

POLYMORPHISM IN THE SCREECH OWL IN EASTERN NORTH AMERICA

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MY aim in this paper is to provide a description of geographical trends in the occurrence of color forms in the Screech Owl (*Otus asio*) and, in particular, to draw attention to what appears to be an unusual pattern of variation within an animal species. This paper is adapted from part of a recently finished and lengthy study of variation in the Screech Owl.

The Screech Owl is continuously distributed and common over much of North America between about 57° N (southeastern Alaska) and 17° N (Oaxaca). East of about 104° W there are two color forms, one with the plumage mainly gray and the other with the plumage mainly rufous. Similar forms occur in other species of *Otus*. In the Screech Owl it is known that at least in some areas rufous is genetically dominant to gray, but the presence of intermediates indicates that the genetic control of color forms is more complex than this.

The existence of two distinct color forms of the Screech Owl has been known since about 1874 when Ridgway (Baird, et al., 1874) realized that rufous and gray birds were of the same species and that the forms were independent of age, sex, or season. Earlier, rufous and gray birds had been variously interpreted as belonging to different sexes or to different age classes. Ridgway later published in many natural history and scientific journals an appeal for information on the frequency of rufous and gray birds, nesting details, and any other data that might help to solve the problem. The information so obtained was passed over to E. M. Hasbrouck who later published an account of his findings (Hasbrouck, 1893). There are a number of inaccuracies in Hasbrouck's paper, as pointed out at the time in a critical review (Allen, 1893). No one has attempted a full survey of the geography of color forms in the Screech Owl since that date. There have been, however, a number of papers discussing the problem in relatively small geographical areas, such as Ontario (Martin, 1950) and parts of Illinois and Wisconsin (Schorger, 1954). There also has been one somewhat inconclusive genetic analysis in Ottawa County, Ohio (Hrubant, 1955).

GEOGRAPHICAL VARIATION IN RELATIVE FREQUENCY OF RUFOUS SCREECH OWLS

Figure 1 shows the distribution and relative frequency (per cent) of rufous Screech Owls in eastern North America. The percentages are based upon 1,778 specimens in the collections listed at the end of this paper and upon

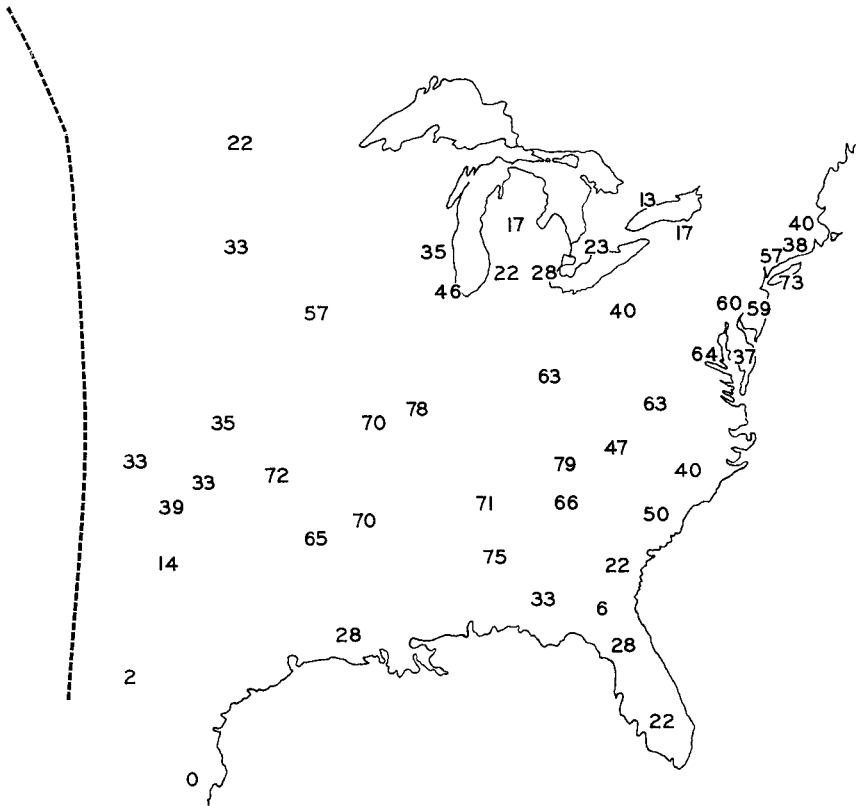


FIG. 1. Relative frequency (per cent) of rufous Screech Owls in North America.

the specimens reported by Schorger (1954) and Stupka (1953). Other published records are omitted because of uncertainty as to their reliability, or because I have re-examined the specimens upon which the reports were based. There is good reason for regarding the sample upon which Fig. 1 is based as representative of the population. Using a series of 2×2 contingency tests, I was unable to detect bias by individual collectors or museums for either rufous or gray birds (details in Owen, ms).

The approximate western limit of rufous Screech Owls in North America is indicated by a broken line in Fig. 1. The Regina region of Saskatchewan is the most westerly point (about 104.6° W) at which rufous birds have been recorded. The southern limit of occurrence of rufous Screech Owls is in Nuevo Leon (or possibly Tamaulipas), Mexico. But there were no rufous birds in a sample of 124 specimens from southeastern Texas (chiefly Cameron County), and it seems likely that the southern limit of regular occurrence of

rufous specimens is at about 30° N in Texas. In the Florida peninsula, rufous birds occur south to the Keys. (The species is absent from the West Indies.)

Thus rufous Screech Owls occur throughout the range of the species in eastern North America; but in no area do they comprise the total population, some gray birds are always present. As shown in Fig. 1, the relative frequency of rufous birds forms a somewhat irregular cline from north to south. The lowest frequencies occur at the northern limits of the range of the species: 22 per cent in northern Minnesota and North Dakota, 17 per cent in the upper part of the Lower Peninsula of Michigan, and 13 per cent around Toronto. Between 30° and 40° N rufous birds frequently comprise 60–70 per cent of the population, sometimes more, as in southern Illinois (78%) and eastern Tennessee (79%). In the Florida peninsula and along parts of the Gulf coast there is a decrease in the relative frequency of rufous birds, but this is caused chiefly by a sharp rise in the frequency of intermediates and not by an increase in the frequency of gray birds. I shall discuss this later. Near the western limit of rufous birds there is a sharp drop in their relative frequency: only 2 per cent in Kerr County, Texas, and less than 40 per cent elsewhere. As already mentioned, there are records of rufous birds west of 100°, but there are no data on relative frequency. Some of the irregularities in the cline depicted in Fig. 1 can doubtless be attributed to inadequate sampling, but the high frequency (73%) of rufous birds on Long Island compared with the surrounding mainland (38–59%) must be mentioned because large samples were examined.

BIMODAL VARIATION IN THE SCREECH OWL

As already mentioned, the low relative frequency of rufous Screech Owls in Florida is largely because of an increase in relative frequency of birds intermediate in coloration. In view of this, I set up a graded series of six specimens, ranging from gray to rufous, against which all other specimens were matched. Young, damaged, and dirty birds were excluded, and, after some experience, I had little difficulty in placing each specimen in one of the six color categories. The following are descriptions of the six birds against which all others were matched. The descriptions refer only to those characters used in placing other specimens into categories; other variation is omitted.

1. Upperparts: gray, shafts of body feathers dark brown or black; numerous fine bars and irregular streaks on each feather; a very light rufous suffusion on many of the feathers (this not present in all specimens). Underparts: white; almost all feathers, except some of those of the lower belly, with heavy dark brown or black streaks surrounding and including the shaft; each feather with 1–3 (sometimes more) bars of variable length and width, each making an angle of about 65° with the streak, such that (especially on the belly) the arrow-shaped markings so-formed point toward the posterior of the bird. The streaks vary in thickness from 10 mm on the feathers of the lower

breast to 2 mm on the feathers of the belly, while the feathers around the vent and on the thighs are generally unpigmented. On the breast and throat the main bars are interspersed with smaller bars giving an almost vermiculated appearance. Occasionally there is a small patch of rufous where the bars make an angle with the streak, and many of the wider streaks and bars are lightly edged with rufous, this, however, is apparent only at close inspection. The general appearance of birds in this category is gray.

Example: male, Washtenaw County, Michigan, 16 October 1950 (UMMZ 151952).

2. Upperparts: as in 1, but the whole back more suffused with rufous, especially in the middle and on the crown and forehead. Underparts: as in 1, but the angles between the bars and streaks with more extensive rufous areas, giving the entire underparts a more rufous appearance, but retaining the same basic pattern. Birds in this category are unquestionably gray.

Example: female, Lenawee County, Michigan, 17 November 1934 (UMMZ 125549).

3. Upperparts: as in 2, but more rufous, especially on the back, crown, and forehead. Underparts: as in 2, but rufous areas still more extensive; basic pattern on the feathers of the belly and breast as in 2, unlike the next category (4). Birds in this category appear intermediate between gray and rufous, but are closer to the gray form on account of the pattern of the feathers of the underparts.

Example: male, Benton County, Arkansas, 17 June 1935 (UMMZ 125587).

4. Upperparts: as in 3, but more rufous, especially on the crown and back; rufous now replaces gray as the dominant color of the upperparts. Underparts: streaked as in 3, but on the belly and lower breast the bars on each feather are largely replaced by broad irregular spots of rufous, one or two on each feather; many feathers of the upper breast and throat similarly patterned, but many also as in 3. Birds in this category obviously intermediate, but on the underparts the pattern approaches that found in 5 and 6 rather than that in 1-3.

Example: male, Washtenaw County, Michigan, 20 October 1929 (UMMZ 152081).

5. Upperparts: more rufous and less heavily streaked than in 4, much more uniform in coloration with less indication of patterning. Underparts: the irregular rufous spots on each feather, noted in 4, occur on most of the pigmented feathers of the underparts; fine barring present on only a few feathers; many feathers with just one large rufous spot; black and dark brown shafts still conspicuous.

Example: male, Walsh County, North Dakota, 18 May 1933 (UMMZ 125620).

6. Upperparts: almost all visible parts of feathers bright rufous; streaks less distinct than in 5 (in some specimens there are no streaks). Underparts: most feathers with one, sometimes two, irregular, bright rufous spots; no bars. The general appearance is bright rufous.

Example: female, Benton County, Arkansas, 11 December 1935 (UMMZ 125597).

It was possible to place 1,320 specimens into the above six color categories. The specimens in this sample are from the entire range of the species east of 100°; that is to say, the area where rufous as well as gray birds occur. Birds in categories 1-2 may be conveniently regarded as gray, those in 3-4 as intermediate, and those in 5-6 as rufous. About 54 per cent of the specimens are gray and 38 per cent rufous, while only 8 per cent are intermediate in coloration. Thus, in eastern North America as a whole, the variation in color has a bimodal distribution. But the degree of bimodality varies geographically, as shown in Table 1.

TABLE 1

RELATIVE FREQUENCY OF COLOR CATEGORIES 1-6 IN SCREECH OWLS IN SELECTED AREAS
OF EASTERN NORTH AMERICA

Area	N	Number of specimens in Color Categories:						Per cent 3-4
		1	2	3	4	5	6	
Minnesota: Roseau and Beltrami counties	27	17	3	0	0	0	7	0
North Dakota: Walsh County	39	21	8	3	1	3	3	10
Illinois: Will, Cook, and Lake counties	15	7	2	1	0	2	3	7
Kansas: Douglas County	24	11	4	2	0	1	6	8
Michigan: Washtenaw and Livingston counties	77	45	12	0	1	3	16	1
Ontario: York County	42	31	2	1	1	0	7	4
Ontario: Middlesex County	23	13	2	0	0	0	8	0
Ontario: Essex County	14	11	0	1	0	0	2	7
Connecticut: Hartford, Litchfield, Middlesex, and Fairfield counties	40	15	5	2	1	2	15	7
New York: Long Island	43	8	2	1	1	1	30	4
New York: Orange, Rockland, and Westchester counties	30	9	3	0	1	1	16	3
New Jersey: Essex, Bergen, Morris, and Union counties	24	5	3	0	0	0	16	0
Maryland: Prince Georges and Montgomery counties	18	4	2	0	0	0	12	0
Washington, D.C.	44	10	3	3	1	1	26	9
Virginia: Fairfax County	13	4	0	0	0	0	9	0
Georgia: Cobb and Fulton counties	31	5	6	0	1	3	16	3
Arkansas: Washington and Benton counties	38	9	0	2	0	0	27	5
Arkansas: Pike County	21	8	0	0	0	1	12	0
Texas: Kerr County	20	19	0	0	0	1	0	0
Texas: Cameron County	99	83	16	0	0	0	0	0
Louisiana: St. Tammany Parish	12	4	3	2	0	0	3	17
Florida: Duval, Columbia, Nassau, Bradford, Alachua, Clay, St. Johns, Madison, and Taylor counties	16	7	6	2	1	0	0	19
Florida: Levy, Putnam, and Volusia counties	11	2	2	1	0	0	6	9
Florida: Brevard, Orange, Citrus, Seminole, Sumter, and Pasco counties	33	6	8	6	3	5	5	27
Florida: Indian River, Polk, Osceola, and Hillsborough counties	30	7	6	4	8	1	4	40
Florida: Martin, Sarasota, Highlands, St. Lucie, Manatee, De Soto, and Okeechobee counties	25	6	4	2	3	7	3	20
Florida: Collier, Palm Beach, and Lee counties	14	4	5	2	2	1	0	29
Florida: Dade and Monroe counties	16	1	8	3	3	1	0	38

Note: For descriptions of color categories see text.

The frequency of birds classified in Color Categories 1-6 in 28 representative areas is given in Table 1. Throughout eastern North America, except in southern Louisiana and in Florida, intermediates (Categories 3-4) comprise 10 per cent or less of the population. In Florida and in southern Louisiana intermediates are more frequent: in central Florida they comprise 40 per cent of the population. Thus, as shown in Table 1, although both rufous and gray birds occur in Florida, the population lacks the bimodality evident throughout the rest of eastern North America.

DISCUSSION

The existence of bimodal or polymodal variation within a species is often referred to as polymorphism, which may be formally defined as: The occurrence together in the same habitat of two or more distinct genetic forms of a species of animal or plant in such proportions that the rarest of them cannot be maintained by recurrent mutation (Ford, 1940). Differences between the sexes, differences between young and older individuals, and seasonal differences are excluded from this definition. Only bimodal or polymodal variation, in which intermediate forms occur at low frequency or are even absent, is considered as polymorphism. Hence an extremely variable species may not necessarily be polymorphic.

It is extremely unlikely that two or more very different phenotypes would be equally adapted to the environment in which they live; a balance of selective forces must be involved, for if not, one form would rapidly replace the other and there would be no polymorphism (Fisher, 1930). Hence the presence of polymorphism in a species probably represents balanced adaptation of the forms to varying environmental conditions.

Nothing is known of the adaptive significance of the polymorphic forms of the Screech Owl, but the existence of a cline in the relative frequency of the forms (Fig. 1) as opposed to random or irregular distribution supports the view that polymorphism in this species is maintained by selection operating along environmental gradients. The cline is not correlated with any obvious environmental factors, but, with the exception of the extreme South (including Florida), rufous birds are more frequent in warmer areas. An earlier attempt to correlate the cline with relative humidity (Hasbrouck, 1893) was based upon inadequate information and cannot be substantiated with the additional material now available. The absence of polymorphism throughout the range of the species in the West is probably the result of environmental factors which prevent its establishment there.

The existence of two distinct forms with few intermediates throughout much of the range of the Screech Owl in eastern North America is indicative of selection for bimodal variation. In most areas, selection must be continually

operating against intermediates, but in Florida, where intermediates are frequent (Table 1), there is presumably a relaxation of selection pressure. The result of this is that while all six color categories occur in Florida, the population is extremely variable, but not polymorphic. Hence in the Screech Owl the unusual situation exists in which polymorphism for color and pattern is maintained over a large geographical area (eastern North America), while in a much smaller area (Florida) the complete range of phenotypes occurs, but the population is not polymorphic. I am not aware of a comparable situation in any other species of animal.

SUMMARY

Throughout most of North America east of about 104° there are two forms of the Screech Owl: one with the plumage mainly bright rufous and the other with the plumage mainly gray. Birds of intermediate coloration also exist, but in most areas they are rare.

The relative frequency of rufous birds varies geographically in the form of a cline from north to south; about a quarter or less of the northern population is rufous, while in the South (the Gulf coast and Florida excepted) up to three-quarters of the population may be rufous.

Screech Owls intermediate in coloration between gray and rufous comprise not more than 10 per cent of the population, except in Florida and the adjacent Gulf coast where they comprise up to 40 per cent. In Florida, Screech Owls are more variable in color and the population lacks the bimodality of other populations in eastern North America. This is probably the result of relaxed selection pressure.

The geography of polymorphism in the Screech Owl appears to be an unusual pattern of variation within an animal species.

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LITERATURE CITED

- ALLEN, J. A.
1893 Hasbrouck on "Evolution and dichromatism in the genus *Megascops*." *Auk*, 10:347-353.
- BAIRD, S. F., T. M. BREWER, AND R. RIDGWAY
1874 A history of North American birds. Baltimore. American Ornithologists' Union. 691 pp.
- FISHER, R. A.
1930 The genetical theory of natural selection. London. Oxford University Press. 291 pp.
- FORD, E. B.
1940 Polymorphism and taxonomy. In "The New Systematics" edited by J. Huxley. Oxford. Oxford University Press. 583 pp.
- HASBROUCK, E. M.
1893 Evolution and dichromatism in the genus *Megascops*. *Amer. Nat.*, 27:521-533, 638-649.
- HRUBANT, H. E.
1955 An analysis of the color phases of the eastern Screech Owl, *Otus asio*, by the gene frequency method. *Amer. Nat.*, 89:223-230.
- MARTIN, N. D.
1950 Colour phase investigations on the Screech Owl in Ontario. *Can. Field-Nat.*, 64:208-211.
- SCHORGER, A. W.
1954 Color phases of the Screech Owl between Madison, Wisconsin and Freeport, Illinois. *Auk*, 71:205.
- STUPKA, A.
1953 Some notes relating to the mortality of Screech Owls in Great Smoky National Park. *Migrant*, 24:3-5.

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