

SPREAD OF THE BLACK PHASE OF THE RED-BACKED SALAMANDER IN MICHIGAN

FREDERICK H. TEST

Department of Zoology, University of Michigan, Ann Arbor

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INTRODUCTION

For the past several years, field studies have produced information on the distribution of the red-striped and the black phases of the small terrestrial salamander, *Plethodon cinereus*, in Michigan. The two phases are similar except for the dorsum, which is black in the latter phase, while in striped individuals a broad reddish band, bounded laterally by black, extends from the head onto the tail. From evidence available, these two color phases appear to be genetically determined, having been found together repeatedly in the same brood. Information obtained to date shows their distribution in northern Michigan, which is discussed below.

The collections serving as a basis for this paper have been made mostly in selected localities by the writer, but in addition specimens in the Museum of Zoology of the University of Michigan have been examined and certain of those records included here. I am grateful to Norman E. Hartweg for the opportunity to study those specimens and to E. C. Hertzler of Kent State University, Ohio, for information on a collection he made at Burt Lake. To the Huron Mountain Club I am much indebted for permission to collect on Club property in northern Marquette County and for various kindnesses while so doing. Alfred H. Stockard kindly made available the facilities of the University of Michigan Biological Station for several short periods of collecting. My wife, Avery R. Test, was an invaluable assistant in most of the collecting. The greater part of this work was supported by grants from the Faculty Research Fund of the Horace H. Rackham School of Graduate Studies.

METHODS OF COLLECTING

The general collector usually is satisfied with a handful of specimens of any single species to establish a locality record. Such small numbers have only limited usefulness. With increasing attention being given to studies which involve moderately large samples, it is to be hoped that collectors will avail themselves of opportunities to obtain larger numbers than is customary. With accurate and precise notes on location and environment, such collections would have considerable value in many kinds of studies, particularly if specimens are collected as found rather than selected. Common sense should be exercised to keep from seriously depleting limited populations, but for at least some species our present evidence (Kline and Fuller, 1932; Test and Bingham, 1948) indicates little danger of so doing.

The area reported upon here is the Upper Peninsula of Michigan and the extreme northern tip of the Lower Peninsula, close to the Straits of Mackinac. Throughout this region the vegetation 100 years ago was largely northern hardwoods on the higher, better soil and white cedar-black spruce forest on the low ground (Gates, 1942; Potzger, 1946). The northern hardwood forest had sugar maple as the principal dominant and mixed with it were various proportions of beech, hemlock, basswood, and yellow birch. Pine forests occurred on the poorer soils. More recently, lumbering operations, fire, and clearing of the land for habitation, agriculture, and recreation have combined to modify greatly the early vegetational pattern. Few areas remain unchanged by cutting. The largest part of the land now forested is covered with either (1) north-

TABLE 1. *Samples of Plethodon cinereus from populations in northern Michigan*

Location	Number of localities sampled	Size of samples	Proportion of striped individuals in per cent
Upper Peninsula			
Ontonagon Co.	8	191	100
Gogebic Co.	4	24	100
Marquette Co.	8	249	100
Alger Co.	3	31	100
Luce Co.	5	65	100
Chippewa Co.	4	27	100
Mackinac Co.			
Gros Cap	1	115	99
2.5 mi. NW Gros Cap	1	55	76
Pte. Aux Chenes	1	58	97
Other localities NW to NE of the 3 listed above	13	1,145	100
Bois Blanc Island	1	79	75
Lower Peninsula (Emmet and Cheboygan counties)			
1.5 mi. W Mackinaw City	1	59	83
1.5 mi. SW Mackinaw City	1	74	95
W end Carp Lake	1	101	94
Sturgeon Bay	1	57	91
1 mi. SW Cross Village	1	36	97
4 mi. WNW Pellston	1	98	98
Douglas Lake region	unknown	77	92
NW side Burt Lake	1	19	100
Colonial Pt., Burt Lake	1	203	95

every individual found was collected except an occasional one which escaped. Records were kept on the color of the latter. Generally, a sample was taken from an area of approximately 3-10 acres, which sometimes was the total area of the woods.

Statistically, a random sample of 100 individuals in which the less common of two types does not occur is said to indicate that this less common type comprises less than 10 per cent of the population (Simpson and Roe, 1939). In this collecting the accuracy of such a sample probably was somewhat greater, for in all woods where the black (the less common) phase occurred, black individuals were found at fairly regular intervals, indicating a rather uniform distribution in the population. It was not possible in all woods to obtain samples of 100 because of scarcity of the salamanders and lack of time, but this regularity of

finding black individuals and the results of taking successive samples from the same area in a number of places elsewhere in Michigan point to the figures obtained as being reliable within 5-7 per cent (Test and Bingham, 1948; Test, unpublished data). Samples of 100 or more have somewhat greater accuracy.

Most of the collecting was done in August and September, with a small amount in early summer. That the season does not affect the proportions of the color phases collected is indicated by the results of numerous samples taken throughout the active season over the same areas in southern Michigan (Test MS.).

Samples were taken from three large populations in the Upper Peninsula, exclusive of Mackinac County where more intensive work was done. In the Porcupine Mountains State Park of Ontonagon County the population was sampled at

five places in the extensive and continuous forest, part of it virgin. Similarly, the Huron Mountains (Marquette County) collection was taken from four parts of a single large population in virgin forest.

In addition, specimens from a number of other localities in the Upper Peninsula have been examined in the Museum of Zoology. Without exception, all of the 587 individuals of *Plethodon* seen from

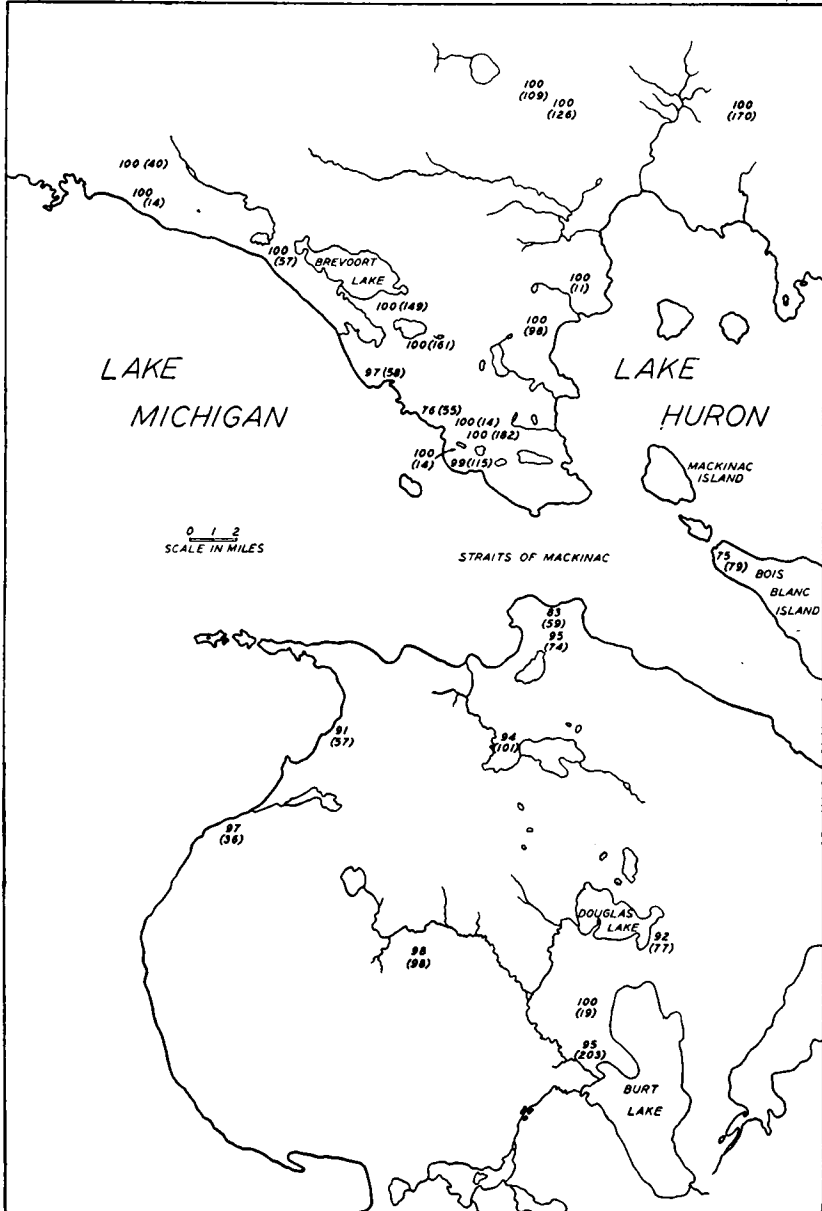


FIG. 2. Sampled populations of *Plethodon cinereus* near the Straits of Mackinac, Michigan. Positions of the figures indicate approximately the localities. The first number of each pair is the percentage of the striped phase in the sample; the number in parentheses is the total number of individuals examined.

the Upper Peninsula outside of Mackinac County have been striped. Collecting localities are shown in figure 1, and the data are listed in table 1.

After black individuals were found in Mackinac County immediately north of the straits, that region was sampled more intensively than the rest of the Upper Peninsula, collections being made at 16 places. Most of these populations are isolated from each other, but a few stations of concentration are connected by regions of low density. In figure 2 it will be seen that only three samples, all from points close to the straits and within a six-mile span, include black salamanders. The 1145 specimens in the other samples from Mackinac County are all striped.

In the vicinity of the southern shore of the straits the situation is different, for all but one of the eight samples show a small and fairly uniform proportion of black individuals. The exceptional sample is too small to be indicative. Museum specimens from the same region (but mostly without exact location data) show proportions similar to those of the majority of our samples: Of 116 from the two counties forming the northern tip of the Lower Peninsula, 91 per cent are striped. About two-thirds of those specimens are from the vicinity of Douglas Lake and are included in figure 2 and table 1.

A single collection made on Bois Blanc Island, immediately east of the straits, has 75 per cent of the specimens striped. Bois Blanc is almost completely forested, but much of the eastern part of the island apparently is uninhabited by *Plethodon* because of severe logging and perhaps fire.

DISCUSSION

It is apparent from the data given above that the black phase of *Plethodon cinereus* is found regularly, though in low proportion, in the northern part of the Lower Peninsula of Michigan. In the Upper Peninsula, however, it is localized in a small area on the northern border of the

Straits of Mackinac. To this part of the picture of distribution in Michigan may be added the knowledge that in southern Michigan the black phase usually forms a considerably larger proportion of the population (Blanchard, 1928; Test and Bingham, 1948; Test, MS.), sometimes exceeding 50 per cent.

The range of the species as a whole extends in general from Georgia north to southern Quebec and westward into Arkansas and Minnesota. Throughout this area there are few data to indicate accurately the proportions of the color phases, but it is known that both occur through most of the range. Westward and northward the black phase apparently becomes less common, and it is unknown, in the literature, west of the Mississippi River. These facts suggest that either the black phase is less well able to exist and reproduce under the environmental conditions of the north and west, or that it is evolutionarily newer than the striped phase and has not had time to spread as far. It may also be possible that each factor is in part responsible.

There have been no studies of the tolerances of the two phases, but they occur together on the Upper Peninsula near the northern limit of the species range. This suggests that different tolerances are, at least, not the sole explanation. Furthermore, environmental conditions found in the northern part of the species range are quite different from those in the western part.

Geological evidence shows that most of Michigan was covered with glacial ice as late as the Second Wisconsin (Tazewell) Substage of glaciation and the straits region as recently as the Fifth Wisconsin or Mankato (Thwaites, 1941). As the ice receded, waters of the tripartite Lake Algonquin, which overflowed the present basins of lakes Superior, Michigan, and Huron, covered the straits and the eastern half of the Upper Peninsula.

Following retreat of the ice and water, there must have been an interval before plant succession on the exposed glacial

drift reached a stage suitable for *Plethodon cinereus*, which is a forest animal. Eventually, however, it must have invaded the glaciated area from the south and slowly followed the ice northward. There is a possibility that the Upper Peninsula has become populated with the striped phase of *Plethodon cinereus* by migration from the west. If it occurred throughout its present range in earlier Pleistocene times, the driftless area of Wisconsin may have served as a refuge from which it migrated eastward into the deglaciated area. An alternative is that the salamander spread northward through Wisconsin and into the Upper Peninsula of Michigan more rapidly than across the Straits of Mackinac. There seems to be little real evidence for a choice between the three possible ways for repopulation of the Upper Peninsula by the striped phase.

If both color phases were waiting, as it were, near the southern limit of the ice sheet, it is difficult to believe that one would not have advanced approximately as rapidly as the other, producing northern populations with a large proportion of black animals. Because of the low proportion actually present, it seems more likely that the black phase invaded the glaciated region later than the striped one and that it has not yet had time to become as abundant in the north nor to spread as far.

The location and localization of the black phase on the Upper Peninsula in the immediate vicinity of the narrowest part of the Straits of Mackinac strongly indicate that it crossed there. All three colonies in which the black phase is represented are adjacent to the coast, as close as suitable conditions occur. (The tip of the peninsula at the straits is not now occupied by *Plethodon* because of the presence of the old city of St. Ignace and surrounding cleared and logged land.) Inland and farther along the coast in both directions nearly 1,150 specimens from 13 populations represent only the striped phase. It is possible that a salamander with a gene or genes for the black condi-

tion crossed the straits in a floating log, for it is well known that this species occurs frequently in logs, often laying its eggs in cavities and probably hibernating there also. It is not difficult to imagine a spring freshet washing such a log into the straits, and wind and current carrying it across. It will be noted that the black phase occurs in fair numbers within two hundred yards of the south shore of the straits even now. That only a single crossing of the black salamander occurred is suggested by the pattern of the three black phase populations on the north shore. Perhaps the landing took place near the present location of the colony containing 24 per cent blacks, at a straight line distance of about eight and a half miles from the nearest part of the Lower Peninsula, with later spread in both directions along the coast, where populations with much lower proportions of that phase now occur. It may also have spread inland a short distance from the landfall, but samples are not available from the most critical area.

Our sample from Bois Blanc Island shows that the black phase has also reached at least one of the islands in the straits and has become well established there. An attempt to find *Plethodon* on Mackinac Island was unsuccessful.

It would be useful to have a time-table in terms of years for the events postulated above. At present only estimates of uncertain validity are available, even for the geological events of the Pleistocene, although current studies of the carbon in peat may provide a much more precise dating. Recent estimates (Thwaites, 1941; Flint, 1947) of the time since the Tazewell Substage of glaciation suggest that perhaps 25,000–50,000 years have elapsed since *Plethodon cinereus* began to invade southern Michigan. Because of the salamander's small size, weak locomotor organs, and peculiarities of habit, we may assume that it spread very slowly. The region about the present Straits of Mackinac remained unavailable to terrestrial animals for a considerable interval

after retreat of glacial ice because of the high level of Lake Algonquin. The period since recession of Lake Algonquin uncovered the eastern part of the Upper Peninsula of Michigan and left the Straits of Mackinac at approximately their present width has been estimated on geological evidence (cutting of the Niagara Gorge) to be 10,000–15,000 years, and recent data from radiocarbon (Flint and Deevey, 1951) suggest that the time may have been only half as long. This period was long enough to allow the striped phase to spread throughout the region of the straits and the Upper Peninsula. In contrast, the much restricted distribution of the black phase in the Upper Peninsula suggests that it crossed the straits only a very few thousand, or perhaps hundred, years ago. Because of human modification of the forests there and consequent isolation of small remnants of the population, spread of the black phase from its present foothold, except by human agency, has ceased. Whether future commercial and agricultural developments wipe out this foothold, or whether re-establishment of suitable forest conditions allows the resumption of normal extension of range, remains to be learned.

SUMMARY

Plethodon cinereus occurs throughout Michigan in suitable forest, forming small isolated remnants of a population that was once largely continuous. In extreme southern Michigan the black color phase forms a large proportion of the population; in the northern tip of the Lower Peninsula less than 10 per cent of the

salamanders are black; on the Upper Peninsula the black phase is apparently confined to a small area at the Straits of Mackinac.

It is probable that the black phase is evolutionarily younger than the red-striped one and so has not had time to reach the limits of the species range. It probably entered Michigan long after the striped phase and only recently (perhaps 200–2,000 years ago) crossed the Straits of Mackinac. It has also reached at least one island in the straits.

LITERATURE CITED

- BLANCHARD, F. N. 1928. Topics from the life history and habits of the Red-backed Salamander in southern Michigan. *Amer. Nat.*, 62: 156–164.
- FLINT, R. F. 1947. *Glacial geology and the Pleistocene Epoch*. New York, John Wiley and Sons. xvii + 589 pp.
- FLINT, R. F., AND DEEVEY, E. S., JR. 1951. Radiocarbon dating of late Pleistocene events. *Amer. Jour. Sci.*, 249: 257–300.
- GATES, F. C. 1942. The bogs of northern lower Michigan. *Ecol. Monog.*, 12: 213–254.
- KLINE, E. K., AND FULLER, N. M. 1932. Interpretation of laboratory findings in rural spring water supplies. *Amer. Jour. Pub. Health*, 22: 691–699.
- POTZGER, J. E. 1946. Phytosociology of the primeval forest in central-northern Wisconsin and upper Michigan, and a brief post-glacial history of the Lake Forest formation. *Ecol. Monog.*, 16: 211–250.
- SIMPSON, G. G., AND ROE, A. 1939. *Quantitative zoology*. New York, McGraw-Hill Book Co. xvii + 414 pp.
- TEST, F. H., AND BINGHAM, B. A. 1948. Census of a population of the Red-backed Salamander (*Plethodon cinereus*). *Amer. Midl. Nat.*, 39: 362–372.
- THWAITES, F. T. 1941. *Outline of glacial geology*. Ann Arbor, Michigan, Edwards Bros. 119 pp. (lithographed).