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First Record of the Rock Vole, *Microtus chrotorrhinus* (Miller) (Rodentia: Cricetidae), in Virginia

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ABSTRACT.— A rock vole, *Microtus chrotorrhinus*, collected in Bath Co., Va., represents the first record of this species in the state. The collection site was at 1,036 m on Allegheny Mountain in George Washington National Forest. The site was characterized by talus and supported a northern hardwood forest.

A subadult male rock vole, *Microtus chrotorrhinus* (Miller), collected in Bath Co., Va., on 28 July 1987, represents the first record to be published of this species in the Commonwealth. The collection site, at 1,036 m elevation on the eastern slope of Allegheny Mountain (38° 14′ N, 79° 49′ W) in the George Washington National Forest, is 16 km N of Mountain Grove. The rock vole was captured on a west-facing slope about 25 m above the channel of Lightner Run, a tributary of Little Back Creek. The nearest of several West Virginia localities where *M. chrotorrhinus* has been collected is about 32 km from this site (Kirkland 1977a, 1977b).

Forty Sherman live traps were set among talus and boulders in a small area approximately 60 m by 60 m, 26-28 July and 12-15 August, 1987, for a total sampling effort of 240 trap nights. Traps were baited with a mixture of rolled oats and peanut butter scented with oil of anise. The rock vole (Virginia Commonwealth University Mammal Collection No. 5006) was captured in a trap set within the talus with the opening of the trap directed under a small rock overhang. Other species captured in the same area were red-backed vole, *Clethrionomys gapperi* (Vigors) (13 specimens); short-tailed shrew, *Blarina brevicauda* (Say) (7); cloudland deer mouse, *Peromyscus maniculatus nubiterrae* Rhoads (3); and masked shrew, *Sorex cinereus* Kerr (1). Eight pitfall traps set along the stream captured *S. cinereus* (4); smoky shrews, *S. fumeus* Miller (3); and rock shrew, *S. dispar* Batchelder (1). These small mammals are some of the same species reported as habitat associates of *M. chrotorrhinus* in West Virginia (Kirkland 1977a, 1977b). In New York, Kirkland and Knipe (1979) also captured the water shrew, *Sorex palustris* Hooper, with *M. chrotorrhinus*. The only known Virginia locality for *S. palustris* is a site along Little Back Creek only 1.6 km from Lightner Run (Pagels and Tate 1976, Pagels 1987).

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The capture site was characterized by talus and supported a northern hardwood forest. Sugar maple, *Acer saccharum*, composed nearly 50% of the trees 10 cm in diameter or greater within 100 m of the collection site. Remaining trees were principally yellow birch, *Betula lutea* (16%); black birch, *B. nigra* (10%); and basswood, *Tilia americana* (10%). Scattered throughout the sampling area were small numbers of American beech, *Fagus grandifolia*; northern red oak, *Quercus rubra*; and hickory, *Carya* sp. No conifers were observed. Understory consisted primarily of mountain maple, *Acer spiratum*; witch-hazel, *Hamamelis virginiana*; and saplings of *A. saccharum*. The most prominent forbs were white snakeroot, *Ageratum altissima*, and Dutchman's pipe, *Aristolochia macrophylla*. Rocks and talus were generally moss-covered, and stumps and fallen trees in various stages of decomposition were prevalent. Severe drought conditions prevailed in much of Virginia, including most montane areas, during summer 1987, and the rocky channel of Lightner Run was nearly dry on the collection date. Long-term climatic data from nearby Marlinton, W.Va., are given by Pagels and Tate (1976).

Based on studies of *M. chrotorrhinus* throughout its range (see Kirkland and Jannett 1982), the following observations can be noted. (1) Boulders, talus, or rocks, as the name rock vole so aptly indicates, are important features of *M. chrotorrhinus* habitat. (2) The rock vole exploits subterranean portions of its rocky environment; subsurface runways are observed and captures in subsurface sets are common. (3) Water, whether surface or subsurface, is an important component of rock vole habitat. (4) *Microtus chrotorrhinus* is most often associated with a suite of small mammals having northern affinities, and in the southern Appalachian Mountains appropriate habitat for all such species is present only at relatively high elevations. (5) Although vegetation associations are variable with respect to the rock vole's habitat preferences in various parts of its range, tree species that predominate at a given collecting site in the southern Appalachian Mountains are kinds with northern affinities, for example, red spruce (*Picea rubens*), sugar maple, and yellow birch.

Existing habitat in the southern Appalachian Mountains that appears suitable for the rock vole is highly fragmented as a result of both natural forces and human activities, especially burning and timbering (Handley 1980). Opportunity for repopulation of sites from which *M. chrotorrhinus* has been extirpated seems negligible because of the lack of avenues of suitable habitat. If *M. chrotorrhinus* is found at other locations in Virginia, these undoubtedly will be protected rocky and/or talus sites that have remained relatively moist throughout historical time. Certain factors provide a moderately optimistic outlook for the rock vole in Virginia: (1) the healthy status of *M. chrotorrhinus* in nearby West Virginia and (2) the presence in Virginia of apparently suitable habitat at some high elevation sites, despite the discontinuity of those sites.

ACKNOWLEDGMENTS.— Collection of the rock vole was made ancillary to a study on the distribution of the northern flying squirrel sponsored by the Nongame Wildlife and Endangered Species Program of the Virginia Department of Game and Inland Fisheries. I am grateful to R. W. Duncan, M. Fies, and K. Terwilliger for their support in that effort. I thank R. Glasgow of George Washington National Forest for his support and encouragement. Station manager B. Bocchicchio, who provided access to the site, and Sara S. Bell, C.M. Kershner, and people at the security station of the Virginia Power Bath County Pumped Storage Station are gratefully acknowledged for many acts of kindness. I am especially grateful to Ms. Bell for much assistance both before and after the collection was made. I thank Dr. C. O. Handley, Jr., for verifying the identification of the vole and Dr. M. F. Johnson for identification of plant species. Dr. G. L. Kirkland, Jr., graciously provided many helpful comments on an earlier draft of the manuscript.

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Occurrence of a Northern Cicada, *Okanagana rimosa* (Homoptera: Cicadidae), in the Southern Appalachians

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ABSTRACT.— The cicada *Okanagana rimosa* (Say) is reported from five mountain counties in North Carolina and one in Tennessee. This represents a range extension southward of ca. 300 miles (485 km) from Rappahannock Co. in northern Virginia.

Virtually all of the relatively large cicadas of the eastern United States are members of the genus *Tibicen*. Although smaller than most of its congeners, *Tibicen canicularis* (Harris) is one of the characteristic forms in the Northeast, and it perhaps extends farther north than any other member of the genus. *Okanagana* is a large genus (several dozen species) of mostly smaller western and southwestern forms. However, according to Davis (1930), *Okanagana rimosa* (Say) and *O. canadensis* (Provancher) are noteworthy in being distributed across much of southern Canada and spilling down into the border states of the United States. The distribution of *O. canadensis* appears to be slightly the more northerly of the two. The most southerly eastern records for *O. rimosa* have been in Pennsylvania, northeastern Ohio, and, as a helpful reviewer reminds us, a specimen collected by Allard (1938) at about 3,500 feet (1,070 m) on Mary's Rock, Rappahannock Co., in northern Virginia.

For a number of years, one of us (E.E.B.) has had an interest in cicadas. He was aware of the statement by Davis (1922) that, from an elevation of 3,900 feet (1,190 m) on Bald Knob, Bath Co., in western Virginia, a friend had brought to him a headless specimen apparently of *T. canicularis* (Harris). Considering the numerous northern organisms that range southward in the mountains, he surmised that the ranges of the small northern forms *O. rimosa* and *T. canicularis* might extend farther south in the Appalachians than had been reported. Consequently, he searched along the Blue Ridge Parkway, then being unaware that his hearing was not adequate to have detected the call of *O. rimosa*. When J.D.B. relocated to Marion, N.C. (Grandfather District, Pisgah National Forest), E.E.B. asked him to be alert for cicadas, especially small ones.

On 14 July 1983, J.D.B. collected a small, newly transformed cicada in a patch of white pines near old N.C. Hwy. 105 (McDowell Co.), which runs along the ridge just west of Linville Gorge and Table Rock. On later examination, this specimen appeared to be a female of *O. rimosa.*

On 22 July we went back up old N.C. Hwy. 105 (SR 1238). The call of the cicada was a fine, long buzz that J.D.B. could hear but that the older ears of E.E.B. failed to pick up then, though he later heard it easily with Bionic Ear® equipment. Beginning about 7 miles (11.3 km) north of the Canal Bridge on Lake James, J.D.B. could hear calls at numerous stops along the road (among mixed pines and hardwoods) over a stretch of about 5 miles (8 km) at an altitude of 2,800-3,300 feet (855-1,005 m). We found two small, conspicuously banded nymphal skins, both on young maples (*Acer pennsylvanicum*) among larger white pines.

On 9 August J.D.B. hand-caught a male specimen about 1 foot (0.3 m) above the ground on a young white pine, just off Forest Service Route 496, 3.2 miles (5.1 km) S of N.C. Hwy. 181), on the E side of Table Rock-Sitting Bear (Hawksbill) Ridge at about 2,800 feet (855 m) (Burke Co.). In the same area the next day, using a .22 caliber shotshell, we collected another male. This specimen was about 18 feet (5.5 m) above the ground, on the underside of, and far out on, a white pine limb. It was nearly invisible in shadow and against a dark blotch of bark.

The cicadas identified as *O. rimosa* agree with: (a) Heath's (1978) characterization of *Okanagana*, with narrow head, widely separated and exposed tymbals, non-retractable uncus, etc.; (b) Say's original description of *O. rimosa* as quoted by Davis (1919), including orange-rufous markings on pronotum, mesonotum, edges of abdominal terga, and bases of wings; (c) Alexander's (1961) provisional key to eastern species of cicadas; (d) Moore's (1966) notations regarding the species in Michigan; and (e) Davis's (1926) notes touching the northeastern region of the country.

Since 1983, in addition to the continued occurrence of the species at the localities noted above, J.D.B. has heard specimens at several other sites.

1984: First noted 12 June, Burke Co. Later heard on the ridge S of Roseboro (Block #135) in Avery Co.

1985: First heard 11 June. Heard 25-28 June in the pines on the Singecat Ridge area, N of Sunnyvale, in McDowell Co.

1986: Heard 5 June on Joe White Mountain, just E of Mortimer, Caldwell Co. Heard during July on Flat Top Mountain, near the Tennessee line in Yancey County.

1987: On 1 May, heard on a knob S of Meadow Creek Mountain, in Cocke Co., Tenn. During June it was heard at several other points in Cocke Co.

These appear to be the first records of *O. rimosa* for the Carolina region. They thus extend its known range some 300 miles (485 km) southward from Rappahannock Co., Va., to the central mountain counties of North Carolina.

Evidently, we have in the mountains not just an isolated brood or two of this cicada, but a moderately widespread population, especially at intermediate elevations where pines are present. Presumably it will show up in some other mountain counties. Although present in considerable numbers, it definitely is not a conspicuous form and must be sought after.

Specimens will be deposited in the collections of the North Carolina Department of Agriculture.

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Distribution and Ecology of the Blackside Dace, *Phoxinus cumberlandensis* (Osteichthyes: Cyprinidae)

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ABSTRACT.— A recent status survey of the blackside dace, *Phoxinus cumberlandensis*, resulted in nine new distributional records and a better understanding of the species ecology. This threatened species is now known from 30 streams; it inhabits approximately 27.0 km of small headwater streams within the Upper Cumberland River basin. Impacts from coal-mining activities have resulted in the loss of the species from seven previously reported localities. Removal of riparian vegetation and increased siltation appear to be the primary degrading factors.

The blackside dace, *Phoxinus cumberlandensis*, is a rare cyprinid restricted to small streams of the Upper Cumberland River basin of Tennessee and Kentucky. The species was first discovered in 1975 and was described by Starnes and Starnes (1978a). A status survey in 1978 recorded the species from 12 sites (Starnes and Starnes 1978b). Additional localities were reported by Starnes (1981), Warren (1981), and Burr and Warren (1986). The biology of the species was described by Starnes and Starnes (1981). The species currently is listed as a threatened species by the U.S. Fish and Wildlife Service.

Phoxinus cumberlandensis has been reported only from the Upper Cumberland River basin. This has been confirmed by extensive surveys in adjacent basins: Kentucky River (Branson and Batch 1981, 1983, 1984), Tradewater and Green rivers (Warren and Cicerello 1982), Big South Fork River (O'Bara and Estes 1984), Little South Fork River (Branson and Schuster 1982), and Powell River (Tennessee Valley Authority 1975). In addition, Harker et al. (1979, 1980) reported on surveys of Tygarts Creek and the Kentucky, Little Sandy, Licking, and Upper Cumberland river basins.

The main purpose of the present study was to determine the current status of *P. cumberlandensis*. Potential threats and habitat requirements were also investigated.

STUDY AREA

The Upper Cumberland River basin has been traditionally defined as that section upstream of Cumberland Falls (McGrain 1966). Although no definitive geological records exist, Cumberland Falls is believed to have been originally located near Burnside, Ky. The present falls are situated approximately 72 km upstream of this presumed origin.

The entire Upper Cumberland River basin is within the Appalachian Plateau Physiographic Province. Three physiographic sections lie within the basin. The Cumberland Mountains section consists of two parallel ridges with altitudes ranging from 600 to 1,295 meters. Headwater streams in this region are generally of steep gradient. The Kanawha section is a dissected plateau characterized by narrow valleys and moderate-gradient streams. The Cumberland Plateau section is a broad plateau of moderate relief. The Pottsville escarpment along the western edge of the plateau contains steep-gradient streams (McGrain 1966).

METHODS AND MATERIALS

Sampling was conducted from October 1984 to August 1985. Collections were made by using seines and backpack electrofishing equipment. The habitat was characterized qualitatively at each site. The analyzed characteristics included substrate, embeddedness, riparian vegatation, stream morphometry, watershed land use, and canopy cover. The approximate length of suitable habitat based on the previously mentioned characteristics was measured upstream and downstream from a known population location. Healthy populations were defined as those that contained two or more year classes and numerically composed more than 25% of the fish community.

RESULTS AND DISCUSSION

Of the 193 sites sampled, 30 contained *P. cumberlandensis* (Table 1). It appears that *P. cumberlandensis* has been extirpated from nine streams (Table 2). Nine new populations were discovered (Table 1), but only the one in Bucks Branch was considered healthy. An estimated 27.0 km of stream were inhabited by *P. cumberlandensis*, but only 13.0 km supported healthy populations.

Five population clusters were found (Table 1). Downstream of Cumberland Falls, five streams were inhabited by *P. cumberlandensis*. The other four population clusters were found in the Straight Creek system (six populations), in the Jellico Creek system (five populations), in the Clear Fork system (five populations), and in four small streams that drain directly into the Cumberland River. These population clusters are extremely important to the continued existence of the species. If conditions improve in adjacent streams, natural recolonization is likely to occur as a result of the fairly large numbers of *P. cumberlandensis* in these population clusters. Reinvasion was documented in the Straight

Table 1. Location, number of individuals collected, and approximate habitat length for all observed *Phoxinus cumberlandensis* populations.

Population cluster/ stream	County, state	No. individuals collected	Approx. length of habitat (km)
Isolated Systems			
Poor Fork	Letcher, Ky.	4	0.8
Brownies Creek	Harlan, Ky.	24	2.0
Davis Branch	Bell, Ky.	10	2.0
Little Clear Creek	Bell, Ky.	12	0.5
Trammel Fork[a]	McCreary, Ky.	15	1.0
Straight Creek Population Cluster			
Straight Creek[a]	Harlan, Ky.	2	1.0
Mill Creek[a]	Bell, Ky.	6	0.4
Sims Fork	Bell, Ky.	14	1.5
Long Branch[a]	Bell, Ky.	2	0.2
Right Fork of Caney Creek[a]	Bell, Ky.	8	0.4
Left Fork of Caney Creek	Bell, Ky.	95	0.8
Clear Fork Population Cluster			
Buck Creek[a]	Whitley, Ky.	2	0.1
Buffalo Creek	Clairborne, Tenn.	2	0.5
Davis Creek	Campbell, Tenn.	2	0.5
Sandlick Creek	Campbell, Tenn.	2	0.5
Elk Creek[a]	Campbell, Tenn.	2	0.8
Cumberland River Population Cluster			
Youngs Creek	Whitley, Ky.	30	2.0
Becks Creek	Whitley, Ky.	1	0.7
Archers Creek	Whitley, Ky.	9	1.5
Bunches Creek	Whitley, Ky.	20	1.5
Jellico Creek Population Cluster			
Bucks Branch[a]	Whitley, Ky.	46	1.4
Rose Branch[a]	Whitley, Ky.	1	0.2
Gum Fork	Scott, Tenn.	12	1.6
Lawson Creek	Scott, Tenn.	1	0.1
Hatfield Creek	Campbell, Tenn.	2	0.3
Cumberland Falls Population Cluster			
South Fork of Dog Slaughter	Whitley, Ky.	1	0.9
North Fork of Dog Slaughter	Whitley, Ky.	2	0.4
Eagle Creek	McCreary, Ky.	4	1.5
Big Lick Branch	Pulaski, Ky.	32	0.9
Middle Fork of Beaver Creek	McCreary, Ky.	21	1.0

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[a] First record of population.

Creek system with the expansion of *P. cumberlandensis* into four streams that were devoid of the species when sampled by Starnes and Starnes (1978b).

Five populations (Poor Fork, Brownies Creek, Davis Creek, Little Clear Creek, Trammel Fork) are isolated and appear to be in jeopardy because of low numbers or inadequate adjacent habitat. These populations could be lost as a result of a single catastrophic event, and natural recolonization would be extremely unlikely because of their isolation.

Fish species typically found in association with *P. cumberlandensis* included creek chub (*Semotilus atromaculatus*), white sucker (*Catostomus commersoni*), blacknose dace (*Rhinichthys atratulus*), stripetail darter (*Etheostoma kennicotti*), and central stoneroller (*Campostoma anomalum*). Some or all of these five species were generally found in each stream containing *P. cumberlandensis*.

Gradient is believed to influence the distribution of *P. cumberlandensis* significantly. In streams of the Cumberland Mountains, the gradient is usually high, which results in large populations of *R. atratulus*. Low-gradient streams (Kanawha section) did not appear to provide suitable hatitat for *P. cumberlandensis*. A 60:40 riffle/pool ratio appears to be preferred by *P. cumberlandensis*. I conclude that 42 of the 193 systems sampled did not historically support populations of *P. cumberlandensis* owing to inadequate habitat (too high or low gradient, streams too large, etc.), whereas the remaining 151 systems have adequate habitat to sustain the species.

Habitat degradation resulting from human activities is the cause of the apparent decline of *P. cumberlandensis*. Major degrading activities are coal mining and associated disturbances (site preparation, road maintenance). During the survey, mining occurred in only one of the 30 watersheds in which the blackside dace was found. That watershed, Sims Fork, was impacted not directly by run-off from the coal mine, but primarily by poor road construction and bridges not adequate to enable the passage of large coal trucks, thus resulting in trucks passing directly through the stream. Coal mining had occurred in five of the other watersheds, but had been stopped because of the current economic state of the coal industry. The absence of blackside dace from 101 of the 151 systems with theoretically adequate habitat for the species could have resulted from coal-mining activities. The remaining 20 systems with appropriate gradient but not inhabited by *P. cumberlanensis* have been degraded by agriculture, road construction, impoundments, or poor forestry practices. Extirpated populations were impacted by coal mining (6), road construction (1), agriculture (1), and drought (1).

Table 2. Streams previously reported to contain *Phoxinus cumberlandensis* and from which the species apparently has been extirpated.

Stream	County, state	Last reported
Colliers Creek	Letcher, Ky.	1979
Cloverlick Creek	Harlan, Ky.	1961
Little Poplar Creek	Knox, Ky.	1976
Louse Creek	Campbell, Tenn.	1979
Trammel Creek	Cambell, Tenn.	1981
Cane Creek	Whitley, Ky.	1977
Marsh Creek	McCreary, Ky.	1981
Ned Branch	Laurel, Ky.	1977
Craig Branch	Laurel, Ky.	1977

Coal mining, either by direct runoff or by secondary disturbances such as poor or inadequate roads and bridges and mine preparation and maintenance, appears to affect two important physical components of the blackside dace habitat, riparian vegetation and substrate. First, riparian vegetation, consisting of hemlock, rhododendron, ironwood, river birch, and sycamore, with canopy cover exceeding 70 percent of the stream is important. The significance of a natural, undisturbed riparian vegetational zone appears to be two-fold: in preventing elevated water temperature due to solar heating, and in providing submerged root systems that appear to be preferred cover. Healthy populations had access to extensive undercut, rooted banks. The riparian vegetational zone is often removed or significantly reduced during mine preparation and in road and bridge construction. Second, it is extremely important that the substrate consist of a cobble-gravel mix in riffles, a bedrock-boulder-silt combination in pools, and silt-free areas just downstream of the riffles. Coal-mining activities increased siltation, thus degrading this preferred substrate.

CONCLUSIONS

The continued existence of the rare and threatened *P. cumberlandensis* appears to depend on a number of factors. Viable population clusters and improved habitat in adjacent streams are necessary for natural recolonization to occur. Further physical isolation of populations would only further jeopardize this species. It is to be hoped that protection under stringent federal and state regulations will improve the possibility for the continued existence of *P. cumberlandensis.*

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ENDANGERED, THREATENED, AND RARE FAUNA OF NORTH CAROLINA

PART II.

A RE-EVALUATION OF THE MARINE AND ESTUARINE FISHES

by

Steve W. Ross, Fred C. Rohde, and David G. Lindquist

This is the second in a series of reports by committees appointed in 1985 by the North Carolina State Museum of Natural Sciences to re-evaluate the faunal lists presented in *Endangered and Threatened Plants and Animals of North Carolina* (John E. Cooper, Sarah S. Robinson, and John B. Funderburg, editors. N.C. State Mus. Nat. Hist., Raleigh, 1977), which is now out of print. The report on marine and estuarine fishes by Ross, Rohde, and Lindquist treats one Endangered species, six Vulnerable species, and four anadromous fishes that, while not formally listed, are of some concern. Five species listed as being of Special Concern in 1977 no longer warrant formal status. The publication includes six original drawings by Renaldo Kuhler.

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Oviposition, Larval Development, and Metamorphosis in the Wood Frog, *Rana sylvatica* (Anura: Ranidae), in Georgia

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ABSTRACT.— Oviposition and development in the wood frog, *Rana sylvatica*, were investigated from February through July of 1987 in the upper Piedmont of Georgia. Egg masses were laid in February and March in groups ranging from 1 to 22 masses. The number of eggs averaged 553 per mass. Mean egg diameter was 2.8 mm. Larvae, which averaged 8.7 mm in total length, hatched 18 to 25 days after oviposition. Larvae had reached a mean total length of 51.6 mm when they metamorphosed 115 to 130 days after hatching. Newly metamorphosed froglets had a mean snout-vent length of 18 mm.

The wood frog, *Rana sylvatica* LeConte, ranges from the tundra in Alaska and Canada to upland areas of Georgia (Martof 1970) and Alabama (Mount 1975). Various aspects of the life history of this frog have been investigated in a number of localities (Martof and Humphries 1959, Herreid and Kinney 1966, 1967, Meeks and Nagel 1977, Howard 1980, Berven 1982a,b, Seale 1982, Seigel 1983). Davis and Folkerts (1986) recently studied the life history of the wood frog in Alabama but did not report specific data on larval development time or size at metamorphosis. The only previous study describing larval development in the southern portion of the wood frog's range was by Meeks and Nagel (1977) in northeastern Tennessee. We present here an account of development in the wood frog in northeastern Georgia.

MATERIALS AND METHODS

This study was conducted in the Piedmont of Habersham Co., Ga., from February through July, 1987. Study areas were small, rain-filled, temporary pools located at Nancytown Lake (NTL; 3.2 km S of Mt. Airy, elevation = 280 m) and Roger's Creek (RC1 and RC2; 6.4 km S of Batesville, 450 m). Eggs were measured, and egg masses were counted from an additional site on the Soque River (SR; 8.0 km W of Demorest, 350 m). NTL, RC2, and SR were woodland pools, whereas RC1 was located in a pasture approximately 200 m from RC2. NTL and RC1 had abundant macrophytic vegetation; RC2 was heavily shaded and had little vegetation; SR was a deep wheel rut in an old logging road and contained no vegetation.

Dates of oviposition were recorded, and egg masses were counted in the study sites and in additional breeding sites that were discovered subsequently. Sample egg masses were removed and preserved in 10% formalin. Eggs were counted in eight separate collected masses, and samples (at least 10 eggs per mass) were taken from six of these masses for determination of egg size. The diameters of both eggs and outer jelly envelopes were measured to the nearest 0.1 mm using a vernier caliper.

Egg masses at NTL, RC1, and RC2 were monitored daily until hatching was complete. Dates when hatching began and ended were recorded. Midday readings of water and air temperatures were taken at NTL and RC1. Maximum depth was determined daily at all three sites. Ten larvae were preserved at hatching in 10% formalin, measured for total length to the nearest 0.1 mm, and staged (after Gosner 1960) with the aid of a dissecting microscope.

A series of tadpoles was collected at RC2 as larvae neared metamorphosis (stages 39-41 of Gosner 1960), preserved in 10% formalin, and measured for total length to the nearest 0.1 mm.

A partial drift fence (after Gibbons and Semlitsch 1982) was constructed along one side of RC2 in order to collect newly metamorphosed individuals. Tadpoles were observed two or three times per week until some of them began developing hind legs, at which time daily monitoring of both the edge of the pool and the drift fence began. Monitoring continued until metamorphosis and dispersal from the pool were complete. Body lengths (snout-vent) of newly metamorphosed froglets were measured to the nearest 0.5 mm in the field using a ruler, and the animals were then released on the opposite side of the fence.

RESULTS

Eggs were first discovered at NTL on 12 February 1987, and newly laid clutches appeared on 13 February. Adult male wood frogs were collected at the site on 12 and 23 February. A total of nine egg masses was located at NTL. These were deposited as individual masses scattered throughout an area covering approximately 35 m^2. Eggs were deposited in RC1 (22 masses) and RC2 (18 masses) from mid-February to 2 March, with most oviposition events occuring from 20 to 24 February. Most egg masses in these ponds were deposited as communal aggregates. Limited breeding activities were observed in three small adjacent ponds, where 1, 2, and 10 individual egg masses were recovered.

Midday water temperatures during periods of oviposition were 3-18° C (mean = 9.1) at NTL and 6-15° C ($\bar{x}$ = 8.9) at RC1. Air temperatures during this period were 1-23° C ($\bar{x}$ = 8.7) at NTL and 5-20° C ($\bar{x}$ = 9.5) at RC1. Maximum depth averaged 9 cm at NTL and 33 cm at RC1 during this time.

Clutch sizes varied from 295 to 706 eggs per mass ($\bar{x}$ = 553 ± 139.05 SD; N = 8). No more egg masses were taken because of the small number of egg masses deposited in each breeding pond (range = 1-22). Eggs averaged 2.8 mm in diameter (range = 2.2-3.3 mm; range in mean diameter per clutch = 2.7-2.9 mm). Outer jelly envelopes averaged 11.2 mm in diameter (eggs = 7.3-14.1 mm; mean per clutch = 10.4-12.3 mm).

Hatching began at NTL on 3 March and continued until 13 March. Hatching began 24 February at RC1 and 26 February at RC2. Hatching was completed 20 March at RC1 and 11 March at RC2. Hatching times ranged from 18 to 25 days after the date of egg deposition. Water temperatures during the hatching period averaged 12.3° C (range = 3-22) at NTL and 11.7° C (range = 6-17) at RC1.

Hatching occurred at stage 20 (gill circulation) at an average total length of 8.7 mm (range = 8.3-9.0). Larvae reached an average maximum total length of 51.6 mm (range = 49.0-55.6) before metamorphosing at an average body length of 17.8 mm (range = 15.0-21.0). The first metamorphosed frog was collected from RC2 on 21 June and the last on 19 July. From the start of hatching to the start of metamorphosis was 115 days, and from the end of hatching to the end of metamorphosis was 130 days. NTL and RC1 were completely dry by the end of April (22 and 25 April, respectively). Complete mortality of larval populations in both sites was assumed, and this was supported by the observation of large numbers of dead tadpoles at each site.

DISCUSSION

Rana sylvatica typically lays eggs in communal aggregates that are hypothesized to represent a thermal adaptation to development in cold climates (Wells 1977, Howard 1980, Seale 1982, Waldman 1982, Waldman and Ryan 1983). In four breeding ponds containing nine or more egg masses in our study, only two (RC1 and RC2) showed signs of communal oviposition. The lack of aggregation of NTL and SR egg masses may have been an aberration created by the small number of clutches in those breeding pools.

Wood frog eggs from Georgia are only slightly smaller than those reported from Alabama (2.9 mm; Davis and Folkerts 1986). The tendency of wood frogs to deposit progressively larger eggs from the north to the south in their geographic range has been noted by several investigators (Herreid and Kenney 1967, Meeks and Nagel 1977, Davis and Folkerts 1986).

Larvae in this study hatched at a smaller size than those in Alabama (10.7 mm; Davis and Folkerts 1986). The size difference is attributable to larvae in Georgia hatching at an earlier stage than those in Alabama (stage 21). Meeks and Nagel (1977) reported a similar hatching size to that in this study but did not report the larval stage at hatching. Herreid and Kinney (1967) reported that Alaskan wood frogs hatch at larval stage 20. Tadpole development time in our study was longer than that reported for wood frogs elsewhere (Hinckley 1882, Bellis 1957, Herreid and Kinney 1967, Meeks and Nagel 1977, Berven 1982b, Davis and Folkerts 1986). Berven (1982b) suggested that temperature was a major factor in variation in wood frog larval development periods.

Maximum total length reached by tadpoles in Georgia was similar to that reported from most parts of the species range (Bellis 1957, Herreid and Kinney 1967, Meeks and Nagel 1977). Size at metamorphosis was similar in Georgia wood frogs to that reported elsewhere (Hildebrand 1949, Bellis 1961, Meeks and Nagel 1977, Berven 1982b).

Catastrophic mortality as a result of premature desiccation of NTL and RC1 emphasizes the risky nature of breeding in temporary pools. Desiccation has been identified as a major selective force for amphibians breeding in temporary ponds (Semlitsch 1987).

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Seasonal Diet of the Margined Madtom, *Noturus insignis* (Osteichthyes: Ictaluridae), in a North Carolina Piedmont Stream

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ABSTRACT.— The diet of four size classes of the margined madtom, *Noturus insignis*, collected during 1 year from New Hope Creek, Orange Co., N.C., was examined. Margined madtoms consumed a wide variety of prey, but most (93.8%) were Diptera, Ephemeroptera, Trichoptera, and Plecoptera. On average, fewer individual prey were consumed during the winter than in any of the other three seasons. Many prey species were most abundant in the madtom's diet when those prey appeared to be most abundant in the stream. The diversity of the madtom's diet increased as the fish increased in size. Small madtoms consumed primarily chironomid larvae (>70% of the diet). Although chironomids were still a major prey item numerically for large madtoms, 65-70% of their diet consisted of other taxa. We hypothesize that the diet of the madtom diversifies with increasing size because large madtoms are able to capture large prey successfully and are able to forage in areas with high current velocities.

The margined madtom, *Noturus insignis* (Richardson), is a common benthic fish in streams of eastern North America from New York to Georgia (Rohde 1980). Despite the margined madtom's widespread distribution, characterization of its diet is based on only three individuals collected by Flemer and Woolcott (1966) between 13 June and 22 December, 1958. Flemer and Woolcott found a dipteran larva, two stoneflies, and unidentified insect and fish remains in the stomachs of the margined madtoms they sampled. The present study had two major goals. First, we wanted to provide more detailed information about the diet of *N. insignis* in the southern part of the species range. Second, we wanted to determine if the diet of margined madtoms changed with either the season or the size of the fish.

METHODS

Margined madtoms were sampled from a series of three riffles and three pools (about 150 m of stream) in New Hope Creek, a fourth-order

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stream that flows through the Duke Forest, in Orange County, N.C., approximately 11 km NE of Chapel Hill. Madtoms were collected using an electroshocker in combination with dipnets, because strong currents and the rocky bottom prevented the effective use of a seine. Shocked fish were captured as they drifted into two large dipnets (0.5 m × 0.25 m) placed on the bottom about 0.5 m downstream from the anode ring. Fish were collected from September 1982 through August 1983 with collection dates approximately 1 month apart (range 27-41 days, $x = 33$ days). We restricted collection to a small section of the stream so that any observed variation in diet would not be a result of variation in prey availability at different sites.

Because madtoms are reported to be nocturnal feeders (Mayden and Burr 1981, Burr and Mayden 1982, Moyle and Cech 1982), collections were made between 1 and 2 hours after sunrise. Fish were preserved whole in 95% ethanol within an hour of capture. In order to assess whether madtoms consumed any prey during the day, fish were collected twice on one date (27 July 1983), once in the morning and again between 1700 and 1800 hours.

Prior to gut content analysis, fish were measured (total length in mm). Then the foregut and intestine were removed. Visual estimations of gut fullness were made for both the foregut and the intestine following the methods of Yoshiyama (1980) and Creed (1985). Evaluation of gut fullness was not initiated until March 1983. Five levels of fullness were used: 0, ¼, ½, 1, 2, of which 0 signifies empty or with traces of food, 1 is full, and 2 is distended. Contents of both the foregut and the intestine were then removed and examined under a dissecting microscope. Prey items were counted and identified to the lowest taxon possible (often genus, occasionally species). These data were pooled by season, because it was not always possible to sample adequate numbers of madtoms in particular months. This was especially true of collections made in January and February, when water levels were high and effective sampling was difficult. The seasons referred to in the results (fall 1982 through summer 1983) encompass the following collection dates: fall - 28.IX, 28.X, 7.XII; winter - 6.I, 9.II, 16.III; spring - 14.IV, 11.V, 21.VI; summer - 27.VII, 25.VIII.

RESULTS AND DISCUSSION

A total of 53 margined madtoms were sampled for gut content analysis. Numbers of madtoms collected in each of the first three sampling seasons were about equal (fall N = 10, winter N = 11, spring N = 12), but about twice as many madtoms were collected during the summer (N = 20).

Table 1. Distribution of 53 margined madtoms collected from New Hope Creek, Orange Co., N.C., by size class and season.

Season	Size class (mm)			
	<31	31-60	61-90	91-120
Fall	0	6	1	3
Winter	0	5	1	5
Spring	0	3	5	4
Summer	1	6	9	4

Madtoms, which ranged from 19 to 113 mm, were assigned to four size classes (Table 1). Fish 31 mm or longer were collected throughout the year. In fall and winter samples, however, most fish were in the 40-50 mm and 95-105 mm ranges, which closely match the ranges of Clugston and Cooper (1960, figure 2) for age 0+ and 1+ fish during fall and winter months. During the spring and summer we collected a number of madtoms from an intermediate size class (61-90 mm). Clugston and Cooper collected madtoms in that same size range during the summer growing season. The data suggest that madtoms in the intermediate size class in our study are probably age 0+ fish growing to age 1 size. We collected only one young-of-the-year madtom, less than 31 mm long (19 mm), in July.

Captured madtoms almost always contained prey. The only exceptions were two small fish (40 and 38 mm) collected in January. In general, fish collected during the winter contained fewer prey than those sampled during the rest of the year (Table 2). Ninety percent of the fish collected from March through August (N = 31) had a foregut fullness of ½ or greater. Most fullness values (84%) for the intestine were ½ or less. These data suggest that the madtoms had fed throughout the night and that processed food was starting to move into the intestine. Four of the five madtoms sampled on the morning of 27 July had a foregut fullness of 1 and the fifth had a foregut fullness of ¼; all had an intestinal fullness of ½ or less. Three of the five individuals sampled that afternoon had no prey in the foregut, and two contained 8 and 42 prey items, respectively; all had an intestinal fullness of ½ or greater. Some prey from the afternoon foregut samples were not broken up, which suggests that they had been consumed recently. In general, however, intestinal fullness increased from morning to afternoon. Therefore, although the general trend was for nocturnal feeding, some madtoms appeared to take prey during the day.

Table 2. Numbers of different prey taxa consumed by 53 margined madtoms collected from September 1982 to August 1983 in New Hope Creek, Orange Co., N.C.[a]

Prey taxon	Season (No. of fish sampled)				Total
	Fall (10)	Winter (11)	Spring (12)	Summer (20)	
Diptera					
Chironomidae (larvae)	264	105	140	455	969
Chironomidae (pupae)	0	0	0	1	1
Tipulidae					
Antocha	1	0	3	1	5
Tipula	0	0	1	0	1
Unid. Tipulidae	6	0	14	31	51
Simuliidae					
Simulium (larvae)	3	47	45	0	95
Simulium (pupae)	0	0	14	0	14
Prosimulium (larvae)	0	3	2	0	5
Heleidae	0	0	0	1	1
Empididae					
Hemerodromia	0	0	2	0	2
Chelifera	0	1	0	0	1
Unid. Empididae	1	1	1	1	4
Chaoborus	5	0	0	0	5
Total Diptera	280	157	222	490	1149
Mean no. Diptera/fish	(28.0)	(14.3)	(18.5)	(24.5)	
Ephemeroptera					
Heptageniidae					
Heptagenia	1	0	1	1	3
Stenonema modestum	1	11	0	4	16
Stenonema sp.	0	0	3	0	3
Plecoptera					
Perlidae					
Acroneuria abnormis	0	4	2	10	16
Phasganophora capitata	0	0	4	0	4
Unid. Perlidae	1	0	1	0	2
Taeniopterygidae					
Taeniopteryx	9	7	0	0	16
Strophopteryx	6	0	0	0	6
Unid. Taeniopterygidae	4	0	0	0	4
Amphinemoura	0	3	3	0	6
Allocapnia	2	0	0	0	2
Unid. Plecoptera	3	3	4	0	10
Total Plecoptera	25	17	14	10	66
Mean no. Plecoptera/fish	(2.5)	(1.5)	(1.2)	(0.5)	
Coleoptera					
Psephenus herricki	0	0	0	1	1
Dubiraphia	0	0	0	6	6
Unid. Coleoptera	0	0	0	1	1
Lepidoptera					
Pyralidae	1	1	1	6	9
Megaloptera					
Sialis	1	0	0	9	10

Stenacron pallidum	0	0	0	1	1
Unid. Heptageniidae	16	16	29	42	103
Ephemerellidae					
Ephemerella dorothea	0	1	4	0	5
Unid. Ephemerellidae	1	1	0	1	3
Isonychia	1	0	14	2	17
Baetis	1	45	266	6	318
Unid. Ephemeroptera	1	1	0	0	2
Total Ephemeroptera	22	75	317	57	471
Mean no. Ephemeroptera/fish	(2.2)	(6.8)	(26.4)	(2.9)	
Trichoptera					
Hydropsychidae					
Cheumatopsyche	5	0	5	2	12
Hydropsyche	0	0	1	1	2
Unid. Hydropsychidae	7	3	0	41	51
Hydroptilidae					
Hydroptila	0	0	0	24	24
Oxyethira	0	0	0	4	4
Leptoceridae					
Oecetis	0	0	0	1	1
Unid. Leptoceridae	0	0	0	1	1
Philopotamidae					
Chimarra	13	1	5	10	29
Dolophilodes	0	0	1	0	1
Unid. Trichoptera	1	0	11	5	17
Total Trichoptera	26	4	23	89	142
Mean no. Trichoptera/fish	(2.6)	(0.4)	(1.9)	(4.5)	
Odonata					
Anisoptera	1	0	0	0	1
Aeshnidae	0	0	0	1	1
Hydracarina	3	0	26	7	36
Crustacea					
Copepoda					
Cyclopoida	0	1	0	0	1
Calanoida	1	0	0	0	1
Isopoda					
Caecidotea	1	0	0	0	1
Cladocera					
Chydoridae	2	0	0	0	2
Unid. Cladocera	1	0	0	0	1
Amphipoda					
Gammaridae	0	2	0	0	2
Ostracoda	0	0	1	0	1
Crayfish	0	0	0	1	1
Fish eggs	0	0	39	0	39
Terrestrial prey					
Hymenoptera	1	0	0	0	1
Unid. terr. insects	2	2	0	1	5
Total	367	259	643	679	1948
Mean no. prey per fish	(36.7)	(23.5)	(53.6)	(34.0)	

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[a] Unid. = unidentifiable beyond taxon listed.

Margined madtoms consumed a wide variety of prey (Table 2). A vast majority of the prey were benthic, but some terrestrial prey were consumed. We assume that the terrestrial prey were encountered on the stream bottom because madtoms were always observed on or in the bottom. Of the benthic prey, immature aquatic insects in four orders dominated in the diet (93.8%); these orders were Diptera, Ephemeroptera, Trichoptera, and Plecoptera.

Dipterans, especially chironomid larvae, were the predominant prey in the diet except in the spring (Table 2). Chironomids were found in all but 2 of the 51 madtoms that contained food in their guts. The mean number of chironomids consumed per fish in the fall and summer was about the same. The number of chironomids eaten was lowest in the winter, which appears to be a result of reduced feeding activity by members of the 31-60 mm size class of madtoms, perhaps as a result of the strong currents present on those dates. A majority of the prey (67%) were consumed by large fish (>90 mm) during the winter. As discussed below, large madtoms consumed fewer chironomids than did small madtoms. Reduction in the number of chironomids consumed in the spring appears to have a different explanation. We observed dense aggregations of large instars of *Baetis* (Ephemeroptera), prior to their emergence in the spring, on the upper surface of many rocks. Encounters between madtoms and *Baetis* probably increased at this time of year. Increased feeding on *Baetis* probably led to reduced feeding on chironomids in the spring. Indeed, there was an inverse relation between the numbers of *Baetis* and of chironomids in the guts of the 12 madtoms collected in the spring ($r = -0.47$, Pearson product-moment correlation). *Simulium* spp. were also observed to emerge in the spring, the season when large instars of this genus are probably encountered most frequently by the margined madtom. *Simulium* pupae were found in the madtom gut only in the spring.

Ephemeropteran nymphs other than *Baetis* were also important in the madtom's diet (Table 2). Heptageniid nymphs were found in the gut throughout the year, with a peak in the summer. About half as many ephemeropterans as dipterans were consumed over the entire year. However, in terms of prey biomass, it is likely that Ephemeroptera often contributed at least as much as Diptera, if not more, to the madtom's diet. In the spring Ephemeroptera outnumbered Diptera and probably contributed more biomass to the diet as well.

There were few apparent trends in the consumption of trichopteran larvae (Table 2). However, consumption of Hydropsychidae and *Hydroptila* was greatest in the summer. Most *Chimarra* were consumed during the summer and fall. The total number of Trichoptera consumed was extremely low during the winter. Overall, low numbers of Plecoptera nymphs were consumed. Winter-emerging stoneflies (e.g. *Taeniopteryx*, *Strophopteryx*, *Amphinemoura*, and *Allocapnia*) were consumed when large instars were most abundant in New Hope Creek.

Our results indicate that the diet of *N. insignis* is similar to that of other species of *Noturus* (Mayden et al. 1980, Mayden and Burr 1981, Burr and Mayden 1982, Miller 1984). Unlike Flemer and Woolcott (1966), we did not find any fish remains in the madtoms sampled. Seasonal variation in the composition of the diet was observed. We believe it is attributable, in part, to seasonal variation in the abundance of different prey taxa. For example, *Baetis*, *Simulium*, and winter-breeding stoneflies were most abundant in the madtom's diet when large individuals of these taxa were most common in the stream. Miller (1984) did not observe seasonal variation in the diet of *Noturus munitus*.

An interesting trend is apparent when the diet of the madtom is analyzed by size class (Table 3). As madtoms increased in size, the proportion of chironomid larvae consumed decreased relative to other prey. That trend in chironomid consumption, though evident during spring, summer, and fall (Table 4), is most pronounced in summer and fall. In winter the proportions of chironomid larvae consumed by the two intermediate size classes were almost identical; only the largest fish had a fairly diverse diet. Chironomids increased in importance for intermediate-sized madtoms (61-90 mm) during the winter, when their movements were probably restricted by swift currents. In the spring, on the other hand, the proportions of chironomids consumed by all size classes were reduced. That appears to be a result of the increased consumption of *Baetis* and Simuliidae by all sizes of madtoms, possibly as a consequence of increased encounter rates with those taxa. In general, though, as madtoms increased in size the importance of chironomids in the diet decreased, while the importance of other invertebrates, primarily Ephemeroptera and Simuliidae, increased. The importance of chironomids as prey for the young of other stream fish has been noted by Allen (1941), Scrimgeour (1986), and Weatherley (1987). Mayden and Burr (1981), Burr and Mayden (1982), and Miller (1984) also noted an increase in the diversity of the diet of other *Noturus* species with increasing size of the fish.

We have considered three explanations for the more diverse diet of large madtoms: (1) small madtoms may be restricted in habitat use by piscivorous predators, (2) movement of small madtoms may be restricted to areas of reduced current velocity, and (3) the mouths of small madtoms are just too small to handle large prey. Because we collected a majority of the madtoms in riffles, where largemouth bass, the dominant

Table 3. Contribution (percent) of major prey taxa to the diet of four size classes of margined madtoms.[a]

Prey taxon	Size class (mm)							
	<31 (N = 1)		31 - 60 (N = 18)		61 - 90 (N = 16)		91 - 120 (N = 16)	
Diptera								
Chironomidae	94.4	(17)	73.1	(32.9)	35.9	(14.4)	26.4	(7.9)
Simuliidae	-	-	0.7	(0.3)	3.0	(1.2)	18.7	(5.6)
Other	-	-	3.2	(1.4)	4.7	(1.9)	2.5	(0.8)
Ephemeroptera								
Baetis	-	-	7.6	(3.4)	25.3	(10.2)	19.5	(5.8)
Heptageniidae	5.6	(1)	2.8	(1.3)	8.7	(3.5)	9.4	(2.8)
Other	-	-	0.4	(0.2)	1.4	(0.6)	3.2	(0.9)
Trichoptera	-	-	6.7	(3.0)	8.7	(3.5)	6.7	(2.0)
Plecoptera	-	-	2.6	(1.2)	3.0	(1.2)	6.1	(1.8)
Miscellaneous	-	-	2.9	(1.3)	9.3	(3.8)	7.6	(2.3)

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[a] Mean number of prey individuals of each taxon consumed per fish are shown in parentheses.

piscivore of New Hope Creek, are absent, the first explanation seems inadequate. In addition, because madtoms are active primarily at night and bass feed primarily during the day, predation risk would probably be low for all size classes of the madtom. We did not directly measure the swimming ability of madtoms under different current regimes. However, two pieces of indirect evidence lend support to the idea that the movement of small madtoms is influenced by current velocity. First, both the total and mean number of prey consumed were lowest in the winter, a period of higher than average discharge and of frequent flooding (Reice 1981; Creed, personal observation). Most of the prey consumed during the winter were eaten by the large madtoms, the only size class also to have a fairly diverse diet. Second, *Simulium* and *Baetis*, which composed about 38% of the diet of madtoms >90 mm

Table 4. Contribution (percent) of chironomids to the diet of four size classes of margined madtoms for each of the four seasons.[a]

Season	Size class (mm)			
	<31 (N = 1)	31 - 60 (N = 18)	61 - 90 (N = 16)	91 - 120 (N = 16)
Fall	- -	79 (37.7 ± 5.9)	56 (20[b])	43 (6.0 ± 3.8)
Winter	- -	67 (2.4 ± 1.3)	65 (46[b])	27 (9.4 ± 2.3)
Spring	- -	42 (19.3 ± 6.8)	15 (9.2 ± 4.3)	18 (9.0 ± 2.7)
Summer	94 (17[b])	81 (49.3 ± 11.8)	51 (13.2 ± 4.1)	42 (6.3 ± 3.9)

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[a] Mean ± 1 SE in parentheses.
[b] No SE shown because sample consists of one individual.

long, were usually found on the upper surface of rocks. This was especially true for the filter-feeding *Simulium*. These taxa made up only 9% of the diet of madtoms <60 mm long. Many of the prey were obviously too large for small madtoms to handle, e.g. late instars of *Acroneuria*, *Stenonema*, *Isonychia*, and Megaloptera, as well as crayfish. Consequently, we favor the idea that diet diversifies with increasing size because the larger madtoms (1) are able to capture larger prey successfully and (2) are able to forage in areas of higher current flow. Our data suggest that the diet of margined madtoms is strongly influenced by size-specific prey capture abilities and current velocity. These and other factors influencing the predatory behavior of many stream fishes, especially nonvisual predators like madtoms, deserve further study.

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Population Dynamics of Adult *Unionicola formosa* (Acari: Hydracarina), a Parasite of *Anodonta imbecillis* (Mollusca: Bivalvia), in West Virginia

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ABSTRACT.— Population dynamics of a parasitic aquatic mite, *Unionicola formosa*, were studied at the McClintic Wildlife Station (West Virginia) in two ponds that supported different densities of the host mussel, *Anodonta imbecillis*. Pond 27 with 26.0 host individuals/m^2 was categorized as a high-density pond, whereas Pond 14 with 8.6 host individuals/m^2 was considered a moderate-density pond. Collections were made monthly from May through November 1986. All hosts in both ponds were infested by female mites, but only 57 of 90 hosts from Pond 14 and 60 of 79 from Pond 27 were infested by males. Intensity of infestation, as mean adult mites/host, was lowest in May (5.4 for Pond 14; 19.7 for Pond 27) and highest in August (12.9 and 31.3) for those ponds. Although the number of mites per host was positively correlated with host shell length for mussels in Pond 27, there was little or no correlation in Pond 14. Mite sex ratios were heavily female-biased at 10.7:1 in Pond 14, and 18.5:1 in Pond 27.

May (1983) demonstrated, by an illustration based upon mathematical modeling, that a relationship existed between the number of animal parasites per host and the host population density. In theory, at relatively high parasite burdens and correspondingly high levels of host mortality, a host population could be regulated by parasitic infestation (Anderson and May 1978). Lanciani (1975) showed that increased numbers of an ectoparasitic water mite, *Hydryphantes tenuabilis* Marshall, reduced the rate of population increase of its aquatic insect host, *Hydrometra myrae* Bueno, in a laboratory setting.

It is often difficult to assess the extent to which a parasite regulates host population growth in nature. Therefore, the primary goal of this study was to evaluate intensity of infestations of a parasitic aquatic mite in two freshwater mussel populations at different densities. This study was carried out during the 7-month seasonal period when mussels are most active, and a secondary objective was to examine changes in seasonal intensity levels of mites in the two host populations. We also attempted to correlate intensity of infestation with host size, a relationship investigated in several previous mite/mussel studies. This paper

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constitutes the first report of the parasitic mite *Unionicola formosa* (Dana and Whelpley, 1836) from West Virginia.

MATERIALS AND METHODS

The subject of this study was a parasitic aquatic mite, *Unionicola formosa,* and its freshwater mussel host, *Anodonta imbecillis* (Say, 1829). Work was carried out in two ponds at the McClintic Wildlife Station, Mason Co., W.Va. The station, outlined on USGS Topographic Map, Cheshire Quadrangle, Ohio–W.Va., is a 2,800-acre (1,135-ha) wildlife sanctuary dotted by 35 ponds and managed by the W.Va. Department of Natural Resources. Ponds 14 and 27 were chosen as study sites because they harbored thriving mussel populations at densities of 8.6 (moderate) and 26.0 (high) *A. imbecillis* individuals per m^2, respectively (Harmon 1987). Pond 14 had a surface area of approximately 1.4 ha. It was a shallow pond (maximum depth of 2.4 m) with a considerable amount of rooted aquatic vegetation (coon-tail, *Ceratophyllum demersum*) arising from a silt/clay substrate. Pond 27 had a surface area of approximately 0.75 ha. It also was shallow (maximum depth of 1.6 m) with a silt/clay substrate. With the exception of a few small shoreline patches of cattail, this smaller pond was virtually devoid of rooted aquatic vegetation.

A host sample was collected, by hand, from each pond monthly from May through November, 1986. Collections were not random because a randomized procedure resulted in a sample containing disproportionately large numbers of mussels in the shell-length range of 65-79 mm. Because one goal was to estimate intensity of infestation relative to host length, some additional effort was made to collect individuals with a shell length <65 mm or >79 mm.

Each mussel was processed at the site where it was collected: cleaned, measured for its shell length with vernier calipers to the nearest 0.1 mm, and opened by severing the adductor muscles with a # 60 autopsy scalpel blade. The entire open mussel was then placed in a separate, labeled (pond designation, date, shell length) jar containing a fixative of 10% buffered formalin acetate. This procedure precluded loss of mites and exchange of mites between hosts. Hosts thus collected and preserved were transported to the laboratory. In the laboratory mites were collected from the bottom of the jars and from host soft tissues with jeweler's forceps and the use of a Zeiss stereomicroscope as needed. Only adult mites were counted. Females were easily separated from males on the basis of two or more of the following criteria: larger body size, presence of eggs, shape of palps, and differences in anal plate morphology (Vidrine 1986). The data from two collections made in the same month were combined.

Counts of female and of male mites were transformed ($\log_{10}$ [Y] for female mites; $\log_{10}$ [Y+1] for male mites). These data were then backtransformed to show mean intensity levels (as mean number of mites per infested host) with 95% confidence limits (Fig. 1A-C). To detect seasonal differences in means, log-transformed data were used in calculating *F*-values (ANOVA) on an AT&T PC 6300 computer with Microstat® general-purpose statistics package developed by ECOSOFT, Inc. A Texas Instruments statistial calculator was used for *t*-tests (Table 1) and regression analyses (Fig. 2 and 3).

RESULTS

A total of 169 *Anodonta imbecillis* individuals—90 from Pond 14 and 79 from Pond 27—were examined for *Unionicola formosa* during the 7-month study period. All host mussels were infested by female mites (Fig. 1A), but male mites were recovered from only 57 of 90 (63.3%) and 60 of 79 (75.9%) hosts in Ponds 14 and 27, respectively (Fig. 1B-C). The sex ratio of *U. formosa* was 10.7:1 (794 females: 74 males) in *A. imbecillis* from Pond 14 and 18.5:1 (1,737 females: 94 males) for the host sample drawn from Pond 27.

Mean intensity levels of female *U. formosa* in *A. imbecillis* individuals from the high-host-density Pond 27 were significantly higher than mean intensities for hosts in the moderate-density Pond 14 for every month sampled from May through September (Table 1; Fig. 1A). There was no statistical difference between the means for October, and no comparison could be made for November when no mussels were taken from Pond 27 (Table 1). Conversely, mean intensity levels of male *U. formosa* in *A. imbecillis* were essentially the same for both ponds in every month in which comparisons could be made (Table 1; Fig. 1B-C).

Although mean intensities of female mites increased seasonally from May through September in Pond 27 (Fig. 1A), those increases were not significant as determined by ANOVA on log-transformed data ($F = 2.166$, 73 df; $P = 0.0671$). Seasonal variations in log-transformed means for female mites in Pond 14 mussels (Fig. 1A) were, however, significantly different ($F = 2.504$, 83 df; $P = 0.0282$). An ANOVA on log-transformed data revealed no significant differences in mean numbers of male mites by season in either pond ($F = 0.059$, 54 df; $P = 0.7681$ and $F = 1.861$, 50 df; $P = 0.1062$ for male mites in mussels from Ponds 27 and 14, respectively).

Adult mites were positively correlated with host shell length in the high-host-density Pond 27 for every month sampled (Fig. 2). Correlations between adult mites and host length in the moderate-host-density Pond 14 were, however, largely nonexistent (Fig. 3).

Fig. 1A. Back-transformed mean number of female mites, i.e. antilog [$\overline{\log Y}$]. Horizontal lines and closed circles indicate mean numbers of *U. formosa* females in host mussels from Ponds 14 and 27, respectively. Vertical lines are 95% confidence limits around the means. Numbers above vertical lines equal host sample size. Because prevalence was 100%, number of infested mussels is the same as sample size.

Fig. 1B. Back-transformed mean number of male mites, i.e. antilog [$\overline{\log Y+1}$]. Horizontal lines indicate mean numbers of *U. formosa* males in host mussels from Pond 14. Vertical lines are 95% confidence limits around the means. Fractions above vertical lines denote prevalence, with denominator the host sample size and numerator the number of hosts infested.

Fig. 1C. Back-transformed mean number of male mites, i.e. antilog [$\overline{\log Y+1}$]. Closed circles indicate mean numbers of *U. formosa* males in host mussels from Pond 27. Vertical lines are 95% confidence limits around the means. Fractions above vertical lines denote prevalence as in Fig. 1B.

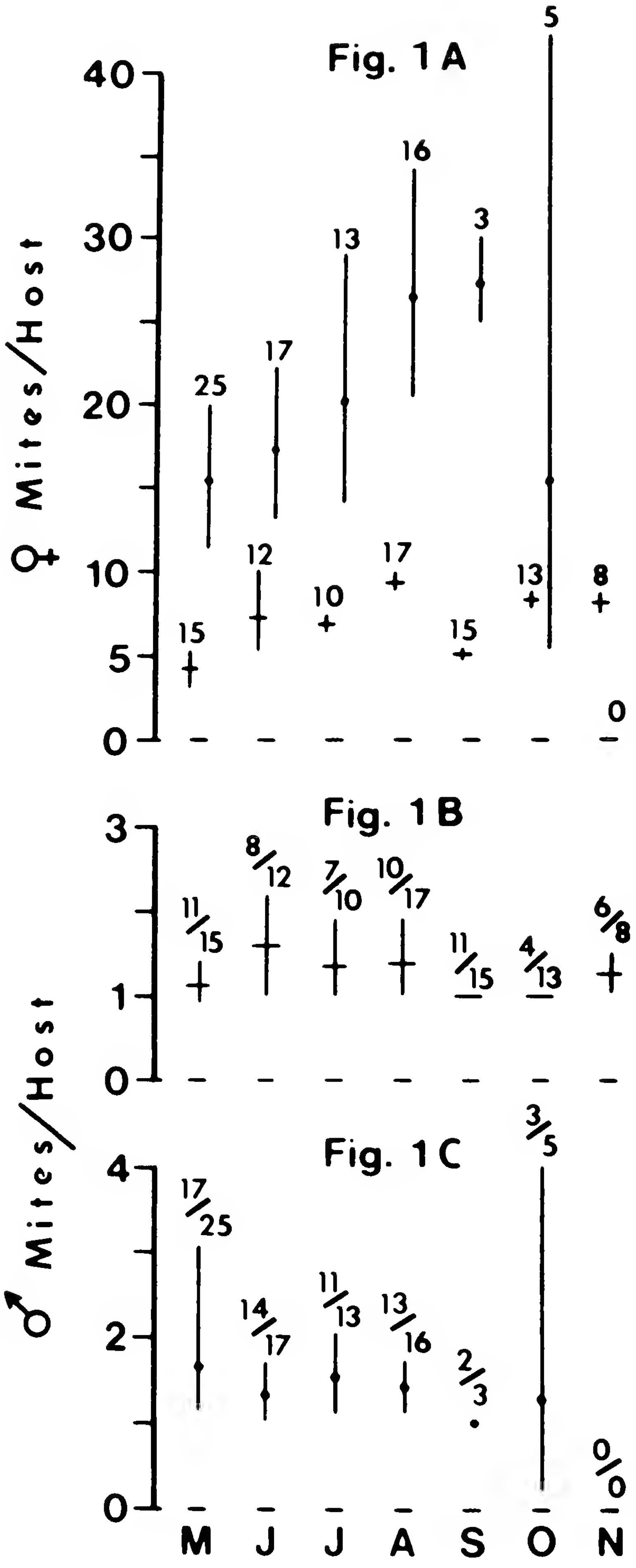

Table 1. Mean numbers of adult *Unionicola formosa* in *Anodonta imbecillis* in two ponds compared by month.[a]

Month	Female mites/host			Male mites/host		
	Pond 27	Pond 14	calculated *t*-value (two-tailed test)	Pond 27	Pond 14	calculated *t*-value (two-tailed test)
May	18.48	4.67	$t_{0.05,38} = 5.05$[b]	1.82	1.18	$t_{0.05,26} = 1.535$
	[1.19]	[0.63]	[= 6.75][b]	[0.42]	[0.33]	[= 1.585]
Jun	19.47	8.25	$t_{0.05,27} = 3.86$[b]	1.43	1.63	$t_{0.05,20} = -0.662$
	[1.24]	[0.83]	[= 4.41][b]	[0.37]	[0.41]	[=-0.667]
Jul	23.50	8.10	$t_{0.05,21} = 3.88$[b]	1.64	1.43	$t_{0.05,16} = 0.693$
	[1.31]	[0.85]	[= 4.31][b]	[0.41]	[0.38]	[= 0.634]
Aug	29.56	12.10	$t_{0.05,31} = 4.41$[b]	1.46	1.50	$t_{0.05,21} = -0.156$
	[1.42]	[0.98]	[= 4.31][b]	[0.38]	[0.38]	[=-0.023]
Sep	27.30	6.80	$t_{0.05,16} = 7.09$[b]	1.00	1.00	$t_{0.05,9}$ = nd[c]
	[1.44]	[0.73]	[= 3.77][b]	[0.30]	[0.30]	= [nd][c]
Oct	20.60	12.80	$t_{0.05,16} = 1.17$[b]	1.33	1.00	$t_{0.05,5} = 1.187$
	[1.19]	[0.93]	[= 1.36]	[0.36]	[0.30]	[= 1.168]
Nov	-	10.50	-	-	1.33	-
	-	[0.92]	-	-	[0.36]	-

[a] Initial *t*-tests based on raw data followed by log-transformed data in brackets.

[b] Significantly different at $\alpha = 0.05$.

[c] nd = not determined (mean = 1.0 and variance = 0 for male mites in mussels from both ponds).

DISCUSSION

The impetus for this study came primarily from two sources: (1) Vidrine's (1980) suggestion that concentrated populations of mussels harbored more *U. formosa* individuals than mussels in areas of lower density; and (2) Dimock's (1985) statement that "no association between the population biology of the host and that of symbiotic mites has yet been established." Vidrine's empirical observation should be evaluated with consideration of his extensive work on aquatic mite/freshwater mussel relationships. The present investigation strengthens, quantitatively, his generalization that mussels in a high-density population (as in Pond 27) harbor significantly greater numbers of female mites than host mussels in a moderate-density situation (as in Pond 14) (Table 1; Fig. 1A). Differences were so striking that mean numbers of female mites

FIG. 2

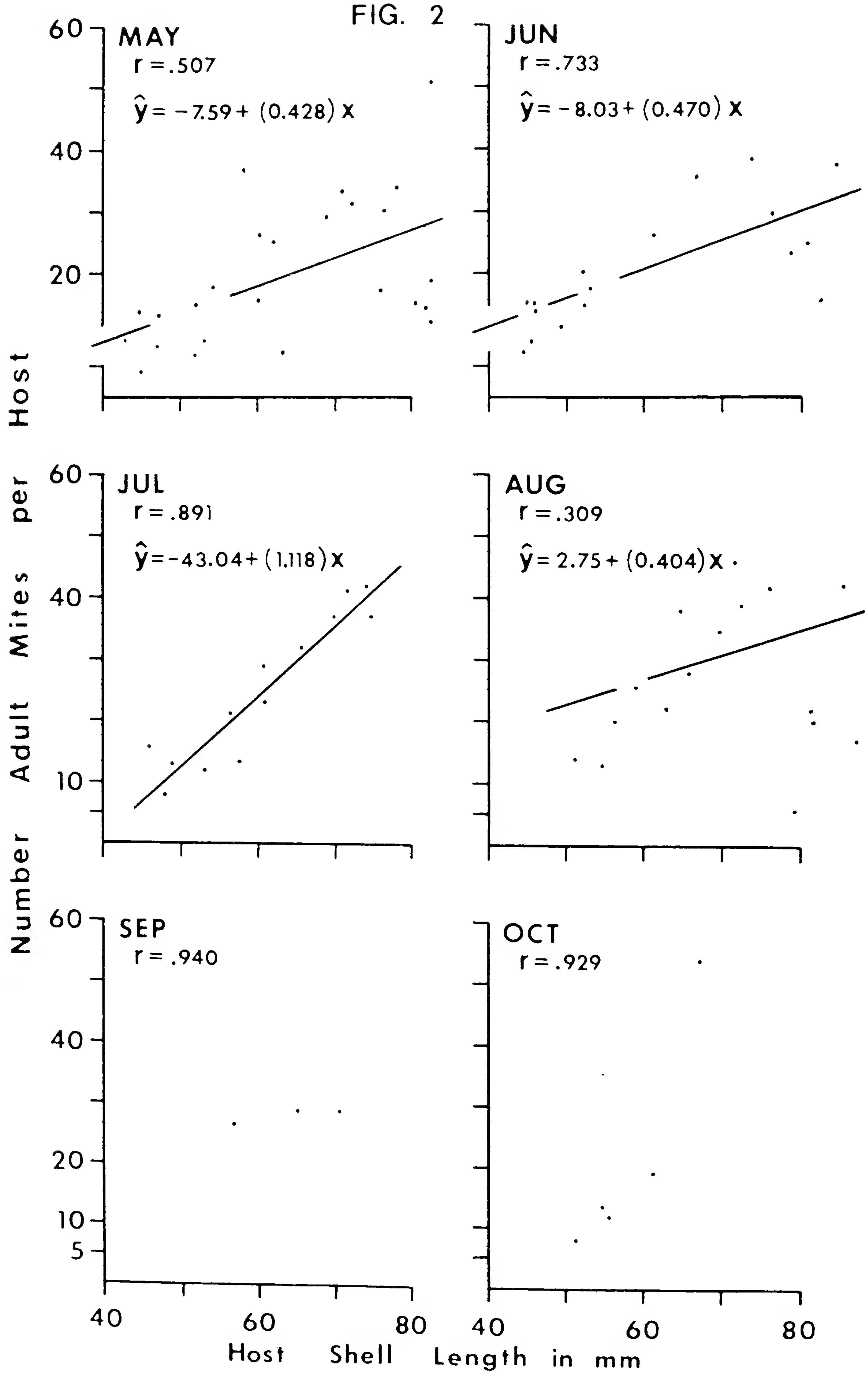

Fig. 2. Scatter diagrams showing monthly relationship between number of adult mites per host and host length. Each dot represents a single host from Pond 27.

FIG. 3

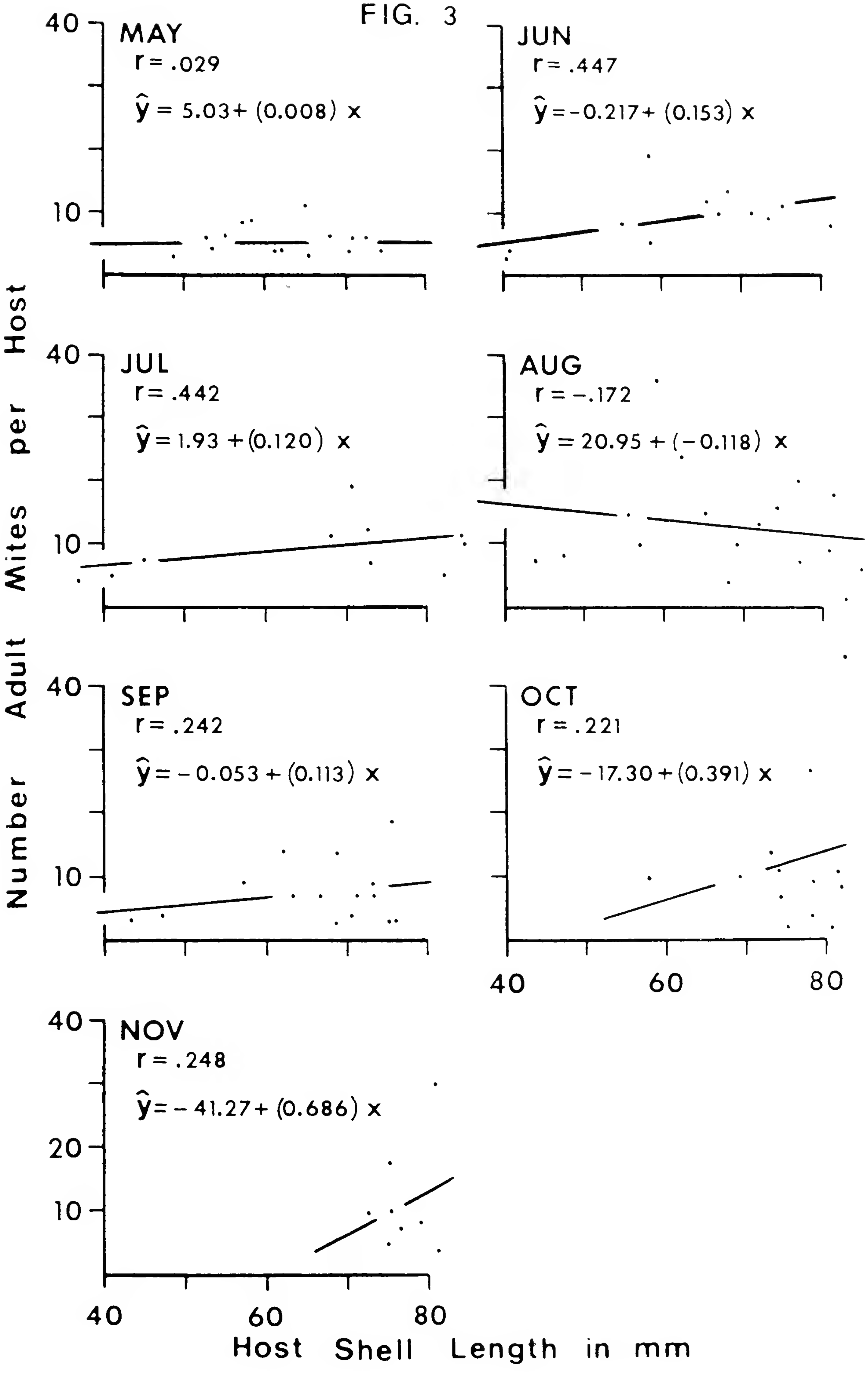

Fig. 3. Scatter diagrams showing monthly relationship between number of adult mites per host and host length. Each dot represents a single host from Pond 14.

recovered from Pond 27 hosts in May, July, and September exceeded the maximum numbers of female mites collected from mussels in Pond 14. Still, these findings must be tempered somewhat because they describe an association between host populations and the populations of their acarine parasites in only two ponds.

Although sex ratios of *Unionicola* species vary considerably (Humes and Jamnback 1950, Mitchell 1965, Gordon et al. 1979, Hevers 1980, Dimock 1983, 1985), a female-biased situation is almost universal. This condition, referred to as "harem-defense polygyny" by Dimock (1985), was also seen in the present study with female: male sex ratios of 10.7:1 and 18.5:1 in Ponds 14 and 27, respectively.

Humes and Jamnback (1950) reported an inverse relationship between prevalence of *Najadicola ingens* (Koenike, 1895) and size of *Elliptio complanata* (Lightfoot, 1786) and *Anodonta cataracta* Say, 1817, whereas Mitchell (1965) found no correlation between host size and any parameter of the population biology of *Unionicola fossulata* (Koenike, 1895). Conversely, Gordon et al. (1979) and Dimock (1985) cited positive correlations between host size and the presence of *U. formosa*, with which our findings in Pond 27 concur (Fig. 2). Previous workers tend to group all sample data on a single scatter plot to show correlations between host shell length and number of mites present. There is a possibility, however, that this approach obscures seasonal correlations. For example, if a disproportionate number of small mussels are examined in the spring, with predominantly larger mussels sampled in the fall, the question then becomes: Is the correlation size-related or season-related? To approach that question we attempted to collect *A. imbecillis* individuals across a broad spectrum of shell lengths for every sample month. Scatter diagrams were then constructed for each month (Fig. 2 and 3). Thus, in Pond 27 (Fig. 2) it is quite apparent that the positive correlations are indeed related to host shell length. The lack of correlation between host length and number of mites present in Pond 14 (Fig. 3) is not easily explained, but the seasonal factor has been removed because of a wide-ranging distribution of host lengths for each month (except for October and November).

An understanding of the growth rates and anticipated life expectancy of *A. imbecillis* individuals reveals why shell length may not be a good indicator of mites present. Harmon (1987) has rather convincingly argued that 70-79 mm will likely be the dominant size class of mussels in a population at McClintic Wildlife Station. Small *A. imbecillis* individuals grow rapidly, approaching their maximum shell length of ~80 mm after 3 to 4 years. Because a 75-mm-long individual could be in its fourth growing season, or in its eighth or ninth, it could be argued that shell length alone provides insufficient information for inferences about numbers of mites present. That argument is strengthened by our data, which suggest that host density should also be considered an important factor in determining the number of mites present per host mussel (Fig. 1A). Dimock (1985) noted that age of host may be correlated with number of mites present because increase in age would allow for increased exposure time to invasive stages of the mite. That is a reasonable conclusion even though no one has convincingly demonstrated how to age members of this mussel species—at least beyond the third growing season—with any degree of confidence. Availability of oviposition sites, as suggested by Mitchell (1965), might be a good estimator of number of mites present relative to host size. Certainly some inventive measure of weight, or of gill area, could be devised to test Mitchell's hypothesis. One feels tempted to assess the influence of mantle cavity volume, and perhaps host tissue response to mite infections as well, although the latter measure may prove exceedingly difficult to describe.

Over the past 3 years we have never been able to collect mussels from McClintic ponds in the winter months (December through February). Our lack of data for March and April is an unfortunate omission. That oversight, coupled with an unexplained population crash of *A. imbecillis* in Pond 27 that began in mid-August of 1986, further restricted our ability to draw definitive conclusions regarding seasonal influences on adult mite infections. Nevertheless, a couple of comparisons can be made. Gordon et al. (1979), whose study period covered the same months as ours, reported no seasonal differences in either prevalence or intensity of *U. formosa* infestations in *A. cataracta.* Our findings were basically similar, i.e. the prevalence was identical for every month sampled (100%) and differences in mean intensities were statistically insignificant for male mites in both ponds and for female mites in Pond 27 (Fig. 1A-C). On the other hand, Dimock (1985) noted seasonal variation for *U. formosa* in *A. imbecillis*: Adult females were most numerous in the winter and least so in late spring and summer. Although we detected significant differences between monthly means for female mites in Pond 14 ($F = 2.504$, 83 df; $P = 0.0282$), there was no seasonal trend. Means for August and September, for example, were widely separated (Fig. 1A). Thus, our knowledge of seasonal influence on populations of *U. formosa* cannot be presented as a simple generalization.

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Reproduction in the Hispid Cotton Rat, *Sigmodon hispidus* Say and Ord (Rodentia: Muridae), in Southeastern Virginia

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ABSTRACT.— The hispid cotton rat, *Sigmodon hispidus* Say and Ord, a species of the southwestern United States that has been moving northward and eastward in this century, was first observed in Virginia in 1940. In this study of the cotton rat in southeastern Virginia, most males were reproductively competent from February through November, embryos were recorded from March through October, and litter sizes were comparable to those from other locations except Kansas. Also unlike the cotton rat in Kansas, animals grew at substantial rates during the winter in Virginia. The hispid cotton rat seems to have adjusted its breeding season in Virginia by the cessation of breeding early in autumn, which permits the last young of the season to attain nearly adult size before winter arrives. Both young and adults are able to maintain and even increase their autumnal body mass throughout the winter. Timing and length of the breeding season and the patterns of body growth suggest that the hispid cotton rat is well adapted to winter, and hence to persistence of the species, in southeastern Virginia.

The hispid cotton rat, *Sigmodon hispidus* Say and Ord, is a cricetine rodent that has dramatically expanded its distribution in the central and southeastern states in historic times (Genoways and Schlitter 1967). First recorded in Virginia from Mecklenberg Co. in 1940 (Patton 1941), it moved northward in the lower Piedmont into Amelia Co. (Lewis 1944) and then north of the James River in central Virginia (Pagels 1977). The current distribution is believed to extend from Virginia Beach westward to points north of Richmond and southwestward through Halifax Co., or approximately throughout the southeastern one-third of Virginia.

Because the hispid cotton rat has tropical affinities (Hall 1981, Zimmerman 1970), it is surprising that the species has been able to extend its range to the present northern limit of its distribution and to cope with winters in such states as Kansas, Tennessee, and Virginia. Furthermore, we expected to observe that this rodent has a shorter breeding season in those marginal populations than in Texas or Mexico, which are closer to the center of distribution for the species. In fact,

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some features of the expected pattern have been reported in Kansas (McClenaghan and Gaines 1978), Oklahoma (Goertz 1965), and Tennessee (Dunaway and Kay 1964), although the details vary somewhat from location to location. Kilgore (1970) examined the possibility that northern populations might have larger litters than central populations as a way of compensating for increased winter mortality; he found significantly larger litter sizes in Kansas than in Texas.

The primary objective of our study was to examine details of reproduction and patterns of body growth in a population of cotton rats at the northern limit of the species distribution on the East Coast. Using monthly samples of live-caught cotton rats that were necropsied and examined for evidence of reproduction, we learned that cotton rats in Virginia suspended breeding from early November through late March, had litters no larger than those in central populations (Texas), and had a larger weight gain in males than in females during the winter.

MATERIALS AND METHODS

From October 1983 to November 1984, cotton rats were obtained using Fitch and Sherman live traps baited with chicken scratch feed (a mixture of wheat, millet, and cracked corn). Although not always attained, the goal was a sample of 30 animals per month. No animals were taken in January or August. The 250-ha study area, an old field in Portsmouth, Va., was dominated by grasses, *Panicum* spp. and *Andropogon* spp.; a spikerush, *Juncus effusus*; and, at the margins, young sweet gum trees, *Liquidambar styraciflua*. Other common species of plants found in the study area were trumpet creeper, *Campsis radicans*; cane, *Arudinaria gigantea*; saltbush, *Iva frutescens*; goldenrods, *Solidago* spp.; and giant ragweed, *Ambrosia artemisiifolia*. Less common were black oak, *Quercus nigra*; grape, *Vitis rotundifolia*; loblolly pine, *Pinus taeda*; smooth sumac, *Rhus copallina*; dogfennel, *Eupatorium capillifolium*; blackberries, *Rubus* spp.; briers, *Smilax* spp.; willows, *Salix* spp.; and cattails, *Typha angustifolia*. Traps were moved from place to place to prevent excessive depletion of the cotton rat at a local site.

All animals $\geq$ 50 g (lower limit of potential breeders) were killed with chloroform in the laboratory and frozen until necropsy, when the following information was recorded for each: (1) body mass (g), (2) overall body length (mm), and (3) length of tail (mm).

Additional data were recorded for females: (1) number of placental scars, (2) number of embryos, (3) uterine mass (uterus + embryos), (4) number of corpora lutea, and (5) parity class. The parity classes were defined as nulliparous females without embryos or placental scars (also lacking well-developed mammary glands and nipples); primiparous females with one set of placental scars and corpora albicantia or with embryos and corpora lutea (but not placental scars or corpora albicantia); and multiparous females with more than one set of placental scars or with embryos, corpora albicantia, and placental scars. In the analysis of body mass, the mass of the uterus was subtracted so that pregnancy would not confound the results.

Additional data were recorded for males: (1) testes position (scrotal or abdominal), (2) paired testicular mass (mg), and (3) condition of epididymal tubules (looped or convoluted). Males were considered to be breeding if the epididymal tubules were convoluted (Jameson 1950). Data are presented as $\bar{x} \pm$ SE.

RESULTS

FEMALES

The most reliable indicator of female reproductive state is pregnancy. Of 148 females, 48% were pregnant. However, no pregnant females were collected from November through February (Fig. 1). The level of breeding in females was high from March through October, when the average pregnancy rate was 68.7% (including October of both 1983 and 1984).

Using the Chi-square test, we found no differences ($\chi^2 = 0.76$, 2 df, $P > 0.50$) in the proportions of females that were pregnant in the April-May, June-July, and September-October bimonthly periods (not sampled in August). Thus, as measured by pregnancy, females bred at a uniform rate during these months of peak activity.

Overall, litter size averaged 5.00 ± 0.284 SE. However, during the peak breeding months of April to October, females averaged 5.18 ± 0.274 embryos per female. There was significant variation in litter size (= embryo counts) throughout the months of the breeding seson (ANOVA: $F = 30.46$, df = 4,62, $P < 0.005$) with largest litters ($\bar{x} = 7.83 \pm 0.984$) in May. In contrast, females in April averaged only 4.18 ± 0.652 embryos per female, and the two pregnant females in October 1983 had one and two embryos, unusually small litters for the cotton rat.

The pregnant females were divided into primiparous (those in their first reproductive experience) and multiparous (experienced breeders) groups to determine whether a difference in litter size was attributable to reproductive experience. Although there was a trend toward larger litters in multiparous females, there was no significant difference between the litter sizes of primiparous ($\bar{x} = 4.76 \pm 0.378$ SE) and multiparous ($\bar{x} = 5.72 \pm 0.371$) females during the "peak" breeding months (ts = 1.74, df = 65, $0.1 > P > 0.05$). Thus, season had greater influence on litter size than age of the female.

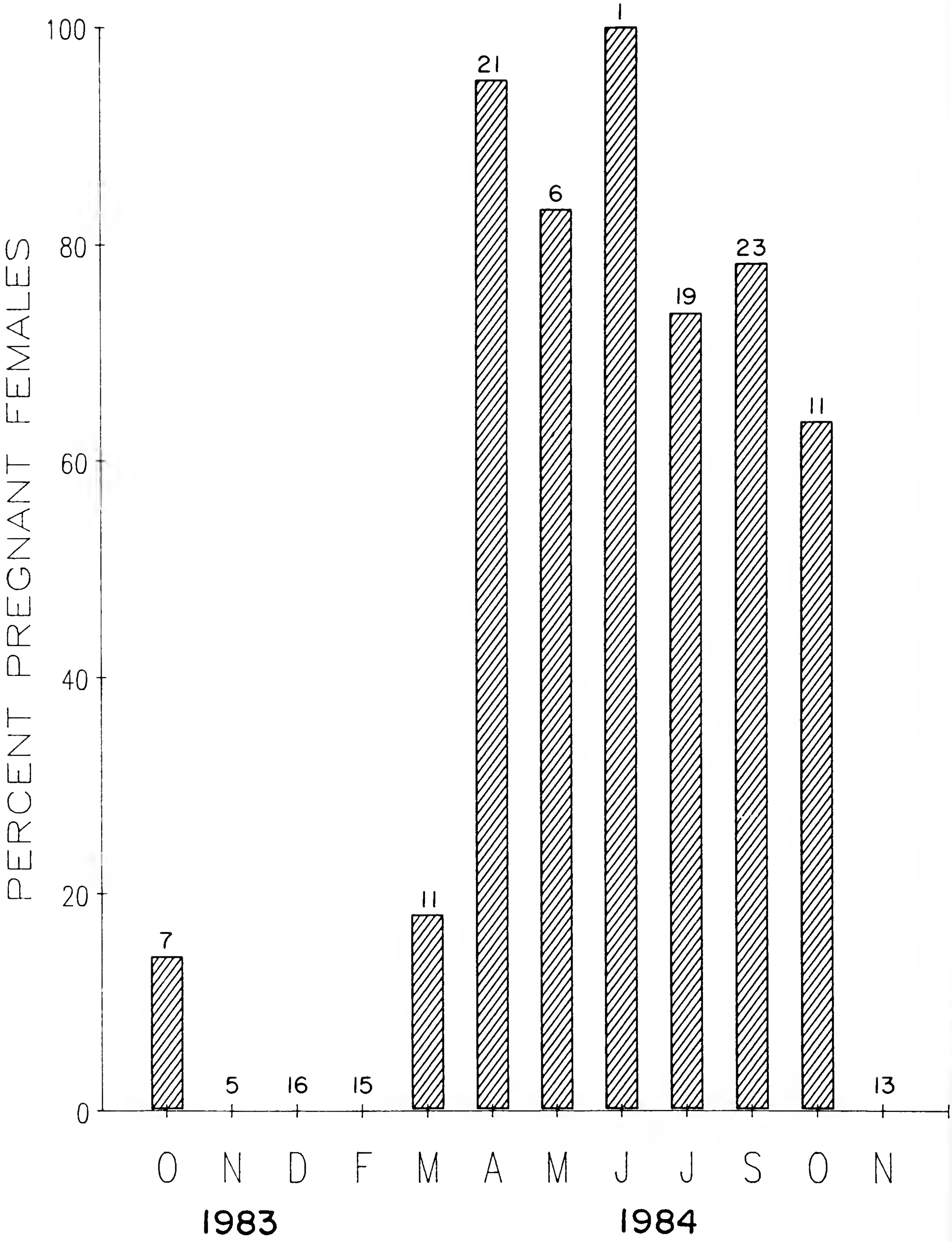

Fig. 1. Monthly percentages of females (≥50 g) that were pregnant. Sample sizes are given above each bar. N = 148. (No collections in January and August.)

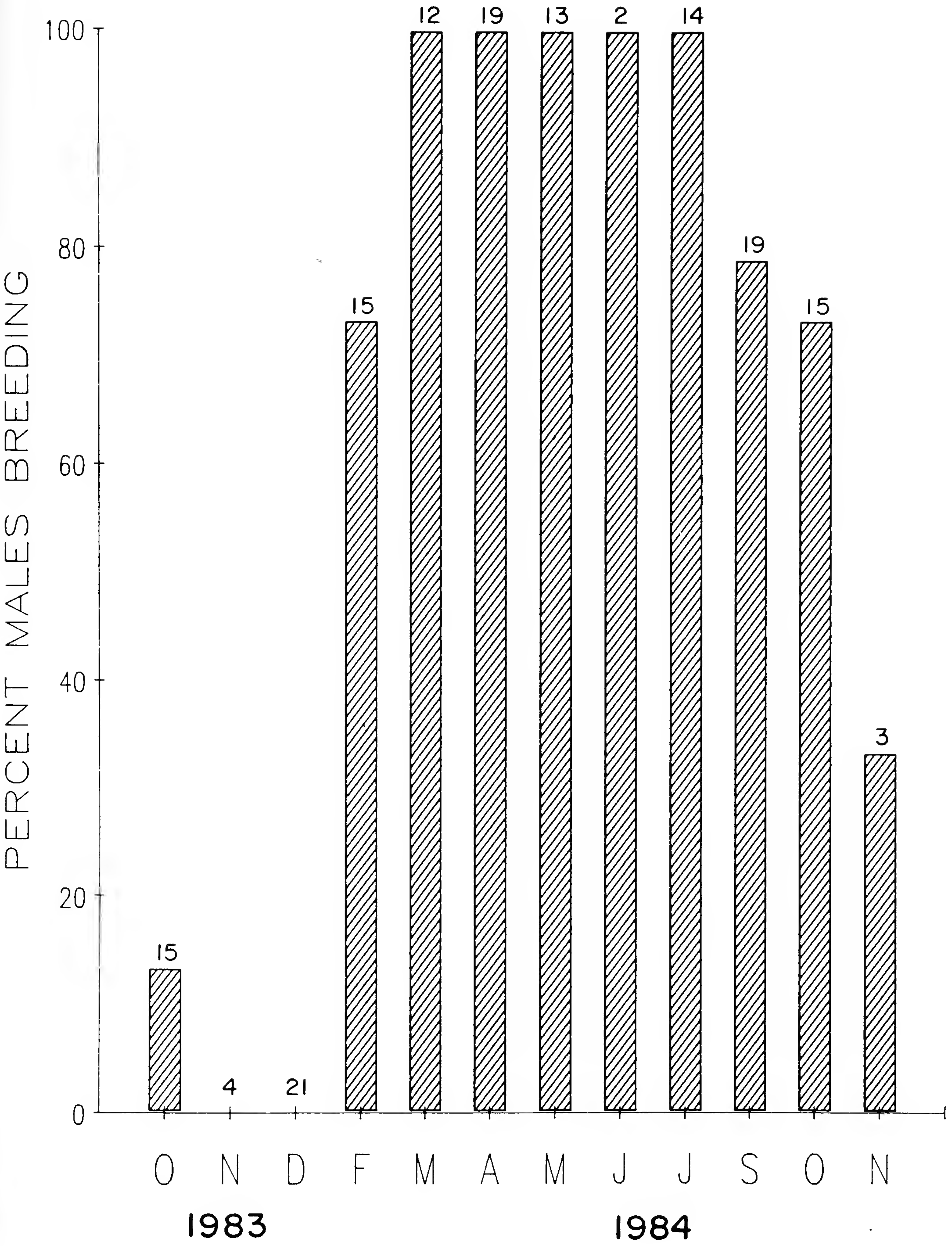

Fig. 2. Monthly percentages of males (≥50 g) that were breeding based on the presence of convoluted cauda epididymides in the testes. Sample sizes are given above each bar. N = 152. (No collections in January and August.)

PRENATAL MORTALITY

Preimplantation mortality, which occurs before the embryo has implanted in the uterine wall, can be estimated by comparing the number of ovulation sites with the number of embryos. After ovulation, the remnant of each ovarian follicle is retained. It quickly enlarges into a corpus luteum, a structure 2.0-2.5 mm in diameter, which can easily be seen and counted. If all ova are fertilized and the resulting embryos are successfully implanted, the number of corpora lutea corresponds exactly to the number of embryos. However, if there are, for example, seven corpora lutea but only six embryos, then one ovum has been lost to preimplantation mortality.

There are two potential obstacles to making accurate estimates of preimplantation mortality. The corpus luteum enlarges quickly as it produces progesterone to maintain the thick wall of the pregnant uterus. However, embryos do not appear as bulges in the uterus until day 10 in the 27-day gestation period (Meyer and Meyer 1944). Thus, for a few days the enlarged corpora lutea indicate pregnancy but no embryos are evident. A second problem is twinning, the production of two embryos from the same ovum. In this study, at least four females were judged to be pregnant (i.e. had enlarged corpora lutea) though no embryos were seen, and there was one case of probable twinning. When these females were eliminated from the analysis, preimplantation mortality averaged 5.7% of 371 ova.

MALES

Reproductive potential (fertility) in males is most reliably indicated by the presence of convolutions in the cauda epididymides, which Jameson (1950) found to be highly correlated with the presence of sperm in the tubules. Relative testicular mass (the ratio of weight of testes to weight of animal) is a fair predictor of maturity, because the testes grow rapidly in late winter prior to the onset of the breeding season. We used both of these indicators of male breeding capability.

Using convoluted cauda epididymides as a criterion, we found that males were fertile longer than females (Fig. 2), from February (73% fertile) to November (33% fertile); from March through July, all males were fertile. According to this criterion, the breeding season of males begins about one month earlier and ends about one month later than that of females.

As is typical of males of many temperate-zone mammals, testes undergo a dramatic regression in late autumn. In *S. hispidus*, the mass of the paired testes of a 120-g male might be 2,000 mg at the height of the breeding season, compared with only 80 mg after testicular regression. With regression, the cauda epididymides lose their convolutions and become looped. Such males are no longer fertile.

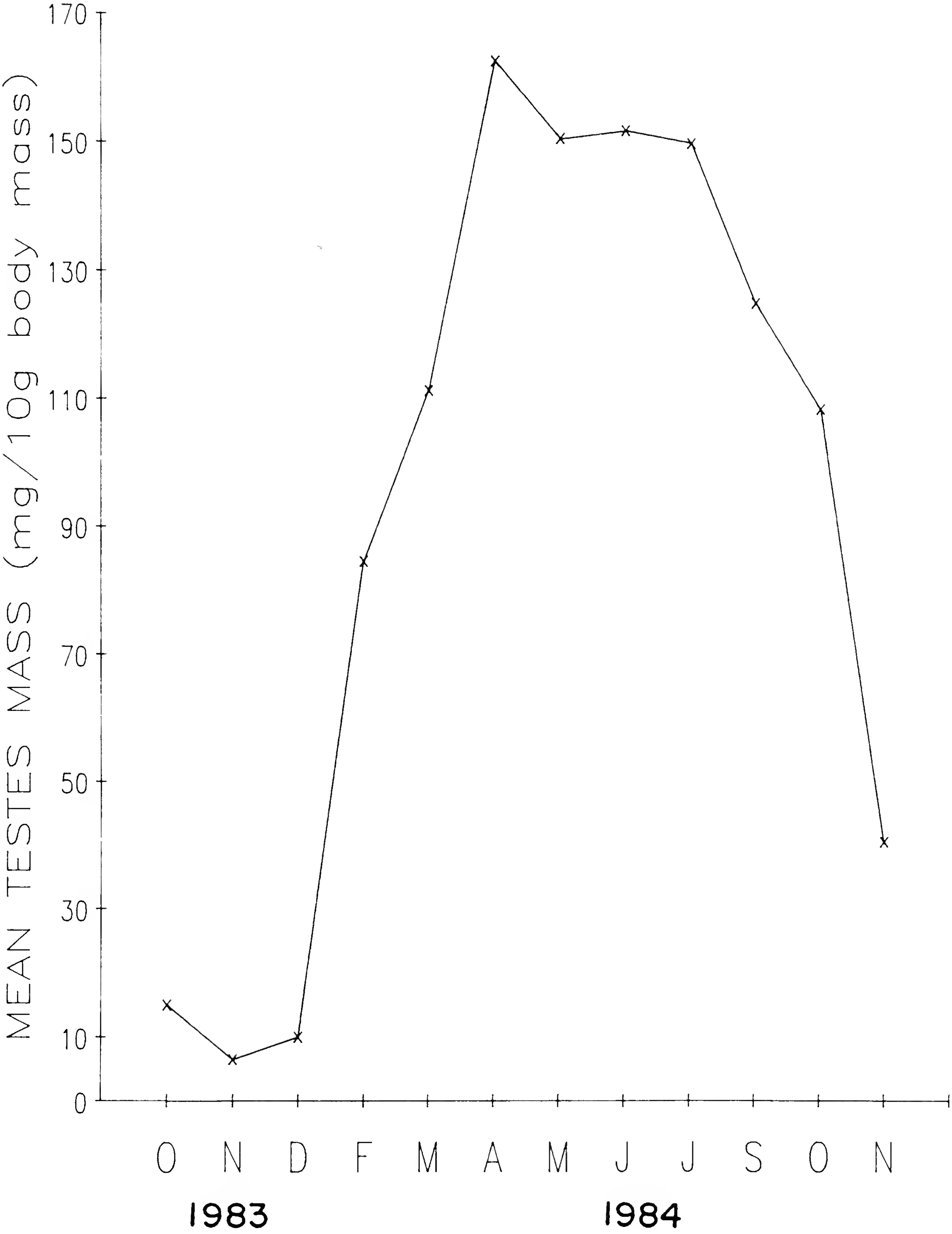

Fig. 3. Mean testicular mass per 10 g of body weight for each month of study. (Sample sizes as given in Fig. 2.)

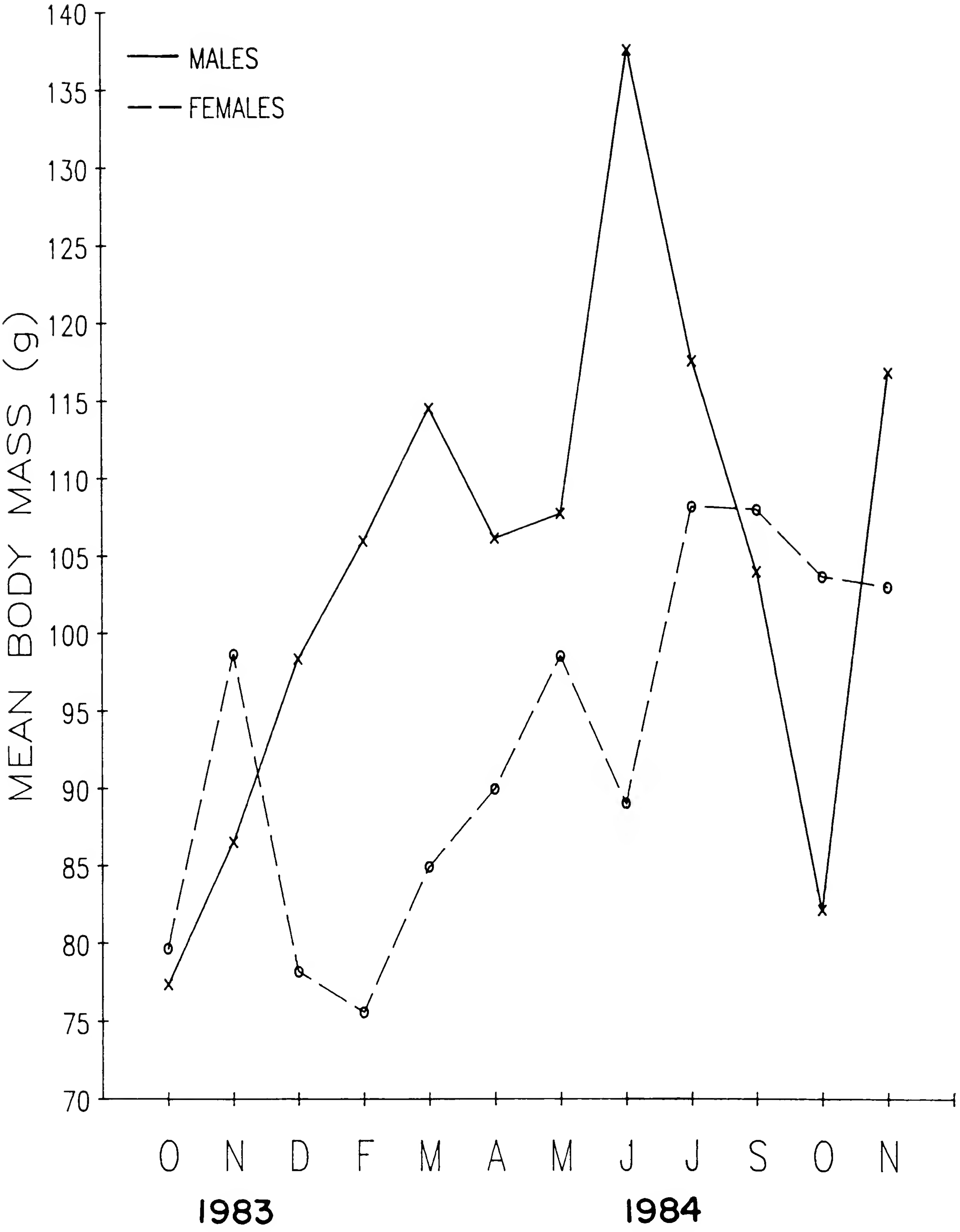

Fig. 4. Mean monthly body masses of male and female cotton rats. (Sample sizes as given in Fig. 1 and 2.)

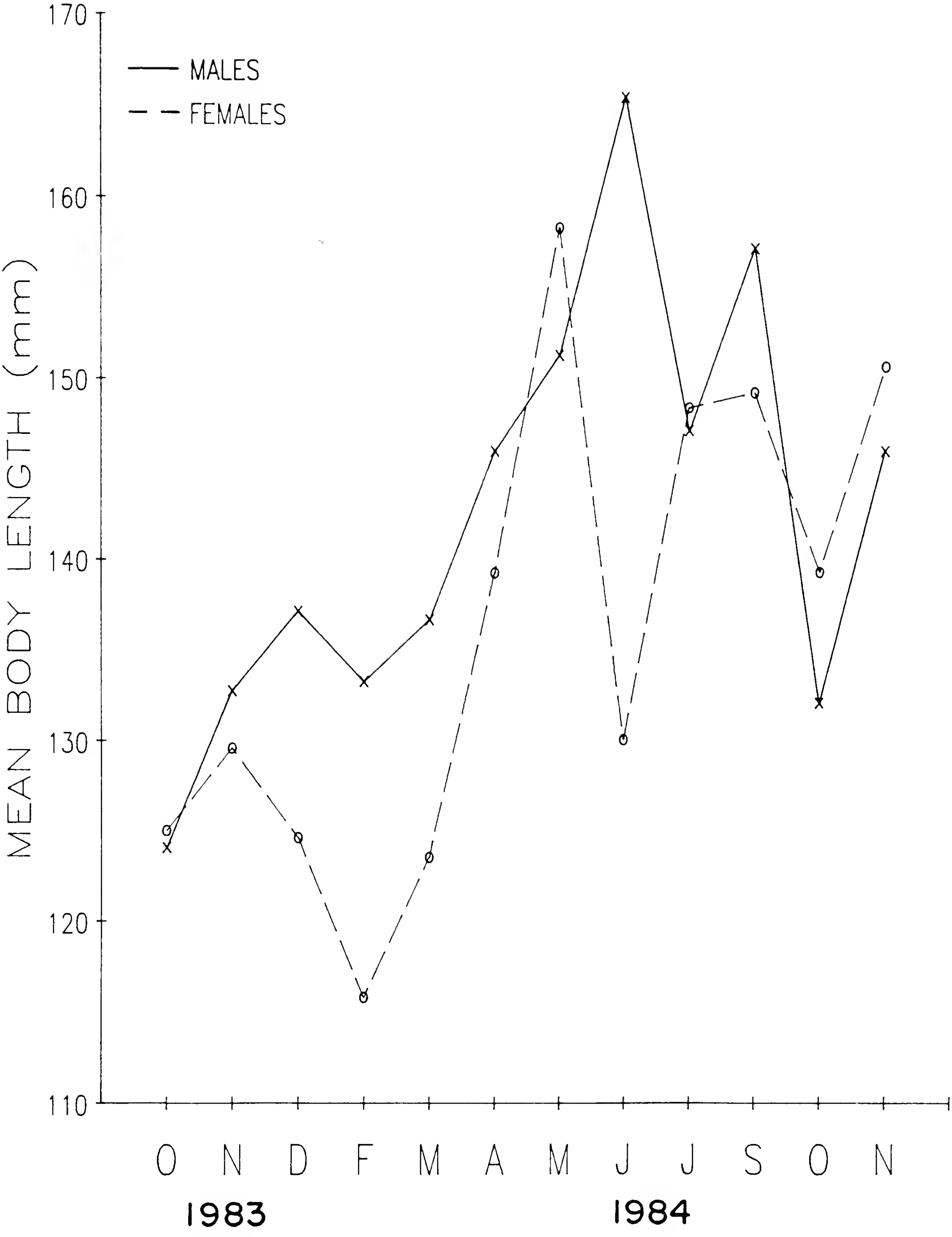

Fig. 5. Mean monthly body lengths (total length minus tail length) of male and female cotton rats. (Sample sizes as given in Fig. 1 and 2.)

Because not all males are of the same size and because testicular mass is approximately proportional to body mass (Keller and Krebs 1970), we computed the testicular mass per 10 g of body mass (Fig. 3). This assessment of male reproduction closely parallels the breeding season of males based on cauda epididymides (Fig. 2). The testes grew rapidly in late winter (February) so that overwintered males were fully mature by March. The somewhat lower fertility rates of males in late summer (September) probably were a result of an increasing proportion of young males included in the samples. However, later decreases in fertility (November and December in Fig. 2 and 3) were primarily a result of testicular regression in adult males.

DYNAMICS OF BODY SIZE

In some parts of the United States, populations of cotton rats have substantial winter mortality (e.g. Dunaway and Kaye 1964, Sauer 1985). Slade et al. (1984) showed that cotton rats surviving the winter in eastern Kansas tend to weigh nearly the same regardless of age; large animals lose mass and young animals entering the winter grow slowly, so that by spring most animals are approximately the same mass. Severe mortality and weight loss in the winter make an evaluation of body weight dynamics particularly important in *S. hispidus* at the northern limit of its distribution, such as in southeastern Virginia.

Of course, chance plays a role in determining the average mass of a sample of field-caught cotton rats, particularly during periods when young animals are entering the trappable population. However, in this study, those effects are minimized because juveniles and small subadults (<50 g) were not collected for necropsy. Overall, males ($\bar{x}$ = 101.48 ± 2.027 g) were significantly heavier than females ($\bar{x}$ = 94.26 ± 1.872 g). Body mass differences were smallest (Fig. 4) at the end of the breeding season (October and November). Males were much larger (20-30 g) than females throughout the winter in this study.

Body length (Fig. 5) showed similar trends, with males averaging 141.11 ± 1.557 mm and females 137.63 ± 1.441 mm. Males had roughly linear growth in body length throughout the late autumn and winter, and the decline in mean length was probably a result of the recruitment of spring-born animals into the trappable populations. Body lengths of males and females were most similar in October and November, a pattern also seen with body mass (Fig. 4).

DISCUSSION

Mammals seem to adjust the breeding rate to the mortality rate at a given location (Sadleir 1969). Mammals, particularly small mammals, can increase reproduction by one or more of the following means:

becoming sexually mature at an earlier age, increasing litter size, or increasing the number of litters per year (extending the breeding season or decreasing the interval between litters). Decreasing the time between litters is achieved by a short gestation period and rapid postnatal development, so that the interval between conception and weaning is minimal. In the most rapidly breeding individuals, mating often occurs within 24 to 48 hours after parturition; consequently, a lactating female frequently is pregnant with the next litter. In general, small mammals in the tropics have small litters and long breeding seasons (Sadleir 1969). However, in temperate locations, small mammals tend to compensate for shorter breeding seasons and increased mortality by producing larger litters (e.g. in *Peromyscus*; Smith and McGinnis 1968). Of the seven species of New World *Sigmodon*, only *S. hispidus* has a widespread and expanding distribution in temperate North America, making it a candidate species to examine for evidence of adjustments in its breeding biology in response to the harsher winter conditions endured by populations colonizing northern locations.

PREGNANCY RATE

Maximum rates of pregnancy were achieved early and sustained throughout the breeding season in Virginia. The observed pregnancy rate often exceeded the theoretically observable maximum pregnancy rate, such as in April when 95% of 21 females were pregnant (Fig. 1). Because bulges in the uterus cannot be detected during the first 9 days of pregnancy, embryos can be counted only for 18 days of the 27-day gestation period. During the peak breeding season, mating usually occurs within 24 hours of parturition, resulting in a 28-day interval between litters. Because embryos can be seen only for 18 days of these 28 days, the theoretical maximum pregnancy rate that can be observed is 18/28, or 64.3%, which is the detectable pregnancy rate if all females are pregnant all of the time. The higher rate in April likely is a result of synchronous breeding at the start of the reproductive season. Breeding synchrony in small mammals diminishes progressively from the start of the breeding season and disappears after the second litters are born, in part because of increasing variation in litter interval among overwintered females but mostly as a result of spring-born females entering the breeding population (at 45-60 days of age for cotton rats).

Nothing is known of the actual litter intervals of cotton rats in natural populations, but longer post-partum mating intervals would lower the maximum observable pregnancy rate below the 64.3% value. The observed pregnancy rate during the breeding season (68.7%) slightly exceeded the theoretical value; that can be explained by sampling error or, more likely, by changes in the behavior of pregnant females.

Randolph et al. (1977) found that the fat accumulated during the last half of pregnancy was used during lactation, when energy demands outstripped the female's speed in processing food. It is plausible that females in the later stages of pregnancy would be increasingly attracted to the high-energy food source (mixed seeds) that was used as bait.

Although Dunaway and Kaye (1964) did not calculate monthly pregnancy rates, they did observe low levels and apparently sporadic breeding throughout what they judged to be a relatively mild Tennessee winter. In Oklahoma, Goertz (1965) found no pregnant females during a severe winter, but he did find pregnant females during November, December, and February of a milder winter. Goertz reported highest pregnancy rates during May to September. Haines (1961) recorded no embryos in Texas cotton rats from October to February, but he did record corpora lutea throughout the year. Haines observed the highest pregnancy rates between February and July, with low rates after September and the lowest rates in December. Thus, the breeding season seems to be somewhat earlier in Texas compared with Tennessee, Oklahoma, or Virginia.

In duration, methods, and analysis, our study most closely parallels that of McClenaghan and Gaines (1978), conducted near Lawrence, Kan. They found no breeding from November through March, which is similar to what we observed in the Virginia population. The pregnancy rate in Kansas was low (30%) in April, highest (over 80%) in May, and generally greater than 70% from June through October. Overall, the patterns of breeding in Virginia and Kansas were similar for both sexes.

Litter Size

Within a species, litter size is affected by several interacting factors, including age, parity, body weight, and nutritional state (Sadleir 1969). In a recent exhaustive review, Cameron and McClure (1988) examined the patterns of breeding in female *Sigmodon hispidus* by evaluating published and unpublished laboratory and field data. Using a stepwise multiple regression analysis on data from 18 studies, Cameron and McClure (1988: table 2) examined the patterns of geographic variation in litter size and the effects of body size on litter size. By finding latitude, longitude, and body length to be significantly associated with mean litter size, their analysis "confirmed the existence of both north-south and east-west variation in litter size." Largest litters were reported for the large females of the north-central states.

A further analysis "indicated that latitudinal and longitudinal variation in litter size were due primarily to differences among subspecies" (Cameron and McClure 1988). Specifically, *S. hispidus texianus*, which had the largest litters at 7.20 ± 0.23 SE, averaged 8.35 ± 0.35 in Kansas but only 5.10 ± 0.37 in coastal Texas (Houston). Nutrition may also contribute to these differences within this subspecies (Cameron and McClure 1988; table 6). Although litters of *S. hispidus virginianus*, the subspecies in Virginia, were significantly larger than those of Mexican and Central American subspecies, they were significantly smaller than those of *S. h. texianus* (Cameron and McClure 1988).

The litter size of 5.00 for Virginia cotton rats lies in the range of values reported from other studies (Cameron and McClure 1988: table 2), although on the low side for "northern populations." Populations from Tennessee averaged 6.1 embryos per litter (Dunaway and Kaye 1961), from Oklahoma 6.0 (Goertz 1965), from western Kansas 6.7 (Fleharty and Choate 1973), and from eastern Kansas 9.0 (McClenaghan and Gaines 1978). Furthermore, laboratory animals derived from Houston, Kansas, and Tennessee populations and raised by McClure at Indiana University remained significantly different in average litter size even after 16-28 generations and 8-12 years in the laboratory (Cameron and McClure 1988: figure 2). Thus, the determination of litter size in *Sigmodon hispidus* is complex, involving both genetic and environmental factors.

Although Lawrence, Kan., and Portsmouth, Va., are both near 37° N latitude, the Kansas winters are longer and colder (average 2° C), in the absence of moderating oceanic effects. In coastal Virginia, snow falls only once or twice a year and periods of freezing weather rarely last more than a few days. Despite the more moderate conditions in Virginia (Cameron and McClure 1988: table 4), the Virginia cotton rats did not breed longer than the Kansas cotton rats, and Virginia litter sizes as well as body sizes were significantly smaller. However, female cotton rats in Virginia were pregnant at nearly maximum levels throughout the breeding season (Fig. 1), and there was a trend ($0.1 > P > 0.05$) for multiparous females to have larger litters than primiparous females. Thus, differences in age of onset of breeding and in longevity (neither of which was measured in these studies) may be important in affecting geographic differences in the dynamics of these populations.

MALE BREEDING

The breeding season of males began in February and lasted to November (Fig. 2). Based on the breeding criterion of convolutions in the cauda epididymides, 73.3% of males were in breeding condition in February and 100% were fertile from March through June. McClenaghan and Gaines (1978), who also used epididymal convolutions to determine breeding condition in males, did not find 100% breeding in any month. Their highest monthly rates were just under 90% in June and August; and in all other months during the breeding season except May, fertility rates were less than 60%. Haines (1961) measured spermatogenesis and found that the production of sperm remained high from February through October (which was the breeding season for males in our study). Dunaway and Kaye (1964), who assessed male reproduction based on live-caught animals, observed that just under 100% of males had descended testes (i.e. were mature) during the June-September period. They noted a decline in the percentages of mature males from October to December, but by January, the proportion of males with descended testes again began to increase.

Testicular mass is closely related to reproductive condition in males (Haines 1961). Our results agree with those of McClenaghan and Gaines (1978), who found testicular mass to be highest from June through September, also the peak breeding months for males as determined by convolutions of the cauda epididymides in the present study. In Kansas, smallest testicular masses were recorded for December, but we found the smallest testicular masses in the October to December period, with dramatic monthly increases from December through April. Testicular mass remained high from April through July and then declined sharply (Fig. 3), probably at first because of the recruitment of young males in the trappable population and later also because of testicular regression of adult males. Goertz (1965) reported large testicular masses from February through September and low values in the remaining months.

In Texas, Haines (1961) reported spermatogenesis in males with the largest testicular masses; he provided perhaps the best available information on the relationship between these two variables. He found the largest average testicular mass per 10 g of body mass during the period from February through August, after which testicular mass declined until November. McClenaghan and Gaines (1978) and Haines (1961) found that testicular regression resulted in a reduction to about 1/30th of the maximum testicular mass, compared with a value of about 1/26th in our study.

BREEDING SEASON

During the breeding season, 68.7% of females were pregnant, and in most of the same months all males were judged to be fertile. The breeding season in males started one month earlier and ended one month later than the breeding season in females. That pattern is common in mammals (Sadleir 1969), and it is interpreted as adaptive in that the energy costs for breeding in females are greater than those in males. As a result of the earlier onset of fertility in males, mature males are ready to copulate and produce fertile matings when females undergo the first estrous cycle of the spring.

The breeding season in Virginia closely paralleled that found by McClenaghan and Gaines (1978) in Kansas. Both locations are at or near the northern limit of distribution for hispid cotton rats; therefore, it is not surprising to find some similarities. Differences also were noted. Although the breeding season in Virginia started a month earlier in both sexes, it lasted until October for females in both Kansas and Virginia. Another similarity in the breeding of *Sigmodon* in these two studies is the percentage of breeding females; the rate was relatively low during the first month in which pregnancies occurred and then rose sharply to near the maximal rate in the following month. In McClenaghan and Gaines (1978), this trend must be inferred because their study ended in April. However, if the high May level at the start of their study can be extrapolated to the preceding April, a large increase in breeding level occurred at the same time in Kansas and Virginia.

In Texas (Haines 1961), the breeding season began in the same month as in Virginia, but it ended one month sooner. This is an unexpected result if we assume that the breeding season has been shortened at more northerly locations because of the constraints of winter on the energy budgets of mammals. We would expect the breeding season to be longer at more southerly locations. Goertz (1965), who found pregnant females in some winter months, believed that breeding was possible in Oklahoma under the favorable conditions of mild winters.

EFFECTS OF BODY SIZE

Several factors affect patterns of body size in *Sigmodon hispidus*, including sex, latitude, subspecies, and nutrition. In some, but not all, populations males are larger than females, and northern populations tend to have larger skeletal sizes and, in some seasons, higher fat content. *Sigmodon h. texianus* is significantly larger than all other subspecies (Cameron and McClure 1988). McClenaghan (1977) found generally larger skull and skeletal variables for cotton rats from northern populations (Kansas and Virginia) than from southern localities (Mexico), but Kansas and Virginia populations differed in only one skeletal feature. However, the seasonal pattern of body growth of Virginia cotton rats differs from that of Kansas cotton rats, in which Slade et al. (1984) found that the large adult animals lost weight over the winter. By contrast, in Virginia, the males in particular gained body mass steadily throughout the winter months (Fig. 4). This pattern of winter increase is evident but less well defined for body length (Fig. 5), although males did increase in length nearly every month from October to May or June.

Mean body mass for females was low in October (79.7 ± 6.77 g) but it rose sharply to 98.6 ± 10.19 g in November. The mean values for December and February were low, indicating that females were not gaining weight during this time. Because there was no breeding during these months, the lower mean mass in winter cannot be a result of the recruitment of young, lightweight animals; therefore, we can assume that females either lose mass or fail to gain significant mass during the winter months. From February through July, the monthly mean mass of females rose steadily, indicating a real increase in body mass during this time. Then, when the young of the year finally entered the trappable population, the monthly mean mass of females (and males) declined.

Patterns of body length were similar to those of body mass. Although both length and mass are measures of body size, length may be a more reliable index of body growth in *S. hispidus* because (1) animals lose mass but not length during starvation or during winter, (2) both sexes divert resources away from growth and towards reproduction during the breeding season, and (3) females store up body fat during pregnancy in preparation for the greater energy demands during lactation (Randolph et al. 1977).

In conclusion, cotton rats in southeastern Virginia seem to be well adapted to the northern limit of their present distribution on the East Coast; their March-to-October breeding season and the sustained growth of overwintering individuals suggest high survival rates of both young and adults during the winter months. The modest litter size may indicate that, unlike Kansas populations, Virginia populations have not been selected for larger litter sizes to compensate for winter mortality.

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Occurrence of the Milliped *Auturus erythropygos erythropygos* (Brandt) in Virginia (Polydesmida: Platyrhacidae)

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The milliped *Auturus erythropygos erythropygos* (Brandt) is known from scattered localities ranging from the Fall Zone of northern North Carolina to the northern Coastal Plain of Georgia and westward into the Kings Mountain inselberg and the western Piedmont Plateau of North Carolina (Shelley 1978, 1982, Filka and Shelley 1980). The northernmost site, 8.3 km (5.2 miles) WSW of Gaston, Northampton Co., N.C, is the only one north of the Roanoke River, and because it is only 3.2 km (2 miles) S of the Virginia border, I (Shelley 1978, 1982) predicted discovery in that state.

A Virginia locality can now be confirmed. I collected two males and one female on 11 May 1988, in Brunswick Co., 9.6 km (6 miles) SE of Lawrenceville, along Va. Hwy. 670 just south of the Meherrin River, about 19 km (11.9 miles) N of the North Carolina state line and due north of the Northampton Co. site. The specimens were encountered in typical habitat for American platyrhacids, under bark and in a moist, rotting oak stump at the base of a wooded slope. They conform to the anatomical illustrations and description of *A. e. erythropygos* (Shelley 1982). Efforts to find the milliped in adjacent counties to the north, east, and west in May and September, 1988, were unsuccessful; therefore, the extent of the population north of the Roanoke River is unknown. Both the Brunswick and the Northampton samples were obtained in May, but those from western North Carolina were recorded in April, July, August, October, and December of other years (Shelley 1982), which suggests that the milliped should be collectable in Virginia during the same months. The Brunswick Co. locality is the northernmost for the species, genus, tribe, and family along the Atlantic Coast and the only known occurrence of the Platyrhacidae in eastern Virginia. *Euryurus leachii* (Gray) occurs in the westernmost counties near West Virginia, Kentucky, and Tennessee (Hoffman 1978).

The Virginia specimens of *A. e. erythropygos* are housed in the North Carolina State Museum of Natural Sciences invertebrate collection, catalog number A4897. The known distribution of the Platyrhacidae in Virginia is depicted in Fig. 1.

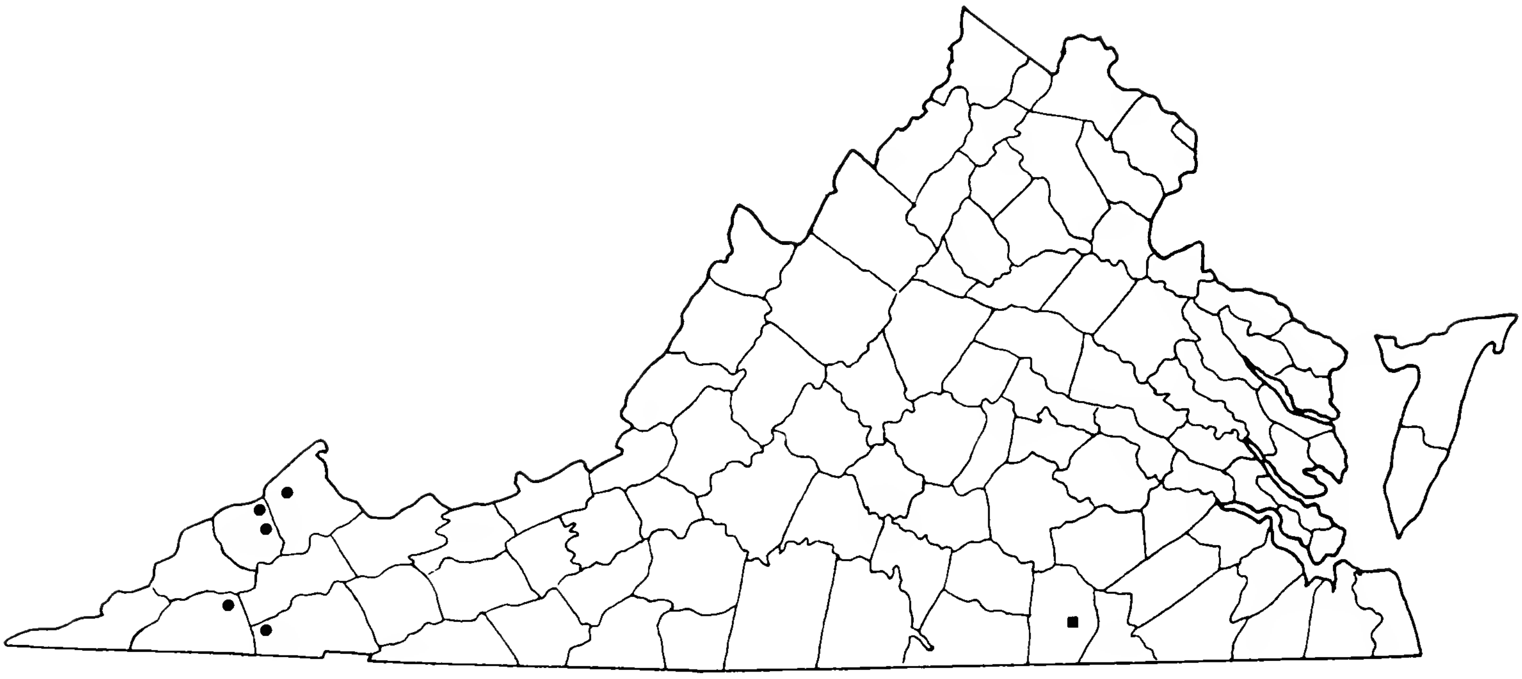

Fig. 1. Distribution of the milliped family Platyrhacidae in Virginia. Dots, *Euryurus leachii*; square, *Auturus erythropygos erythropygos*.

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Kleptoparasitism of a River Otter, *Lutra canadensis,* by a Bobcat, *Felis rufus,* in South Carolina (Mammalia: Carnivora)

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ABSTRACT.— In January 1985, a bobcat, *Felis rufus,* was observed robbing a river otter, *Lutra canadensis,* of an American coot, *Fulica americana.* Observations of interactions between these two carnivores are practically nonexistent. This observation indicates that bobcats can assume an aggressive kleptoparasitic mode of behavior toward river otters.

Bobcats, *Felis rufus,* are opportunistic in prey selection, usually choosing abundant and easily captured prey (Pollack 1951, Beasom and Moore 1977, King et al. 1983). Carrion is also consumed (McCord 1974). In spite of this general foraging strategy, there are no published reports describing interspecific prey-stealing behavior (i.e. kleptoparasitism) by the bobcat. I observed a case of kleptoparasitism involving a bobcat and a river otter, *Lutra canadensis.* The incident occurred on Par Pond, a 1,120-ha cooling reservoir located at the Savannah River Plant, Barnwell Co., S.C.

At 1645 hours on 21 January 1985, while observing waterfowl with a spotting scope from the reservoir dam, I observed a river otter swimming. The otter climbed onto a 1-m ice shelf along the shoreline. Approximately 50 American coots (*Fulica americana*), 15 pied-billed grebes (*Podilymbus podiceps*), 5 buffleheads (*Bucephala albeola*), and 10 lesser scaup (*Aythya affinis*) were feeding in the vicinity of the otter. The otter remained on the shore approximately 1 minute, returned to the water, and swam toward the feeding aggregation of waterfowl about 45 m away. After approaching within 10 m of several coots, the otter submerged; it resurfaced in 35 seconds and began swimming to shore with a coot in its mouth. The coot's wing was flapping as the otter climbed onto the ice shelf. The otter then plucked the breast feathers and fed upon the breast. Feeding continued as the abdominal cavity was opened and a portion of the viscera consumed. At this point, the otter appeared startled, quickly looked about, and jumped into the water. A bobcat came into view and appeared to emit a snarl as the otter swam

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from the shoreline. The bobcat picked up the coot and quickly made its way into the thick vegetation that bordered the shoreline. Upon later inspection of the site of the interaction, all that remained were coot feathers and some entrails.

Weather conditions were uncommonly harsh in the area on 21 January, with winds out of the northwest at 8-10 km/hr and an air temperature of -5° C. The incident took place approximately 75 m from my location on the dam.

This incident is unique in the literature not only because of the kleptoparasitism by a bobcat but also because the bobcat displaced an atypical competitor, a river otter, from a prey item. A report of a bobcat killing a young river otter is the only previously documented description of a direct interaction between these two mammalian carnivores (Young 1958).

Several incidents of river otter predation upon aquatic birds have been documented. Meyerriecks (1963) reported a river otter preying upon a common gallinule (*Gallinula chloropus*) in Florida. In Alaska, Quinlan (1983) found that river otters killed over 75% of the immature fork-tailed storm-petrels (*Oceanodroma furcata*) and Leach's storm-petrels (*O. leucorhoa*) in a single colony. Cahn (1937) observed a river otter's unsuccessful attempt to catch a coot in Ontario, Canada. Most studies of river otter food habits have found that birds make up a minor portion of the diet (Loranger 1981, Knudsen and Hale 1968, Stenson et al. 1984).

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A DISTRIBUTIONAL SURVEY OF NORTH CAROLINA MAMMALS

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Spring Movement Patterns of Two Radio-tagged Male Spotted Turtles

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ABSTRACT.— Spring movements of male spotted turtles (*Clemmys guttata*) on the upper Coastal Plain of South Carolina may be extensive. Movement in 24 hours for two turtles equipped with small radio transmitters ranged from 0 to 423 m. The typical activity pattern involved a series of movements throughout each pond that was occupied, followed by overland travel to the next nearest body of water. Backtracking to previously occupied habitats was observed only once. These movements may reflect mate-search activity and support the concept of "transient behavior."

Males turtles of many species appear to move greater distances than females at certain times of the year (Chelazzi and Francisci 1979, Morreale et al. 1984, Parker 1984, Berry 1986, Gibbons 1986). This difference is thought to be representative of divergent reproductive strategies between the sexes, but other explanations for movement are possible, including seasonal migrations to and from overwintering sites and departure from an unsuitable habitat (Gibbons 1986). In general, the reproductive strategy hypothesis predicts that male reproductive success is dependent on the number of mating opportunities available (Trivers 1972, Williams 1975, Maynard Smith 1978). Under this assumption, a male turtle's reproductive success could benefit by increasing movements in search of females during the breeding season (Morreale et al. 1984). Occasionally, movements are extensive and some males may act as "transients," moving regularly throughout the active season without recrossing areas previously traversed (Kiester et al. 1982, Parker 1984). Observations of the spotted turtle, *Clemmys guttata* (Schneider), made during a study of its seasonal activity patterns in South Carolina (Lovich 1988), support the concept of extensive movements by males during the breeding season. The purpose of this note is to report those observations.

The study site was located along Risher Road on the Savannah River Plant in Barnwell Co., S.C. This area is characterized by scattered, shallow, ephemeral marshes, and cypress-tupelo ponds separated by pine plantations and clearcuts. Two adult male *C. guttata*, designated ACJ and ACI, were collected on 2 March 1987 and equipped with small radio transmitters. The plastron lengths of the turtles were 93 mm and 99 mm, respectively. A transmitter was attached to the posterior portion of each carapace and accounted for 10% or less of the animal's mass. The turtles were released at the respective points of capture on 6 March and located daily until 15 April. From 15 to 23 April, positions were determined every 48 hours. Both turtles were periodically brought back to the laboratory during the study period for battery replacement or transmitter-package repair. In spite of the downtime, 35 observations of movement were obtained for each turtle. Every attempt was made to minimize disturbance to the turtles during tracking. After each turtle was located, the straight-line distance to the previous point of capture was measured with a meter tape or determined from aerial photographs.

A summary of major movement patterns is shown in Fig. 1. Movements in 24 hours ranged from 0 to 423 m. Twenty-two percent of all daily changes in location were greater than 100 m. Rates of movement reached 20.7 m/hour with a mean of 2.7 m/hour. The distances moved between captures did not differ significantly between the two turtles (Mann-Whitney U = 617; df = 1; P = 0.80). ACJ moved a total of 2,750 m and ACI 1,843 m. The greatest straight-line distance achieved from original point of capture was more than 1,000 m for each turtle. During these movements, each animal occupied three separate aquatic habitats (marshes and ponds) (Fig. 1). Known time spent in each habitat ranged from 4 to 20 days. The typical activity pattern involved a series of movements through an aquatic habitat followed by overland movements (up to 2 days) to the next nearest body of water. Return by an individual to a previously occupied aquatic habitat was observed only once.

Detailed descriptions of short-term movements have not previously been reported for this species. However, Ernst (1968) found that a small proportion of *C. guttata* in a Pennsylvania population returned to the original point of capture 4 to 64 days after being moved 805 m upstream from his study site. Netting (1936) reported movement of *C. guttata* from an upland hibernation site to a small swamp, but provided no further data. Ernst (1976) found that normal daily movements (based on hand recaptures) were rarely more than 20 m, but males were occasionally captured up to 250 m from water during the mating season. Seasonal microhabitat selection was reported by Ward et al. (1976), but daily movement data were not provided. The results of the present study, although provisional, suggest transient behavior (as defined by Kiester et al. 1982, Parker 1984) as well as oriented long-distance movement in male *C. guttata*. Because these movements occurred during the mating season (Ernst 1976), they may be a reflection of mate-search activity, as suggested by Morreale et al. (1984). It is not likely that these short-term

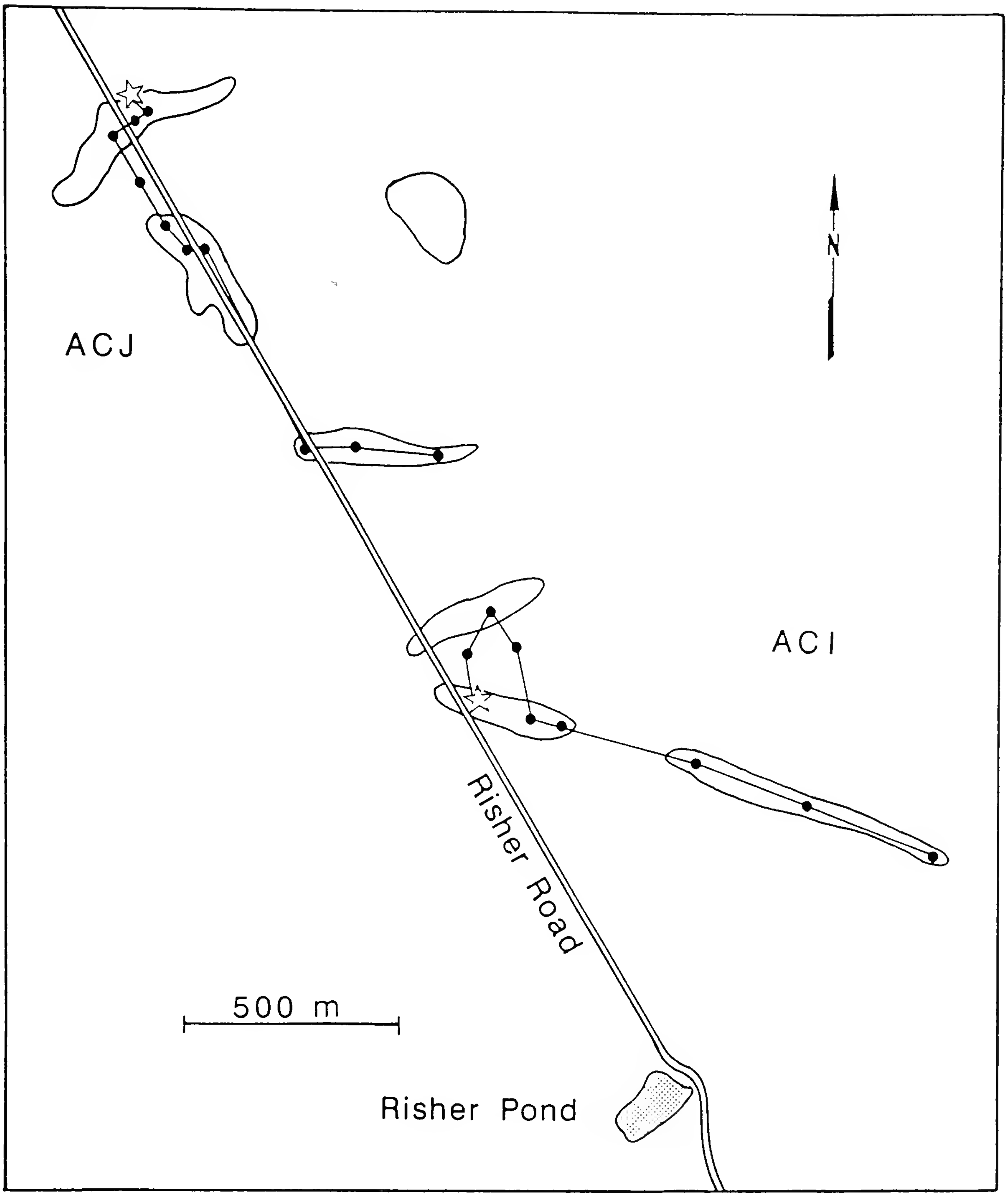

Fig. 1. Map of study area showing major aquatic habitats (temporary marshes and ponds) along Risher Road. Paths represent major movement patterns and do not include every capture point. Starting points are designated with a star.

movements were in response to major changes in the aquatic habitats since water levels remained relatively stable during the period of study. Additionally, no correlations between environmental temperatures and turtle movements were detected.

Comparative data are not available for females, but I predict that they will show greater site fidelity than males. Ernst (1970) reported similar home-range size in male and female *C. guttata*, but his results may be an artifact of long-term hand recapture techniques. Kiester et al. (1982) considered radiotelemetry to be a basic prerequisite for determining transient behavior in turtle populations.

The possible importance of transient males in maintaining gene flow between adjacent turtle populations was suggested by Kiester et al. (1982). In fact, genetic exchange among populations of freshwater turtles in adjacent aquatic habitats has been demonstrated electrophoretically (Scribner et al. 1984). The phenotypic homogeneity exhibited by the widely distributed spotted turtle (Ernst and Barbour 1972) may be a result of this behavior.

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ENDANGERED, THREATENED, AND RARE FAUNA OF NORTH CAROLINA

PART I.

A RE-EVALUATION OF THE MAMMALS

Edited by Mary Kay Clark

This book is a report prepared by a committee appointed in 1985 by the North Carolina State Museum of Natural Sciences to re-evaluate the list of mammals presented in *Endangered and Threatened Plants and Animals of North Carolina* (John E. Cooper, Sarah S. Robinson, and John B. Funderburg, editors. N.C. State Mus. Nat. Hist., Raleigh, 1977), which is now out of print. Committee members were Mary Kay Clark, David A. Adams, William F. Adams, Carl W. Betsill, John B. Funderburg, Roger A. Powell, Wm. David Webster, and Peter D. Weigl. The report treats 21 species listed in the following status categories: Endangered (5), Threatened (1), Vulnerable (6), and Undetermined (9). Most species accounts discuss the animal's physical characteristics, range, habitat, life history and ecology, special significance, and status (including the rationale for the evaluation and recommendations for protection) and provide a range map and an illustration of the animal's external characters. Ruth Brunstetter and Renaldo Kuhler illustrated the book. An introductory section contributed by Ms. Clark discusses the changes in status that occurred in the decade between 1975 and 1985. It also mentions efforts to protect marine mammals and includes a checklist of the cetaceans known from North Carolina.

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New Records of the Distribution and the Intestinal Parasites of the Endangered Northern Flying Squirrel, *Glaucomys sabrinus* (Mammalia: Sciuridae), in Virginia

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ABSTRACT.— Three specimens of *Glaucomys sabrinus* are reported from localities in the mountains of Grayson and Highland counties, Virginia. Thirty-three other *G. sabrinus* were captured and released at or near these sites. Only one specimen had been previously recorded in Virginia, in Smyth Co. Five sites where we captured *G. sabrinus* had a mean elevation of 1,354 m (1,097-1,615 m), and the southernmost sites were at the greatest elevation. The typical habitat was a mixed forest of red spruce or other northern-type conifers and northern hardwoods. Three species of intestinal nematodes were recovered from the squirrels: *Citellinema bifurcatum*, *Strongyloides robustus*, and *Syphacia thompsoni*.

The northern flying squirrel, *Glaucomys sabrinus* (Shaw), has an extensive distribution in the northern United States and Canada. In the southern Appalachian Mountains it is extremely rare and is considered a relict of the ice ages. It is known from only a few scattered populations in West Virginia, Tennessee, North Carolina, and Virginia (Wells-Gosling and Heaney 1984). In 1985, both subspecies of the northern flying squirrel that occur in the southern Appalachians, *G. s. fuscus*

Brimleyana 16:73-78, July 1990

Miller and *G. s. coloratus* Handley, were listed as federally endangered by the U.S. Fish and Wildlife Service. Weigl (1987) summarized factors considered as major threats to survival of these subspecies. Among these are loss of habitat, competition with the southern flying squirrel, *G. volans* (L.), and a parasitic nematode (*Strongyloides* sp.), a form that is harbored by the southern flying squirrel without apparent harm but that may be lethal or debilitating when transferred to *G. sabrinus.*

The present report on *G. sabrinus* in Virginia updates distributional data and provides information on its intestinal parasites. Some ecological data are included herein. Payne et al. (1989) provide a more extensive description of plant communities associated with *G. sabrinus* in the southern Appalachians, including Virginia.

The only previously recorded specimen of *G. sabrinus* in Virginia was trapped in 1959 by Handley at 1,615 m on Whitetop Mountain in Smyth Co. (Handley 1980). The animal was captured in a snap trap attached to a red spruce bole in a mixed forest of red spruce (*Picea rubens*), yellow birch (*Betula lutea*), and sugar maple (*Acer saccharum*) within a few hundred meters of an almost pure stand of red spruce.

In December 1985, one of us (J.R.B.) found the remains of a female northern flying squirrel along the headwaters of a creek at 1,478 m in Grayson Co., 7.6 km E of the Smyth Co. site. The remains were under the edge of a large rock and partially covered with leaves. Tracks of a mink, *Mustela vison* Schreber, leading to and from the spot were evident in the snow around the carcass and indicated predation as the cause of death. The vegetation was a mixed forest of Fraser fir (*Abies fraseri*) and red spruce, with American beech (*Fagus grandifolia*), yellow birch, and red maple (*Acer rubrum*) the most prevalent canopy hardwoods and with rhododendron an important understory component. In April 1986, two specimens were taken about 336 km NE of the Smyth Co. site, in the Laurel Fork area of Highland Co. These specimens were also taken along a headwater stream. They were accidentally trapped in Museum Special mouse traps during a study of the fleas of Virginia by one of the authors (R.P.E.). These specimens were captured in a northern hardwood forest dominated by yellow birch, American beech, and sugar maple. An almost pure stand of young red spruce was within 10 m of the capture site. Mountain laurel (*Kalmia latifolia*) was the dominant understory plant. This locality, at 1,158 m, is about 19 km E of Cheat Bridge, the nearest locality from which *G. s. fuscus* has been taken in West Virginia (C. W. Stihler, personal communication). Several irregularly oriented mountain ridges separate the two sites.

In addition to the specimen records, 33 northern flying squirrels were captured and released at 4 of 22 nest-box locations in Virginia during an ongoing study that was initiated in 1985 (Fies and Pagels 1988). The locations included the Grayson site (19 captures) where the specimen apparently killed by a mink was found and the Smyth Co. site (10 captures) of Handley's (1980) first record in 1959. The other sites were in Highland Co., approximately 5 km S (1 capture) and 20 km S (3 captures), respectively, of the site where the snap-trapped specimens described above were taken. These sites, at 1,097 m and 1,219 m, were also mixed forests characterized by red spruce and various northern hardwood species.

In West Virginia, where a nest-box and live-trapping study of *G. sabrinus* has been under way for several years (Stihler et al. 1987), of more than 60 captures, *G. sabrinus* was taken only in spruce or spruce-northern hardwood forests (K. B. Knight and C. W. Stihler, personal communication). However, as we found at one of our Highland Co. sites where a stand of red spruce was 10 m away, red spruce does not necessarily characterize the point of capture. Weigl (1987) observed, "Although often associated with spruce-fir forests, this form is more commonly captured in adjacent stands of mature hardwoods . . . ." It is curious that no spruce or fir trees were present within miles of the capture site of a specimen taken in 1935 in Tennessee (Handley 1953). Payne et al. (1989) found red spruce in their transects at all 13 sites where *G. sabrinus* was collected. Nearly all data indicate that both northern-type conifers and northern hardwoods are necessary components of the habitat of *G. sabrinus.*

The specimens from the Highland Co. site were examined for parasites. Both of the squirrels harbored nematode parasites. The large female (VCU 4629) had *Syphacia thompsoni* (3 males, 10 females) in the cecum, *Strongyloides robustus* (31 females) in the anterior 10 cm of the small intestine, and a single male *Citellinema bifurcatum* also in the anterior small intestine. The smaller female (VCU 4630) had a female *S. robustus* in the anterior 10 cm of the small intestine and 11 male *S. thompsoni* in the cecum.

Only the formalin-fixed intestinal tract of the Grayson Co. specimen (VCU 4615) was available for parasitological study. Two female *S. robustus* were found in the anterior small intestine, and two male *S. thompsoni* in the cecum. Unsporulated coccidean oocysts that averaged 21.8 μm by 14.3 μm were present but uncommon. By gross examination slight hyperemia of the intestine was noted in the area surrounding the 31 individuals of *S. robustus.*

All of these nematode species have been reported from sciurid hosts in Virginia previously (Davidson 1976, Eckerlin 1985, Parker 1968, 1971, Price 1928) and from *Glaucomys sabrinus* elsewhere in the United States (Eckerlin 1974, Rausch and Tiner 1948), but they have not previously been recorded from this host in Virginia. Voucher specimens of *Citellinema bifurcatum*, *Strongyloides robustus*, and *Syphacia thompsoni* have been deposited in the Helminth Collection of the U.S. National Museum of Natural History with accession numbers 79566, 79567, and 79568, respectively.

The presence of only male *S. thompsoni* in the two squirrels that had this species deserves comment. Although life cycle data for this nematode are not available, it is generally agreed that male oxyurids do not survive more than a short time after the females have been fertilized. Consequently, females usually outnumber males, but we found 2 males and 11 males in the absence of females. A unisexual infection of 32 male *S. thompsoni* was reported from the red squirrel, *Tamiasciurus hudsonicus* (Erxleben), in Wisconsin (Tiner and Rausch 1949). It was suggested that the unusual sex ratio could be attributed to the occurrence in an unnatural host. *Glaucomys volans* is the type host for *S. thompsoni,* but the high prevalence in *G. sabrinus* suggests that the latter species also is a suitable host. Clearly, more data are needed to clarify the relationship between *S. thompsoni* and *G. sabrinus*.

The Highland Co. specimens (both skin and skull), VCU 4629, female, and VCU 4630, female, measured respectively: total length 260, 250; tail vertebrae 120, 110; hindfoot 35, 36; ear 24, 26. The only standard measurements available for the Grayson County specimen are length of tail vertebrae 139 mm and hindfoot 38 mm. The partial museum skin is deposited in the Virginia Commonwealth University Mammal Collection (VCU 4615, female).

That *G. sabrinus* was only recently taken in the Laurel Fork area in Highland Co., which has been sampled periodically over many years, suggests that the squirrel is rare. However, it also suggests that the apparent rarity may at least in part reflect the difficulty in trapping this animal or the inadequacy of collecting techniques that have been used. Weigl (1978) found that *G. sabrinus* and *G. volans* occasionally occur in the same woodlot although perhaps only temporarily. Further, Weigl (1978) found in captive populations that *G. volans* was able to control nests more often than *G. sabrinus* could and that it was much more aggressive than *G. sabrinus* in defending home area. One of us (J.F.P.) handled and ear-tagged numerous *G. volans* at the Highland Co. sites before and after the captures of the northern flying squirrels. C. O. Handley, Jr. (personal communication) observed numerous individuals of *G. volans* at one of the sites as much as 50 years ago. The species have coexisted at Stuart Knob in West Virginia for at least 36 years (Stihler et al. 1987). However, again perhaps suggestive of its great rarity, low trappability, or temporary coinhabitance of the sites, we have had no recaptures or new captures of *G. sabrinus* at the Highland Co. locations to date. Finally, it has also been noted that *G. volans* carries a parasitic nematode of the genus *Strongyloides*, and it has been suggested that this nematode is lethal to *G. sabrinus* (Weigl 1977). Each of the three *G. sabrinus* that we were able to examine and report here harbored *S. robustus*, and it appeared that each was a healthy adult animal until its death. In West Virginia, Stihler et al. (1987) reported that "the 1 northern flying squirrel for which parasitological data are available was infected with *Strongyloides*, but there was no evidence this was debilitating." Certainly, these data are limited and more study is needed on all aspects of the biology of *G. sabrinus*, including its interactions with *G. volans*, if we are to develop guidelines for its recovery.

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Age Estimates for a Population of American Toads, *Bufo americanus* (Salientia: Bufonidae), in Northern Virginia

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ABSTRACT.— Age estimation by skeletochronology was made on adult female and male *Bufo americanus* from a small population in northern Virginia. This breeding population consisted predominantly of males 3-4 years old and females 4-5 years old. Size and age were not closely correlated, i.e. the larger toads were not necessarily older. Large males did not appear to have an advantage over the small in mating; average SVL of amplectic males (64.5 mm) was similar to that of calling males (64.8 mm). First breeding occurred in late March or early Arpil and appeared dependent upon water temperatures greater than 11°C in breeding ponds.

An old technique for the estimation of age in amphibians and reptiles, skeletochronology, has recently gained renewed interest. The use of bone layers to estimate the ages of frogs or snakes has occurred irregularly since the early 1900s; however, the technique received considerable criticism because of the researchers' inability to demonstrate that each bone layer represents the same time period. This criticism has been addressed by several European herpetologists (e.g. Castanet 1985), who have used known-aged or captive-raised animals to test the annual deposition of a single bone layer in elements of the appendicular skeleton.

Hemelaar and van Gelder (1980) studied two populations of the European toad, *Bufo bufo* (L.) and demonstrated that a single periosteal layer was deposited each year. Their experimental demonstration was simple, but elegant. They marked toads so that each could be recognized individually and then removed bone samples in successive years. This procedure showed that an extra layer was present in the second year. In an attempt to repeat their experiment, Zug initiated a mark and recapture study of an American toad (*Bufo americanus* Holbrook) population in a suburban park in northern Virginia. Owing to the transitory nature of the population and an irregular sampling regime, a Hemelaar/van Gelder-type study could not be repeated, although we

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were able to estimate the ages of some marked individuals. In this report, we summarize our skeletochronological analyses and natural history observations.

MATERIALS AND METHODS

Each spring from 1983 through 1988, the toads breeding in Eakin Park (Fairfax Co., Va.) have been censused. In 1983-85, the toads were captured, measured, weighed, and individually marked. The toads were marked uniquely by removing the distal two phalanges using the 1-2-4-7 coding technique (Ferner 1979). The toe tips were immediately preserved in 10% buffered formalin and 3-12 months later prepared histologically (see Zug and Rand 1987). The first digit (1 and 10) of the hand was not used because injury to the "thumb" could have affected the reproductive activities of the males. The numbers of individuals marked were: 1983, 19; 1984, 40; 1985, 13. In subsequent years, all toads were counted and their location and behavior were noted.

Two age estimates can be derived from the histological slides: (1) the number of periosteal layers observed, complete and incomplete, and (2) the sum of the number of complete layers observed and the estimated number of layers partially and completely resorbed. The estimate of resorbed layers is based on Hemelaar's (1985: figures 2,3) graphic technique for the estimation of periosteal growth in *B. bufo*. *Bufo americanus* and *B. bufo* are equivalent-sized species; therefore, they are assumed to have similar growth rates. The use of Hemelaar's technique and the potential difficulties with the assumptions are discussed in later sections.

Each toad's snout-vent length was measured with dial calipers to the nearest 0.1 mm (though measuring a live, struggling toad is, at best, accurate to 1.0 mm). Weights were taken on Pesola spring scales to the nearest 1 g. Air and water temperatures were recorded with a Muller and Weber quick reading cloacal thermometer to the nearest 0.2° C.

Histological sections were examined independently by the two authors. Heather Kalb (HK) reviewed all the slides; selected the best section of the phalanx for each individual; and measured the diameters of the central marrow cavity, the endosteal ring, and each periosteal layer (Mark of Skeletal Growth, MSG) as delineated by a LAG (Line of Arrested Growth), across the dorsoventral axis of the phalanx. Because all toads were caught in early spring and had not begun a new growth cycle, the outside diameter of the phalanx represents the last LAG. The number of measured MSGs equals the total number of incomplete and complete periosteal layers present in each phalanx. George Zug (GZ) counted the total number of MSGs on the sections identified by HK, but without knowledge of HK's counts and measurements. These data serve to estimate the age of the individual toads based on the standard skeletochronological assumption that each MSG (= one growth cycle) represents one year in the life of a toad.

RESULTS

AGE ESTIMATES AND POPULATION STRUCTURE

The initial goal of the mark and recapture study was to repeat Hemelaar/van Gelder's confirmation of the addition of one new MSG each year. Only one marked toad (a male) was caught in a subsequent year. This toad showed two MSGs in 1984 and three MSGs in 1985. Because of the poor recapture rate, marking was discontinued after 1985.

Comparison of MSG counts. Independent counts permit the evaluation of the precision of data collection and the "legibility" of the MSGs in this sample. Of the total sample (N = 69), 61 phalangeal sections could be read by both observers; 46 counts (75%) were identical, 13 differed by ±1 and two by ±2. The differences were examined by the Wilcoxon matched-pairs signed-rank test ($z = 3.26$, $P = 0.0006$). This nonparametric test evaluates the null hypothesis that the differences between the two observers' counts are random. The z value rejects that hypotheses, because when different, GZ's counts are less than HK's counts with only one exception.

Age estimates. All subsequent discussions of age are based on HK's counts and measurements. Examination of the phalangeal histology suggested that the first year's periosteal growth layer (MSG) had been resorbed in many of the Eakin Park toads. To correct our age estimates for the lost MSGs, we needed to determine the number of MSGs lost from each toad's phalanx. Hemelaar's graphic technique (1985: figures 2,3) offered a mechanism for such a determination. We selected a maximum diameter of 220 μm for the first LAG/MSG (= first year's periosteal growth), because 12 toads showed minimum LAG diameters <220 and toads with resorption/endosteal core diameters <220 had minimum MSG diameters >230 μm. By establishing a minimum first-year MSG diameter, the minimum MSG diameter data for each toad could be assigned to a year class (Fig. 1). The assignment of each toad's minimum MSG to a year class locks the larger MSG diameters for that toad into subsequent year classes. We then summed the diameters for each age class and calculated MSG diameter means and standard deviations for each class (Fig. 1). The estimated age for each toad is, thus, the number of MSG diameters measured plus the estimated

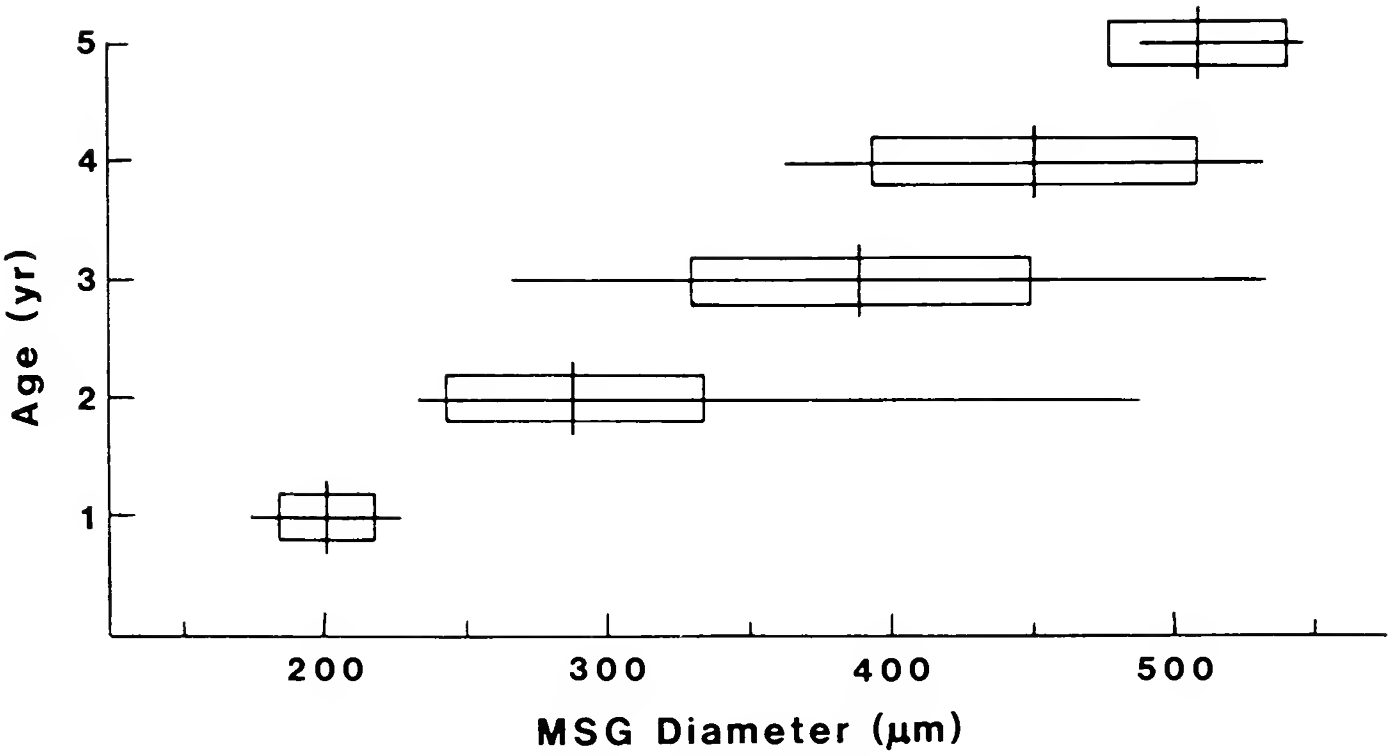

Fig. 1. The relationship between MSG (marks of skeletal growth) diameters and age in *Bufo americanus* from Eakin Park, Fairfax Co., Va.

number of MSGs lost (i.e. 0, 1, or 2 years in this data set). Because a LAG forms each winter and periosteal growth begins anew each spring, we accept the hatching of tadpoles as age 0 and each subsequent spring as a "birthdate"; therefore a toad with two MSGs and captured in spring 1988 hatched and metamorphosed in 1986.

Population structure. The following interpretations are based on the total of the number of MSGs seen and the number of MSGs estimated to have been lost. In 1983, Zug marked 19 adult toads; age estimates are available for 16 toads. Males ranged from 2 to 4 years and females from 4 to 5 years (Fig. 2). In 1984, 53 adults were seen, 41 marked, and ages estimated for 31; the age range is the same as for 1983 toads. Fifteen toads were seen and marked in 1985; ages estimated for 14 with a similar age distribution as in 1983-84.

Estimated age and body size. There is no significant correlation between age and body size (snout-vent length; SVL). In males (N = 46), the correlation coefficient is low (r = 0.20, $P > 0.05$), and when all toads with estimated age (N = 61) are examined, the correlation is marginally better (r = 0.45, $P < 0.01$). In contrast, the correlation (r = 0.92) is significant for the association of weight and length (wt = -103.89 + 2.08 SVL) for all toads captured.

Age and size in amplectic toads. Since all males captured were calling and the females were moving toward the male choruses or in

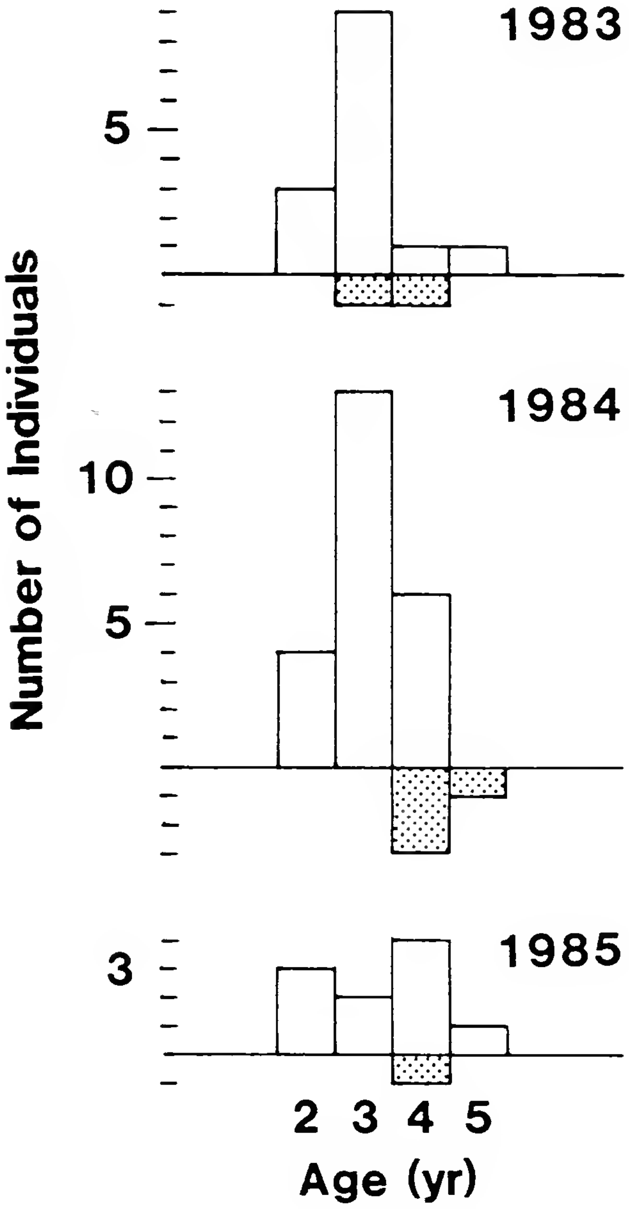

Fig. 2. Age (estimated) distributions for the Eakin Park, Fairfax Co., Va., population of breeding toads from 1983 through 1985. Males are plotted above the horizontal line, females (stippled) below the line.

amplexus, we assumed that our sample contained all adults. Male (N = 51) SVL averaged 64.8 mm (51.1-74.3, SD = 4.76), and female (N = 10) SVL averaged 82.3 mm (71.4-92.6, SD = 7.30). The males in amplexus (N = 9) had a mean of 64.5 mm SVL (51.5-71.4, SD = 6.51); the females in amplexus (N = 9) had a mean of 80.6 mm SVL (71.4-92.6, SD = 7.58). In 1983, the four amplectic males were three (N = 3) and four years old; the five amplectic males in 1984 were 2 (N = 2), 3 (N = 2), and 4 years old. No amplexus was observed in 1985. The females were 4-5 years in 1983-84.

PHYSICAL ENVIRONMENT AND BREEDING

Dates of first breeding. First breeding, i.e. presence of amplectic pairs, was observed on 8 April 1983, 5 April 1984, and 28 March 1987. On 29 March 1985, males were calling and several females were observed entering the breeding pond, but no amplexus occurred while GZ was present. In 1986, the first major chorus did not occur until 21 April; no females were observed on that date. No major choruses occurred in 1988, although a few males called for the first time on 3 April; because no *Bufo* egg strings were located from April through mid-May, it appears that breeding did not occur.

Air and water temperatures. The means and ranges of temperatures observed during breeding were: air 12.8°, 10.0-19.5°C; water 13.2°, 11.0-17.0°C; N = 10. These data include temperatures recorded subsequent to first breeding as well as at first breeding.

Breeding sites. The study area is a suburban park that encompasses a small permanent stream and its valley, abutted on the north and south by housing developments. The park includes a mix of hardwood forest, cattail marsh, and mowed grass tracts. Three aquatic sites are generally available for toad spawning: (west to east) a temporary woodland pond (ca. 20 m, maximum length), a cattail marsh (ca. 70 m) with lagoon-like extensions into adjacent forest, and a permanent man-made pond (ca. 25 m) at the edge of a recreational field. In 1983, an amplectic pair was found in the flooded grass area adjacent to the woodland pond. In 1984, amplectic pairs occurred in the marsh and subsequently in the woodland pond. First and subsequent breeding activities were observed in the woodland pond in 1985. The 1986 chorus occurred in the permanent pond. First and second breeding activity in 1987 occurred in the marsh, third in the permanent pond, and fourth in the pond and marsh. A few males were calling for the first time on 3 April 1988 in the permanent pond; during subsequent visits an occasional male was heard in various localities, but no breeding was observed in 1988.

DISCUSSION

The single recaptured toad with an additional MSG after 1 year is not confirmation of the "annual deposition of a periosteal layer" assumption. It does, however, indicate that the Eakin Park *B. americanus* produce one MSG each year, and our age estimates are based on that assumption.

The blind protocol for determining the number of MSGs permits an evaluation of the legibility of the growth layers and the accuracy of the observers. The agreement of our observations for 75% of the toads and a difference of one MSG in 21% of the toads indicate a moderately high reliability of the counts. The Wilcoxon sign test shows a conservative bias for the GZ counts, but it does not invalidate the use of the counts for estimating age. To avoid inconsistency, only the HK data were used in estimating ages.

We made a number of other assumptions in our skeletochronological analysis, and these assumptions weaken the precision and reliability of our age estimates. Procedurally, it is desirable to record MSG counts and measurements from the same region in the same bone. We used penultimate phalanges in most cases, and those phalanges derived from the second through fourth digits of the left or right hand. Using phalanges from different digits and occasionally the ultimate phalanx should not alter the number of visible MSGs, but it will increase the variation in MSG diameters. Further, the maximum diameter of the first MSG was selected in part on the basis of Hemelaar's data (1985) on *B. bufo*, a different though similar-sized species of toad. Even though the preceding factors may have increased the variation of our MSG measurements, the range of diameters for each year class (Fig. 1) is comparable to Hemelaar's (1985: figures 2,3) data. Therefore we believe that the resulting age estimates are reasonably accurate, and if used as a unit rather than individually, they provide a reliable picture of the age structure of this American toad population.

The only other age structure data for *B. americanus* derives from a population in central Illinois (Acker et al. 1986), nearly identical in latitude to Eakin Park. In the Illinois population, males 2-3 years old and females 3-4 years old were the most numerous age classes. This pattern does not match that of the Eakin Park population, although the age range is nearly identical for the two populations. The most striking difference between the two populations is the absence of 2-year-old females at Eakin Park and the presence of few 4-year-old and no 5-year-old males in Illinois. Although not wishing to overinterpret these data, they do suggest that the average lifespan for male American toads seldom exceeds 4 years.

Size and age are not correlated in either the Illinois or the Eakin Park population. Both populations have females significantly larger than the males, although the Illinois females are smaller (65-84 mm SVL). The males of the two populations are approximately equal in size (Illinois, 55-75 mm SVL).

The average size of Eakin Park ampletic males was nearly identical to the average for the entire male population. Indeed, the smallest male captured was in amplexus; thus, these data suggest that nonrandom mating by larger toads is not operating in the Eakin Park population. Although large male *B. americanus* have a mating advantage in some populations (e.g. Gatz 1981), this advantage is not evident or clear-cut in all populations (e.g. Kruse 1981, Wilbur et al. 1978). Our samples are, however, too small to evaluate nonrandom mating critically in the Eakin Park population.

The Eakin Park breeding population is fairly mobile. It is not tied tightly to a single site, but has shifted between four major open-water areas during the 6 years of observations. Perhaps this is typical of American toad populations; however, we have been unable to find comparable data in the literature.

Breeding activity in *B. americanus* was associated with the first warm rain in late March or early April. The controlling factor seemed to be water temperature. Males did not call if the water temperature fell below 11°C, and cold fronts following a spring rain stopped chorus activity.

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Small Mammals in the Great Dismal Swamp of Virginia and North Carolina

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ABSTRACT.— Small mammals were surveyed in a range of habitats in the Great Dismal Swamp of Virginia and North Carolina. The survey is based on three chronologically overlapping studies, each lasting 15-18 months and for which the results have been reported separately. A different trapping method was used in each of the three studies: nest boxes, Fitch live traps, or pitfall traps. Only two species of mammals, both arboreal, were taken in nest boxes, compared with 10 and 9 species in Fitch live traps and pitfall traps, respectively. The Fitch live traps had a much higher catch rate per 1,000 trap-nights than either of the other methods. However, pitfall traps were more efficient at catching *Sorex longirostris fisheri* and *Synaptomys cooperi helaletes*, two mammals that were previously believed to be rare. Although the catch rates were comparable in nonforested habitats and in forest, more individuals and more species were obtained in the former. At least 5 of the 12 collected species do not occur in the forests. These studies added *Sigmodon hispidus* to the mammals known from the Dismal Swamp, and the results suggest that *Peromyscus gossypinus* no longer occurs in the swamp.

The Great Dismal Swamp, which lies close to the Atlantic Ocean in southeastern Virginia and northeastern North Carolina, is a wooded swampland that is flooded annually from December through March or April. The soils, which range from sandy through deep peat, are saturated throughout the winter, but in years of extreme drought, fires sometimes burn deeply into the organic soils and also destroy large areas of forest. These physical factors, flooding and fires, and attempts to control them, have had marked effects on the past and present biota of the swamp.

The Dismal Swamp encompassed a diversity of habitats before human attempts to change it. Where the soils burned deeply, bald cypress trees, *Taxodium distichum*, often flourished when the normal hydroperiod returned. Where hot, shallow fires occurred, the regeneration of dense stands of Atlantic white cedar, *Chamaecyparis thyoides*, sometimes resulted, and other conditions favored the development of large stands of cane, *Arundinaria gigantea*, the only native American bamboo.

Slightly elevated "mesic islands" supported oaks and even beeches, trees that are typical of the upland habitats in the region. Thus, the Dismal Swamp that developed after the recession of the Wisconsin glacier from the region 8-10 thousand years ago was a swampland of vegetational diversity, a diversity maintained by a regime of flood and fire.

The flooding cycle is in part a result of the unusual geology of the swamp, which includes an escarpment on the western boundary and underlying impervious clays that prevent the rapid loss of rainfall to an underground aquifer. Thus, water moves slowly eastward toward the old duneline that forms the eastern boundary. In the winter months, reduced evapotranspiration and moderate rainfall combine with a high water table to inundate many sections of the swamp.

Since the Colonial Period, many land developers have attempted to exploit the swamp. Even George Washington participated in a scheme to drain and clear the swamp and convert it to farmland. Invariably those efforts failed, and always the swamp returned to forested swampland. However, the lowered water table resulting from the construction of ditches and the suppression of fires in this century has changed the character of the forest. Today, the Dismal Swamp forests are predominantly black gum, *Nyssa sylvatica*, water gum, *Nyssa aquatica*, and red maple, *Acer rubrum*, with scattered patches of bald cypress and Atlantic white cedar. The formerly extensive areas of cane and evergreen shrub thicket have been greatly reduced (Musselman et al. 1977). Stands of cane now are virtually absent except where preserved or maintained by human activity, such as the 3- to 5-year mowing treatment under a powerline. As a result, the swamp is moving slowly and inexorably in the direction of domination by maple and gum trees, and towards less vegetational diversity. We must assume that this will not favor the biota, including the mammals, which has become adapted to life in a physically harsh and biologically variable environment. In an effort to conserve this distinctive swamp forest, the Union Camp Corporation donated nearly 19,000 ha of land within the Great Dismal Swamp to the Nature Conservancy in 1973, which in turn deeded the land to the U.S. Fish and Wildlife Service (USFWS). In 1974, the USFWS created the Great Dismal Swamp National Wildlife Refuge, which has grown through other donations and purchases to its present size of more than 45,000 ha, about three-fourths of which is located in Virginia.

In their efforts to attract buyers, early land developers often greatly exaggerated the numbers and kinds of wildlife in their descriptions of the swamp (Handley 1979). The first accounts of what actually was present were written in a U.S. Geological Survey annual report (Shaler 1890). Shortly afterwards, a major collecting effort was made by the

U.S. Department of Agriculture's Bureau of Biological Surveys, directed by C. Hart Merriam. Between 1895 and 1898, teams of investigators studied and collected in the swamp for a total of 23 weeks. As a result, several new taxa of mammals were described from the swamp, including a southeastern shrew, *Sorex longirostris fisheri* Merriam, and a short-tailed shrew, *Blarina brevicauda telmalestes* Merriam, each of which is much larger than its nearby upland subspecies; a Pleistocene relict population of southern bog lemming, *Synaptomys cooperi helaletes* Merriam; and a distinctive muskrat, *Ondatra zibethicus macrodon* (Merriam). A meadow vole, *Microtus pennsylvanicus nigrans* Rhoads, was described from the North Carolina section of the swamp (Rhoads and Young 1897). Thus, from the first investigations it was clear that there were several unusual mammals in the Great Dismal Swamp. (Although named as distinct species, these mammals have since been relegated to subspecies status, as shown here.)

The few attempts to study Dismal Swamp mammals in this century have been summarized by Handley (1979), who had access to the unpublished data and field notes of government surveys conducted in the Dismal Swamp. The early studies (1895-1906 period) indicated that the small-mammal fauna was dominated by forest-dwelling species [white-footed mouse, *Peromyscus leucopus leucopus* (Rafinesque); cotton mouse, *Peromyscus gossypinus gossypinus* (LeConte); golden mouse, *Ochrotomys nuttalli nuttalli* (Harlan); and *B. brevicauda*], with other rodents and shrews contributing to a total of 12 species (Handley 1979). Handley speculated, as others had done, that some of the species may have disappeared as a result of the changes in the water level and the vegetation within the swamp.

Breidling (1980, see also Breidling et al. 1983) trapped briefly on, and measured the food production of, small plots in four forest types in the swamp. The only other previous study was conducted in late winter and spring of 1980, when Rose (1981a) set lines of pitfall traps under a powerline in the northwestern section of the Dismal Swamp in an effort to catch *S. c. helaletes* and *S. l. fisheri*. Within a short time he had caught as many *S. l. fisheri* as had previously been taken in the swamp, and rediscovered *S. c. helaletes*, which had not been reported in this century (Rose 1981b). This short study (Rose 1981a) provided the preliminary information for a 12-month project funded by the USFWS's Office of Endangered Species, which sought to determine the status of *S. l. fisheri* and *S. c. helaletes* and to determine the critical habitats for these taxa. The grant provided support for the following studies: (1) Dismal Swamp forest mammals, in which nest boxes were used to evaluate arboreal small mammals (Walke 1984, Rose and Walke 1988);

(2) the demography of mammals living in an opening and along an ecotone within the forest, in which live traps were used (Stankavich 1984); and (3) the distribution and habitats of small mammals in the Dismal Swamp (Everton 1985), in which pitfall traps were used. Together those studies form the basis for this paper. Our objectives were to determine the status of the two rare species and to learn more about the distribution and abundance of the small mammals of the Dismal Swamp.

MATERIALS AND METHODS

Each study involved 15-18 months of field work, conducted during the period October 1980 through February 1982, during which time the region was in a severe drought.

Walke (1984) tested the idea of Breidling et al. (1983) that forest mammals are present in low numbers because of the poor quality and unpredictability of the food supply, by the use of four large grids (on 1.96 ha, with 8 × 8 sites at 20-m intervals), each with the 64 tree-mounted nest boxes designed to be suitable for use by arboreal *P. leucopus* and *O. nuttalli*. In the two experimental grids, 100 g of mixed seeds and lab blocks was added to each nest box whenever it was examined. The two control grids had nest boxes that provided shelter and hay for building nests, but did not have supplemental food. Nest boxes were examined at biweekly intervals (later at weekly intervals when activity levels increased) to catch animals and to evaluate evidence of their activity (presence of nests, food caches, and scats).

Because her live-trapping study was conducted during a drought, Stankavich (1984) studied small mammals in what might be considered ephemeral habitats. Fitch live traps (one per station) were set at 7.6-m intervals in two rectangular grids (0.38 and 0.40 ha) under a 40-m-wide 110-kv powerline located in the northwest corner of the swamp. These grids were placed between the pairs of grids of nest boxes in an effort to monitor the movements of small mammals from one habitat to another. The two grids differed in amount of flooding and in composition of vegetation, with one dominated by cane and the other by thick herbaceous vegetation, primarily *Panicum* grasses and spikerush, *Juncus effusus*; sections of the latter grid remained flooded even in the drought. Trapping was conducted for 2 days every 2 weeks from October 1980 through February 1982. (On frequent visits since, the second grid has been totally flooded, some sections to 1-m depths.)

Everton (1985) used 0.25-ha grids, each consisting of a 5-by-5 plot with a water-filled no. 10 tin can, sunk so that the lip was flush with the ground surface, as a pitfall trap at each station. Pitfall traps were

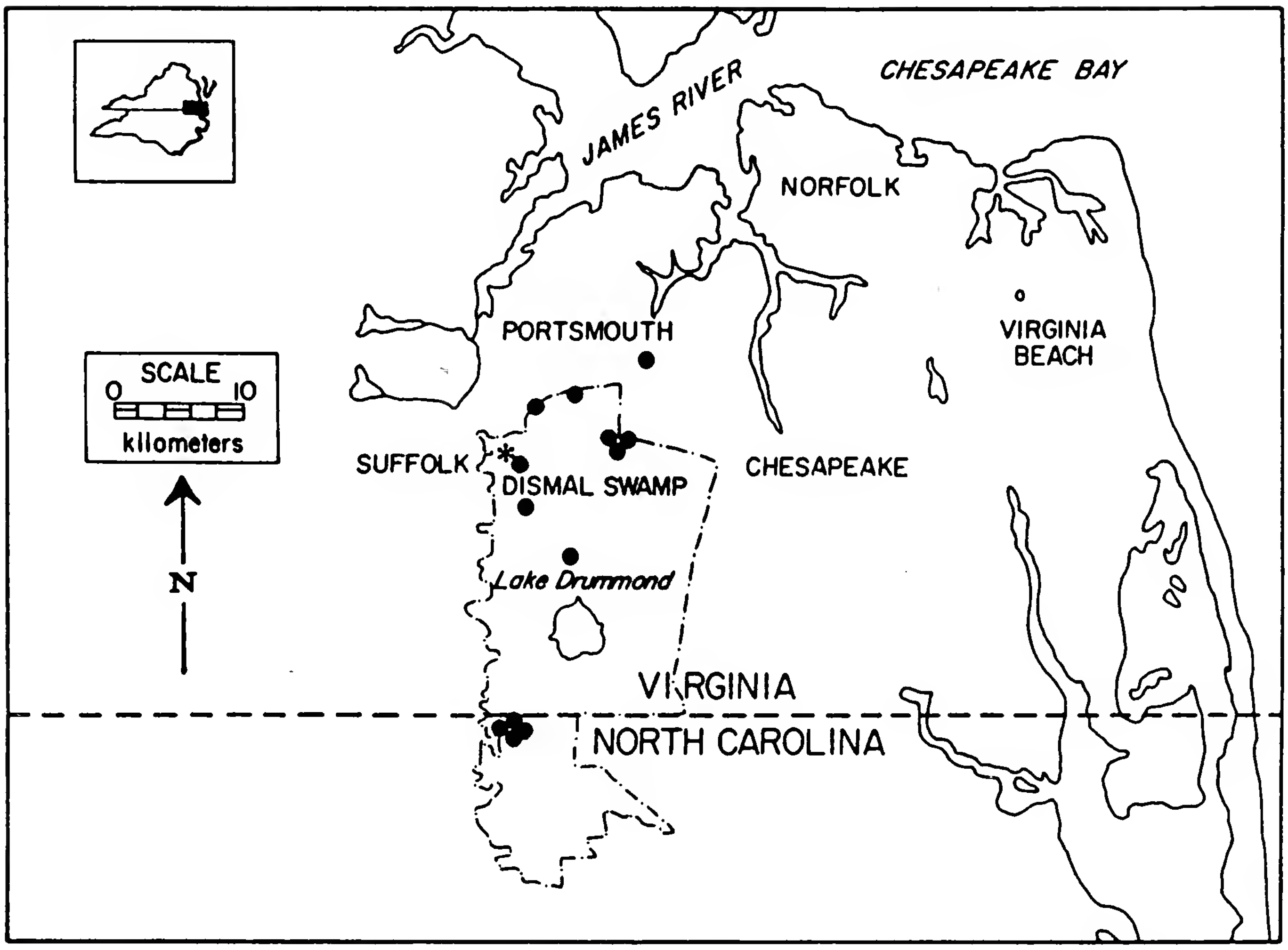

Fig. 1. Map showing the location of the live-trap and nest-box study grids (*) and the 13 pitfall study grids (•) in the Great Dismal Swamp of Virginia and North Carolina. The boundary encloses the current Great Dismal Swamp National Wildlife Refuge. The inset at upper left shows the location of the map area in eastern Virginia and North Carolina.

chosen because of their proven effectiveness in catching shrews, lemmings, and other species that are difficult to catch with conventional snap or live traps. Ten grids were placed in a range of nonforested habitats, and three grids were set in mature forests. Locations of the study grids in the Dismal Swamp are shown in Fig. 1.

RESULTS

A total of 359 small mammals were taken during the 18 months encompassed by the three studies (Table 1). Live and pitfall trapping yielded similar results, both in numbers of individuals (155 and 159) and in numbers of species (10 and 9). The nest boxes yielded 45 individuals of two arboreal species. In the three studies collectively, the three most numerous species were *B. brevicauda*; the eastern harvest mouse, *Reithrodontomys humulis humulis* (Audubon and Bachman); and *P. l. leucopus*. Five or fewer specimens were taken of each of the following:

the least shrew, *Cryptotis parva parva* (Say); the marsh rice rat, *Oryzomys palustris palustris* (Harlan); the hispid cotton rat, *Sigmodon hispidus virginianus* Gardner; the woodland vole, *Microtus pinetorum scalopsoides* (Audubon and Bachman); and the house mouse, *Mus musculus* L. Between 26 and 44 individuals each were trapped of *S. l. fisheri*, *O. n. nuttalli*, *M. p. nigrans*, and *S. c. helaletes*. *Peromyscus g. gossypinus*, one of four most common small mammals in the early studies, was absent.

Combining the data from the three studies, 301 mammals of 12 species were taken from 12 nonforested study grids (Table 2), compared with 58 specimens of four species from seven forested sites. Trapping efforts in the two habitat types were not comparable; 79.5% of the 64,653 trap-nights were conducted on nonforested grids. Nevertheless, the catch rates of 5.857 and 4.376 individuals per 1,000 trap-nights were similar. The nonforested sites included wet grassland dominated by *M. p. nigrans*, dry grassland dominated by *R. h. humulis*, and young pine plantations and regenerating forest up to 15 years old dominated by *S. l. fisheri*, *B. brevicauda*, and *S. c. helaletes*. Habitats with young trees and plentiful grasses frequently yielded the greatest numbers of individuals and species. The mature forests were mostly red maple and black gum, which predominate throughout the Dismal Swamp, but one forest site also had numerous loblolly pines, *Pinus taeda*, indicating drier conditions and a slightly higher elevation.

Although live and pitfall trapping yielded comparable numbers of individuals (Table 1), the capture efficiencies of these methods differed substantially. Expressed as a catch rate per 1,000 trap-nights, live trapping was more than three times as efficient (11.962 vs. 3.454) as pitfall trapping (Table 3). Capture efficiencies were comparable only for *B. brevicauda* and *M. p. scalopsoides*, although the sample size is exceedingly small for the latter species. The only other species taken by pitfall trapping at even half of the catch rate of live trapping was *S. c. helaletes*. *Sorex l. fisheri* and *C. p. parva* were taken only with pitfall traps, whereas *O. p. palustris, S. h. virginianus,* and *M. musculus* (one or two individuals of each) were live-trapped only. Interestingly, for the arboreal mice, the catch rate using nest boxes was two or three times greater than that using pitfall traps (Table 3), and for *P. l. leucopus*, the nest box was slightly less than half as efficient as the live trap (0.45 vs. 1.133 per 1,000 trap-nights).

These studies nearly double the amount of information about small mammals in the Dismal Swamp (Table 4). The earliest studies (summarized in Handley 1979) focused heavily on forested sites, so the finding that *P. leucopus* and *O. nuttalli* (both arboreal) and the litter-dwelling *B. brevicauda* were the most common mammals is not surprising.

Table 1. Numbers of individual small mammals taken in a range of habitats using three different trapping methods during concurrent studies in the Great Dismal Swamp of Virginia and North Carolina.

Species	Live trapping	Pitfall trapping	Nest-box trapping	Total	Percent[a]
Southeastern shrew *Sorex longirostris*	0	44	0	44	12.26
Short-tailed shrew *Blarina brevicauda*	14	51	0	65	18.11
Least shrew *Cryptotis parva*	0	5	0	5	1.39
Marsh rice rat *Oryzomys palustris*	1	0	0	1	0.28
Eastern harvest mouse *Reithrodontomys humulis*	71	5	0	76	21.17
White-footed mouse *Peromyscus leucopus*	14	10	36	60	16.71
Golden mouse *Ochrotomys nuttalli*	22	3	9	34	9.47
Hispid cotton rat *Sigmodon hispidus*	2	0	0	2	0.56
Meadow vole *Microtus pennsylvanicus*	13	13	0	26	7.24
Woodland vole *Microtus pinetorum*	3	1	0	4	1.11
Southern bog lemming *Synaptomys cooperi*	13	27	0	40	11.42
House mouse *Mus musculus*	2	0	0	2	0.56
Total individuals	155	159	45	359	
Total species	10	9	2	12	

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[a] Percent refers to the proportion of that species to the total individuals (359) taken in the study.

Table 2. Number and percent (of individuals within a species) of small mammals taken in 12 nonforested and 7 forested study grids in the Dismal Swamp.

	Nonforest habitat (51,399)[a]		Forest habitat (13,254)[a]	
Species	Total	Percent of individuals	Total	Percent of individuals
Sorex longirostris	40	91	4	9
Blarina brevicauda	59	92	6	8
Cryptotis parva	5	100	0	0
Oryzomys palustris	1	100	0	0
Reithrodontomys humulis	76	100	0	0
Peromyscus leucopus	21	35	39	65
Ochrotomys nuttalli	25	74	9	26
Sigmodon hispidus	2	100	0	0
Microtus pennsylvanicus	26	100	0	0
Microtus pinetorum	4	100	0	0
Synaptomys cooperi	40	100	0	0
Mus musculus	2	100	0	0
Total individuals	301	83.6	58	16.4
New individuals per 1,000 trap-nights	5.857		4.376	
Total species	12		4	

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[a] Numbers in parentheses are the total number of trap-nights in that habitat.

The studies of Handley (8 days in 1953), Breidling (on four forest plots for 1 week in each of three seasons in 1979 and 1980), and Rose (two study sites over 2 months in 1980) were brief or restricted to a few sites. By contrast, the current studies lasted 15-18 months each, and together evaluated the mammals on 19 study grids. Our studies recorded one new species for the swamp, *S. h. virginianus*. Two individuals were recaptured

Table 3. Comparison of trapping efficiencies for three methods of trapping small mammals, expressed as the number of new individuals taken per 1,000 trap-nights.

Species	Live trapping[a]	Pitfall trapping[b]	Nest-box trapping[c]
Sorex longirostris	0	0.993	0
Blarina brevicauda	1.133	1.151	0
Cryptotis parva	0	0.113	0
Oryzomys palustris	0.008	0	0
Reithrodontomys humulis	5.747	0.113	0
Peromyscus leucopus	1.133	0.158	4.512
Ochrotomys nuttalli	1.781	0.068	1.128
Sigmodon hispidus	0.016	0	0
Microtus pennsylvanicus	1.052	0.293	0
Microtus pinetorum	0.024	0.023	0
Synaptomys cooperi	1.052	0.542	0
Mus musculus	0.016	0	0
New individuals per 1,000 trap-nights	11.962	3.454	5.640

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[a] 12,354 trap-nights.
[b] 44,320 trap-nights
[c] 7,979 trap-nights.

several times over a 2-month period on the driest live-trap grid. For the first time in this century, *O. p. palustris* (one specimen in live trap) and *M. p. scalopsoides* (four specimens in live and pitfall traps) were collected. No specimens of *P. g. gossypinus* were collected in these studies, and only two have been collected in this century [in 1933 by Dice (1940)]. We can conclude that its numbers and distribution have declined, and perhaps it is now absent from the swamp forests. The largest apparent increases in numbers were for the shrews, because pitfall traps were used, and *R. h. humulis*, most of which were taken in live traps.

Table 4. A comparison of the results of small mammal studies conducted in the Dismal Swamp, based on Handley (1979), recent studies [Handley's 1953 in Handley (1979), Breidling et al. 1983, Rose 1981a], and the present studies.[a]

Species	1895-1906	1953-1981	Present studies	Total	Percent of total individuals
Sorex longirostris	14	16	44	74	10.03
Blarina brevicauda	37	19	65	121	16.40
Cryptotis parva	1	2	5	8	1.08
Oryzomys palustris	16	0	1	17	2.30
Reithrodontomys humulis	16	1	76	93	12.60
Peromyscus gossypinus	29	0	0	29	3.93
Peromyscus leucopus	78	40	60	178	24.12
Ochrotomys nuttalli	36	19	34	89	12.06
Sigmodon hispidus	0	0	2	2	0.27
Microtus pennsylvanicus	7	6	26	39	5.28
Microtus pinetorum	4	0	4	8	1.08
Synaptomys cooperi	21	7	40	68	9.21
Mus musculus	7	3	2	12	1.63
Total individuals	266	113	359	738	
Total species	12	9	12		

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[a] Dice (1940) caught four *Peromyscus leucopus* and two *P. gossypinus* near Lake Drummond in 1933.

DISCUSSION

The results of our three studies substantially advance our understanding of the distribution and abundance of Dismal Swamp mammals. One species, *S. h. virginianus*, was recorded in the swamp for the first time, and *P. g. gossypinus* probably is now absent. Thus, the total remains at 12 species of small mammals, as in the 1895-1906 period (Table 4). However, we now have information about mammals in nonforested habitats as well as large sample sizes for several species.

The arboreal *P. l. leucopus* and *O. n. nuttalli* are common today, as in the past, and so is *B. brevicauda* (Table 4). The species showing the largest numerical increases in collections conducted during this decade, including the results of Rose (1981a), were *S. l. fisheri*, *S. c. helaletes*, and *R. h. humulis* (Table 4). That substantially larger numbers were recorded has two causes: the use of different trapping methods and the greater sampling effort in nonforested habitats (Table 2). Early studies relied heavily on snap or break-back traps. In our research, all 44 *S. l. fisheri* were taken with pitfall traps (Table 1), an expected result because this shrew is rarely collected by any other means (Rose 1980), and most *R. h. humulis* (93%) were taken in live traps. These two methods yielded all *S. c. helaletes* (Table 1).

The Dismal Swamp southern bog lemming, *S. c. helaletes*, a distinctive relict subspecies, remains enigmatic as a study subject. We noted the cuttings and green dropping of this species at the start of the study on one live-trap grid, but we did not catch any *S. c. helaletes* until the tenth month of trapping, after which we caught 11 in the span of a few weeks on that grid. Pitfall trapping yielded *S. c. helaletes* from nearly half of the nonforested grids, and we determined that it sometimes was common. The same can be said of the Dismal Swamp southeastern shrew, *S. l. fisheri*; it was found on more than half of the pitfall grids and it, too, was locally abundant, especially in habitats in early succession. Thus, we determined that these two supposedly rare species, whose status was a particular objective of the pitfall trapping, were widespread and sometimes common. However, because the upland subspecies of the southeastern shrew, *Sorex longirostris longirostris* Bachman, is found nearby, *S. l. fisheri* has been listed by the USFWS as threatened (FR 51,287: 26 September 1986). That decision was made because the drying conditions created by ditching and draining may favor the movement of the *S. l. longirostris* into the Dismal Swamp, thereby potentially resulting in interbreeding and perhaps genetic swamping of the restricted and less common *S. l. fisheri*. On the other hand, *S. c. helaletes* has never been Federally listed, because it is widespread (1,000-km^2 area), colonizes early-successional stages and persists there until the forest matures, is locally abundant, and is isolated by 300 km from the nearest conspecific subspecies. Thus, although *S. c. helaletes* was believed by some investigators to be extinct, it apparently is thriving.

The second reason that we were able to collect these three species in numbers indicating that they are common is that the live- and pitfall-trapping studies focused on nonforested habitats (Table 2). Overall, 91% of *S. l. fisheri* and 100% of *R. h. humulis* and of *S. c. helaletes* were taken from nonforested habitats. These habitats ranged from fields with purely herbaceous vegetation to natural or planted stands of trees up to

15 years old. As long as grasses remained in the understory, *S. c. helaletes* persisted. *Sorex l. fisheri* persisted even in mature forests with no grasses, but at lower densities than in early seral stages. *Reithrodontomys h. humulis* were restricted to early seral stages, i.e. those with few saplings or shrubs, where they attained densities as great as 25/ha on live-trapping grids (Stankavich 1984). Trapping in areas dominated by herbaceous vegetation no doubt contributed to the relatively large number of *M. p. nigrans* compared with previous studies (Table 4). Clark et al. (1985), working in and near Carolina Bays and pocosins in North Carolina, also reported 3-5 times higher capture success when trapping on edges or in fields compared with the interior of pocosins.

Five species (*C. parva, O. palustris, S. hispidus, M. pinetorum,* and *M. musculus*), each represented by one to five specimens, were found only in nonforested habitats (Table 2). Except for *S. hispidus*, all had been collected in the past, usually in low numbers, and should be considered as minor species in the Dismal Swamp. For example, *C. parva* is most abundant in the region in dry oldfield habitats (Rose 1983, Everton 1985), habitats that are absent in the Dismal Swamp. Although little is known of the ecology of *O. palustris*, it is highly aquatic and therefore well adapted to live in swamps. The decline in numbers of *O. palustris* (Table 4) may be more apparent than real, or it could indicate a loss of habitat. *Sigmodon hispidus*, first reported from Virginia (Mecklenburg Co. in 1940) by Patton (1941), has been expanding its range throughout the Midwest and East. In Virginia, it has crossed the James River near Richmond (Pagels 1977), but its northward path is blocked in eastern Virginia by the Chesapeake Bay. As a species that is well adapted to the dry grassland of the Southwest, *S. hispidus* probably is poorly adapted to conditions of long-term inundation of its habitat, particularly if winters are relatively cold. Furthermore, the species is found primarily in habitat dominated by grasses and other herbaceous vegetation, and it seems not to tolerate much woody vegetation in its habitat. Although patches of suitable habitat may be produced by fires or clearcutting, that habitat will probably occur in remote sections of the swamp, where it is separated from the closest source populations of *S. hispidus* by large expanses of unsuitable cover.

The woodland vole, *M. pinetorum*, also called the pine vole, usually is associated with the edge of forest and oldfield. Although *M. pinetorum* sometimes is common in well-drained upland forests in the region, it apparently is not common in the seasonally flooded forests of the Dismal Swamp. Finally, *M. musculus*, introduced to North America from Europe during colonial times, usually is a commensal of man or is restricted to disturbed areas such as recently plowed fields, croplands, or the earliest successional stages. In general, *M. musculus* does not coexist with native mammals once the latter become well established. Because there are no buildings or croplands, there is today relatively little disturbed habitat in the Dismal Swamp, except for that resulting from an occasional fire or blowdown. Hence, there is little opportunity for *M. musculus* to flourish. Except for *S. hispidus*, which was not found prior to these studies, the five species that we found in lowest number (1-5) also were present, but rare to uncommon, in the early studies of the Dismal Swamp (Table 4).

The numbers of different individuals taken by the three methods differed substantially in these studies (Table 3). Higher catch rates for almost all species were obtained in live traps compared with pitfall traps. The exception was *B. brevicauda*, for which the rates were comparable. One thing we learned in the pitfall-trapping study was that most of the animals were taken in the first 2-4 weeks. Catch rates dropped off sharply thereafter. On grids established midway in the study, we placed plastic snap-on lids on the pitfall traps after a month of trapping, and weeks later reopened them. These grids had higher catch rates, i.e. yielded more animals over fewer weeks of trapping. Had we used this technique throughout the study, the catch rates for pitfall trapping would have been substantially higher.

Besides yielding moderate catch rates, live traps are also useful because individuals can be trapped repeatedly and marked to obtain information on growth, reproduction, and density. The primary advantage of pitfall traps is that some species, particularly *S. longirostris*, rarely are taken by any other means. An additional advantage is that, unlike live traps, pitfall traps can be checked at irregular intervals, e.g. weekly or biweekly, which permits a large amount of information to be obtained in relation to the time spent tending the traps. Especially for locations deep inside the Dismal Swamp, pitfall traps are useful even though the catch rate is lower than for live traps (and based on Wiener and Smith 1972, much lower than it would be for snap traps).

The relatively high number of *O. nuttalli* (22, Table 1) and the catch rate for this form in the live-trap grids were surprising, particularly because other studies in the swamp have shown it to be less common than *Peromyscus*. We believe our success resulted from the habitat sampled, because the powerline right of way provided a large amount of ecotone, which seems to be ideal for *O. nuttalli* (Layne 1958). All but one of the *O. nuttalli* in the nest-box study also were taken at the ecotone. These results reinforce Dueser and Shugart's (1978) suggestion that *O. nuttalli* is a habitat specialist and requires the complex vegetational structure provided along the edge of a forest. In the forest proper, however, *P. l. leucopus* remained most common, as seen in the nest-box study (Table 1). In the live-trap study, most of the *P. l. leucopus* also were trapped at the edges of the grids, i.e. in the ecotone.

In conclusion, these studies showed the supposedly rare Dismal Swamp subspecies of *S. l. fisheri* and *S. c. helaletes* to be widespread and locally abundant. However, *S. l. fisheri* is affected by interbreeding with a nearby upland race and now is listed as threatened by the USFWS. Our studies nearly double the amount of information for small mammals in the Dismal Swamp, documenting one additional species (*S. hispidus*) and one probable loss (*P. gossypinus*) in this century. The slightly higher catch rate (= abundance) and greater numbers of species from nonforested habitats suggest that any management plan that creates clearings or other vegetational heterogeneity will promote the diversity and abundance of small mammals in the Dismal Swamp. Fortunately, the management plan recently developed for use in the Great Dismal Swamp National Wildlife Refuge calls for the implementation of such management measures.

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THE SEASIDE SPARROW, ITS BIOLOGY AND MANAGEMENT

Edited by

Thomas L. Quay, John B. Funderburg, Jr., David S. Lee, Eloise F. Potter, and Chandler S. Robbins

The proceedings of a symposium held at Raleigh, North Carolina, in October 1981, this book presents the keynote address of F. Eugene Hester, Deputy Director of the U.S. Fish and Wildlife Service, a bibliography of publications on the Seaside Sparrow, and 16 major papers on the species. Authors include Arthur W. Cooper, Oliver L. Austin, Jr., Herbert W. Kale, II, William Post, Harold W. Werner, Glen E. Woolfenden, Mary Victoria McDonald, Jon S. Greenlaw, Michael F. Delany, James A. Mosher, Thomas L. Merriam, James A. Kushlan, Oron L. Bass, Jr., Dale L. Taylor, Thomas A. Webber, and George F. Gee. A full-color frontispiece by John Henry Dick illustrates the nine races of the Seaside Sparrow, and a recording prepared by J. W. Hardy supplements two papers on vocalizations.

"The Seaside Sparrow, with its extensive but exceedingly narrow breeding range in the coastal salt marshes, is a fascinating species. All the authors emphasize that the salt marsh habitat is at peril. . . . The collection is well worth reading." — *George A. Hall, Wilson Bulletin.*

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Recent Changes in the Freshwater Molluscan Fauna of the Greenfield Lake Basin, North Carolina

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ABSTRACT.— The molluscan fauna of the Greenfield Lake basin has undergone significant changes in recent years. In surveys conducted from January 1984 through October 1987, 16 species of mollusks were found in the basin. Twelve of those species were recorded from the basin for the first time; 15 species previously recorded in the basin were not found. The most noticeable change was the almost total elimination of the Unionidae. Changes in the molluscan fauna of the Greenfield Lake basin have probably been caused by a combination of factors and events. Those agents of change are still at work today and undoubtedly keep the molluscan population of the lake from ever establishing any type of equilibrium. Partial winter drawdowns are believed to be the most damaging aspect of the water management presently undertaken in the watershed. Pollution from non-point sources has probably also played a role in changing the fauna.

Mollusks in Greenfield Lake, in Wilmington, New Hanover Co., N.C., were frequently sampled by malacologists during the early part of the twentieth century. Records of those collections are scattered in the literature, but a comprehensive survey of the fauna has never been undertaken.

Because of its prominence in the literature of freshwater malacology on the south Atlantic slope, any changes in the molluscan fauna of Greenfield Lake are of general interest. Because of the available data on prior species occurrence, a comprehensive survey was undertaken to assess what changes have taken place in the composition of the lake's molluscan fauna.

Many of the taxa cited in this paper are in need of systematic revision. Resolving taxonomic problems was not a purpose of this study, but the subject has to be addressed because of the abundance of synonyms for some species and the revisions that have taken place since the time of the first Greenfield Lake records. A synonymy section has therefore been included to deal with this problem to the level necessary

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for identification of species. Gender problems in the species names used by previous authors have not been rectified.

HISTORY OF GREENFIELD LAKE

Greenfield Lake was created prior to 1750 by the impoundment of a small low-lying stream located south of Wilmington to provide a source of fresh water for a nearby rice plantation and for the operation of grist and saw mills. The rice plantation, lake, and surrounding lands were known collectively as "Greenfields" (Moore 1968). The surface elevation is 1.85 m above mean sea level, the surface area is 75 ha, and the drainage basin is approximately 1,100 ha. Maximum depth is approximately 2.5 m.

The City of Wilmington purchased the lake in 1925 for use as a public park, and a circumferential road approximately 8 km long was constructed as a public works project during the Great Depression (Moore 1968). In 1935, fallen trees were removed from the lake and the surrounding area was landscaped (Moore 1975). Removal of marsh grasses and additional snags took place in 1945 for mosquito control (Appleberry 1945).

Today, Greenfield Lake is well within Wilmington, and its watershed is almost completely developed. Land use consists primarily of residential and commercial areas with open space in the form of a golf course and small, isolated tracts of woodlands. Lands immediately adjacent to the lake are still used as a public park, which is a major recreation center for Wilmington.

Urbanization of the watershed has resulted in a decreased detention time for storm waters and, consequently, an increased introduction of nutrients, pesticides, and metals into Greefield Lake. Breaks in sewer lines on the bottom of the lake and sewage overflow from nearby manholes during storms have also added large pulses of nutrients. The latter are now a major problem and in recent years have contributed to severe algal blooms (*Lyngbya*). Control has been attempted through algacides (chelated copper and dichlobenil); introductions of the exotic fishes tilapia, *Tilapia aurea* (Steindachner), and grass carp, *Ctenopharyngodon idella* Valenciennes; and partial drawdowns during the winter months to desiccate and freeze the algae. Central portions of the lake have been dredged in attempts to remove nutrient-laden sediments and deepen the lake beyond the photic zone.

All of the tributaries leading into Greenfield Lake have been channelized to improve drainage in the basin. Maintenance of the channels is periodic and is confined to portions upstream of Lakeshore Drive, the perimeter road. The outlet creek below the dam has been channelized to its confluence with the Cape Fear River and has changed from a freshwater system to an intermittently brackish one.

HISTORICAL COLLECTIONS

Documentation of the historical occurrence of species in the lake was taken from published literature. Records from unpublished collections in museums and universities were not sought. In summarizing her private collection of North Carolina freshwater mollusks plus those in the Academy of Natural Sciences, Philadelphia, and in the Museum of Zoology of the University of Michigan, Dawley (1965) provided several Greenfield Lake citations of both bivalves and gastropods. However, this work was not exhaustive, as major mollusk collections, such as those at Harvard University and the National Museum of Natural History, were not searched. Early in this century, Bartsch searched for *Planorbis magnificus* (Pilsbry, 1903), which had been first described from "the lower Cape Fear River." He found that snail to be fairly abundant in the lake; discovered and described another new planorbid, *Planorbis eucosmius* (Bartsch, 1908); and noted but did not describe two other apparently new mollusks. Bartsch's (1908) discussion of the habitat of *P. magnificus* provides the only available description of the aquatic macrophyte community in Greenfield Lake early in this century. Rehder (1949) reported *Campeloma rufum* (Haldeman, 1841) from the lake in his discussion of land and freshwater snails collected during his travels through the region. Walter (1954) reported *Pseudosuccinea columella* (Say, 1817) from the lake in his discussion of the range of the species but did not disclose the source of the record. Porter (1985) reported forms of *Campeloma* believed to be *C. geniculum* (Conrad, 1834) from Greenfield Lake and mentioned other species of gastropods reported by Dawley (1965).

Records of Bivalvia from Greenfield Lake deal principally with the Unionidae and were summarized by Johnson (1970), who recorded eight species from the lake or the creek below the spillway: *Lampsilis radiata* (Gmelin, 1791), *Villosa delumbis* (Conrad, 1834), *Villosa vibex* (Conrad, 1834), *Anodonta couperiana* (Lea, 1842), *Anodonta imbecillis* (Say, 1829), *Uniomerus tetralasmus* (Say, 1831), *Elliptio complanata* (Lightfoot, 1786), and *Elliptio lanceolata* (Lea, 1828). *Elliptio fisherianus* (Lea, 1838) was recorded from the lake by Bailey (1940), and Morrison (1972) mentioned that *Anodonta imbecillis, A. couperiana,* and *A. teres* (Conrad, 1834) occur there. Porter (1985) reported *Anodonta cataracta* (Say, 1817) and, in citing correspondence with J. P. E. Morrison, also reported *E. fisherianus, A. teres, Villosa vaughaniana* (Lea, 1838), and *Lampsilis ochracea* (Say, 1817) from the lake. Heard (1963, 1965) reported Greenfield Lake specimens of *Musculium transversum* (Say, 1829) and *Eupera cubensis* (Prime, 1865). Walter (1954) also reported *E. cubensis* from the lake in his discussion of the range of the species but did not disclose the source of the record.

All published records from the Greenfield Lake system are summarized in Table 1. Names are presented as published without regard to subsequent taxonomic revisions or the possibilities of misidentifications, which are discussed later.

SYNONYMY

Most of the collections cited in Table 1 are old, and the names have undergone substantial taxonomic revision. The following brief discussion of synonymy brings these historical records into a modern taxonomic framework. Species names are still considered valid if they appear in Table 1 and are not discussed below.

GASTROPODA

Clench (1962) synonomized the three forms of *Campeloma rufum* (Haldeman, 1841) with three separate species. *Campeloma rufum* was synonymized with *C. crassulum* Rafinesque, 1819, a species of the Great Lakes-St. Lawrence and the Mississippi drainages. *Campeloma r. meridionale* (Pilsbry, 1916) was synonomized with *C. limum* (Anthony, 1860), and *Campeloma r. geniculiforme* (Pilsbry, 1916) was synonymized with *C. geniculum*. Which form Rehder (1949) collected in Greenfield Lake is unknown, and the ranges of *C. geniculum* and *C. limum* reported by Burch (1982) make either species a possibility.

The genus *Gillia* Stimpson, 1865, has not been revised. *Gillia crenata* (Haldeman, 1840) has not been synonymized with any other forms; however, modern taxonomic keys make no reference to this species. Specimens of *G. crenata* in the National Museum of Natural History are being treated as *G. altilus* (Lea, 1841) (A. G. Gerberich, personal communication).

Although its taxonomic status is still in doubt, *Planorbis eucosmius* (Bartsch, 1908) has been transferred to the genus *Helisoma* Swainson, 1840 (Burch 1982). Burch (1982) speculated that *P. eucosmius* may simply be a juvenile form of *H. anceps anceps* (Menke, 1830), whereas Fuller (1977) assigned *P. eucosmius* to the South American genus *Taphius* H. & A. Adams, 1855. Proper taxonomic placement will not be possible until additional specimens are acquired for soft-tissue analysis.

Planorbis magnificus (Pilsbry, 1903) was transferred to *Planorbella* Haldeman, 1842, by Baker (1945) and the species epithet emended to the feminine *magnifica. Planorbis* Muller, 1774, refers to Palearctic and Ethiopian forms (Burch 1982).

Table 1. Published records of freshwater mollusks from the Greenfield Lake drainage basin.

	Authority[a]										
Species	1	2	3	4	5	6	7	8	9	10	11
GASTROPODA											
Viviparidae											
Campeloma geniculum	x		x								x
Campeloma rufum				x							
Lymnaeidae											
Pseudosuccinea columella										x	
Planorbidae											
Planorbis eucosmius						x					
Planorbis magnificus					x	x					x
Hydrobiidae											
Gillia altilis	x										x
Gillia crenata	x										x
Liogyrus sp.						x					
Ancylidae											
Laevapex diaphanus	x										
BIVALVIA											
Unionidae											
Elliptio complanata							x				
Elliptio fisherianus	x		x				x				x
Uniomerus tetralasmus							x				
Anodonta imbecillis	x	x					x				
Anodonta couperiana		x					x				
Anodonta teres		x									x
Anodonta cataracta											x
Villosa delumbis							x				
Villosa vaughaniana											x
Villosa vibex							x				
Lampsilis radiata							x				
Lampsilis ochracea											x
Sphaeriidae											
Limosina sp.						x					
Eupera cubensis								x		x	
Musculium transversum									x		

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[a] (1) Dawley 1965, (2) Morrison 1972, (3) Bailey 1940, (4) Rehder 1949, (5) Pilsbry 1903, (6) Bartsch 1908, (7) Johnson 1970, (8) Heard 1965, (9) Heard 1963, (10) Walter 1954, (11) Porter 1985.

The genus *Liogyrus* Gill, 1863, is now considered a subgenus of *Amnicola* Gould, 1841 (Burch 1982).

BIVALVIA

Johnson (1970) synonymized *Elliptio fisheriana* (Lea, 1838) with *E. lanceolata* (Lea, 1828). Davis (1984) determined that *E. fisheriana* was distinct from *E. lanceolata* and that *E. folliculata* (Lea, 1838) and *E. producta* (Conrad, 1836), which had also been synonymized with *E. lanceolata* by Johnson (1970), were also distinct from it and from each other. Johnson (1984) synonymized *E. producta* with *E. angustata* (Lea, 1831). The ranges of these species are uncertain, and which species occurred historically in Greenfield Lake is unknown.

Uniomerus tetralasmus (Say, 1831) is still a valid species, but south Atlantic drainage *Uniomerus* are now considered to be *U. obesus* (Lea, 1831) (Johnson 1984).

Johnson (1970) synonymized *Anodonta teres* with *A. cataracta* and *Villosa vaughaniana* with *V. delumbus*. However, *Anodonta teres* and *Villosa vaughaniana* are still regarded as distinct by some researchers (e.g. Porter 1985, Turgeon et al. 1988).

The genus *Limosina* Clession, 1872, is synonymous with *Eupera* Bourguignat, 1877 (Heard 1965). *Eupera cubensis* (Prime, 1865) and *Musculium transversum* (Say, 1829) are still considered to be valid names.

METHODS

All of the major tributaries, the nearshore lake bottom out to a distance of about 10 m, and the creek downstream of the dam were sampled between January 1984 and October 1987. Eighteen stations were investigated and are shown in Fig. 1. During January 1984 and again in January 1986, the lake was drained for several weeks, and the substrate for 6-30 m from the bank was exposed. This permitted thorough searches, although some mollusks may have retreated with the receding water. Because movements of unionids during such events have been shown to be random (Samad and Stanley 1986), the species obtained are considered to be representative. The central portions of the lake could not be sampled, as soft sediments and deep water made collecting by the methods used impossible. Summer collections of gastropods were made by sweeping a fine-mesh net through floating aquatic macrophytes, by raking mats of submerged aquatic macrophytes, and by hand. The creek below the dam was sampled by hand and by raking during low tides in summer 1985 and during the winter drawdown. Approximately 40 man-hours were spent in collecting.

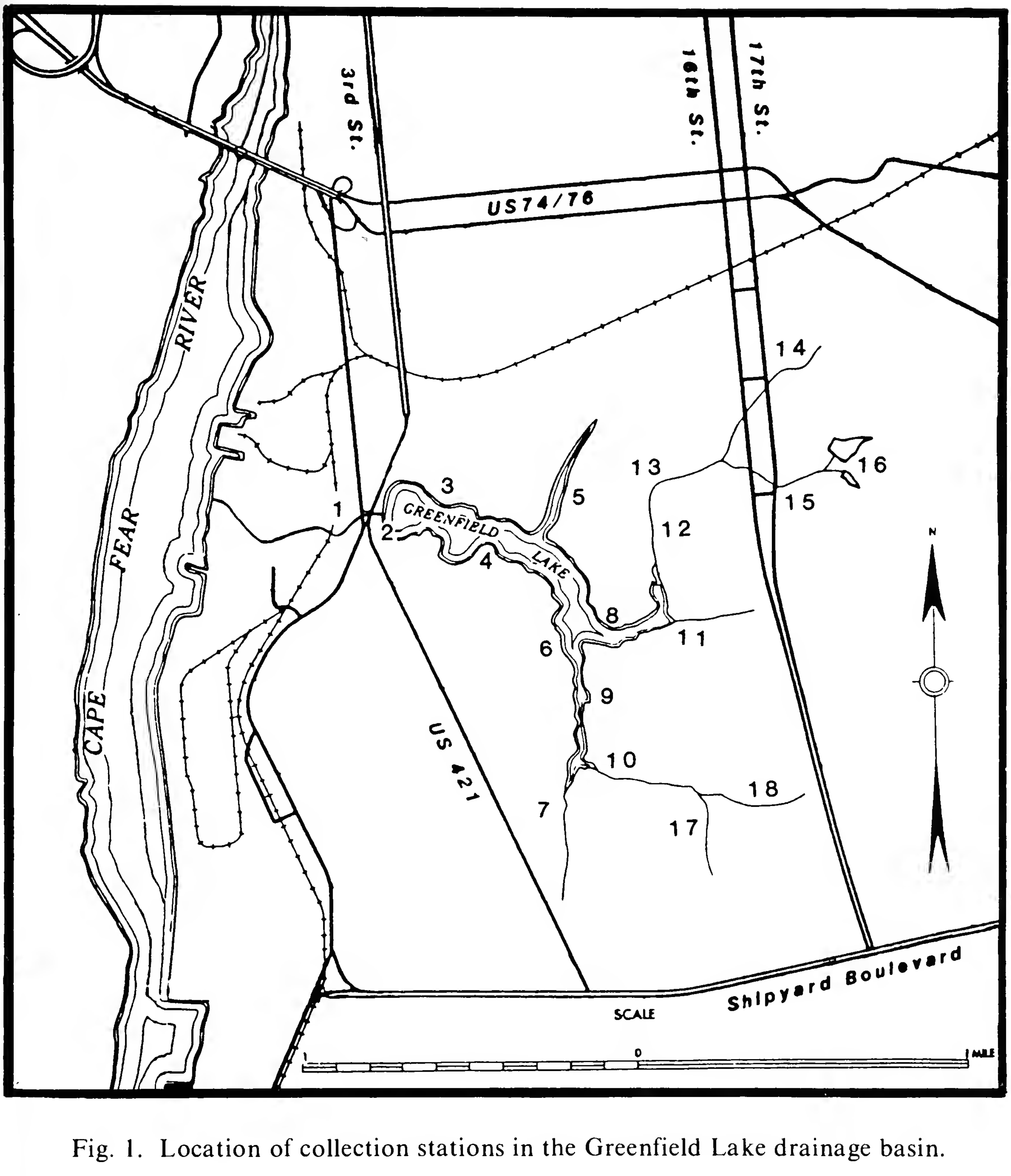

Fig. 1. Location of collection stations in the Greenfield Lake drainage basin.

Salinity measurements in the creek below the dam were taken during and after the 1986 drawdown. All measurements were taken from surface waters and determined by using a refractometer.

Identifications of Unionidae were made using Johnson (1970). Sphaeriidae were determined from Herrington (1962) and Burch (1975), and the nomenclature follows Burch (1975). Gastropods, excepting the Ancylidae, were identified using Burch (1982), and his nomenclature is used. Identification and nomenclature of the Ancylidae follow Basch (1963).

RESULTS

Sixteen species of mollusks, 10 gastropods and 6 bivalves, were collected from Greenfield Lake, its tributaries, and the creek below the spillway (Table 2). Twelve species were recorded from the lake or the drainage basin for the first time, and 15 species previously reported were not relocated.

Campeloma decisum occurred in only one tributary. *Planorbella trivolvis* and *Helisoma anceps* were relatively common throughout the lake in the nearshore area. *Pseudosuccinea columella* was found in quiet waters of the finger portions of the lake but was absent from the main body of the lake. Because of the fragility of the shell of *P. columella*, occasional waves may render the main body of the lake unsuitable habitat for that species. *Menetus dilatatus* and *Gyraulus deflectus* were common in the upper end of the lake. *Gyraulus parvus* was found only in the golf course ponds of Station 16. *Ferrissia fragilis* was common on leaf litter and trash throughout the lake.

Anodonta is the only unionid genus now occurring in the basin. *Anodonta* species are normally associated with lentic habitats, and all live specimens were obtained from the upper portions of the lake. *Anodonta cataracta* may be common in the central portions of the lake; numerous valves of this species were found at the interior base of the dam during the drawdown period. Three forms of *A. cataracta* occur in the lake: a form with dorsal and ventral margins roughly parallel, a form with a broadly rounded ventral margin, and a form with a concave ventral margin.

Only one valve of *Andonta imbecillus* was found during the present study, in the fall of 1987 on a spoil pile resulting from rechannelization of the tributary at Station 13. Despite extensive searches of other spoil piles, no additional specimens could be located, and none were found during drawdowns. Because this tributary was at least temporarily disrupted, the status of *A. imbecillus* cannot be determined. It is at best extremely rare, and perhaps it is extirpated from the Greenfield Lake basin.

Table 2. Species of freshwater mollusks collected from Greenfield Lake with collection stations.

Species	Collection stations
GASTROPODA	
Viviparidae	
Campeloma decisum (Say, 1817)	12, 13, 15
Lymnaeidae	
Pseudosuccinea columella (Say, 1817)	9, 11, 16, 17, 18
Physidae	
Physella hendersoni (Clench, 1925)	3, 4, 6, 8, 11, 18
Physella heterostropha (Conrad, 1834)	4, 7, 8, 10, 11, 16, 18
Planorbidae	
Gyraulus deflectus (Say, 1824)	6, 8, 10
Gyraulus parvus (Say, 1817)	16
Menetus dilitatus (Gould, 1841)	7, 10
Planorbella trivolvis (Say, 1817)	4, 5, 12
Helisoma anceps (Menke, 1830)	6, 8, 17
Ancylidae	
Ferrissia fragilis (Tryon, 1863)	3, 7, 8, 10, 11, 14
BIVALVIA	
Mactridae	
Rangia cuneata (Gray, in Sowerby 1831)	1
Cyrenidae	
Polymesoda caroliniana (Bosc, 1802)	1
Unionidae	
Anodonta cataracta (Say, 1817)	2, 7, 10, 12, 13
Anodonta imbecillus (Say, 1829)	13
Sphaeriidae	
Musculium transversum (Say, 1829)	5, 15
Sphaerium occidentale (Prime, 1853)	4

Sphaeriid clams were numerically the most abundant bivalve mollusks in the lake system. High densities of *Sphaerium occidentale* and *Musculium transversum* were discovered under algal mats in nearshore areas during the January 1984 drawdown, but numbers were much reduced in the summer of 1987.

Only *Rangia cuneata* (Gray, in Sowerby 1831) and *Polymesoda caroliniana* (Bosc, 1802), both brackish-water species, occur in the creek below the spillway. Salinity appears to be the limiting factor for freshwater species in this area as tides bring brackish water from the Cape Fear River into the creek. Surface salinity measurements taken during February 1986 indicate a range of 0 parts per thousand (ppt) to 5 ppt when the lake was being reimpounded after a drawdown and there was no water being released from the lake. Concentrations up to 3 ppt were observed during normal summer releases from the lake. Hopkins et al. (1973) note that *R. cuneata* is restricted to areas where salinity is below 15 ppt most of the time and may occupy portions of creeks and tidal rivers where salinities are continuously below 1 ppt for extended periods.

DISCUSSION

Distributions of many species in the lake appear to be spotty based on the collection station records (Table 2). Differences between stations may be caused by microhabitat conditions, by disturbance histories, or by differing efficiency of collecting at each station. Species of mollusks not recorded in this survey may yet be found to exist in the lake.

MISIDENTIFICATIONS IN HISTORICAL RECORDS

The record of *Laevapex diaphanus* by Dawley (1965) may be based on a misidentification of *L. fuscus*; she did not mention the source of the specimen or the determination. *Laevapex diaphanus* typically inhabits rock bottoms in slowly flowing waters, and I have collected it on debris in swamp streams near Wilmington. However, *L. fuscus* is fairly common in southeastern North Carolina, and it would be more likely than *L. diaphanus* to have occurred in the lacustrine habitats provided by the lake.

Campeloma geniculum may also have been misidentified, because it is difficult to separate from *C. decisum*. In discussing current taxonomy of the genus *Campeloma*, Clench (1962) correctly remarked that "few genera among our North American freshwater mollusks are in a more confused state." Bailey (1940) states that Pilsbry examined specimens of *C. geniculum* from the lake and referred to them as "a rather unusually rounded form of the species." That would imply that the specimens may have been *C. decisum*, which is separated from *C. geniculum* by its more rounded shoulders (Burch 1982). Rehder (1949) collected *C. rufum* (which would now be synonymized with either *C. geniculum* or *C. limum*, see Synonymy above) from Lake Waccamaw, approximately 50 km W of the study area, as well as from Greenfield Lake. *Campeloma* that had characteristics of both *C. geniculum* and *C. decisum* were noted by Porter (1985) in his collections from Lake Waccamaw, and one specimen that had characteristics of *C. geniculum* was found during the present survey. *Campeloma geniculum* is generally expected to have a more southern range, but a population is certainly possible in southeastern North Carolina.

CHANGES IN THE MOLLUSCAN FAUNA

All of the species recorded during this survey are common natives and were probably present in the lake in prior years but were simply not mentioned in previously published accounts.

Neither *Planorbella magnifica* nor *Helisoma eucosmius* has survived in Greenfield Lake, as Fuller (1977) conjectured. Until recently both of these species were considered extinct by some authors (Opler 1976, Imlay 1977, Palmer 1985), but *P. magnifica* has recently been found in Orton Pond, approximately 40 km S of Greenfield Lake (Adams and Gerberich 1988). *Helisoma eucosmius* has not been located at Orton Pond, but the habitat appears to be suitable for it.

Campeloma geniculum was not positively identified from the lake. One specimen of what appeared to be this species was collected at Station 15, but owing to the difficulties associated with separating it from *C. decisum* and the fact that only one was encountered, the specimen was counted as *C. decisum.*

Gillia altilus and members of the genera *Amnicola* and *Laevapex* were not found in this study. Suitable habitat for these species has probably been eliminated by changes in the lake.

By comparing Tables 1 and 2, it can be seen that virtually all of the gastropods collected during this study represent new species records for the lake. Of the species represented in Table 2, only the identifications of the Physidae are uncertain. The species *Physella hendersoni* and *P. heterostropha* could be expected to occur in Greenfield Lake. These species are difficult to separate based on shell characters, and Burch (1982) provides only illustrations. *Physella heterostropha* tends to be more robust than *P. hendersoni*, and it was on this character that the species were separated. "Robustness," however, is a very weak taxonomic character.

Changes in the molluscan fauna of the lake are most dramatically shown in the virtual elimination of the Unionidae. Only two species, *Anodonta cataracta* (= *A. teres*) and *A. imbecillus*, are found in the Greenfield Lake system today compared with 10 that were recorded historically. The loss of *Anodonta couperiana* from the lake, previously suspected by Shelley (1987), has been confirmed. *Eupera cubensis*, a sphaeriid also previously reported from the lake, could not be relocated. When the decline of the Unionidae began is impossible to place. However, since Bailey collected *Elliptio fisheriana* in 1940 and Morrison mentioned three species of *Anodonta* in the lake in 1972, it would appear that this is a recent and rapid phenomenon.

The two brackish-water species, *Rangia cuneata* and *Polymesoda caroliniana*, and the freshwater sphaeriid, *Sphaerium occidentale*, are the only new records of bivalves from the Greenfield Lake basin.

POSSIBLE CAUSES OF CHANGE

Degraded water quality has been a persistent problem in Greenfield Lake in recent years, and its decline has been brought about primarily by the urbanization of the watershed. Elevated levels of nutrients, pesticides, and metals and the occurrences of algal blooms have been documented or suspected to have adverse effects on mollusks (Havlik 1987, Havlik and Marking 1987) and have probably done so in the lake. Several fish kills that occurred in the lake during the study period were attributed by local authorities to low levels of dissolved oxygen resulting from excess nutrients. The copper-based algacides used to control *Lyngbia* may be adversely affecting the entire benthic macroinvertebrate community. Havlik and Marking (1987) report that copper sulfate is toxic to freshwater bivalves at concentrations of 2 to 18.7 mg/liter in acute exposures and as low as 25 parts per billion in long-term exposures. Hanson and Stefan (1984) studied the effects of long-term copper sulfate application on lakes in Minnesota and found that the normal functioning of the ecosystems were severely disrupted. Long-term effects that were discovered included copper accumulation in lake sediments, changes in species composition from game fishes to rough fishes, disappearance of macrophytes, and severe reductions in benthic macroinvertebrates.

The water quality of tributaries of Greenfield Lake may have changed over time, because of improved drainage in the upper portions of its basin and the removal of groundwater from the underlying aquifer by residential wells. Bartsch (1908) states that Greenfield Lake was spring fed at the time of his collection, but much of the present freshwater input comes from runoff. In addition, groundwater in the vicinity of the lake may be polluted. If so, it may take many years for pollutants entering the lake to be purged, even if similar pollutants from overland runoff are curbed.

I suspect that the factor most damaging to the unionid populations has been winter-season partial drawdowns. They have a twofold purpose: to permit removal of nearshore trash and debris and to kill the exposed algae mats through cold temperatures and desiccation. These drawdowns have had, and continue to have, a profound effect on the mollusks of the lake ecosystem, because all mollusks occurring in this exposed area are subjected to desiccation and to nighttime temperatures that are frequently well below freezing. *Anodonta cataracta* killed by exposure were observed in several locations. Long (1983) noted significant mortality of *A. cataracta, A. imbecillis,* and *Lampsilis radiata* in a Maryland reservoir when summer water levels were drawn down rapidly. Samad and Stanley (1986) found that *Elliptio complanata* and *L. radiata* were almost totally eliminated by drawdowns of a lake in Maine. Libois and Hallet-Libois (1987) found that thin-shelled unionids such as *Anodonta* suffered high mortality during a 3-week drawdown of the River Meuse in Belgium. From those studies, and the observations gathered here, it appears clear that as long as drawdowns are used as a management measure in Greefield Lake, the unionid population cannot recover.

Not all of the effects of drawdowns are obvious and direct. Lake drawdowns drastically reduce the amount of nearshore habitat available for the fish community and were observed to result in substantial mortality of fish through strandings, increased predation by wading birds and gulls, and cold shock. This loss to the fishery is directly related to the health of the unionid population, because the Unionidae rely on a fish host for the glochidial stage of their life cycle. A reduction in the species diversity or abundance of fishes will, therefore, reduce the number of glochidial hosts available.

Drawdowns also reduce the cross-sectional area of the impounded portions of tributaries. This reduction in cross-section, with tributary inflow remaining the same, causes an increase in water velocities in normally lacustrine areas, and that results in a massive shifting and redistribution of the bottom sediments. Several *Anodonta cataracta* were observed with trails in the sand behind them, apparently attempting to reestablish themselves. While shifting substrates can be a normal occurrence in lotic environments, the lacustrine organisms of the lake probably have difficulty coping with such changes.

During reimpoundment, which takes from 2 to 3 weeks, virtually no fresh water is released from the dam. Therefore, undiluted waters from the Cape Fear River reach the base of the dam with each high tide, and all fish and benthic organisms in the outlet stream are exposed to abnormally high salinities. *Uniomerus tetralasmus* and *Villosa vibex* were recorded below the spillway by Johnson (1970), and Dawley (1965) reported *Gillia altilis* from that area. Habitat for those species has been altered by increased salinity levels.

As discussed previously, all of the tributaries of Greenfiled Lake have been channelized to enhance drainage. These creek channels are periodically maintained by dragline, which results in almost total removal of all benthic organisms and aquatic vegetation. The consequences of such actions for molluscan populations are undoubtedly profound; Greenfield Lake and its tributaries will be repopulated only from undisturbed waters upstream or downstream of the maintenance area or from outside sources. Because channels run from the lake all the way to the headwaters, recolonization is presumed to be very slow.

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John White and the Earliest (1585-1587) Illustrations of North American Reptiles

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ABSTRACT.— Five paintings of reptiles executed by John White between 1585 and 1587 are the earliest known depictions of North American herpetozoa. They represent the box turtle, *Terrapene carolina*; the diamondback terrapin, *Malaclemys terrapin*; the loggerhead, *Caretta caretta*; a West Indian iguana, *Cyclura* (*cychlura*?); and a crocodilian (*Crocodylus acutus*?). Black-and-white reproductions of the paintings are provided, as well as a brief account of White's role in the history of North American exploration.

It is well recognized (e.g. Smith and Smith 1973) that Francisco Hernândez was the earliest naturalist to depict American reptiles and amphibians, through his travels in Mexico from 1570 to 1577. Lamentably, his manuscript of 15 folio volumes with many illustrations was destroyed by fire in 1671, but not before it had been extensively revised, abridged, amended, and plagiarized by several authors. An abridged version appeared under Hernandez's name in 1628, augmented in 1649 (see Hulton and Quinn 1964), and the earliest annotated excerpts appeared under the authorship of Francisco Ximênez in 1615. Only black-and-white copies of the original illustrations have survived. The next illustrations of North American species of reptiles and amphibians, by a naturalist, did not appear until 1743, in Catesby's famed monograph (cf. Adler 1979).

Between the dates of Hernandez's and Catesby's works, and indeed only shortly after the earlier of the two, in the period from 1585 to 1587, John White prepared numerous watercolor paintings, drawings, and maps while living on Roanoke Island, N.C., or while traveling in its vicinity and in the West Indies. Of his work dating from 1577 to 1590, about 75 paintings remain, including one of uncertain origin; 62 depict animals, plants, Indians, and geography of the areas he visited in the New World. All of these are replicas White made of the originals, which are now all lost (Quinn 1955). Five of the 62 paintings depict reptiles; others of biological interest include 6 of plants, 13 of fishes, 6 of birds, and 7 of various invertebrates. White's many other paintings, known

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through copies made by others, were not preserved. In their time, all were widely known, widely admired, and usually poorly imitated. His Indian paintings, copied notably by DeBry, were for centuries the primary basis for European concepts of native Americans.

The first generally available reproduction of the entire collection of 75 paintings appeared in color, copied from tinted photostats, not the originals, in a single volume by Lorant (1946). An elaborate, handsome analysis and reproduction followed 18 years later in a two-volume work published by, and drawing exhaustively upon the resources of, the British Museum (Hulton and Quinn 1964). Hulton (1965, 1984) also reproduced the White paintings and drawings, and Cumming, Skelton, and Quinn (1972), in a beautifully illustrated book on North American explorations, reproduced four of the five reptile paintings by White, two in color.

All the works cited above included most or all of at least the American drawings, including the reptiles. However, none of the reptile paintings had been reproduced for general public access prior to 1946, and none of the three works in which they subsequently appeared had been prominently noted by herpetologists. In order to bring White's contributions more generally to the attention of herpetologists, we here reproduce in monochrome all five reptile paintings, with the cooperation of the Trustees of the British Museum, where all of White's known extant replicas are located.

Although White's reptile paintings have never been given much attention by herpetologists, they were first discovered as early seventeenth-century copies (by a near descendant of White's) in a portfolio acquired in 1709 or shortly thereafter by Sir Hans Sloane, and now in the British Museum. Sloane had numerous copies made of these copies, and in turn, Catesby in 1731-1743 copied seven of Sloane's copies of White's paintings in his "Natural History," among them the "iguana." Lorant (personal communication) sought the assistance of the authorities in the British Museum (Natural History) in identifying the reptile paintings, and for the Hulton-Quinn volumes Doris M. Cochran of the U.S. National Museum of Natural History and J. C. Battersby of the British Museum (Natural History) furnished expert comments on identifications, expanding on the identifications detailed in Quinn (1955). Howard H. Peckham, Helen T. Gaige, and Carl Hubbs prepared a locally distributed pamphlet for a meeting in Ann Arbor, Mich., of the American Society of Ichthyologists and Herpetologists in 1946, bearing a reproduction of White's sea turtle painting as its frontispiece, for a display of rare books in the Clements Library of the University of Michigan. We are not aware of any other herpetological attention,

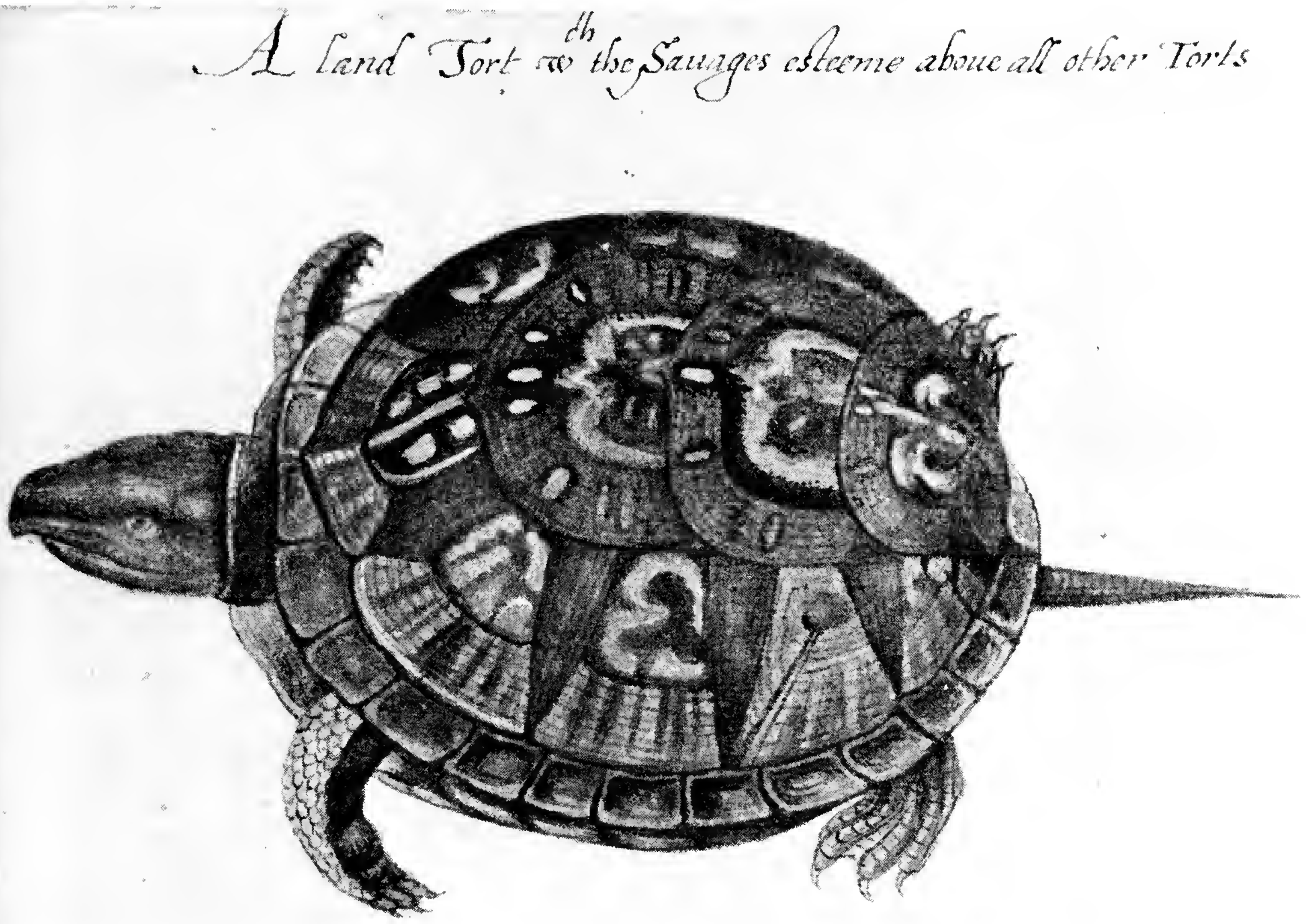

Fig. 1. *Terrapene carolina* (?)*carolina* (L.), as depicted by John White. Reproduced from a watercolor of 187-mm greatest straight-line object dimension.

although the box turtle painting is reproduced in color in Borland (1975).

The Cochran identifications of the three turtles are unimpeachable (Hulton and Quinn 1964). One painting clearly depicts *Terrapene carolina* (L.), presumably *T. c. carolina* (Fig. 1); another represents *Malaclemys terrapin* (Schoepff), presumably *M. t. centrata* (Latreille) (Fig. 2); and a sea turtle (Fig. 3) is readily identifiable as *Caretta caretta caretta* (L.). All three species occur widely on the Atlantic coast and could easily have been taken near Roanoke Island, where White spent most of his time. The subspecies of all three turtles are here suggested on the basis of geographic probability, not depiction of subspecific characters. Cochran noted (Hulton and Quinn 1964) that the *Caretta* is shown with too long a tail and with a pattern too regular and contrasty, and that the *Malaclemys* is improperly shown with six fingers and toes on the right side. Two species are shown with the wrong number of marginals (too many for *Terrapene*, too few for *Malaclemys*).

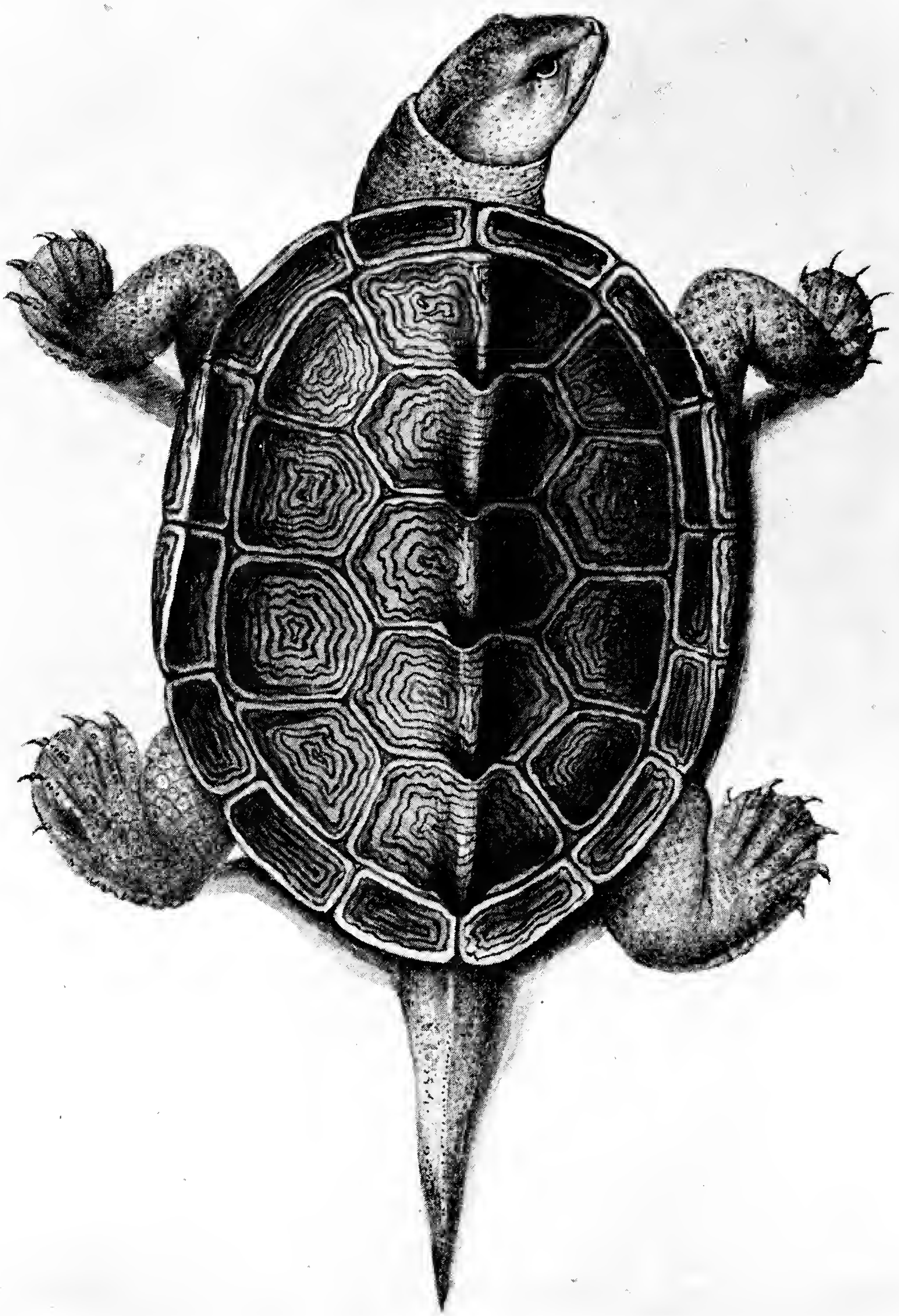

Fig. 2 *Malaclemys terrapin* (?)*centrata* (Latreille), as depicted by John White. Reproduced from a watercolor of 243-mm greatest straight-line object dimension.

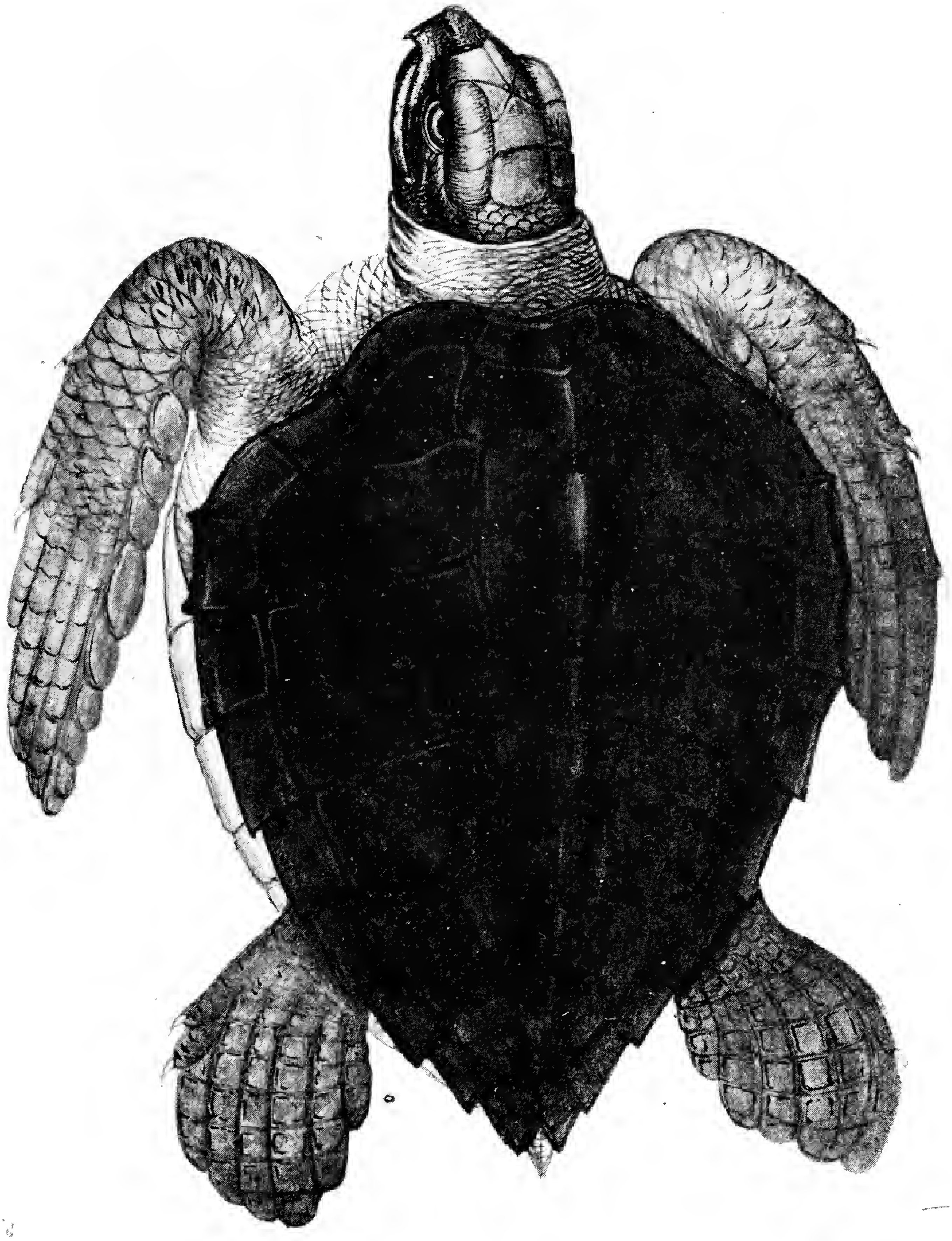

Fig. 3. *Caretta caretta caretta* (L.), as depicted by John White. Reproduced from a watercolor of 221-mm greatest straight-line object dimension.

The single lizard illustrated (Fig. 4) is more of a problem. It is not a temperate North American species, and it is obviously one of the large, herbivorous iguanines. Because White's voyages took him into the northern West Indies, where *Cyclura* is the only abundant large iguanine, there is little doubt that some member of that genus is represented. In Lorant's book the species is identified as *Cyclura carinata*, which occurs (Schwartz and Henderson 1988) only on Booby Cay, Bahama Islands, and on Turks and Caicos islands. Cochran and Battersby (Hulton and Quinn 1964) could only conclude that some *Cyclura* species was represented, admitting some resemblance to *C. carinata*. However, Dr. Albert Schwartz, to whom we turned for help in identifying the species, explicitly eliminated *C. carinata* from reasonable consideration because of its low dorsal crest scales. He also regarded *C. cornuta* (with conspicuous spiny verticils on tail), *C. ricordi* (conspicuous spiny verticils on tail), and *C. rileyi* (low crest scales) as equally improbable subjects. The most likely species, he suggests, is *C. cychlura*, which not only agrees structurally but occurs widely in the Bahamas, on Andros (the largest island of that group) as well as on others. Because the journals of White's travels describe repeated landings in the Bahamas, it seems very likely that *C. cychlura* (Cuvier) is indeed the species depicted. *Cyclura nubila* of Cuba and the Cayman Islands and *C. collei* of Jamaica, though structurally in agreement, are less likely candidates on the basis of probable infrequency of visits by White. However, identification cannot be certain, for White did travel extensively in the West Indies (Hakluyt 1589), and furthermore could well have seen specimens of virtually any species transported by native traders or by explorers such as Francis Drake, with whom he frequently associated.

The remaining illustration (Fig. 5) represents a crocodilian and is labeled "Allagatto" on the painting, but it is identified as *Crocodylus acutus* (Cuvier) (*"Crocodilus americanus"*) in Lorant. Cochran (Hulton and Quinn 1964) regarded the drawing as impossible to identify, showing features of both *Alligator* and *Crocodylus*, but she concluded that it most likely represents *Alligator mississippiensis* (Daudin). She also noted that the inscription indicating a length of 3 feet, 4 inches, and an age of 1 month, must be in error; the age would certainly be more than 2 years at that size. In White's time the alligator occured commonly in the vicinity of Roanoke Island, as well as northward into Virginia and southward throughout Florida. White could have seen specimens of it anywhere in his travels in what are now parts of Virginia and North Carolina. However, he also explored the northern West Indies, where the alligator does not occur but the crocodile was common. Thus, we agree that either species could easily have been illustrated. Although his chances of exposure to the alligator were obviously much more numerous than chances of exposure to the crocodile, the features shown certainly more closely conform with those of a crocodile than an alligator. The label "Allagatto" is just as likely a corruption of the Spanish "el lagarto," applied to the crocodile in the West Indies, as of "alligator" (also a corruption from Spanish), applied to *Alligator*. The light color and narrow straight jaws are particularly significant. We conclude that the crocodile significantly influenced the depiction, even if it is a composite. The crocodile does occur in Florida, but only at the extreme southern tip; White did not reach any part of Florida, his two paintings of Floridians having been copied from the work of Jacques Le Moyne de Morgues.

There is also the possibility, brought to our attention by Dr. Adler, that White could have been influenced in his depiction of the crocodilian by illustrations widely circulated in Europe by that time of the similar *Crocodylus niloticus* of Egypt. In view of the reasonably close accuracy of his other paintings, we assume that White did not have a chance to examine any crocodilian very closely, else his depiction would have been more faithful to the subject. Hence, the influence of extraneous impressions, as of *C. niloticus* illustrations of his era, should not be excluded as a possibility in the apparent absence of close observations of the American species.

The preceding identifications were adopted by Hulton (1984) from a preliminary version of this article that he kindly reviewed in 1981.

Despite the flaws now evident in White's herpetological paintings when compared with modern illustrations, in the context of his era his drawings are remarkably superior, surpassing any others executed for several succeeding generations, including the works of Catesby (1731-43) and Bartram (1791). His stature as a natural history artist is unequalled and merits as much honor as is commonly awarded, for example, to Audubon in a much later era. Because all of his paintings that now survive are replicas of originals now lost, it is likely that some fidelity to the originals has been lost.

White's five paintings are the earliest known for North American and West Indian reptiles, and the earliest now in existence for any reptiles of the western hemisphere. They are not the earliest published illustrations, however, because they were not reproduced for the general public until Lorant included them in his 1946 work.

Although mass-reproduced with accuracy only in the past 35 years or so, some of White's painting were redrawn many times in works in the preceding centuries, beginning with the Sloane (1709-14?) portfolio of 112 leaves of drawings (now only 110). In the Sloane volume the

Fig. 4 *Cyclura* (?)*cychlura* (Cuvier), as depicted by John White. Reproduced from a watercolor of 200-mm greatest straight-line object dimension.

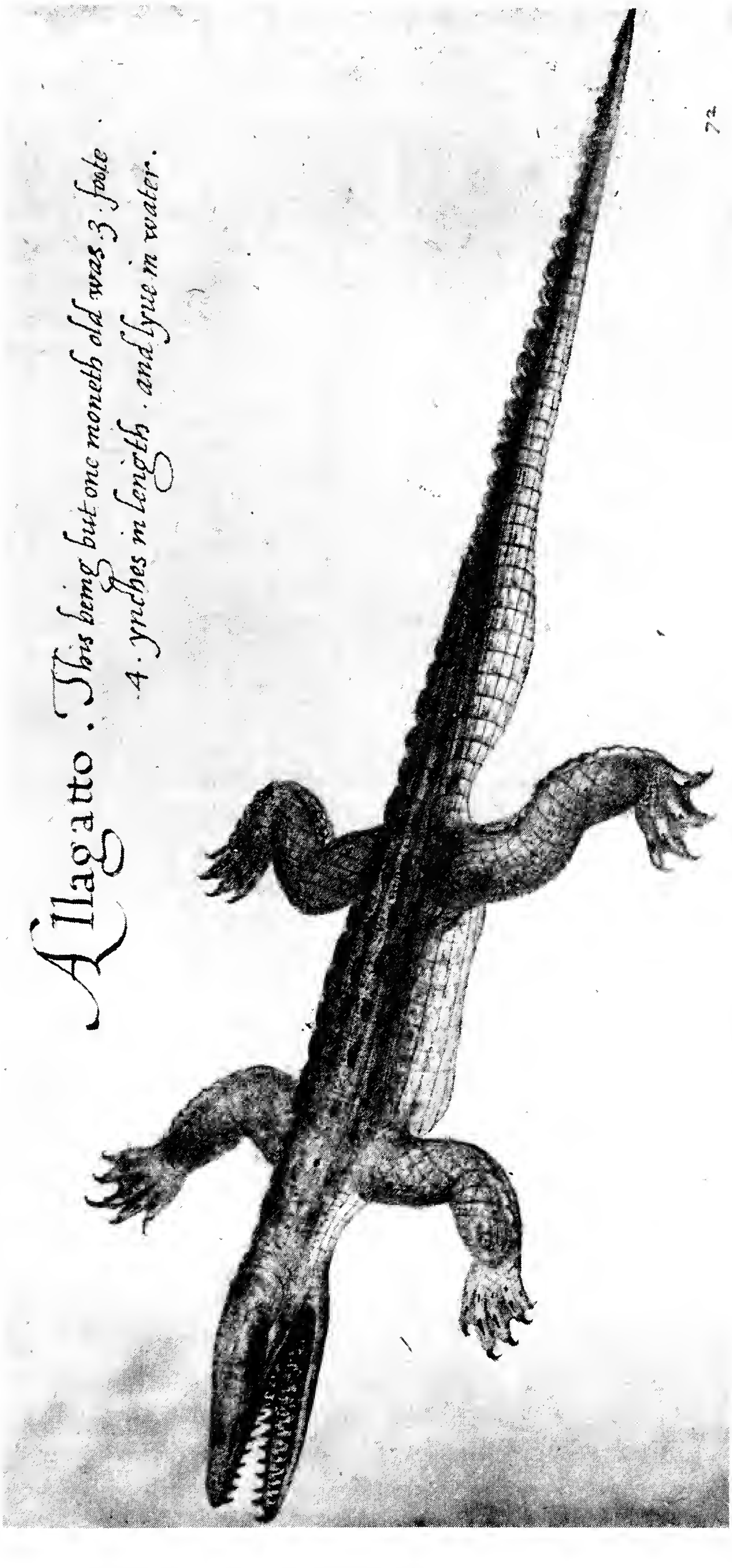

Fig. 5 (?)*Crocodylus acutus* (Cuvier), as depicted by John White. Reproduced from a watercolor of 218-mm greatest straight-line object dimension.

Cyclura and crocodilian, as well as a skink and a snake, were present among the 44 drawings adapted from originals by White that are now lost. Catesby copied his "iguana" from the *Cyclura* (Hulton and Quinn 1964). The monochrome reproductions of these two additional reptiles (Hulton and Quinn 1964) are too inaccurate (whether originally so or from unfaithful copying) to identify satisfactorily. Cochran (in Hulton and Quinn 1964) regarded the snake as "probably" a *Lampropeltis*, whereas we suggest that *Nerodia* is a more likely model. She thought the skink was "probably" a mature male *Eumeces fasciatus* (L.), although noting that *E. inexpectatus* and *E. laticeps* also occur in the vicinity of Roanoke Island and could possibly have been represented in the painting.

There are only two other redrawn versions of White's herpetological paintings of early date, both noted in Hulton and Quinn (1964). One is a 1589 work by Walter Bigges ("A summarie and true discourse of Sir Francis Drake's West Indian Voyage . . ."), showing an "iguana" and an "alligator or crocodile" drawn by Baptista Boazio from White's figures, here reproduced as Fig. 4 and 5. A "turtle" also shown in that volume is too crudely stylized to be identifiable; its uncertain source is apparently not White. The second is John Mountgomery's manuscript of 1588-1589 ("A treatice concerning the navie of England . . ."), in which White's *Caretta* is shown quite clearly in a corner of a large naval panorama. According to Hulton (1984), this is "the earliest known copy of a John White drawing."

The only other herpetological subject matter in Hulton and Quinn's illustrations is some stylized snakes decorating the bodies of some Pict warriors illustrated in manuscripts by Lucas de Heere, about 1575 (Hulton and Quinn 1964).

Although numerous non-herpetological paintings by White were republished in subsequent years, not until the 1930s were the reptiles reproduced faithfully in color. One unique, complete set of all of White's paintings was copied by a Miss Bessie Barclay for the Newport News public schools, and five other sets consisting of tinted photostats were prepared under the direction of Mrs. Sonia Tregaskis (Hulton and Quinn 1964). One of the Tregaskis sets is at the University of Michigan and was the source of the reproduction in the pamphlet by Peckham, Gaige, and Hubbs (1946), and in the book by Lorant (1946), which finally brought White's work to rank-and-file accessibility. Hulton and Quinn (1964) pursued their definitive work with the conviction that Lorant's book, "though useful, was unfortunately marred by the entirely unreliable quality of the plates and text alike"—an opinion universally shared by academic reviewers.

The history of John White is shrouded with uncertainties (Quinn 1955). He was an Englishman of sufficient stature to be appointed by

Sir Walter Raleigh as governor of a group of 113 men and women sent in 1587 as a second attempt to establish a colony on Roanoke Island, "Virginia" (now North Carolina). White, along with the eminent scientist Thomas Harriot, had gone with the earlier group in 1585, stayed with them on the island for a year, and returned (as did the rest of the colonists) with Sir Francis Drake to England in 1586. The second group that White accompanied in 1587 did not fare particularly well; only a little more than a month after their arrival on Roanoke (22 July 1587), White departed again (27 August 1587) for England to procure supplies for the colonists. In that interval, on 18 August 1587, his daughter Eleanor, wedded to Ananias Dare, gave birth to the first child born of English parents in America—Virginia Dare. A second child (name and sex unknown) was born on Roanoke Island to Dyonis and Margery Harvey, just a week or so later.

Unfortunately, war with Spain was then imminent, and hence supplies, ships, and personnel were diffcult to obtain. Not until 1590, three years after his departure to obtain succor for the colonists, was it possible for White to return to Roanoke Island, where little trace of the colonists, including White's daughter and granddaughter, was found. Thus ensued the mystery of the "Lost Colony," famous in the history of early English settlement in America. Quinn (1985) concluded that most migrated to southeastern Virginia, where they lived peacefully with a friendly Indian tribe until about 1607, when they were massacred by Powhatan's tribe. The rest, a very small group, remained for a time on Roanoke Island, but ultimately moved to nearby Croatoan Island to await White, presumably living with Indians there, but their fate is unknown.

White retired into virtual obscurity in Ireland shortly after the unsuccessful relief mission returned to England. His career as an administrator and governmental leader was ignominious, but not so his visual records of paintings, drawings, and maps, executed less than a quarter of a century before the first successful English colonization took place in Virginia.

John White's role as herpetologist was a small facet of the large part he played in early American history and of the contribution he made to the image of America among educated Europeans. He was a gifted artist of the first rank in his time. Although direct credit was long in coming, since his copiers gained far greater fame than he, his paintings created images of native North America that linger today on both sides of the Atlantic, to a considerable extent as a result of his collaboration with Harriot (1588). White's Lost Colony has fostered legends that continue to stimulate the imaginations of those who have concern for colonial American history.

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by

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Genetic Patterns and Population Structure in Appalachian *Trechus* of the *vandykei* Group (Coleoptera: Carabidae)

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ABSTRACT.— The genus Trechus is diverse and widespread in the southern Appalachian region. A majority of its species are alpine endemics, altitudinally restricted to elevations above 1,350 m. Five taxonomic subgroups of the *vandykei* species group of *Trechus* were examined electrophoretically to assess patterns of differentiation within and between taxa. Genetic differentiation within subgroups is slight to moderate, suggesting that gene flow between local populations is maintained or has only recently been interrupted. Differentiation between subgroups is moderate to very great, indicating complete genetic isolation at present. Varying degrees of affinity between subgroups are consistent with the hypothesis that speciation has resulted from lineage vicariance caused by fluctuating Pleistocene climates. The *vandykei* group belongs to the endemic southern Appalachian subgenus *Microtrechus*, which probably originated southwest of a lowland dispersal barrier, the Asheville basin and the French Broad River valley. Electrophoretic data indicate that the *vandykei* subgroup has dispersed northeast of this lowland relatively recently. Affinities of this subgroup with isolates in the Great Smoky and Unicoi mountains, rather than the *pisgahensis* subgroup in the Great Balsam Mountains immediately south of the Asheville basin, suggest that this lowland has been a dispersal barrier throughout the Pleistocene and earlier. Dispersal of *Microtrechus* species east of the Asheville basin and of *Trechus*, s. str., species west of the lowland probably occurred across the narrow French Broad River gorge and the mountain chains along the North Carolina-Tennessee border.

More than three-fourths of North American species of the carabid beetle genus *Trechus* occur in the southern Appalachians. In this region

Trechus exceeds all other carabid genera in taxonomic diversity (Barr 1985a). Nearly 55 *Trechus* taxa are known from the region at present; a great majority of them are alpine endemics isolated at elevations above 1,350 m. Much of the diversity in this genus is a result of lineage vicariance associated with fluctuating climatic regimes during the Pleistocene. Presumably ancestral *Trechus* species were more continuously distributed at lower elevations during colder, wetter climates associated with glacial maxima. However, the warmer, drier interglacial climates made lowlands inhospitable to most trechines and resulted in vertical contraction and fragmentation of ranges. The present insular pattern of distribution of alpine *Trechus* taxa is a direct result of the recent climatic regime (Barr 1962, 1979, 1985a).

Evolution in Appalachian *Trechus* has also been influenced by the Asheville basin, a major lowland drained by the French Broad and Pigeon rivers. The two subgenera represented in the region, *Trechus,* s. str. (males with two protarsomeres enlarged, dentate, and setose beneath), and *Microtrechus* (males with only one protarsomere so modified), are essentially separated by the Asheville basin and the French Broad River. *Microtrechus*, endemic to the Unaka mountain province, appears to have evolved west of the basin, in isolation from subgenus *Trechus*, s. str., to the east (Barr 1962, 1979). However, occurrence of a limited number of *Microtrechus* species east of the French Broad River and a few *Trechus,* s. str., species west of the river suggests that the barrier has recently been breached (Barr 1985a). In general, the area southwest of Asheville exhibits greater endemicity and diversity in many groups of carabids, and carabids in the mountains northeast of Asheville are taxonomically much closer to carabid species and genera in the mountains of western Virginia and eastern West Virginia (see Barr 1969 for summary). The eyeless, wingless, edaphobitic species of *Arianops* (Coleoptera: Pselaphidae) also show much the same pattern (Barr 1974; for a detailed discussion of the evolutionary impact of the Asheville lowland, see Barr 1985a).

Morphological differences between closely related isolates of *Trechus* are often subtle, involving quite minor, though consistent, characters. The taxonomy of the isolates belonging to the *vandykei* species group of *Microtrechus* has proven especially difficult. Twelve upland isolates—all more or less morphologically distinct and strictly allopatric—are known from western North Carolina and eastern Tennessee (Fig. 1. shows all known localities except Joanna Bald, in the Snowbird Mountains). Beetles in this group are quite small (total length means <3 mm) and characteristically inhabit the superficial layers of moist or wet litter in the forest floor and carpets of loose, wet, fluffy mosses. Local populations are often quite abundant, exhibiting densities of about 20 to 80 individuals per square meter. The *vandykei* group is represented in the Black-Great Craggy and Bald mountains east and north of Asheville, and to the west in the Great Smoky, Newfound, Unicoi, Cheoah, Snowbird, Tusquitee-Valley River, and Great Balsam ranges. An apparent relict population occurs on Whiteside Mountain, where the Cowees meet the Blue Ridge escarpment. Nevertheless, some curious distributional gaps exist: Populations assignable to this group have not been found elsewhere in the Cowees, on the Toxaway Mountain spur off the Great Balsams, in the Plott Balsams (between the Smokies and Great Balsams), nor in the Nantahalas, despite special efforts to collect them there. Discontinuity is also found in the chain of higher peaks along the Tennessee-North Carolina border, with the *vandykei* group represented on Sandymush Bald and Camp Creek Bald, but not on Tennessee Bluff in between. *Trechus* taxa assignable to other species groups are relatively abundant in these areas where the *vandykei* group is absent.

Although extensive collecting over the past quarter century has well established the altitudinal restriction of these isolates, such negative evidence does not totally preclude the possibility of some limited gene flow across lowlands. In fact, one specimen of *T. bowlingi* has been taken in Greenbrier Cove, in the Great Smokies, and one specimen of *T. tusquitee* was taken near Old Road Gap along the north approach to Tusquitee Bald, both specimens near elevations of about 900 m. Also, several altitudinally restricted species, including *T. bowlingi*, occur at about 950 to 1,050 m on the north (Tennessee) side of the Great Smokies, where cool microclimates prevail as cold air flows down from the crest through deep ravines. However, the rarity of specimens at lower elevations indicates only that minimal gene flow across lowlands is possible, not that it is significant.

In this study we examine a suite of closely related *Trechus* taxa (the *vandykei* species group) using the technique of gel electrophoresis. This technique permits us to look at another set of characters, enzymatic proteins, thus providing data complementary to biogeographic and morphological considerations. Electrophoretic data are easily quantified and permit insight into relative degrees of biochemical differentiation. The underlying genetic basis of electrophoretic variation can usually be inferred, allowing us to determine whether or not limited gene flow exists between geographically and altitudinally isolated populations. Although most of the isolates sampled are restricted to single peaks, three are more widely distributed in major, continuous uplands—*T. vandykei* in the Black and Great Craggy mountains, *T. bowlingi* in the Great Smoky Mountains, and *T. pisgahensis* in the Great Balsam

Mountains, including Pisgah Ledge. We sampled three populations of *vandykei* and four populations each of *bowlingi* and *pisgahensis*; thus differentiation between local populations within the same continuous upland can serve as a baseline for comparing taxa on isolated peaks.

The isolates within the *vandykei* species group can be arranged in five subgroups, each bearing one of the five available trivial names of taxa assigned to the species group. Although all 12 isolates differ to a greater or lesser extent in minor morphological characters and will be the subject of a subsequent taxonomic paper (Barr, in preparation), we propose no new names in this paper. The subgroups are as follows.

1) *vandykei* subgroup—(a) *T. vandykei* Jeannel (1931), Black and Great Craggy mountains and adjacent Blue Ridge, Yancey Co. and MacDowell Co., N.C.; three other isolates on (b) Camp Creek Bald, Greene Co., Tenn., and Madison Co., N.C.; (c) Big Bald, Unicoi Co., Tenn., and Yancey Co., N.C.; and (d) Unaka Mountain, Unicoi Co., Tenn., and Mitchell Co., N.C.

2) *bowlingi* subgroup—one isolate, *T. bowlingi* Barr (1962), widespread in the eastern two-thirds of the Great Smoky Mountains National Park, Tenn. and N.C.

3) *tusquitee* subgroup—(a) *T. tusquitee* Barr (1979), Tusquitee Bald, Macon Co., Clay Co., and Cherokee Co., N.C.; two other isolates on (b) Joanna Bald (Snowbird Mountains), Graham Co. and Cherokee Co., N.C.; and (c) Cheoah Bald, Graham Co. and Swain Co., N.C.

4) *haoe* subgroup—one isolate, *T. haoe* Barr (1962), known only from Haoe Lead above Joyce Kilmer Memorial Forest, Unicoi Mountains, Graham Co., N.C.

5) *pisgahensis* subgroup—(a) *T. pisgahensis* Barr (1979), widely distributed in the Great Balsam Mountains and their eastern arm, Pisgah Ledge, in Buncombe Co., Haywood Co., Jackson Co., and Transylvania Co., N.C.; two other isolates on (b) Sandymush Bald, Newfound Mountains, Haywood Co. and Madison Co., N.C., and (c) Whiteside Mountain, Jackson Co. and Macon Co., N.C.

METHODS

A total of 19 populations representing 11 of the 12 known isolates of the *vandykei* group were sampled during the summer in 1982, 1983, and 1984 for electrophoretic analysis. [We were unable to recollect the Joanna Bald population discovered in 1960 (Barr 1962), although other *Trechus* (*Microtrechus*) species belonging to the *nebulosus* group were found there in some abundance.] Beetles were collected by sifting forest-floor litter or moss from a hardware-cloth basket into a plastic dishpan, where they could be removed with an aspirator or by hand. The most productive microhabitat proved to be damp, but not excessively wet, litter in *Rhododendron* thickets. Beetles were transported to the laboratory in 4-ounce glass or plastic jars cooled in an ice chest. During the summer of 1982, specimens were maintained alive in a refrigerator at the Highlands Biological Station prior to electrophoresis, which was also conducted at the Station. Beetles collected at the end of the summer in 1982 and all 1983 and 1984 collections were returned alive to the University of Cincinnati; after identification and sexing they were placed individually into 400-μl microcentrifuge tubes and frozen at -80° C until used for electrophoresis.

Electrophoresis was conducted on vertical polyacrylamide slab gels with a Hoefer Scientific SE600 system. Single beetles were ground in approximately 40μl of grinding buffer (0.01M Tris-HCl, pH 7.0, containing 0.001M EDTA, 1% Triton-X, and 25% sucrose). Initial screening dictated that only a single sample could be obtained from each specimen because of the beetles' small size, low enzyme activity, or both. Ten enzymatic systems were surveyed: alkaline phosphatase (ALP), carbonic anhydrase (CAH), esterase (EST), hexokinase (HEX), malate dehydrogenase (MDH), mannose phosphate isomerase (MPI), phosphoglucose isomerase (PGI), phosphoglucomutase (PGM), superoxide dismutase (SOD), and xanthine dehydrogenase (XDH). Only five systems, to include eight presumptive loci, could be consistently scored in all individuals of all taxa: CAH (1 locus), EST (2 loci), MDH (2 loci), PGI (1 locus), and SOD (2 loci). Staining techniques for these systems were adapted from Brewer (1970), Harris and Hopkinson (1976), and Shaw and Prasad (1970).

All data analysis was accomplished with a FORTRAN-77 version of the BIOSYS-1 Program developed by Swofford and Selander (1981). This program contains routines for population genetic analysis as well as procedures for the production of phenograms and other types of phylogenetic analyses.

RESULTS

For practical purposes, the 19 populations sampled were assigned to the five subgroups whose limits and distribution are described in the introductory section. Locations of the sampling sites and the abbreviations employed for them throughout this paper are presented in Table 1, and their relative geographic configuration is shown in Fig. 1. The sampled *vandykei* group populations (except those of Sandymush Bald and Cheoah Bald) coexist with larger *Trechus* species of other groups; see Barr (1985a) for details of the various species guilds to which the *vandykei*-group isolates belong.

Table 1. Location of sampling sites for *Trechus* beetles in North Carolina and Tennessee.

1) *vandykei* subgroup			
BA	Balsam Gap	N.C.:	Buncombe Co. and Yancey Co., at juncture of Black and Great Craggy mountains
BB	Big Bald	N.C.:	Yancey Co./Tenn.: Unicoi Co., near summit
CC	Camp Creek Bald	N.C.:	Madison Co./Tenn.: Greene Co., near summit
MM	Mount Mitchell	N.C.:	Yancey Co., near summit
SN	Snowball Mountain	N.C.:	Buncombe Co., 3 km W of Craggy Dome
UN	Unaka Mountain	N.C.:	Mitchell Co./Tenn.: Unicoi Co., 10 km E of Erwin
2) *bowlingi* subgroup			
CG	Collins Gap	N.C.:	Swain Co./Tenn.: Sevier Co., Clingmans Dome Road
HE	Heintooga Overlook	N.C.:	Haywood Co., eastern Great Smokies
RC	Ramsay Cascades	Tenn.:	Sevier Co., 4 km W of Mount Guyot
WP	Walker Prong	Tenn.:	Sevier Co., at US 441 bridge over Walker Prong
3) *tusquitee* subgroup			
CH	Cheoah Bald	N.C.:	Graham and Swain counties, 5 km S of Stecoah, just west of summit
TU	Tusquitee Bald	N.C.:	Cherokee Co., Clay Co., and Macon Co., immediately south and east of summit
4) *haoe* subgroup			
HA	Haoe Lead	N.C.:	Graham Co., ridge north of Joyce Kilmer Memorial Forest
5) *pisgahensis* subgroup			
BG	Beech Gap	N.C.:	Haywood Co., just north of gap, 2 km W of Devils Courthouse
BP	Bearpen Gap	N.C.:	Haywood Co., just north of gap, 4 km WNW of Beech Gap
DG	Deep Gap	N.C.:	Jackson Co., west side, 4 km SE of Balsam
MP	Mount Pisgah	N.C.:	Henderson Co. and Transylvania Co., 0.5 km E of summit
SM	Sandymush Bald	N.C.:	Haywood Co. and Madison Co., 5 km E of Cove, at summit
WH	Whiteside Mountain	N.C.:	Jackson Co., 4 km SW of Cashiers, summit

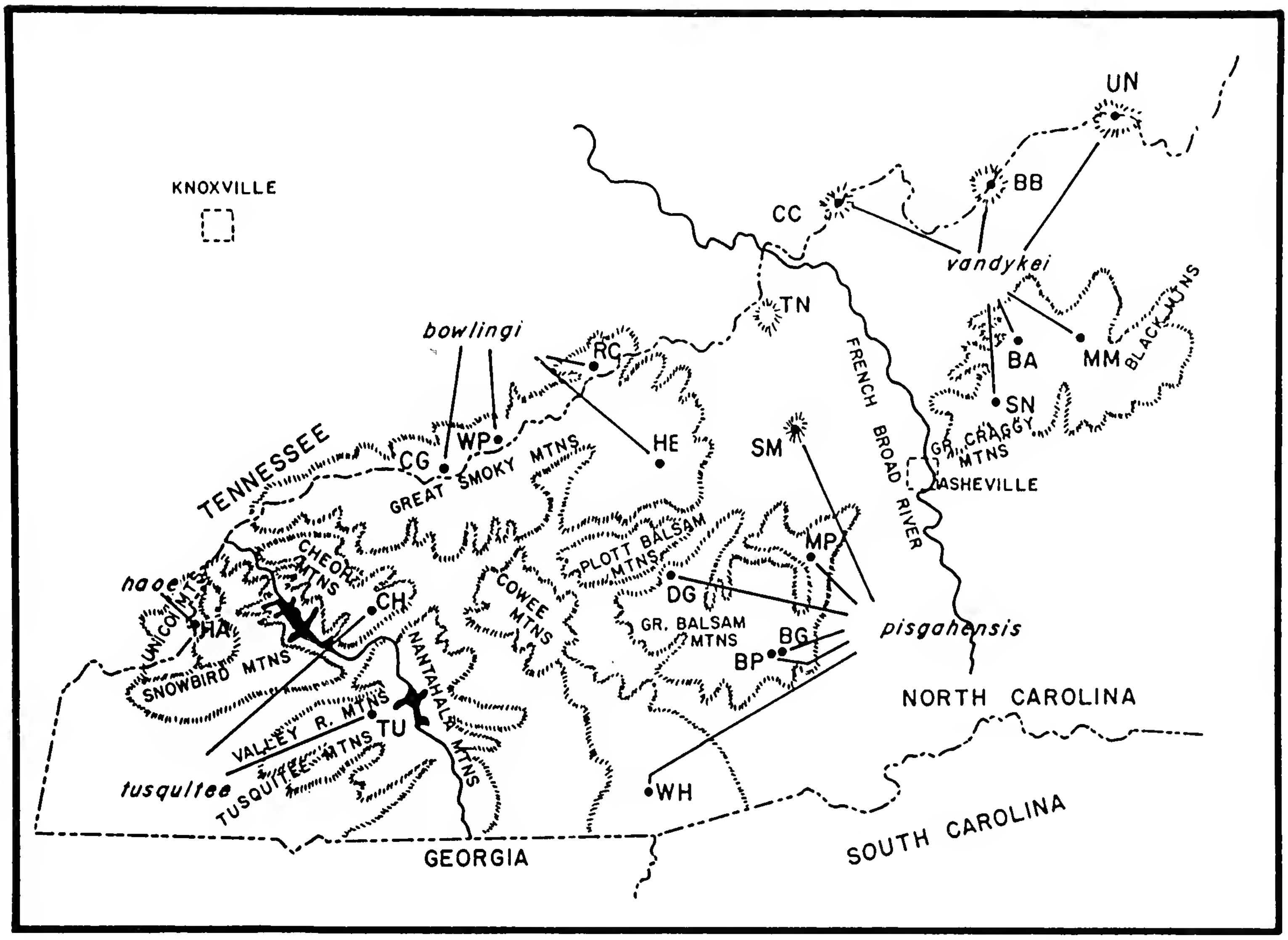

Fig. 1. Map of the Unaka mountain region, showing locations of *Trechus vandykei* species-group populations examined in this study. Subgroup designations of populations are as follows: *bowlingi*—CG Collins Gap, HE Heintooga Overlook; RC Ramsay Cascades, WP Walker Prong; *haoe*—HA Haoe Lead; *pisgahensis*—BG Beech Gap, BP Bearpen Gap, DG Deep Gap, MP Mount Pisgah, SM Sandymush Bald, WH Whiteside Mountain; *tusquitee*—CH Cheoah Bald, TU Tusquitee Bald; *vandykei*—BA Balsam Gap, BB Big Bald, CC Camp Creek Bald, MM Mount Mitchell, SN Snowball Mountain, UN Unaka Mountain.

Six of the eight loci examined were monomorphic, with the same electromorph fixed in all populations of all taxa examined (Table 2). The remaining two loci, CAH and PGI (Table 2, part B), were variable within and/or between populations. Four of the five subgroups showed very similar patterns of genetic variability (Table 3), with all local populations variable at both the CAH and PGI loci; i.e. average polymorphism (P) = 0.25, and average heterozygosity (H) ranged between 0.059 and 0.110 for these subgroups. The *pisgahensis* subgroup exhibited less genetic variation. Only the PGI locus was variable in this subgroup, and only in three of the six populations studied, such that P = 0.08 and H = 0.009 (Table 3).

Table 2. Electromorph frequencies at eight electrophoretic loci for 19 populations of the *Trechus vandykei* species group.[a]

	pisgahensis						*tusquitee*		*haoe*	*vandykei*							*bowlingi*		
	BG	BP	DG	MP	SM	WH	CH	TU	HA	BA	MM	SN	BB	CC	UN	CG	HE	RC	WP
CAH																			
n	26	18	7	10	18	8	18	41	23	45	79	21	36	30	10	57	18	4	31
A																0.518	0.889	0.750	0.323
B							0.111									0.211	0.111		0.194
C							0.444	0.159								0.123		0.250	0.435
D									0.891	0.878	0.772	0.833	0.958	0.883	0.900	0.088			0.048
E							0.444	0.841								0.061			
F									0.109	0.122	0.228	0.167	0.042	0.117	0.100				
null	1.000	1.000	1.000	1.000	1.000	1.000													
PGI																			
n	17	13	20	34	16	26	31	35	35	38	48	23	25	47	16	20	20	17	19
A														0.011	0.031	0.025			0.026
B							0.177	0.300	0.271	0.684	0.760	0.761	0.580	0.872	0.719	0.450	0.475	0.353	0.816
C										0.211	0.188	0.130	0.060		0.250				
D	0.941	1.000	1.000	0.926	0.844	1.000	0.710	0.486	0.729				0.280	0.117		0.525	0.475	0.618	0.158
E				0.074	0.156		0.113	0.214		0.105	0.052	0.109	0.080				0.050	0.029	
F	0.059																		

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[a] Monomorphic loci (6) with the same electromorph fixed in all populations: EST-1; EST-2; MDH-1; MDH-2; SOD-1; SOD-2. Monomorphic and/or polymorphic loci (2): CAH, PGI.

Table 3. Genetic variability at eight enzymatic loci for five subgroups of the *Trechus vandykei* species group.

Population	N[a]	P[b]	H[c] Observed	H[c] Expected
		bowlingi		
CG	27.8	0.25	0.123	0.150
HE	16.0	0.25	0.095	0.095
RC	6.3	0.25	0.029	0.117
WP	25.0	0.25	0.056	0.124
Mean		0.25	0.076	0.122
		haoe		
HA	21.9	0.25	0.059	0.075
		pisgahensis		
BG	15.8	0.125	0.015	0.014
BP	13.6	0.0	0.0	0.0
DG	9.5	0.0	0.0	0.0
MP	15.1	0.125	0.018	0.017
SM	17.4	0.125	0.023	0.034
WH	12.9	0.0	0.0	0.0
Mean		0.063	0.009	0.011
		tusquitee		
CH	15.5	0.25	0.117	0.134
TU	26.8	0.25	0.102	0.113
Mean		0.25	0.110	0.124
		vandykei		
BA	25.5	0.25	0.096	0.087
BB	27.9	0.25	0.075	0.083
CC	32.5	0.25	0.056	0.055
MM	37.3	0.25	0.083	0.093
SN	14.4	0.25	0.090	0.086
UN	9.9	0.25	0.056	0.078
Mean		0.25	0.076	0.080

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[a] Mean sample size per locus.

[b] Proportion of polymorphic loci per population.

[c] Average proportion of heterozygous loci per individual.

Genotype frequencies at variable loci in each population were tested statistically for fit to expectations under Hardy-Weinberg Equilibrium (HWE). Three statistical tests were used to test correspondence of the data to HWE: Chi-square goodness of fit with Levene's (1949) correction for small sample size, an exact probability test analogous to Fisher's exact test, and—in cases where three or more electromorphs occurred in a population—a Chi-square test with pooling. Because sample sizes were relatively small (i.e. almost always < 50 per population), and the Chi-square test is less reliable when expected values for some classes are small (Sokal and Rohlf 1981), we chose to reject the null hypothesis of HEW only when all tests applied indicated statistically significant ($P < 0.05$) deviation from HWE. Sixteen populations were variable at the PGI locus, and in all cases at least one test was not significant ($P > 0.05$), suggesting that none deviates from HWE.

Two populations of the *bowlingi* subgroup (CG and WP; Fig. 1) were found to deviate significantly from HWE expectations at the CAH locus by all three tests. For the remaining 11 variable populations, however, HWE at the CAH locus could not be rejected by one or more statistical tests. Two separate collections, one in 1983 and the other in 1984, were made at both the CG and WP sites. Further, the two collections were made at slightly different, though proximate, microhabitats within each site. In contrast, the HE and RC *bowlingi* locations were sampled on a single date and at single sites in each location. Thus deviation from HWE at the CAH locus for the CG and WP locations may reflect temporal and/or microspatial heterogeneity in gene frequency in these populations. However, the fact that no such genetic heterogeneity is evident at the PGI locus for these two locations argues against this contention. Further, because 27 of the 29 cases of variable loci in populations meet our conservative requirements for fit to HWE, it is difficult to ascribe much significance to these two exceptions from available data.

Variation among populations within subgroups was examined using F-statistics and a Chi-square contingency analysis (Workman and Niswander 1970) (Table 4). Significant heterogeneity in gene frequency ($P < 0.05$) occurs among populations in the *bowlingi, tusquitee,* and *vandykei* subgroups at both the CAH and PGI loci. The six *pisgahensis*-subgroup populations, which are monomorphic for the same allele at the CAH locus, show significant heterogeneity in allele frequency at the PGI locus. For those subgroups in which significant heterogeneity in allele frequencies was observed, genetic differentiation can be described as slight ($F_{ST} < 0.05$) to moderate ($0.05 < F_{ST} < 0.15$) (Table 4). Rogers' Genetic Similarity (S) calculated over all loci produces values of

Table 4. *F*-statistics and heterogeneity Chi-square values for four subgroups of the *Trechus vandykei* species group.

Subgroup	F_{IT}[a]	F_{IS}[b]	F_{ST}[c]	χ^2[d]
		CAH locus		
bowlingi	0.670	0.613	0.147	56.825***
pisgahensis	—	—	—	—
tusquitee	0.157	0.033	0.128	22.906***
vandykei	0.018	-0.011	0.029	15.747***
		PGI locus		
bowlingi	0.199	0.094	0.166	24.153***
pisgahensis	0.184	0.114	0.078	32.506***
tusquitee	0.175	0.146	0.034	6.857**
vandykei	0.122	0.062	0.065	104.830***

[a] F_{IT} = correlation between uniting gametes relative to the gametes of the total IT population.

[b] F_{IS} = average correlation over subdivisions of uniting gametes relative to those of their own subdivision.

[c] F_{ST} = correlation of random gametes within subdivisions relative to gametes of the total population.

[d] ** = $P < 0.01$; *** = $P < 0.005$.

approximately 0.90 or greater for comparisons between local populations within subgroups (Table 5).

Differentiation between subgroups is substantial in some cases. Intersubgroup genetic similarities (Table 5) range from values that are not very different from infrasubgroup similarities (*haoe* vs. *vandykei,* S = 0.921) to values suggesting more distant affinity (*pisgahensis* vs. *vandykei,* S = 0.776). Clustering of Rogers' Distance values for the 19 populations using UPGMA (Sneath and Sokal 1973) produces five clearcut groupings (Fig. 2.). The six populations of the *pisgahensis* subgroup form the most distinct cluster. Thus, this subgroup, which appears to have lower genetic variability than the other four, is also the most biochemically dissimilar of the five subgroups (i.e., S = 0.826 for all between-subgroup comparisons). Closer affinities are observed between the cluster containing the two *tusquitee*-subgroup populations and the cluster of the four *bowlingi* populations. The six populations in the fourth cluster include all of the populations of the *vandykei* subgroup,

Table 5. Rogers' (1972) coefficients of genetic similarity (S) for comparisons of five subgroups of the *Trechus vandykei* species group.[a]

	Number of populations	*bowlingi*	*pisgahensis*	*tusquitee*	*vandykei*
bowlingi	4	0.930 (0.895-0.96)			
pisgahensis	6	0.826 (0.794-0.849)	0.990 (0.980-1.000)		
tusquitee	2	0.881 (0.858-0.904)	0.850 (0.828-0.875)	0.931	
vandykei	6	0.857 (0.826-0.903)	0.779 (0.770-0.806)	0.831 (0.819-0.853)	0.970 (0.945-0.986)
haoe	1	0.867 (0.840-0.888)	0.849 (0.847-0.852)	0.876 (0.862-0.890)	0.921 (0.906-0.943)

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[a] Values shown are averages of pairwise comparisons of appropriate populations. Values in parentheses are the ranges of values appropriate to each comparison.

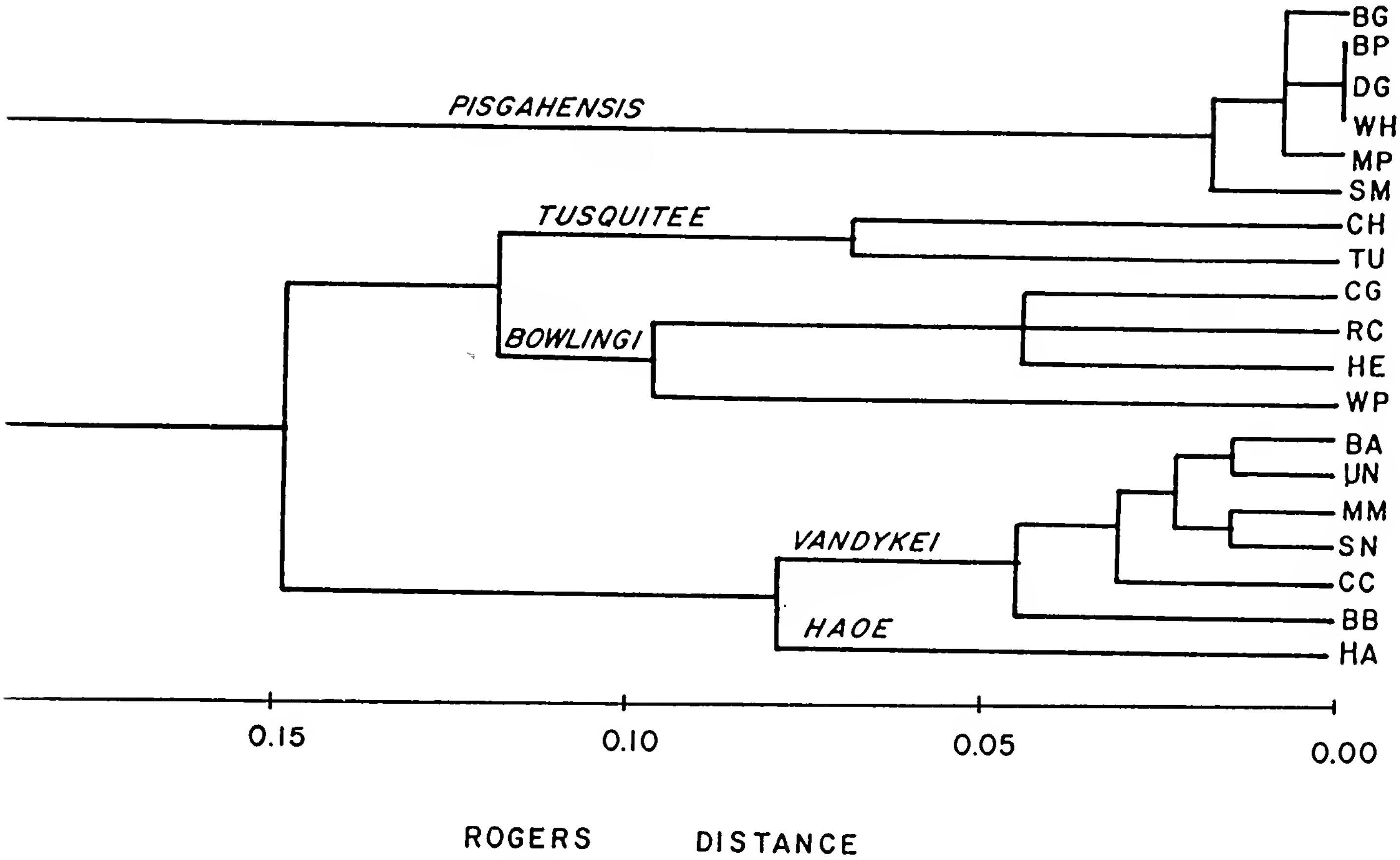

Fig. 2. UPGMA dendrogram of 19 populations of the *Trechus vankydei* species group, generated from Rogers' Distance values for eight biochemical loci.

and the single *haoe* population has its closest affinities with this subgroup.

Genetic differentiation can also be described using Nei's (1977) gene diversity. In this analysis the total gene diversity observed (H_T) can be apportioned among the various levels of a specified hierarchy (Table 6). We recognize four hierarchical levels of gene diversity: (1) within colonies (populations), H_C; (2) among populations within subgroups, D_{CS}; (3) between subgroups within regions, D_{SR}; and (4) between regions, D_{RT}, where the two regions are the areas northeast and southwest of the Asheville basin, respectively. Approximately 4-5% of total gene diversity is attributable to differences between infrasubgroup populations (D_{CS}). More than 50% of gene diversity is a result of differentiation between subgroups (D_{SR} and D_{RT}). Differentiation between subgroups within regions (D_{SR}) appears to be as great as (PGI) or greater than (CAH) differentiation between regions (D_{RT}) (Table 6).

Affinities between various subgroups can also be seen in the geographic patterns of certain diagnostic electromorphs at the two variable loci (Table 2). Electromorph "C" at the PGI locus is restricted to populations in the northeast region, where it occurs in all but the CC (westernmost) population of the *vandykei* subgroup. Conversely, electromorph "D" at the PGI locus is present in only two *vandykei* subgroup populations (CC, BB), where it occurs at low frequency. However, electromorph "D" occurs in all populations in the southwest region and is generally the most frequent PGI electromorph in these populations. If dispersal from southwest to northeast took place along the mountains on the Tennessee-North Carolina border, it is significant that the "D" electromorph occurs in populations on the first two major summits (CC and BB) east of the French Broad River and not elsewhere. At the CAH locus the "D" and "F" electromorphs, which are the only CAH variants present in the northeast populations, are either rare ("D") or absent ("F") in southwest populations, with one exception. The exception is the single peripheral population of *T. haoe* (HA), in which both electromorphs occur at frequencies comparable to those seen in *vandykei*-subgroup populations of the northeast region (Table 2). The *pisgahensis* subgroup can be distinguished from all other subgroups by the presence of a "null" allele at the CAH locus. This enzyme system, which stains intensely and consistently in the other 13 populations sampled, fails to yield any zones of staining in the six *pisgahensis*-subgroup populations examined.

DISCUSSION

Analysis of the electrophoretic data in this study suggests that altitudinal isolation of subgroups in the *vandykei* species group of *Trechus* is complete. The very great genetic differentiation between subgroups ($F_{ST} = 0.533$), the fixation of a unique allele in one subgroup (CAH locus in *pisgahensis*), and the restriction of alleles to geographic regions (e.g. PGI electromorph "C" to the northeast region) indicate an absence of gene flow between subgroups and regions at present. The *pisgahensis* subgroup appears to have been isolated for the longest period of time. Not only does it have a unique allele fixed at the CAH locus, but it also shows a marked reduction in heterozygosity, which is consistent with long-term isolation. This result is evidence that the Asheville basin, which lies between the ranges of the *pisgahensis* and *vandykei* subgroups, may have been an effective dispersal barrier to these beetles even during glacial maxima; consequently, the earlier taxonomic treatment of *vandykei* and *pisgahensis* as geographic races of the same biological species (Barr 1979) requires modification.

The degree of differentiation between populations within subgroups provides a basis for interpreting divergence between subgroups. For those subgroups whose component populations are isolated by lowland barriers (i.e. *pisgahensis, vandykei, tusquitee*), differentiation within the subgroup is only slight to moderate ($F_{ST} < 0.15$). Assuming that gene flow is no longer maintained between such isolates, these data suggest that the break in gene flow has been relatively recent, possibly as recent

Table 6. Analysis of gene diversity at two electrophoretic loci in 19 populations of five subgroups of the *Trechus vandykei* species group[a].

Locus	Number of alleles	H_T	H_C/H_T	D_{CS}/H_T	D_{SR}/H_T	D_{RT}/H_T
CAH	7	0.761	0.303	0.038	0.673	-0.014
PGI	6	0.585	0.582	0.049	0.187	0.182
Means	13	0.673	0.442	0.044	0.430	0.084

[a] H_T = total gene diversity. H_C = gene diversity within colonies (local populations). D_{CS} = gene diversity among populations within subgroups. D_{SR} = gene diversity between subgroups within regions. D_{RT} = gene diversity between regions.

as post-Wisconsian. In fact, differentiation among populations of *bowlingi* is as great as that observed within the three "multi-isolate" subgroups mentioned above. The *bowlingi* populations, however, are sampled from an abundant species continuously distributed over the upland area in the eastern two-thirds of the Great Smoky Mountains, the most extensive mountain range in the region. Furthermore, *bowlingi* is sympatric and usually syntopic with different assemblages of other, more narrowly distributed *Trechus* species in different parts of its range (Barr 1962, 1979). Thus, differentiation in *bowlingi* could result from longer, stepwise pathways of gene flow, but it may also reflect local adaptation to a broader spectrum of microhabitat heterogeneity throughout its more extensive geographic range.

Biochemical, biogeographical, and morphological affinities (Barr 1979) between (a) *bowlingi* and the *tusquitee* subgroup and (b) *haoe* and the *vandykei* subgroup suggest a relatively recent common ancestor in each case. Other relationships between subgroups are vague, suggesting that the associated speciation events occurred in the more distant past. The present data do permit some speculation as to the route of dispersal of the *vandykei* species group from the southwest to the northeast region. As previously noted, the taxonomic hypothesis that *vandykei* and *pisgahensis* belong to the same biological species (Barr 1979) is rendered untenable on two counts: (1) the electrophoretic data indicate that *pisgahensis* (and its morphologically related Sandymush and Whiteside isolates) is the most distinct biochemically and least variable of the five *vandykei*-group clades, suggesting more distant affinity with *vandykei* and longer-term isolation than had previously been postulated; and (2) the *vandykei* subgroup has a much stronger affinity with *haoe*, the similarity being most striking at the CAH locus, where both subgroups not only have the same two electromorphs but have them in very similar frequencies. *Trechus haoe* and *T. vandykei* are readily differentiated by morphological characters (Barr 1962); furthermore, they occupy the western and eastern extremes of the geographic region tracked by the entire *vandykei* group.

It appears that the *vandykei* subgroup dispersed across the French Broad River valley by a route farther north than previously suggested, probably along the chain of high mountains on the Tennessee-North Carolina border, then south into the Blacks, Great Craggies, and adjacent high Blue Ridge. The electrophoretic data clearly are in accord with biogeographical and morphological data supporting this hypothesis; the only representative of *Microtrechus* in the northeast region other than the *vandykei* subgroup isolates is *T. inexpectatus* (Barr 1985b), described from Camp Creek Bald (CC), the first major peak encountered as one proceeds eastward along the Tennessee-North Carolina border from the French Broad River valley. Going in the opposite direction, from northeast to southwest across the French Broad, the first major peak encountered is Tennessee Bluff (Cocke Co., Tenn., and Madison Co., N.C.); two *Trechus* s. str. taxa occur on Tennessee Bluff, an undescribed species related to *T. scopulosus* (Barr 1962, 1979) and the only subspecies (undescribed) of the abundant, widely distributed (northwest North Carolina, northeast Tennessee, southwest Virginia, eastern West Virginia) polytypic *T.* (*T.*) *hydropicus* known from the southwest region (Barr, in preparation). The hypothesis of an earlier, more remote separation of subgenus *Microtrechus* from *Trechus* s. str. during a period of isolation in the Unaka region west of the Asheville basin is thus supported not only by "center of origin" considerations but by additional biochemical and biogeographical data.

More difficult to explain are the close affinities between *T. haoe* (Unicoi Mountains) and the *vandykei* subgroup, given that, at present, the range of *T. bowlingi* in the Great Smoky Mountains intervenes. One possible but speculative scenario (Barr 1985a) for evolution of the *vandykei* group includes the following sequence:

1) An ancestral species diverged from *Microtrechus* by occupying the niche of small predator in superficial litter; among southern Appalachian *Trechus* spp., only the *vandykei* group isolates occupy that niche at present (Barr 1985a).

2) The ancestral species split into populations in the two major mountain ranges of the southwest region, the Smokies (GSM) and the Great Balsams-Pisgah Ledge (GBM).

3) The GBM population dispersed northward and southward, but only relict populations survive in the Newfound Mountains to the north and on Whiteside Mountain to the south. The GSM population, however, dispersed to the northeast along the Tennessee-North Carolina border and southwest into the Cheoah, Snowbird, Tusquitee-Valley River, and Unicoi mountains.

4) In the Smokies, the extensive upland area and microhabitat heterogeneity (patchiness) favored colonization and speciation in other species groups of *Trechus*; the *vandykei*-group isolate was subject to strong selection pressure for niche divergence to permit coexistence. Meanwhile, colonies dispersing to the northeast and southwest evolved less rapidly; consequently, they are more similar to each other than to *bowlingi*, the species that now occupies the Smokies.

5) An early offshoot of the GSM population eventually colonized the mountains southwest of the Smokies—Tusquitee Bald, Joanna Bald, and Cheoah Bald. Finding only one, two, or no competing *Trechus* species, they diverged less rapidly than the GSM ancestor. Possibly they represent an evolutionary stage intermediate to the beetles that dispersed northeastward and the present-day, more derivative species now found in the Smokies, *T. bowlingi*.

6) Meanwhile, the original GSM ancestral type crossed the French Broad River valley and successively colonized CC, BB, the Blacks-Great Craggies to the south, and finally Unaka Mountain to the northeast. A relict population of the southwesterly dispersal survives in the Unicoi Mountains as *T. haoe*. The two peripheral subgroups have evolved less (at least biochemically) than the parental populations they left behind in the Smokies.

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