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AN ECOLOGICAL AND BIOMETRIC INVESTIGATION OF THE NESTING OF THE FOUR-TOED SALAMANDER, HEMIDACTYLIUM SCUTATUM (SCHLEGEL) IN VIRGINIA

BY

John Thornton Wood

A THESIS SUBMITTED IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF ARTS

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INTRODUCTION

Reported here are observations on the nesting of the Four-toed Salamander, *Hemidactylium scutatum* (Schlegel), in Virginia. This species is frequently regarded as rare in areas where its nesting or hibernation are not known. Prior to this report it was so considered in Virginia, and less than a score of adult specimens from this state were found in the collections of the major museums. During this investigation 59 per cent of the nests found in the field were collected with their attending females and studied; this included 144 nests containing over 16,000 eggs, 250 adults, 4 juveniles, and 82 larvae that emerged from eggs at or shortly after the time of collection. The present report is based upon the examination of 224 nests in 21 localities, in 13 of the 100 counties of Virginia.

The abundance of suitable nesting areas for *Hemidactylium* on the Virginia coastal plain, and the numbers of specimens found in the few habitats explored, suggests that this species is common in eastern Virginia. In relative abundance it appears to rank fifth in this region, exceeded in numbers by *Eurycea bislineata bislineata* (Green), *Desmognathus fuscus fuscus* (Raf.), *Diemyctylus viridescens viridescens* (Rafinesque), and *Plethodon cinereus*

cinereus (Green) and their related subspecies.

Eggs of Hemidactylium scutatum (Schlegel) were first noted by Hughes (1886) in Indiana, and subsequently "rediscovered" by Bishop (1920) in New York. They have been reported in Michigan by Blanchard (1922, 1923, 1928, 1934a, 1934b, 1936), in Massachusetts by Dunn (1926), in Pennsylvania by Pawling (1939), in Kentucky by Green (1941), and in Tennessee by King (1944). Investigations of nesting conditions have been reported in some detail in Michigan (Blanchard, ibid.) and New York (Bishop, ibid., 1941; Gilbert, 1941). The nesting of Hemidactylium in Virginia is compared with reports from these states.

Acknowledgement is made to all persons who aided in this study. Assistance in field work was provided by W. T. Allen, L. T. DuVal, S. B. Forrest, I. L. Fuller, Jr., O. K. Goodwin, J. B. MacArthur, Jr., and C. D. Monemous, Jr. Dr. P. M. Patterson made the taxonomic diagnoses of mosses and hepatics involved in nests. Hemidactylium scutatum in the United States National Museum collection were made available by Dr. D. H. Cochran, and in the American Museum of Natural History collection by C. M. Bogert. Dr. S. C. Bishop encouraged this study and donated his last copy of his excellent out-of-print publication (1920) on this species. Valuable criticism of the manuscript was provided by Dr. R. P. Ash, Dr. O. F. Schuette, Dr. E. R. Sohns and William

Vogt. Special thanks are expressed to Dr. J. T. Baldwin, Jr. and Dr. J. L. McHugh for advice on the treatment of the data and criticism of the manuscript.

Figure 1. A typical Hemidactylium scutatum (Schlegel) nesting area near Five Forks, James City County, Virginia (figure 2, locality 13); a shallow, stagnant pond in a cypress-beech-holly woods.

NESTING HABITATS

Two conditions were noted in most nesting sites, still or slowly moving water and some material close to the water in which eggs could be placed in concealment. These conditions were filled by a variety of types of water areas, and a number of "thin" mosses, "deep" mosses, sedges, hepatics, and other suitable concealment materials. Nests were examined in the 18 localities mapped in figure 1, and in two Piedmont counties: APPOMATTOX, 2 miles NNW of Appomattox; and CHARLOTTE, ½ mile N. of Phenix. Nesting in one additional coastal plain county, reported by J. A. Fowler (letter, 25 March, 1950) is as follows: FAIRFAX, between New Alexandria and Dyke.

In Virginia nests of Hemidactylium are found near meandering, shallow, slow-water streams in bogs; by ponds ranging in size up to ten acres; beside seepage springs; and adjacent to stagnant pools in drainage ditches and temporary brooks. Most nests are near the water surface (Bishop, 1920; Blanchard, 1922), usually between three and eight inches from it. The water area ranges in depth from less than an inch in some seepage springs to several feet in the larger ponds.

In two instances egg groups were found from three to ten feet from the nearest surface water. On March 24,

1950 a nest (A-1927) was collected in a ravine 2 miles NE of Gloucester Court House (figure 2, locality 5). The eggs were found suspended from the rhizoids of a "deep" moss, Thuidium delicatulum (Hedw.) Mitt., in a crevice on top of a log three feet from surface water. A mucky area extending from the water to the log suggested that formerly water had been in closer association with the nest. On March 25, 1950 three nests (A-1966, A-1968, A-1970) were collected in a ravine 2 miles NE of Lightfoot (figure 2, locality 10). These nests were in crevices in "deep" mosses, Climacium americanum Brid. and Mnium cuspidatum Hedw., on a bank by a mucky area more than ten feet from surface water. In selecting a nesting site female Hemidactylium scutatum migrate to the nesting areas, enter the water, and swim for an undetermined period, finally emerging from the water to pick a concealment immediately adjacent to the water surface (Blanchard, 1934). In the above mentioned cases it is probable that surface water was in close association with the nesting sites prior to egg-laying.

Water adjacent to nesting sites is usually clear and still, although it may be the "black" water typical of cypress swamps. Nests near moving water were found in moss hummocks growing over cypress knees by bog streams. The flow of water beside these nests did not exceed 0.2 miles per hour.

Nothing is reported in the literature on the pH of waters adjacent to nests of Hemidactylium. The mean of five determinations made March 27, 1950 at Five Forks (figure 1; figure 2, locality 13) was pH 5.0 .

Hemidactylium nests have been noted in deciduous biomes (Bishop, 1920; Blanchard, 1922). In Virginia nesting sites are found in both deciduous and coniferous woods. Nests have been found frequently beneath the following trees: cypress, (Taxodium distichum (L.)); loblolly pine, (Pinus taeda L.); holly, (Ilex opaca Ait.); sycamore, (Platanus occidentalis L.); beech, (Fagus grandifolia Ehrh.); white oak, (Quercus alba L.); and chestnut oak, (Quercus prinus L.). The type of trees near a water area appears to have little correlation with the suitability of the area as a nesting site for Hemidactylium; several habitats were found in deforested areas or open bogs. A typical cypress-holly-beech nesting habitat near Five Forks (figure 2, locality 13) is illustrated in figure 1.

Although Hughes (1886) first noted Hemidactylium eggs in moss, it remained for Bishop (1920) to identify eggs with sphagnaceous habitats. Gilbert (1941) found nests in New York in several genera of mosses: Climacium, Mnium, Sphagnum, and Thuidium. Nests have been found in Virginia in mosses of these four genera and nine others: Atrichum, Aulacomnium, Cirriphyllum, Entodon, Eurhynchium, Hypnum, Leptodictyum, Leucobryum, and Plagiothecium. Providing a

moss contains or covers crevices in which eggs can be deposited, its suitability as a nesting habitat appears to be determined by its proximity to water in nesting areas.

Nests are often found in hummocks containing mosses of several genera, sedges of the genus Carex, and occasionally hepatics. The following genera of Hepaticae were involved: Lophocolea, Pallavicinia, Scapania, and Teleranea. The mosses and hepatics in nesting habitats, and number of nests associated with them, are compiled in table I.

Occasionally nests are found in other types of habitats. Blanchard (1922) noted some nests in southern Michigan in crevices in the sides of rotted, water-soaked logs, and under the loose bark of stumps. Of the 224 nests examined in Virginia, 78 per cent (175) were in mosses, sedges, and hepatics; 17.9 per cent (40) were suspended from the rhizoids of moss over crevices in logs or banks; and 4.1 per cent (9) were in less usual habitats listed in table II.

TABLE II

NESTS IN UNUSUAL HABITATS

No. of Nests	Habitat	Counties
4	Inside of rotted planks, boards, and logs.	James City, Mathews, Lancaster, and York.
2	Under the loose bark of logs.	Elizabeth City.
2	In damp mounds of pine needles and bark.	James City.
1	In a hollow cypress knee.	James City.

Figure 2. Locations of the Hemidactylium scutatum (Schlegel) nesting sites found on the Virginia coastal plain.

No.	County	Locality
1	RICHMOND	4 mi. WSW of Warsaw;
2	LANCASTER	Lively;
3	LANCASTER	1/4 mi. N. of Gray's Pt.;
4	MIDDLESEX	3 mi. S. of Saluda;
5	GLOUCESTER	2 mi. NE of Glou. Ct. Ho.;
6	MATHEWS	1/2 mi. SE of Mathews;
7	CHARLES CITY	4 mi. SSE of Holdcroft;
8	JAMES CITY	2 mi. NE of Jolly Pond;
9	JAMES CITY	3/4 mi. W. of Jolly Pond;
10	YORK	2 mi. NE of Lightfoot;
11	JAMES CITY	4 mi. NW of Williamsburg;
12	YORK	1/2 mi. N. of Williamsburg;
13	JAMES CITY	1/2 mi. W. of Five Forks;
14	YORK	Yorktown area;
15	WARWICK	1½ mi. E. of Denbigh;
16	WARWICK	1/2 mi. E. of Harpersville;
17	ELIZABETH CITY	Buzzard's Roost area;
18	ELIZABETH CITY	Fox's Store area.

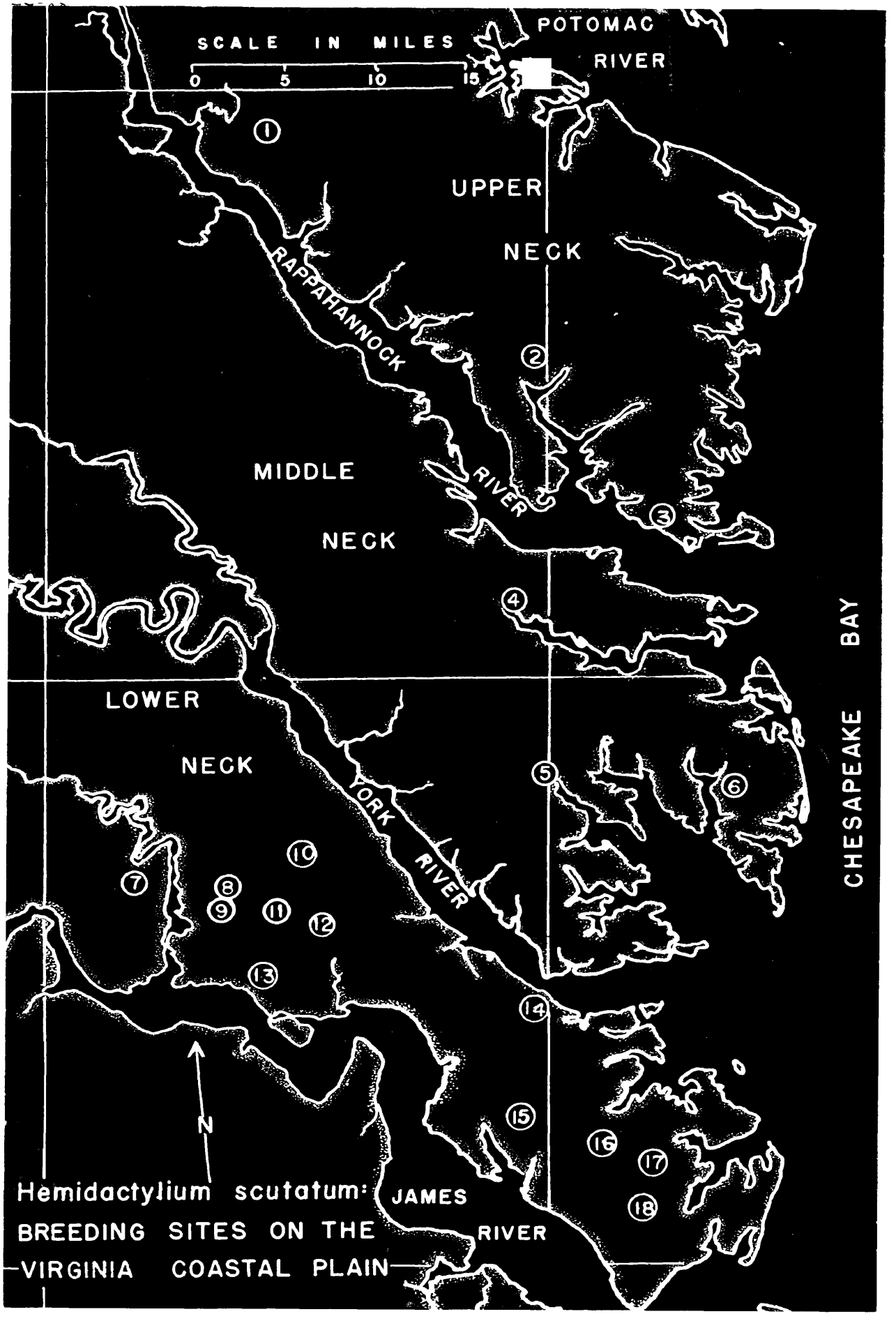


Figure 2. Locations of the Hemidactylium scutatum (numbered) nesting sites found on the Virginia coastal plain.

EGG-LAYING

On February 24, 1951 three nests of recently deposited Hemidactylium eggs were found near Five Forks (figure 2, locality 13). This date, the earliest on which recently deposited eggs have been found in the field in eastern Virginia, is from six to seven weeks earlier than the date on which egg-laying is reported to commence in southern Michigan (Blanchard, 1934) and New York (Bishop, 1941).

Blanchard (1934) reported that egg-laying in Michigan started in mid-April, and was completed before May. It is probable that the period in which the majority of Hemidactylium deposit their eggs in Virginia is also about of two weeks duration. In 1951 80 per cent of the 18 females collected February 24th were gravid, and had no large ova in their oviducts; this is interpreted as meaning that they had not started to lay their eggs. Nine days later, on March 4th, only 17 per cent of 94 females were found in this condition. Only two per cent of all females collected after March 10th were gravid.

Off-season egg deposition was first indicated by a nest of 22 hatching eggs found March 4th, 1951 near Denbigh (figure 2, locality 15) by O. K. Goodwin. This nest is discussed in the section on incubation.

Bishop (1941) reports that Hemidactylium eggs are deposited in nest cavities which often have the appearance of being formed by turning movements of the females, but in some instances it is evident that the females have merely exploited natural cavities in the mosses. All nests examined in Virginia appear to result from the selection of natural crevices by the females, and the shape of the crevices to some extent determine the shapes of the egg groups. The outer envelopes of the eggs are adhesive, and as the eggs are deposited they adhere together in compact clusters in "deep", loose mosses like Thuidium; in "thin", dense mosses like Plagiothecium the eggs are spread over a large surface in a single compact layer.

Blanchard (1922) specified that the eggs are placed "either just under the moss covering of an old stump or root or entangled in moss rhizoids and grass roots, not in the earth below the roots not in the moss and grass above the roots." In Virginia 78 per cent of the nests were found above the roots, among the shoots and leaves of mosses, hepatics, and sedges; 17.9 per cent were attached to rhizoids and roots. The latter was noted in the Cirriphyllum habitat 2 miles NNW of Appomattox, where egg groups were suspended over crevices in the bank from the rhizoids of this "thin" moss.

Sometimes females exploited habitats with very

confining crevices such as those listed in table II. In these nests eggs were often scattered over a large surface, and frequently they were not in contact with one another. The space limitations of these habitats did not prevent numbers of females from forming composite nests. Separate nests of 528 and 438 eggs were found in mounds of pine needles, and a composite nest under loose bark contained 284 eggs.

Bishop (1941) noted that Hemidactylium turns "upside down" to deposit eggs. This behavior is characteristic of a number of salamander species which lay their eggs in water, attaching them to the lower surface of some support. Similar behavior has been observed for several species of salamanders that deposit their eggs in terrestrial situations. In Virginia the Four-toed Salamander usually follows this behavior pattern when depositing eggs in crevices in loose moss hummocks where some freedom of movement is afforded. However, eggs in some nests could not have been deposited in this way because of the shape of the nesting crevice. Examples of these nests are the egg groups found on the vertical surfaces of boards around seepage springs near Williamsburg (figure 2, locality 12) and Mathews (figure 2, locality 6). In the laboratory females have been observed depositing eggs on vertical surfaces; they accomplish this in aquaria while "standing on their heads".

On March 23, 1950 near Yorktown (figure 2, locality 14), and on March 4, 1951 near Denbigh (figure 2, locality 15) nests were observed which had been deposited in exposed positions on top of moss hummocks. It seems doubtful that these eggs were deposited by females in the "upside down" position.

In many nesting sites the majority of nests were found in moss hummocks along the banks of ponds, but in habitats containing little islands of floating moss-covered logs, sedge hummocks, or cypress knees, many nests were found in locations females could reach only through swimming. On March 27, 1950 there were 28 nests around the pond near Five Forks (figure 1); 19 of these were on islets, and the remaining nine were on the bank (4), or on moss-covered logs extending out from the bank (5). The females had departed from many of the nests on this date.

INCUBATION PERIOD

Bishop (1941) reports the incubation period to be variable, depending on temperature, moisture, "and perhaps other factors." In New York, as a result of field observations of egg-laying and hatching, Bishop (ibid.) found that it varies from 52 to 60 days. Laboratory-reared embryos emerged in 30 days (Bishop, 1920). One egg-group deposited March 4, 1951 near Five Forks, James City County, Virginia, was observed May 3rd with larvae emerging; this establishes an incubation period of 61 days for this nest.

Egg mortalities are common , especially during April in nesting areas on the Virginia coastal plain. Dead eggs are found more frequently in Sphagnum than in other mosses; mortalities are more common in composite nests than in small egg-groups. Dead eggs are distinguished from living ones by their opaque or milky appearance, as contrasted with the transparent or translucent envelope of living eggs. The causes of these mortalities have not been determined, but Bishop (1920) reports that excessive moisture is lethal to laboratory-incubated eggs, and Green (1941) cites a case in which natural mortality occurred in a wet habitat. Since several Virginia egg groups successfully passed through their incubation submerged, it is probable that excessive moisture is not a direct cause of egg mortality.

No data on the temperatures of nests and of adjacent air and water were found in the literature. A group of nine nests near Five Forks (figure 2, locality 13) were checked on March 25, 1950, and these readings with the identity of the mosses surrounding the eggs are compiled in table III. Nest temperatures were measured with the thermometer bulb in contact with the egg clusters; air temperatures were measured five cm. above the nest hummocks, and water temperatures were taken adjacent to the nests.

TABLE III

NEST, AIR, AND WATER TEMPERATURES; (°C.)

Nest No.	Air Temp.	Nest Temp.	Water Temp.	Moss around eggs
1	31.0	24.5	21.5	Thuidium
2	27.0	24.0	21.0	Thuidium
3	29.5	24.0	22.0	Thuidium
4	29.5	25.0	23.0	Thuidium
5	29.0	23.5	22.5	Thuidium
6	28.0	24.0	23.0	Thuidium
7	28.0	23.0	21.0	Thuidium
8	29.0	21.0	21.0	Sphagnum
9	28.0	19.0	21.0	Sphagnum

Nests in Thuidium habitats were intermediate in temperatures between those of adjacent air and water. They were always more closely correlated with the latter. The two nests in Sphagnum had temperatures below or equal to that or adjacent water. Further studies are needed to determine whether the differences in temperatures of nests in Sphagnum and Thuidium are sustained through the incubation period. If so, it is possible that different rates of embryonic development occur in these mosses.

The extent of the incubation period of the egg group found hatching on March 4, 1951 near Denbigh (figure 2, locality 15) is unknown. It undoubtedly exceeded the length of the incubation period experienced by embryos developing in March and April. If incubation takes about 60 days normally, and incubation was not retarded in this brood, the eggs were laid during the first week of January; it seems more likely that the eggs were deposited during the fall months.

THE RELATION OF THE NESTING OF VIRGINIA HEMIDACTYLIUM TO OTHER SPRING EVENTS

As related to other spring events in southern Michigan Hemidactylium egg-laying occurs when hepaticas (Hepatica triloba Chaix) are beginning to bloom, and spring peepers (Hyla crucifer crucifer Weid) are beginning to chorus (Blanchard, 1922). This correlation was not noted in eastern Virginia in 1951. Hepaticas were blooming in Yorktown ravines one month prior to the initiation of Hemidactylium egg-laying, and the spring peepers were not heard from until two weeks after the Hemidactylium spawning. In 1951 the egg-laying of the Two-lined Salamander, Eurycea bislineata b. X cirrigera coincided with the blooming of hepatica in Yorktown, and the spring beauty (Claytonia virginica L.) and bloodroot (Sanguinaria canadensis L.) were blooming when Hemidactylium started to lay their eggs.

Blanchard (1934) further notes that Michigan Hemidactylium emerge from hibernation "many days, perhaps three weeks, after the spotted salamanders have mated and laid their eggs." In 1951 in the Williamsburg area (figure 2, locality 12) a few Ambystoma maculatum (Shaw) deposited their eggs three or four days before Hemidactylium started depositing eggs, but the period in which most eggs were deposited by both of these species (Feb. 24th to Mar. 10th) coincided.

NUMBER OF EGGS IN HEMIDACTYLIUM NESTS

The number of eggs in 141 Hemidactylium nests collected in Virginia in 1950 and 1951 are plotted in figure 3. Individual nest complements ranged from six to 868 eggs, with the mode consisting of nests containing from 30 to 40 eggs. Gilbert (1941) considers Hemidactylium nests in New York containing more than 40 eggs as probably the product of more than one female. If this is true in Virginia, 74 per cent of the nests collected in the field contained the products of more than one female.

In examining 47 nests in Pennsylvania, Pawling (1939) found none containing more than 50 eggs; the maximum count of eggs in 32 nests in New York was reported by Gilbert (1941) as 68. Bishop (1941) reports only a single composite nest from New York. In marked contrast with this are Blanchard's (1934) records of 120, 173, 247, 250, 320, 435, 487, 644, and 1,110 eggs in Michigan nests. The tendency toward composite nests in Virginia parallels this behavior in Michigan.

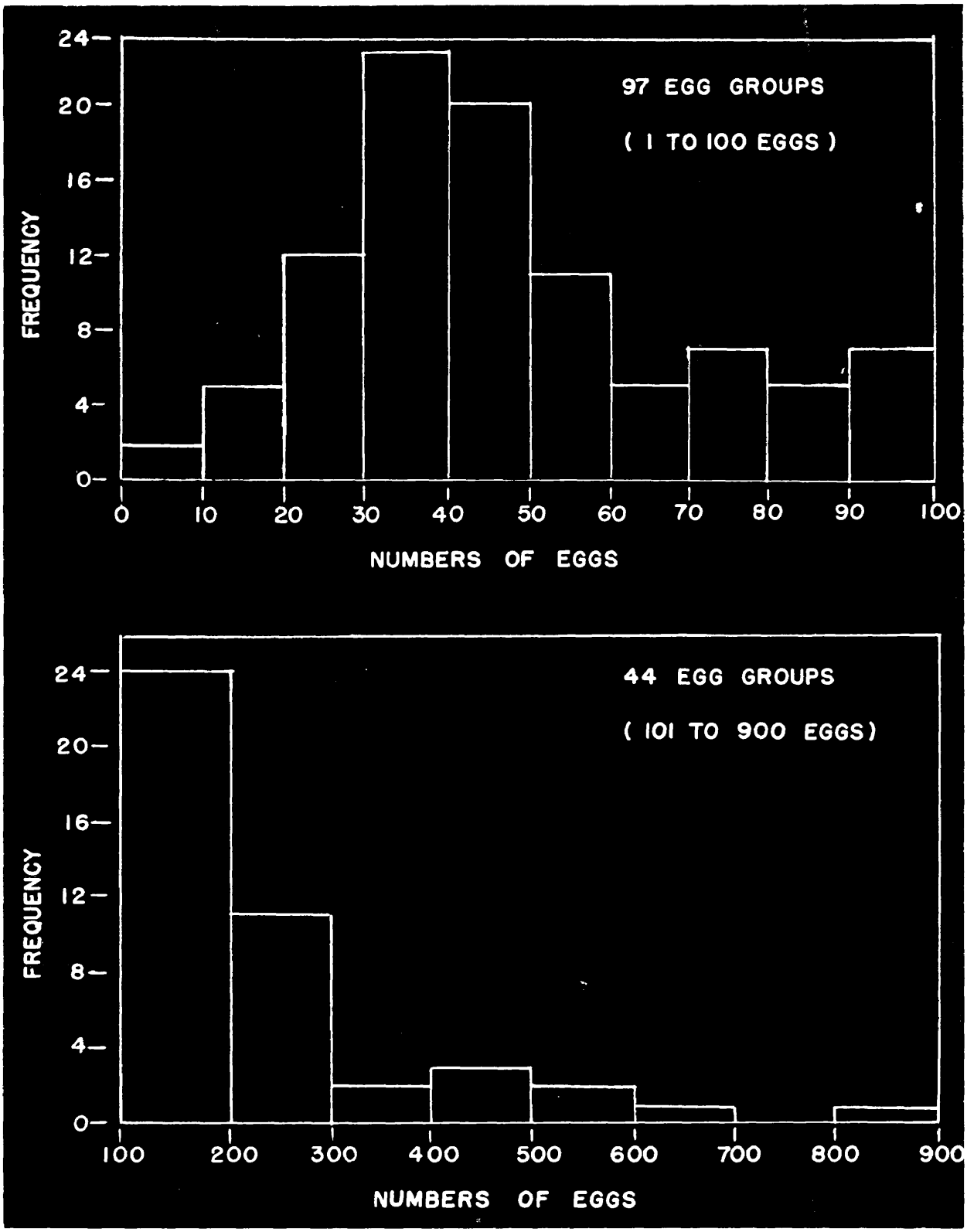


Figure 3. The number of eggs counted in 141 nests of Heniocetylium scutum (Schlegel) in Virginia.

THE RELATION OF THE FEMALE FOUR-TOED SALAMANDER TO THE NEST

The sex of adult Hemidactylium attending nests was determined by Blanchard (1922) through dissecting 40 specimens; all were females. The dissection of 244 adults collected in Virginia nesting sites verified this report; 243 females, one male. The male was found at a nest also attended by a female.

No one has determined why females are found at nests after egg-laying; no aggressive behavior which could be interpreted as guarding has been noted in Virginia, although Gilbert (1941) reports "guarding" in New York State. Noble (1930) reports that the female of Ambystoma opacum (Gravenhorst) remains with her eggs merely because of exhaustion. If this is true of Hemidactylium it would be expected that following a period of recuperation the female would abandon the nest. A further incentive to stimulate females to leave the nests might be the hunger drive. On March 18, 1950 it was observed that females remain with the nests both night and day; dissections of 243 females at nesting sites showed that all specimens had empty stomachs. The digestive rate in salamanders is so slow that this is strong evidence that feeding is rare while females are attending nests.

The position of the attending female in relation to the egg mass has been described by Bishop (1920) as follows: "In every instance the female was found either partly coiled upon the eggs or about them." In Virginia, to the contrary, females are found beneath the eggs in most habitats, and are rarely either upon the eggs or coiled about them. In the Cirriphyllum habitat in Appomattox County the nests were deposited in crevices of an eroded brook bank, attached to the rhizoids of the moss. Some of the females were found lying on the egg groups in this case.

In New York females remain with the nests throughout the incubation period (Bishop, 1941) and in every nest a female was found "guarding" the eggs, even though the majority of the eggs showed an advanced stage of development (Gilbert, 1941). In Michigan, too, females usually attend their nests until the time of hatching unless the nests are closely associated with other nests, in which case all but one of the females usually deserts the nests, and "only occasionally will even two remain,"(Blanchard, 1934). In contrast to these reports, in Virginia 24 per cent of the nests collected during the first three weeks after the egg-laying period were unattended (table V), and toward the end of the incubation period (mid-April to May) few females are found attending nests. The exodus of females from the nesting sites is evidenced by the difference in average number of eggs per female in tables IV and V.

TABLE IV

NESTS COLLECTED DURING THE FIRST NINE DAYS OF EGG-LAYING

No. of Females	No. of Nests	Total No. of Eggs	Av. No. of Eggs per Nest	Av. No. of Eggs per Female
0	0	0	0	0
1	23	1277	56	56
2	14	1354	97	48
3	7	921	132	44
4	2	939	180	45
Totals:	46	4,011		

Average number of eggs per female: 50.2

TABLE V

NESTS COLLECTED DURING THREE WEEKS FOLLOWING EGG-LAYING PERIOD

No. of Females	No. of Nests	Total No. of Eggs	Av. No. of Eggs per Nest	Av. No. of Eggs per Female
0	23	3,201	140	∞
1	57	4,747	83	83
2	13	2,522	194	97
3	3	698	233	79
Totals:	96	11,168		

Average number of eggs per female: 121

Av. No. of egg per female in nests still attended by females: 86.3

Table IV includes counts of eggs and females in 46 nests collected from Warwick and James City Counties between February 24th and March 4th, 1951. Table V is based upon similar data from 96 nests collected in 1950 and 1951 between March 10th and April 4th, a period of three weeks following completion of egg-laying. After March 10th the numbers of eggs attended by one, two, and three females was greater by from 49 to 102 per cent than the numbers of eggs attended March 4th and earlier; this is evidence of the tendency to form composite nests, and of desertion of females from these nests after egg-laying. The average number of eggs per female in Table V, 121, greatly exceeds an average based upon the number of eggs per female in nests still attended, because 23 nests containing 3,201 eggs had been deserted. A comparison of the average number of eggs per female in Tables IV and V shows that a 141 per cent increase (from 50.2 to 121 eggs) has occurred. By April 5th, here estimated as the mid-point in the incubation period, 3 of every 5 females have deserted the nests.

Desertion of composite nests can occur early in the egg-laying period. Using Bishop's (1941) average of 50 eggs deposited per female, a nest of 695 eggs collected March 4, 1951 near Denbigh, Warwick County, must have been deposited by 14 females, but it was attended by 5; nine had departed by the time the egg-laying season was only nine days old.

SIZE GROUPS

The use of total length in a size study of Hemidactylium scutatum is unsatisfactory because it is not possible to distinguish between a specimen with a normal tail and another with a nearly full-sized regenerated tail. The tail of Hemidactylium is usually lost at the basal constriction; of 39 Virginia specimens with damaged or regenerated tails, 38 had lost the tail at this point. The extensive variation in tail lengths, as contrasted with head and body lengths, are demonstrated by Blanchard and Blanchard (1931). Nevertheless all size studies in the literature are based upon total lengths, and for purposes of contrast these measurements are used in this report in addition to the far superior snout-vent measurements.

Total lengths of adult females in southern Michigan varied from locality to locality; three series studied by Blanchard and Blanchard averaged 74.1 mm., 74.7 mm., and 83.7 mm . Bishop (1941) noted that New York females averaged 70.9 mm. In Virginia 204 adult females from nesting sites averaged 78.4 ± 2.9 mm., ranging from 60.5 to 94.5 mm.

Snout-vent lengths of 243 adult females, four yearlings, and 82 recently emerged larvae in Figure 4

show the size classes of Hemidactylium in Virginia nesting areas. Comparison of this data with the excellent studies of Blanchard and Blanchard (1931) verifies the interpretation of the group of four juveniles as yearlings. Year-classes are not evident in the adult females; the age of the recently emerged larvae is from a few hours to one week, yearlings are from 10 to 12 months old, and adults are 22 or more months old.

Blanchard and Blanchard (1931) report Hemidactylium attain fecundity in Michigan during their third year of life; in Virginia females attain maturity during their second year of life, and deposit their first eggs at an age of 22 months.

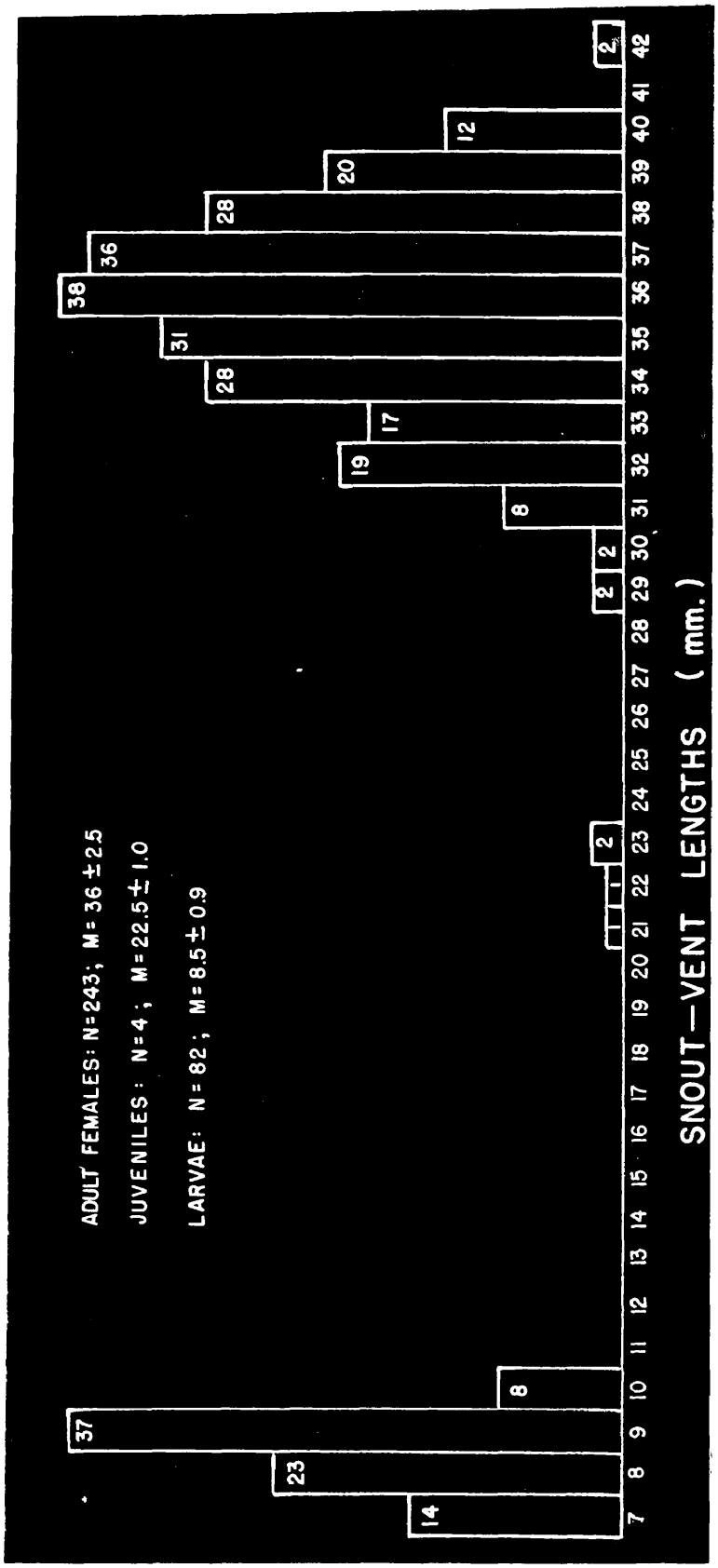


Figure 4. Snout-vent lengths of Hemidactylium scutatum from nesting sites in Virginia.

THE NUMBER OF EGGS PRODUCED AND LAID BY HEMIDACTYLIUM SCUTATUM (SCHLEGEL)

Ova counts in 58 gravid females were plotted against snout-vent lengths in Figure 5. In 32 of these specimens all large ova were in the ovaries; in the remaining 26 females from one to ten large ova were in the oviducts in addition to those in the ovaries. This group included specimens which had deposited a part of their ova; specimens with oviducal eggs were accordingly regarded as unsuitable for use in the determination of the size of large ova complements. A line, based on females with ovarian ova only, was plotted to fit these data by the method of least squares; a good lineal correlation was evident between snout-vent lengths and numbers of ova (Figure 5). Blanchard (1936) plotted the lengths of 217 southern Michigan females against their ova complements and found a wide scatter; the correlation was not highly significant. His use of total lengths rather than snout-vent lengths introduced the variable tail lengths which may have concealed the correlation.

Other differences between the Michigan series and Virginia specimens involve the number of large ova in gravid females; Virginia specimens have from 29 to 80 large ova, but southern Michigan specimens have only from 6 to 46 (Blanchard, 1936). The magnitude of this difference

suggests that different physiological races are involved; a question raised by Blanchard (1936) in regard to the apparent differences between Michigan and New York females.

Blanchard (1936) selected 50 nests each attended by one female and containing a complement of eggs not in excess of the potential production of one southern Michigan Hemidactylium. He compared the average number of eggs in these nests with the average number of large ova in gravid females; the values were approximately the same. This was interpreted as meaning that normally all eggs are laid in one nest, and this nest is attended by the female laying these eggs. To test these conclusions 57 Virginia nests were selected on the same basis, with the number of eggs not in excess of the maximum large ova complements of Virginia specimens. The snout-vent lengths of attending females are plotted against the numbers of eggs in nests they attended (Figure 6). The wide scatter of these data shows that the correlation is not strong. Since, in Figures 5 and 6, the snout-vent lengths are a common factor, the dissimilarity in the slope of the lines indicates that there is not a close relationship between numbers of ova in females and numbers of eggs in nests. Gilbert (1941) also noted a lack of correlation between numbers of eggs in nests in New York, and lengths of attending females, though he attributed this to the small size of the sample he used.

The scatter of the data in Figure 6 suggests that

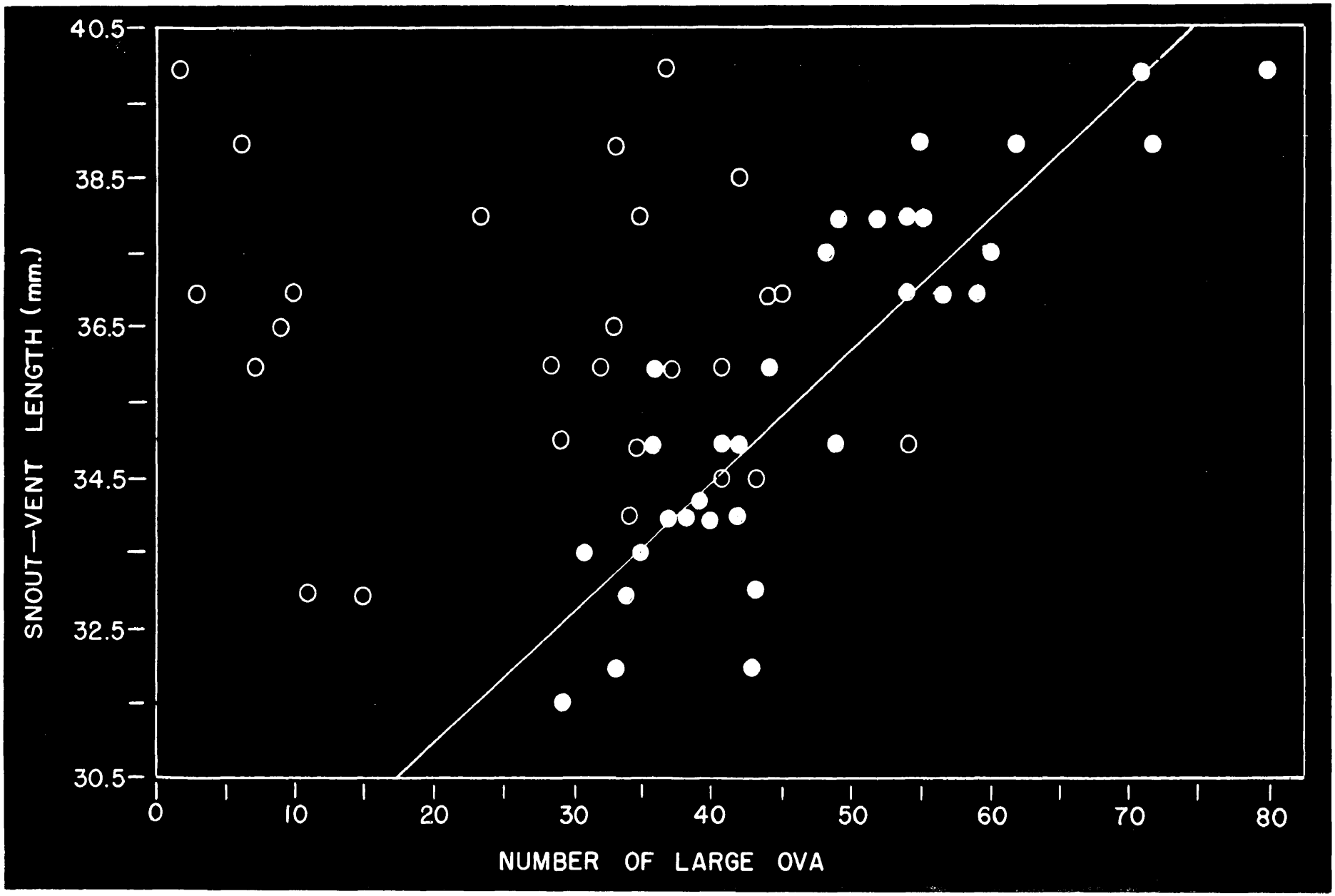
many points below the line represent small composite nests and that some points above the line may represent partial depositions or loss of eggs. The number of small females in Figure 6 found with large numbers of eggs can only be accounted for by assuming inclusion of composite nests. These composite nests are so small that it seems possible they contain less than the full egg complements of two females, suggesting that one female is interrupted in the process of egg-laying by the intrusion of a second specimen, and she departs from the nest having deposited only a part of her complement. The second female then adds her egg complement, resulting in a nest containing a larger number of eggs than would be expected from the attending female.

The behavior dynamics of Hemidactylium in nesting sites are little understood, but desertions of females from composite nests have been mentioned earlier. Evidence that suggests females may normally deposit less than their full complement of large ova are the 12 nests (8.5 per cent of all examined) containing fewer eggs than the minimum number noted in a gravid Virginia specimen.

Undoubtedly some eggs are lost during collecting; losses prior to collecting are indeterminate. Whether females successfully void their ovaries of all large ova during egg-laying is of importance in interpreting the points above the line in Figure 6. Blanchard (1936) states that

all large ova are normally deposited by Michigan specimens, though he cites one exception. All large ova are not normally deposited by Virginia Hemidactylium; in 186 dissections of females with "spent" ovaries it was noted that more half the specimens contained resorbed or partially resorbed large ova. These appeared as aggregations of melanin, occasionally accompanied by yolk, scattered through the ovaries. Retained resorbed ova did not number more than ten in any specimen examined. It is interesting that in Cryptobranchus alleganiensis (Daudin) the failure to complete ova deposition has been attributed to the inefficiency of the mechanism for transfer of the ova into the funnels of the oviducts (Smith, 1916).

Figure 5. The snout-vent lengths of 58 gravid female Hemidactylium scutatum (Schlegel) plotted against their large ova complements; dots denote females (32) in which large ova were all in the ovaries, and circles represent females (28) in which one or more ova have entered the oviducts. The line, based on females having ovarian ova only, was determined by the method of least squares.


40.5
38.5
36.5
34.5
32.5
30.5
SNOUT—VENT LENGTH (mm.)
0
10
20
30
40
50
60
70
80
NUMBER OF LARGE OVA

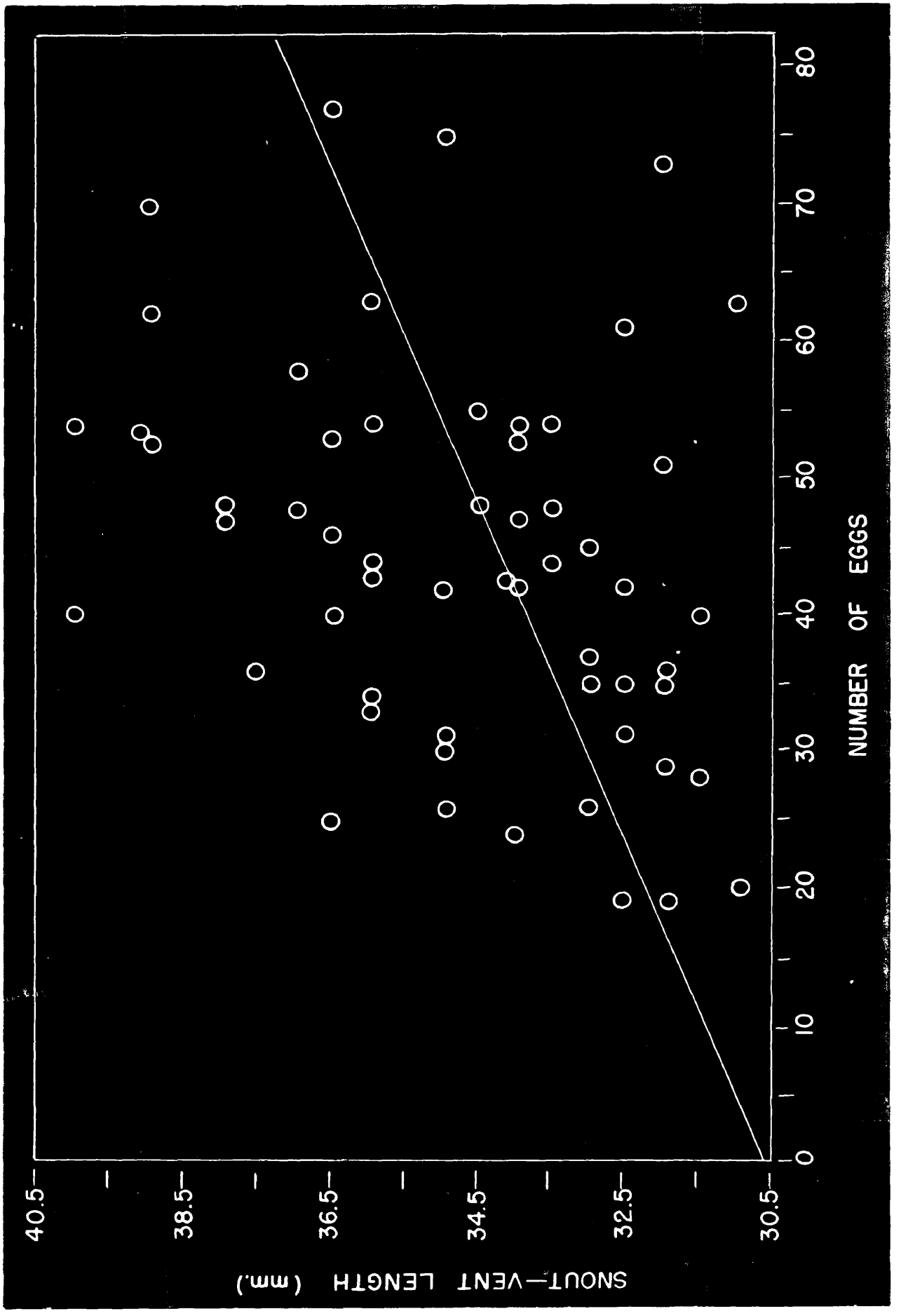


Figure 6. Snout-vent length of 57 attending females plotted against the egg complements in their nests; the line is fit to these data by the method of least squares.

SUMMARY

1. Hemidactylium scutatum (Schlegel) is a common salamander on the Virginia coastal plain.

2. Nests are usually situated within a few inches of still or slowly moving water in crevices in hummocks of mosses, hepatics, and sedges.

3. Nests are found in deciduous and coniferous woods; cypress, loblolly pine, holly, sycamore, beech, white oak and chestnut oak have been noted in nesting areas.

4. Eggs are found in mosses of these several genera: Atrichum, Aulacomnium, Cirriphyllum, Climacium, Entodon, Eurhynchium, Hypnum, Leptodictyum, Leucobryum, Mnium, Plagiothecium, Sphagnum, and Thuidium. If a moss contains natural crevices in which eggs can be deposited, its suitability as a nesting site appears to be determined by its proximity to water in a nesting area.

5. Nests are frequently found in hummocks composed of several mosses, species of sedges (genus Carex), and occasionally hepatics of the following genera: Lophocolea, Pallavicinia, Scapania, and Teleranea.

6. A few nests were found in mounds of pine needles, inside of rotted logs and boards, under loose bark on logs, and in hollow cypress knees.

7. In 1951 Hemidactylium egg-laying in habitats on the Virginia coastal plain started six to seven weeks earlier than it does in New York and southern Michigan; the first groups of recently deposited eggs were found February 24th.

8. Egg-laying by Michigan Hemidactylium is consummated in a two week period; in 1951 only two per cent of the females collected after March 10 were gravid, thus most egg-laying took place between February 24th and March 10th.

9. Off-season egg-laying was noted for the first time; on March 4, 1951 a nest of hatching eggs were collected near Denbigh, Warwick County.

10. No Virginia nests appeared to have been formed by turning movements of the females; they probably result from the exploitation of natural crevices.

11. In Michigan eggs are found attached to the rhizoids of moss and roots of grass; Virginia nests observed in 1950 and 1951 were usually placed above the roots, among the leaves and shoots in moss-hepatic-sedge hummocks, but in "thin" moss habitats eggs were suspended from rhizoids.

12. Composite nests of 528, 438, and 284 eggs have been found in confining crevices in mounds of pine needles and beneath bark.

13. The placement of eggs in nests suggests that females deposit their eggs in an "upside down" position in most habitats; in vertically oriented nests they may deposit eggs while "standing on their heads", and in two cases eggs on top of hummocks were found, strong evidence that on some occasions females may deposit eggs while in the "ventral surface toward ground" position.

14. Some nests were located along banks of ponds; many were located on islets in pools,which could have been reached by swimming females.

15. The incubation period of one nest near Five Forks, James City County, was noted to be 61 days.

16. Egg mortalities are probably not the direct result of excessive moisture; several egg groups have successfully passed through their incubation period while submerged.

17. A few measurements of temperature indicate the possibility of different rates of incubation in Sphagnum and Thuidium habitats.

18. The number of eggs in the 144 nests studied in this report

ranged from 868 to as few as six; this range in numbers of eggs approximates conditions reported for southern Michigan, and is at variance with the tendency toward small egg groups indicated by reports from Pennsylvania and New York.

19. Adult Hemidactylium attending nests or in nesting sites in Virginia were found through dissections to be female in 243 cases, male in one.

20. Exhaustion may be a factor in the behavior of females after egg-laying; the hunger drive may be the stimulation that causes some females to leave the nests they have been attending prior to the time of hatching.

21. Females are usually beneath egg groups in nests, not on top of them or coiled about the eggs, as reported in New York.

22. In New York and southern Michigan Hemidactylium females are reported to attend their nests until the time of hatching unless the nests are composites; in Virginia females remain with small nests longer than they do with large composites, but less than five weeks after egg-laying 24 per cent of the nests examined had been deserted --- at this time three of every five females had departed from the nesting sites. Few females are found with eggs toward the end of the incubation period.

23. Size groups of recently emerged larvae, juveniles, and adult females are well-separated; the age of the larvae ranges from a few hours to one week, juveniles are regarded as "yearlings" of from ten to 12 months of age, and adults include all females of 22 months or older.

24. There is a good lineal correlation between the snout-vent lengths of 32 Virginia gravid Hemidactylium and the numbers of their large ova; prior to egg-laying these females had from 29 to 80 large ova in their ovaries.

25. There is no strong correlation between numbers of eggs in nests and the snout-vent lengths of attending females.

26. Females may not void all of their large ova during egg-laying; more than half of 186 females dissected after egg-laying were found to contain from one to ten large ova which were being resorbed in their ovaries.

27. Of the number of eggs normally laid, all may be placed in one nest, but the fact that 8.5 per cent of the nests contained less than the minimum number of ova in a gravid female suggests that some females may spawn part of their complement in each of two or more nests.

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TABLE I

MOSSES AND HEPATICS SURROUNDING HEMIDACTYLIUM NESTS

County and Locality	No. of Nests	Species of mosses and hepatics
APPOMATTOX: 2 mi. NNW of Appomattox.	31	Cirriphyllum boscii (Sch.) Grout Thuidium delicatulum (Hedw.) Mitt.
CHARLES CITY: 4 mi. SSE of Holdcroft. (Fig. 2, Loc. 7)	2	Climacium kindbergii (R. & C.)Grout Hypnum patientiae Lindb., var. demissum Schimp Mnium cuspidatum Hedw.
CHARLOTTE: ½ mi. N. of Phenix.	5	Entodon seductrix (Hedw.)C. Muell. Eurhynchium serrulatum(Hedw.)Kindb. Mnium cuspidatum Hedw. Thuidium delicatulum (Hedw.) Mitt.
ELIZABETH CITY: Buzzards Roost area. (Fig. 2, Loc. 17)	2	Unidentified.
ELIZABETH CITY: Fox's Store area. (Fig. 2, Loc. 18)	2	Eurhynchium serrulatum(Hedw.)Kindb.
FAIRFAX: Between New Alexandria and Dyke.	1	Sphagnum (reported in letter from J. A. Fowler, March 25, 1950)
GLOUCESTER: 2 mi. NE of Gloucester C. H. (Fig. 2, Loc. 5)	3	Thuidium delicatulum (Hedw.) Mitt.
JAMES CITY: ½ mi. W. of Five Forks. (Fig. 2, Loc. 13)	79	Atrichum crispum (James) Sull. Climacium americanum Brid. Climacium kindbergii(R.&C.) Grout Pallavicinia lyellii(Hook.) S.F.Gray Scapania nemorosa (L.) Dum. Sphagnum imbricatum Hornsch Sphagnum palustre L. Teleranea nematodes (Aust.) Howe Thuidium delicatulum (Hedw.) Mitt.

TABLE I (CONT'D.)

MOSSES AND HEPATICS SURROUNDING HEMIDACTYLIUM NESTS

County and Locality	No. of Nests	Species of mosses and hepatics
JAMES CITY: 3/4 mi. W. of Jolly Pond. (Fig. 2, Loc. 9)	1	Aulacomnium palustre (W.& M.)Schw. Leucobryum glaucum (Hedw.)Schimp.
JAMES CITY: 2 mi. NE of Jolly Pond. (Fig. 2, Loc. 8)	8	Sphagnum. (Other mosses and hepatics unidentified.)
JAMES CITY: 4 mi. NW of Williamsburg. (Fig. 2, Loc. 11)	1	Sphagnum.
LANCASTER: 1/4 mi. N. of Gray's Point. (Fig. 2, Loc. 3)	5	Unidentified.
LANCASTER: Lively. (Fig. 2, Loc. 2)	1	Unidentified.
MATHEWS: ½ mi. SE of Mathews. (Fig. 2, Loc. 6)	5	Hypnum patientiae Lindb., var. demissum Schimp. Plagiothecium micans (Sw.)Paris, var. fulvum (Hook. and Wils.)P.
MIDDLESEX: 3 mi. S. of Saluda. (Fig. 2, Loc. 4)	5	Unidentified.
RICHMOND: 4 mi. WSW of Warsaw. (Fig. 2, Loc. 1)	2	Unidentified.
WARWICK: ½ mi. E. of Harpersville. (Fig. 2, Loc. 16)	7	Atrichum crispum (James) Sull. Climacium americanum Brid. Sphagnum imbricatum Hornsch., var. affine (R.& C.)Warnst. Thuidium delicatulum (Hedw.) Mitt.

TABLE I (CONT'D.)

MOSSES AND HEPATICS SURROUNDING HEMIDACTYLIUM NESTS

County and Locality	No. of Nests	Species of mosses and hepatics
WARWICK: 1½ mi. E. of Denbigh. (Fig. 2, Loc. 15)	52	Climacium americanum Brid. Climacium kindbergii (R. & C.) Grout Entodon seductrix (Hedw.) C. Muell. Eurhynchium serrulatum (Hedw.) Kind. Hypnum curvifolium Hedw. Hypnum patientiae Lindb. Leptodictyum riparium (Hedw.) Warnst Leptodictyum trichopodium (Schu.) W. Leucobryum glaucum (Hedw.) Schimp Lophocolea bidentata (L.) Dum. Lophocolea cuspidata (Nees.) Limpr. Lophocolea heterophylla (Schr.) Dum. Mnium cuspidatum Hedw. Pallavicinia lyellii (Hook.) S.F.Gray Plagiothecium micans (Sw.) Paris Sphagnum palustre L. Thuidium delicatulum (Hedw.) Mitt. Thuidium microphyllum (Hedw.) Best
YORK: 2 mi. NE of Lightfoot. (Fig. 2, Loc. 10)	3	Climacium americanum Brid. Mnium cuspidatum Hedw.
YORK: ½ mi. N. of Williamsburg. (Fig. 2, Loc. 12)	1	Unidentified.
YORK: Yorktown area. (Fig. 2, Loc. 14)	10	Thuidium delicatulum (Hedw.) Mitt. Sphagnum