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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

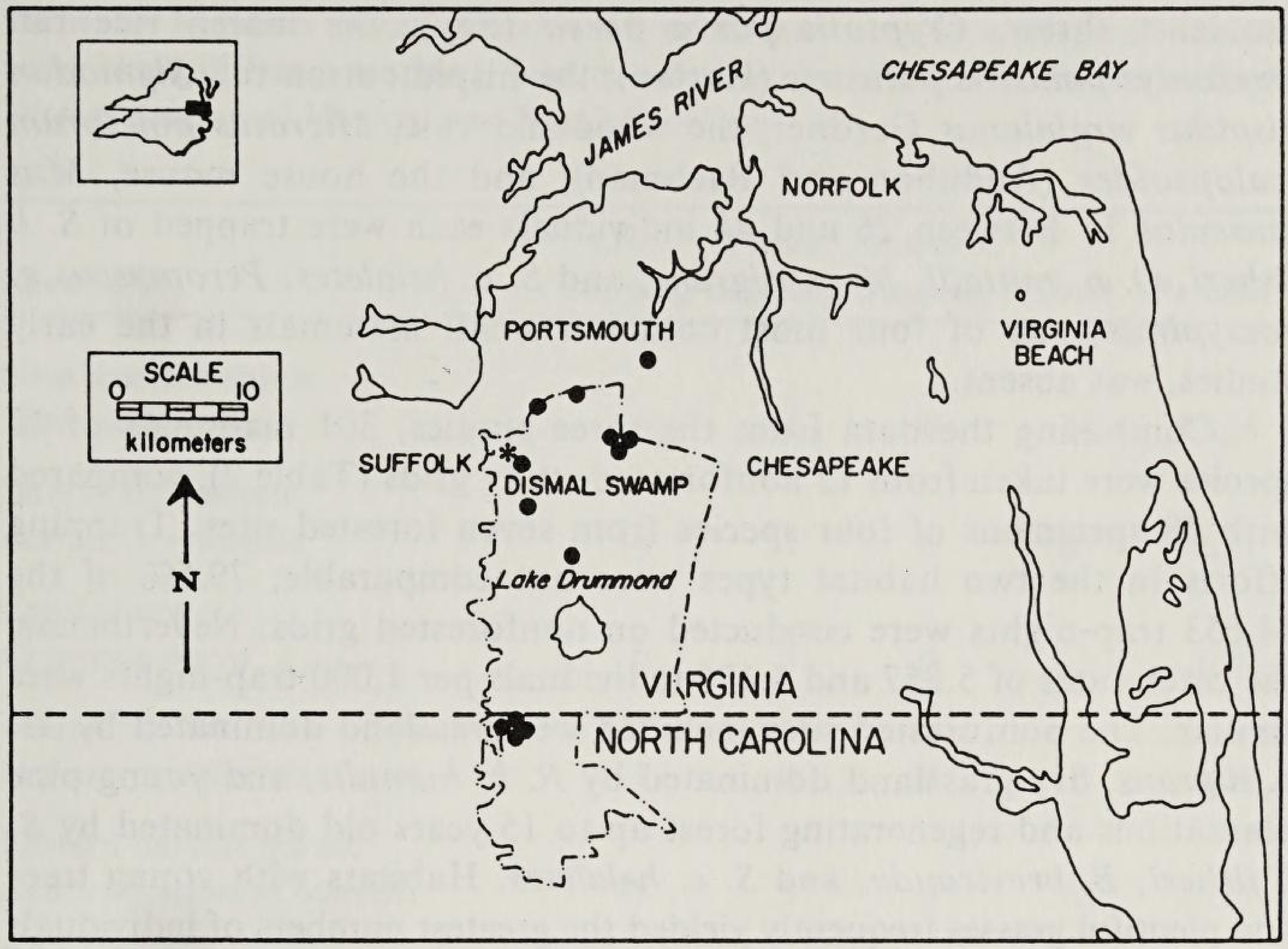

Fig. 1. Map showing the location of the live-trap and nest-box study grids (*) and the 13 pitfall study grids (•) in the Great Dismal Swamp of Virginia and North Carolina. The boundary encloses the current Great Dismal Swamp National Wildlife Refuge. The inset at upper left shows the location of the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

[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.

Species	Nonforest habitat (51,399)[a] Total	Nonforest habitat Percent of individuals	Forest habitat (13,254)[a] Total	Forest habitat 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	

[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

[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		

[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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