virginia sneezeweed, occurs in the landscape between these two complexes (DNH files). The Loves Run complex includes 12 ponds (Ponds 20-31) and the greatest distance between the outermost ponds is approximately 4.5 km. This complex also includes the largest pond in the SVSP system. A gas pipeline right-of-way separates Ponds 21-28 from Pond 20 and Ponds 29-31 (see Plate 8). Less information is available about this complex than the Maple Flats Pond Complex because most recent field studies were conducted in the latter area. However, earlier botanical work (Carr 1937, 1938) recognized several of these ponds. The Loves Run Pond Complex should also include Shenandoah Acres, a botanically significant pond identified by Carr in the 1930s and visible on 1937 aerial photography, that has been converted to a swimming lake. It was not investigated during this study. Several other ponds are visible on the 1937 photography that appear slightly southwest of the currently defined Loves Run complex; their current status is unknown. The Loves Run Pond Complex was forested in 1937 and continues to be forested to the present.

Pond 20 (Plate 6)

Pond 20 (Quarles Pond, Quarles Lake, Green Pond) is the largest sinkhole pond in the entire SVSP study area. Although not measured, it appears to be slightly larger than the man-made Maple Flats North Pond when viewed on aerial photographs. It is a large circular pond and appears to contain water permanently. It has a soft bottom with deep organic matter. Carr (1938) referred to it as Green Pond and noted that it was strikingly different from other ponds in the region, due to its abundance of spatterdock (*Nymphaea lutea* ssp. *advena*). During visits on 18 March and 27 April 1988, many red-spotted newts, cricket frogs, and *Rana* spp. tadpoles were observed. No *Ambystoma* spp. were observed. Painted turtles are present. On 23 March 1995 the surface was covered with emergent macrophytes. It does not contain golden club, as does Spring Pond, but has patches of *Scirpus torreyi* (T. Wieboldt, pers. obs.). Pond 20 is located along the gas pipeline right-of-way adjacent to USFS land and is privately owned. In 1988, the owner considered stocking sport fish in the pond, but was not believed to have done

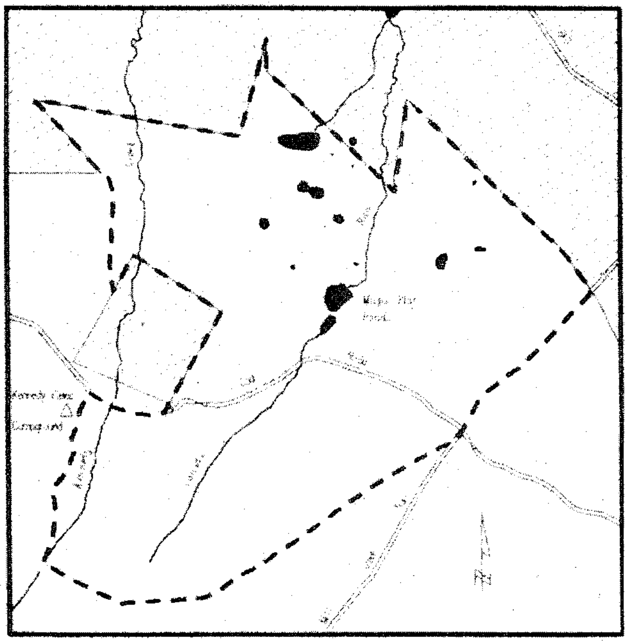


Fig. 6a.
Proposed boundary for the Maple Flats Research Natural Area.

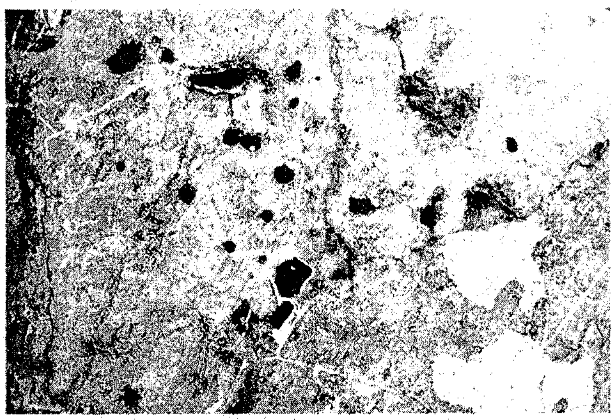


Fig. 6b.
Maple Flats sinkhole pond complex, circa 1985.

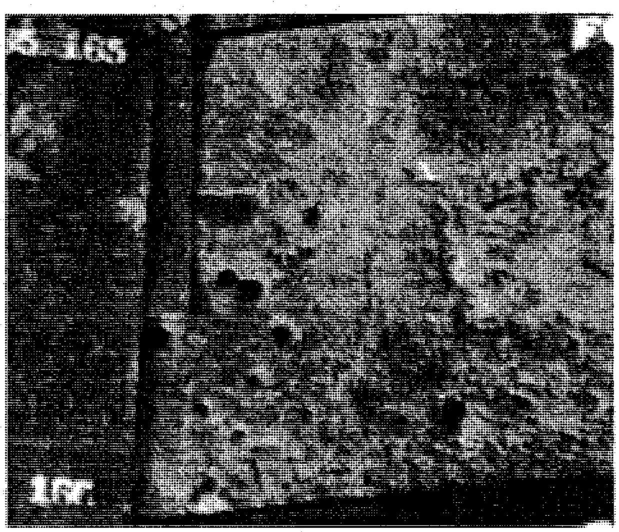


Fig. 6c.
Maple Flats sinkhole pond complex, September 1937.

Fig. 6. (a) Proposed boundaries for the Research Natural Area (RNA), (b) Aerial photograph of the Maple Flats Pond Complex, circa 1985, (c) Aerial photograph of the Maple Flats Pond Complex, September 1937.

so. He was also concerned about USFS plans to sell timber on the slope above the pond which could have impacted the pond via runoff.

Pond 21 (Plate 6)

Pond 21 is an elliptically-shaped, permanent pond. It is approximately 1.0 m deep but has a soft organic bottom that is at least 20 cm deep. Vegetation includes bladderwort (*Utricularia* sp.) and coontail (*Ceratophyllum* sp.). A mixed hardwood forest surrounds the pond. A steep embankment covered with *Rhododendron* borders the southern edge of the pond. The pond was full on 13 April 1988 when red-spotted newts and *Rana* spp. tadpoles were captured and painted turtles were observed basking. No *Ambystoma* larvae were dipnetted. The pond was also full on 21 April 1989 and 23 March 1995.

Pond 22 (Plate 6)

Pond 22 is a small, shallow pond with a leaf litter bottom. It contained some water on 13 April 1988. Pond 22 is located on private property and in 1988 was bordered by a clearcut on two sides. It may be a suitable *Ambystoma* breeding site in wet years.

Pond 23 (Plate 6)

Pond 23 is a small, elliptical, shallow (< 1 m deep), seasonal pond. A panic grass, *Panicum rigidulum*, grows throughout the firm-bottomed pond. A mixed hardwood forest surrounds the pond and the north side is edged with greenbrier. The pond contained some water on 13 April 1988, 21 April 1989, and 23 March 1995. Red-spotted newts, wood frog eggs, marbled salamander larvae, spring peepers and cricket frogs were found on the latter date. Marbled salamander larvae were also found on 21 April 1989.

Pond 24 (Plate 6)

Pond 24 is a shallow swale with grasses and *Sphagnum*. It is connected to Pond 25 when water levels are high. It is surrounded by hardwood forest. It contained some water on 13 April 1988 when red-spotted newts, marbled salamander larvae, and cricket frogs were captured. It contained water on 23 March 1995, but no vertebrates were observed.

Pond 25 (Plate 6)

Pond 25 is a large, shallow pond surrounded by hardwood forest. The pond edge is surrounded by greenbrier and *Sphagnum*. Pond 25 was full on 13 April 1988. It was also full on 21 April 1989 when red-spotted newts were observed. Pond 25 is similar in vegetative structure to Ponds 10, 33, and 34. *Ambystoma* sp. larvae, red-spotted newts, and spring peepers were observed here on 23 March 1995.

Pond 26 (Plate 7)

Pond 26 is a small, shallow depression. It probably holds water only in exceptionally wet years. It was dry on 13 April 1988 when we captured a northern water snake (*Nerodia sipedon*) under a log at the pond's center. The pond was also dry on 21 April 1989 and 23 March 1995. Pond 26 is shown to be full in a 10 March 1985 aerial photograph.

Pond 27 (Plate 7)

Pond 27 is a large circular pond that is several (> 3.0) meters deep when full. The pond is surrounded by an oak-dominated hardwood forest. The pond basin is covered with panic grass with the exception of a 30 m diameter circle of spikerush (*E. acicularis*) at the pond center. The pond was dry on 13 April 1988 and 21 April 1989. On 23 March 1995, the pond contained water in the center circle, at a depth of 0.5 m. Red-spotted newts were observed mating, wood frog egg clusters were present, marbled salamander larvae were observed eating the wood frog eggs, and spring peepers were calling. Red-backed salamanders (*Plethodon cinereus*) were observed under logs within the pond margin. Pond 27 was full on 10 March 1985 and dry on 16 March 1979 based on aerial photographs. Based on vegetation within the basin, Pond 27 appears not to have filled completely in many years. We categorize Pond 27 as filling infrequently; however, perhaps the underlying geology or hydrology has changed and the pond basin has lost its water resistant lining. Quarry activity in the region may be a concern.

Pond 28 (Plate 7)

Pond 28 is a large circular pond near Pond 27. It is 1.0 m deep when full, but fills infrequently. The pond is surrounded by an oak-dominated hardwood forest. The pond basin is covered with panic grass (*P. rigidulum*). The pond has always been dry when visited (13 April 1988, 21 April 1989, and 23 March 1995). Aerial photos indicate that it was dry on 16 March 1979 and full on 10 March 1985. There have been no sampling efforts to determine faunal composition.

Pond 29 (Plate 7)

Pond 29 is a large pond, similar in size to Pond 27, and was completely dry when visited on 27 April 1988. Sapling Virginia pine (*Pinus virginiana*) was invading the basin and downed woody debris (logs) was present. Aerial photos from 10 March 1985 show Pond 29 empty when all other nearby ponds (Ponds 27, 28) that fill very infrequently were full of water. Perhaps the water-resistant lining has been broken due to the dissolution of the limestone underneath. Geological and hydrological investigations are needed. On 27 April 1988, numerous red-spotted newts (red eft stage) and red-backed salamanders were found under log debris in the pond basin. Many slimy salamanders (*Plethodon cylindraceus*) were found under rocks along the inside edges of the pond basin. On 23 March 1995 there was no free water in the pond, but the center was moist and a young pin oak was growing in the center of the pond.

Pond 30 (Plate 7)

Pond 30 is a shallow pond that is slightly smaller than Pond 29. It was dry when visited on 27 April 1988 and had been impacted by 4-wheelers. It was shown to contain water on a 10 March 1985 aerial photograph. Pond 30 has been called Grassy Pond (DNH files).

Pond 31 (Plate 7)

Pond 31 is a small shallow pond adjacent to Pond 30. It was dry when visited on 27 April 1988. It has also been impacted by 4-wheeler use. Aerial photographs from 10 March 1985 indicate some standing water.

SHERANDO POND COMPLEX

The Sherando Pond Complex lies approximately 2-3 km east of the Maple Flats Pond Complex (Fig. 1). Five ponds (Ponds 32-36) occur in this group (Fig. 4). They are all in private ownership, although the properties border USFS land. Hardwood forest surrounds these five ponds, in contrast to other remnant ponds in the Sherando vicinity which have been altered and surrounded by agriculture, since at least 1937. These ponds are important in the overall metapopulation conservation of the SVSP system. At least one rare amphibian species is believed to breed in at least one of the ponds. Turtles originally captured in Pond 10 in the Maple Flats Pond Complex, a distance of 2.5 km, have been observed in Pond 34. The ponds were visited by us with permission from the tenants.

Pond 32 (Plate 8)

Pond 32 is a large, very deep, circular pond, exceeding 6.0 m deep when full. It is surrounded by forest but has an open canopy. The bottom substrate is firm. Two private homes are on the pond's edge. The tenant informed us that Pond 32 nearly dries in some summers. On 18 May 1988 the pond was full and the water was clear enough to see the bottom. Marbled salamander larvae, *Rana* spp. tadpoles, red-spotted newts, northern water snakes, and various invertebrates were dipnetted. Painted turtles were seen. We were told that goldfish had been stocked in 1987, but all had died during low water conditions the subsequent year. On 21 April 1989 the pond was again full. Pickerel frogs (*Rana palustris*) were calling and trout had been reportedly stocked in the pond. Pond 32 was called Blue Pond by Carr (1937-38).

Ponds 33 and 34 (Plate 8)

These are shallow, somewhat irregular-shaped ponds, that are approximately 0.7 m deep with profuse growth of grasses and *Sphagnum*. They are connected when the water is high and both are east of a gravel road which leads to private homes on the property. On 18 May 1988, Pond 33 was dry and Pond 34 contained some water. Both ponds were full on 21 April 1989. Painted turtles and northern watersnakes were captured on 18 May 1988. Ponds 33 (west) and 34 (east) have been called Double Pond (C. E. Stevens, pers. comm.).

Pond 35 (Plate 8)

Pond 35 is a large shallow pond with a soft bottom and Carr (1938) classified it as a permanent pond. On 18 May 1988, we collected invertebrates, red-spotted newts, and green frogs. No *Ambystoma* larvae were found. On 21 April 1989 it was also full and many painted turtles were observed. Pond 35 was called Maple Pond by Carr (1938).

Pond 36 (Plate 8)

Pond 36 is a very small sinkhole that has been partially filled with trash. It contained some water on 18 May 1988, but was dry on 21 April 1989. No faunal information is available.

DISCUSSION

The Value of Isolated Wetlands to Biodiversity

Isolated depressional wetlands of varying sizes, hydrology, and geologic origin occur throughout the eastern United States. The importance of such isolated wetlands to biodiversity has been overlooked in the past, but is becoming increasingly recognized (Dodd, 1992; Burke & Gibbons, 1995; Buhlmann, 1998; Semlitsch & Bodie, 1998; Semlitsch, 1998). Isolated wetlands have been called different names depending on the region and their perceived origins (Lide, 1997; Sharitz & Gibbons, 1982; Schalles et al., 1989). For example, Carolina bays dot the southeastern Coastal Plain landscape from Georgia north to Delaware, but are most abundant in the Carolinas (Sharitz & Gresham, 1998). A cluster of sinkhole ponds, known as the Grafton Ponds Complex, is found in the Virginia Coastal Plain in York County (Pettry et al., 1979; Bliley & Pettry, 1979; Sankey & Schwenneker, 1993). Woodland vernal pools are recognized as important and threatened habitats in the northeastern United States for amphibians (Stone, 1992; Klemens, 1993; Kenney, 1994; Madison, 1997).

The Shenandoah Valley sinkhole ponds are unusual due to their location within the Blue Ridge physiographic region and their geologic origins. Sinkholes are a prominent feature of karst landscapes, such as the Cumberland Plateau (Holsinger & Culver, 1988). However, karst sinkholes rarely hold water due to the solution of limestone. In fact, surface streams often disappear underground in karst landscapes. However, Shenandoah Valley sinkhole depressions often have impermeable bottoms, permitting water retention and, hence, the existence of the unique sinkhole ponds. Because of the isolated position of the Shenandoah Valley sinkhole ponds, relative to other isolated wetlands complexes described above, and because the ponds themselves date back at least to the Pleistocene (Hack, 1965), it is not surprising that the floral and faunal communities of the SVSP system are unique and contain disjunct populations and rare and endemic species (Carr, 1938; Fleming & Van Alstine, 1999; Knox, 1999; Mitchell & Buhlmann, 1999; Roble, 1999).

Variation in SVSP Hydrology

Within the SVSP system, variation in hydrology among ponds promotes unique faunal and floral communities. No two ponds in the system are identical. Variation in hydroperiods, which results in a range of permanent to highly ephemeral ponds, is the underlying reason for the collectively significant biodiversity, and why it is essential to protect the entire system. Each species of rare plant, vertebrate, and insect is known from only a few of the ponds (Fleming & Van Alstine, 1999; Mitchell & Buhlmann, 1999; Roble, 1999). However, nearly every pond contains an element record for a species of conservation interest (Virginia Division of Natural Heritage, unpubl. data).

Variation in amphibian faunal assemblages is directly related to hydroperiod (Semlitsch, 1987; Pechmann et al., 1989; Mitchell & Buhlmann, 1999). For example, bullfrogs require ponds that hold water continuously for more than one year in order for larval development to be completed. Wood frogs and ambystomatid salamanders, such as spotted, tiger, and marbled salamanders, require fish-free ponds that usually contain water from late autumn through early summer (Hopey & Petranka, 1994). Because of year to year variability in hydroperiod of individual ponds, it is the large number of ponds in each complex that maintains the viability of populations within the system. For example, at eight ponds monitored over a 6-year period, 1987-1992, amphibian metamorphosis was successful at four (1991) to seven (1987) ponds depending on the year and rainfall (K.A. Buhlmann & J.C. Mitchell, unpublished data). Therefore, in some years, some ponds, such as Pond 2, can be sink habitats (e.g., Pulliam, 1988; Pulliam & Danielson, 1991) in which no larvae are recruited to the adult population or larvae are forced to transform at smaller body sizes (Semlitsch, 1988a; Mitchell & Buhlmann, 1999). Other ponds, such as Pond 13, may be source populations because they successfully rear metamorphic adults every year, and perhaps produce excess individuals that can disperse and recolonize other sites. In theory, sink populations alone are not viable populations because over the long term, mortalities exceed recruitment (Pulliam, 1988). Identifying source and sink populations is critical in the design of effective landscape conservation models.

Metapopulations and Landscape-level Management

The diversity of pond types is responsible for the diversity of plants and animals in the SVSP system. It is the collective complex of ponds that make this area important, and it is in that context that we must focus landscape-level, metapopulation conservation and management efforts. Fragmentation of habitat can lead to local population extinction (Noss, 1987; Opdam, 1991). Therefore, connectivity of habitats among ponds becomes an important management consideration (Beier & Loe, 1992; Beier & Noss, 1998) due especially to the variation in suitability among years exhibited by different ponds. Dispersal movements, microhabitat requirements, and use of corridors in terrestrial habitats by amphibians and reptiles, as well as other organisms, has received increased research attention in recent years (Buhlmann et al., 1993; Buhlmann, 1998; Burke & Gibbons, 1995; Dodd, 1995; 1996; Semlitsch, 1981; 1983a). Adult amphibians may move greater than 1 km away from wetland breeding sites (Williams, 1973; Dodd, 1996), and mean distances for pond-breeding salamanders was estimated at 164 m for 95% of the population (Semlitsch, 1998). For nearly all amphibians and reptiles, the terrestrial habitat adjacent to aquatic breeding sites is equally as important as the ponds. Both habitats are required for populations of these species to exist (Bennett et al., 1970; Burke & Gibbons, 1995; Buhlmann, 1998; Dodd & Cade, 1998). From an amphibian perspective, terrestrial habitats that protect individuals from desiccation and freezing, and that provide suitable soil structure required for a fossorial existence (e.g., Semlitsch, 1983b) are essential. Therefore, before activities such as clearcutting are conducted, efforts should be made to protect appropriate terrestrial habitat surrounding ponds and maintain corridors between ponds and pond complexes. No timber operations should be conducted within 200 m of pond borders. Such activities have detrimental effects on the population dynamics of amphibian populations (deMaynadier & Hunter, 1995; Means et al., 1996; Palis, 1997; Petranka et al., 1993).

Other Threats to the SVSP System

The larger landscape perspective needs to be considered when designing long term conservation and management plans for the SVSP complex. Some ponds have already been lost due to agriculture, increasing human population size and associated new housing developments, filling, or conversion to swimming lakes. Some ponds have been impacted by off-road vehicle (ORV) users. Some ponds have been stocked periodically with game fish that negatively affect the breeding success of native amphibians (Semlitsch, 1988b) and likely alter trophic dynamics (e.g., Taylor et al., 1988). Ponds have been left isolated in the fragmented landscape throughout the Sherando area north of the pond complexes addressed in this paper (Fig. 5).

The SVSP system lies in the region of the Appalachians that receives acid precipitation in the form of sulfuric and nitric acid from prevailing westerly winds (Galloway et al., 1983; Hyer et al., 1995). Acid levels in streams in the Blue Ridge and Ridge and Valley physiographic provinces in Virginia have increased over the past several decades and atmospheric pH values of 4 or less are not uncommon (Webb et al., 1989; Camuto, 1991). Acid-base chemistry studies of some of the ponds in the SVSP system (Downey et al., 1999) reveal that nearly all of the sinkhole ponds are acidic and that some exhibit pH readings low enough to be potentially harmful to plants and animals. Two-year average pH values for 28 ponds range from 4.74 to 6.0 and corresponding acid neutralizing capacity levels range from -30.4 to 22.2, indicating no neutralizing capacity in the system (Downey et al., 1999). In addition, acidity can increase quickly to about pH 4.0 during some rain events in some ponds. High acid levels are known to be detrimental to amphibians and invertebrates by reducing embryo and larval survival, and affecting behavior (Dunson & Connell, 1982; Freda, 1986; Freda & Dunson, 1986; Freda & Taylor, 1992; Kutka, 1994). Risk from anthropogenic pollution should be assessed for at least all rare and listed species in the SVSP system, based on current knowledge about acid conditions.

Conservation of the Shenandoah Valley Sinkhole Pond System

The Loves Run Pond Complex has been designated as a Special Interest Area by the USFS. The Maple Flats Pond Complex, located largely on U.S. Forest Service property and encompassing 272.8 hectares (Smith, 1991), may be designated as a Research Natural Area (Fig. 6a). An adjacent pond on private property, Kennedy Mountain Meadows, has been under conservation agreement between the landowner and The Nature Conservancy. However, despite these encouraging efforts, the focus of conservation needs to be expanded. Cooperative conservation agreements should be initiated with owners of ponds on all adjacent private lands. All isolated wetlands, no matter how small, are important for maintaining biodiversity across the landscape (Semlitsch & Bodie, 1998). Management strategies should not be limited to the ponds themselves, but also include appropriate terrestrial buffer habitats and provide corridors and landscape linkages to other ponds and pond complexes.

The Shenandoah Valley Sinkhole Pond system represents a wealth of biodiversity that is part of the natural heritage of the Commonwealth of Virginia and the Appalachian region. Progressive management, protection, and conservation efforts must be pursued jointly among federal and private landowners, and state and local governmental agencies to ensure that the legacy of the area is preserved for future generations and to prevent significant biodiversity losses.

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LITERATURE CITED

Beier, P., & S. Loe. 1992. A checklist for evaluating impacts to wildlife movement corridors. Wildlife Society Bulletin. 20:434-440.

Beier, P., & R. F. Noss. 1998. Do habitat corridors provide connectivity? Conservation Biology 12:1241-1252.

Bennett, D. H., J. W. Gibbons, & J. C. Franson. 1970. Terrestrial activity in aquatic turtles. Ecology 51:738-740.

Bliley, D.J. & D.E. Pettry. 1979. Carolina bays on the Eastern Shore of Virginia. Soil Scientific Society of America Journal. 43: 558-564.

Buhlmann, K.A. 1987. Summary of Activities and Report of Findings. Contract # 00-3383-7-445. Unpublished report and photographs to the George Washington National Forest, Harrisonburg, VA. 34 pp.

Buhlmann, K. A. 1998. Ecology, terrestrial habitat use, and conservation of a freshwater turtle assemblage inhabiting a seasonally fluctuating wetland with emphasis on the life history of *Deirochelys reticularia*. Ph.D. Dissertation, University of Georgia, Athens, GA. 176 pp.

Buhlmann, K. A., & J. C. Mitchell. 1988. Field surveys for amphibians and reptiles on the George Washington National Forest: Summary of activities and results 1 March 1988-2 October 1988. Unpublished report to the George Washington National Forest, Harrisonburg, VA. 28 pp.

Buhlmann, K. A., & R. L. Hoffman. 1990. Geographic distribution: *Ambystoma tigrinum tigrinum*. Herpetological Review 21:36.

Buhlmann, K. A., J. C. Mitchell, & C. A. Pague. 1993. Amphibian and small mammal abundance and diversity in saturated forested wetlands and adjacent uplands of southeastern Virginia. Pp. 1-7 *In* S. D. Eckles, A. Jennings, A. Spingarn & C. Wienhold (eds.), Proceedings of a Workshop on Saturated Forested Wetlands in the Mid-Atlantic Region: the State of the Science, Annapolis, MD.

Burke, V. J., & J. W. Gibbons. 1995. Terrestrial buffer zones and wetland conservation: a case study of freshwater turtles in a Carolina bay. Conservation Biology 9:1365-1369.

Camuto, C. 1991. Dropping acid in the southern Appalachians. Trout 32(Winter):16-23, 26-33, 36, 38-39.

Carr, L. G. 1937. Utriculariaceae of Augusta County. Claytonia 4:23-24.

Carr, L. G. 1938. Coastal plain plants in southeastern Augusta County, Virginia, in the Valley and Blue Ridge Provinces. Virginia Academy of Sciences Proceedings 1937-38:1-6.

Craig, A. J. 1969. Vegetational history of the Shenandoah Valley, Virginia. Geological Society of America Special Paper 123:283-296.

deMaynadier, P. G., & M. L. Hunter, Jr. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Reviews 3:230-261.

Dodd, C. K., Jr. 1992. Biological diversity of a temporary pond herpetofauna in north Florida sandhills. Biodiversity and Conservation 1:125-142.

Dodd, C. K., Jr. 1995. The ecology of a sandhills population of the eastern narrow-mouthed toad, *Gastrophyrne carolinensis*, during a drought. Bulletin Florida Museum Natural History 38:11-41.

Dodd, C. K., Jr. 1996. Use of terrestrial habitats by amphibians in the sandhill uplands of north-central Florida. Alytes 14:42-52.

Dodd, C. K., Jr., & B. S. Cade. 1998. Movement patterns and the conservation of amphibians breeding in small, temporary wetlands. Conservation Biology 12:331-339.

Downey, D.M., S. Wirtz, K.R. Kruer, & S.P. Douglas. 1999. Water chemistry assessment of the Shenandoah Valley sinkhole ponds, Augusta County, Virginia. Banisteria 13:53-65.

Duffy, D. L. 1991. The geomorphology of alluvial fan deposits on the west flank of the Blue Ridge, Augusta County, Virginia. M.S. Thesis, Old Dominion University, Norfolk, VA. 118 pp.

Dunson, W.A., & J. Connell. 1982. Specific inhibition of hatching in amphibian embryos by low pH. Journal of Herpetology 16:314-316.

Fleming, G.P., & N.F. Van Alstine. 1999. Plant communities and floristic features of sinkhole ponds and seepage wetlands of southeastern Augusta County, Virginia. Banisteria 13:67-94.

Freda, J. 1986. The influence of acidic pond water on amphibians: a review. Water, Air and Soil Pollution 30:439-450.

Freda, J., & W.A. Dunson. 1986. Effects of low pH and other chemical variables on the larval distribution of amphibians. Copeia 1986:454-466.

Freda, J., & D.H. Taylor. 1992. Behavioral response of amphibian larvae to acidic water. Journal of Herpetology 26:429-433.

Galloway, J.N., S.A. Norton, & M.R. Church. 1983. Freshwater acidification from atmospheric deposition of sulfuric acid: a conceptual model. Environmental Science & Technology 17:541A-545A.

Gorey, J. G. 1984. Proposal to designate Maple Flats Sinkhole Ponds as a Special Interest Botanical Area. Unpublished report of The Nature Conservancy, Charlotteville, VA. 5 pp.

Hack, J. T. 1965. Geomorphology of the Shenandoah Valley, Virginia and West Virginia, and origin of the residual ore deposits. U.S. Geological Survey Professional Paper 484 :1-84.

Holsinger, J. R., & D. C. Culver. 1988. The invertebrate cave fauna of Virginia and a part of eastern Tennessee: Zoogeography and Ecology. Brimleyana 14:1-162.

Hopey, M.E., & J.W. Petranka. 1994. Restriction of wood frogs to fish-free habitats: how important is adult choice? Copeia 1994: 1023-1025.

Hyer, K.E., J.R. Webb, & K.N. Eshleman. 1995. Episodic acidification of three streams in Shenandoah National Park, Virginia, USA. Water, Air and Soil Pollution 85:523-528.

Kenney, L.P. 1994. Wicked big puddles, a guide to the study and certification of vernal pools. Reading Memorial High School Vernal Pool Association, Reading, MA. 58 pp. + appendices.

Klemens, M.W. 1993. Amphibians and Reptiles of Connecticut and adjacent regions. State Geological and Natural History Survey of Connecticut. Bulletin No. 112. Hartford, CT. 318 pp.

Knox, J.S. 1997. A nine year demographic study of *Helenium virginicum* (Asteraceae), a narrow endemic seasonal wetland plant. Journal of the Torrey Botanical Society 124: 236-245.

Knox, J.S., F.W. Stearns, Jr., & C.K. Dietzel. 1999. Factors controlling the distribution and abundance of the narrow endemic, *Helenium virginicum* (Asteraceae): Antiherbivore defense? Banisteria 13:95-100.

Kochel, R.C. 1987. Holocene debris flows in central Virginia. Pp. 139-155 *In* J.E. Costa & G.F. Wieczorek (eds.), Debris Flows/Avalanches: Process, recognition and mitigation. Geological Society of America. Reviews in Engineering and Geology, Volume VII.

Kochel, R.C. 1992. Geomorphology of alluvial fans in west-central Virginia. Pp. 47-60 *In* G.R. Whittecar (ed.), Alluvial fans and boulder streams of the Blue Ridge Mountains, west-central Virginia. Old Dominion University, Norfolk, VA. 128 pp.

Kutka, F.J. 1994. Low pH effects on swimming activity of *Ambystoma* salamander larvae. Environmental Toxicology and Chemistry 13:1821-1824.

Lide, R. F. 1997. When is a depression wetland a Carolina bay? Southeastern Geographer 37:90-98.

Madison, D. M. 1997. The emigration of radio-implanted spotted salamanders, *Ambystoma maculatum*. Journal of Herpetology 31:542-551.

Means, D. B., J. G. Palis, & M. Baggett. 1996. Effects of slash pine silviculture on a Florida population of flatwoods salamander. Conservation Biology 10:426-437.

Mitchell, J. C. 1994. The Reptiles of Virginia. Smithsonian Institution Press, Washington, D.C. 352 pp.

Mitchell, J.C., & K.A. Buhlmann. 1999. Amphibians and reptiles of the Shenandoah Valley Sinkhole Pond System in Virginia. Banisteria 13:129-142.

Noss, R. F. 1987. Protecting natural areas in fragmented landscapes. Natural Areas Journal 7:2-13.

Opdam, P. 1991. Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies. Landscape Ecology 5:93-106.

Pague, C. A., & K.A. Buhlmann. 1991. Eastern tiger salamander, *Ambystoma tigrinum tigrinum*. Pp. 431-433 *In* K. Terwilleger (Coord.), Virginia's Endangered Species. McDonald and Woodward Publishing Company, Blacksburg, Virginia.

Palis, J. G. 1997. Distribution, habitat, and status of the flatwoods salamander (*Ambystoma cingulatum*) in Florida, USA. Herpetological Natural History 5:53-65.

Pechmann, J. H. K., D. E. Scott, J. W. Gibbons, & R. D. Semlitsch. 1989. Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. Wetlands Ecology and Management 1:3-11.

Pennak, R. W. 1978. Freshwater Invertebrates of the United States, 2nd Ed. John Wiley and Sons, New York. 803 pp.

Petranka, J. W., M. E. Eldridge, & K. E. Haley. 1993. Effects of timber harvesting on southern Appalachian salamanders. Conservation Biology 7:363-370.

Pettry, D.E., J.H. Scott, & D.J. Bliley. 1979. Distribution and nature of Carolina bays on the Eastern Shore of Virginia. Virginia Journal of Science 30: 3-9.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652-661.

Pulliam, H. R., & B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. American Naturalist 137:S50-S66.

Rawlinson, E. S., & L. G. Carr. 1937. Plants of Spring Pond, Augusta County, Virginia. Claytonia 3:36-40.

Roble, S. R. 1999. Dragonflies and damselflies (Odonata) of the Shenandoah Valley Sinkhole Pond system and vicinity, Augusta County, Virginia. Banisteria 13:101-127.

Sankey, R.T., & B.W. Schwenneker. 1993. Ecology of the Grafton Ponds Sinkhole Complex in Eastern Virginia. Pp. 576-582 *In* M.C. Landin (ed.), Wetlands: Proceedings of the Thirteenth Annual Conference of the Society of Wetland Scientists. New Orleans, LA., June 1992. South-Central Chapter SWS, Utica, MS. 990 pp.

Schalles, J. F., R. R. Sharitz, J. W. Gibbons, & G. J. Leversee. 1989. Carolina bays of the Savannah River Plant. SRO-NERP-18, DOE Environmental Research Park Program, Aiken, SC. 70 pp.

Schwartz, R.E., & D.M. Kocka. 1999. Wildlife management activities in Big Levels, Augusta County, Virginia: an overview. Banisteria 13:11-15.

Semlitsch, R. D. 1981. Terrestrial activity and summer home range of the mole salamander (*Ambystoma talpoideum*). Canadian Journal of Zoology 59:315-322.

Semlitsch, R. D. 1983a. Terrestrial movements of an eastern tiger salamander, *Ambystoma tigrinum*. Herpetological Review 14:112-113.

Semlitsch, R. D. 1983b. Burrowing ability and behavior of salamanders of the genus *Ambystoma*. Canadian Journal of Zoology 61:616-620.

Semlitsch, R. D. 1987. Relationship of pond drying to the reproductive success of the salamander *Ambystoma talpoideum*. Copeia 1987:61-69.

Semlitsch, R. D. 1988a. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. Ecology 69:184-192.

Semlitsch, R. D. 1988b. Allotopic distribution of two salamanders: effects of fish predation and competitive interactions. Copeia 1988:290-298.

Semlitsch, R. D. 1998. Biological delineation of terrestrial buffer zones for pond-breeding amphibians. Conservation Biology 12:1113-1119.

Semlitsch, R. D., & J. R. Bodie. 1998. Are small, isolated wetlands expendable? Conservation Biology 12:1129-1133.

Sharitz, R. R., & J. W. Gibbons. 1982. The ecology of southeastern shrub bogs (pocosins) and Carolina bays. U.S. Fish and Wildlife Service, Division of Biological Services, Washington, D.C.

Sharitz, R. R., & C. A. Gresham. 1998. Chapter 14: Pocosins and Carolina Bays. Pp. 343-377 *In* M. G. Messina & W. H. Conner (eds.), Southern Forested Wetlands: Ecology and Management. Lewis Publishers, Boston, MA.

Smith, L.R. 1991. Biological diversity protection on the George Washington National Forest. Natural Heritage Technical Report 91-1. Virginia Department of Conservation and Recreation, Division of Natural Heritage, Richmond, 151 pp.

Stone, J.S. 1992. Vernal pools in Massachusetts: aerial, photographic identification, biological and physiographic characteristics, and state certification criteria. M.S. Thesis, University of Massachusetts, Amherst, MA. 98 pp.

Taylor, B. E., R. A. Estes, J. H. K. Pechmann, & R. D. Semlitsch. 1988. Trophic relations in a temporary pond: larval salamanders and their microinvertebrate prey. Canadian Journal of Zoology 66:2191-2198.

Webb, J.R., B.J. Cosby, J.N. Galloway, & G.M. Hornberger. 1989. Acidification of native brook trout streams in Virginia. Water Resources Research 25:1367-1377.

Whittecar, G.R., & D.L. Duffy. 1992. Geomorphology and stratigraphy of late Cenozoic alluvial fans, Augusta Co., Virginia. Pp. 79-112 *In* G.R. Whittecar (ed.), Alluvial fans and boulder streams of the Blue Ridge Mountains, west-central Virginia. Old Dominion University, Norfolk, VA. 128 pp.

Williams, P. K. 1973. Seasonal movements and population dynamics of four sympatric mole salamanders, genus *Ambystoma*. Ph.D. Dissertation, Indiana University, Bloomington, IN.