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GEOGRAPHIC VARIATION OF THE SCREECH OWLS OF THE DESERTS OF WESTERN NORTH AMERICA

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Screech Owls (*Otus asio*) occur widely across the deserts of the southwestern United States and the northwestern states of México. In these arid regions they range from the oak and piñon belts of the mountains down through the desert scrub habitat of the lowest basins and river valleys. Mesquite brush, even when well scattered and not more than six feet in height, and widely spaced palo verdes, ironwoods and the larger cacti are adequate plant cover for the desert races of this species. Nocturnal foraging for insects and rodents on or near the ground requires but sparse vegetation, and daytime concealment and nest sites are probably the needs that limit these owls to the vicinity of the dense, larger-trunked, even if low, desert shrubs or to the large cacti or streamside cottonwoods in which woodpecker cavities are frequent. In especially favorable terrain, male owls stationed on territories may be spaced less than one hundred yards apart, although the interval is more commonly two hundred to four hundred yards. They are, then, an abundant small raptor, much more abundant, and hence we may say more successful, than their diurnal raptorial counterparts of the same areas, the Sparrow Hawks, Loggerhead Shrikes and Road-runners.

The area of concern in our study of Screech Owls lies south of central Nevada and Utah, west of the continental divide in the main, and east of the desert divides of southern California; it extends south through Sonora and Baja California. This area is essentially the lower Colorado River drainage basin and the watersheds of the trough of the Gulf of California. Some adjoining parts of the Great Basin region are involved.

In this area and about its margins eight races of Screech Owl are currently recognized. It is not proposed that any more be recognized, although one does require renaming. The object of our study has been, then, to clarify the nature of the differences in the races, to describe the clines in characters running through the complex and their general environmental correlations, and to indicate the points of maximum change in characters which may serve as somewhat arbitrary race boundaries. The races involved in the area are *Otus asio cineraceus* in the northeast, *O. a. suttoni* marginally in the southeast, *O. a. sinaloensis* in southern Sonora, *O. a. gilmani*, herein renamed, in the center of the Colorado trough, *O. a. inyoensis* in the Great Basin, *O. a. quercinus* on the western desert border, and *O. a. cardonensis* and *O. a. xantusi* in the central and southern parts of the peninsula of Baja California.

Special effort has been exerted for a period of twenty years to collect western Screech Owls in order better to understand the wide range of racial variation in this species. The impetus for this work came from the realization that these owls could be taken in numbers much greater than formerly by nocturnal hunting employing the whistled imitation of the principal trilling note of the western races to induce aggressive calling, and often approach, on the part of the owl. Use of this technique was begun by Loye Miller and independently by Edouard C. Jacot and in time it was adopted by a number of other field students. Among those whose nocturnal activity has also contributed extensively to the collections now before us are Joe T. Marshall, Jr., Alden H. Miller, Ward C. Russell and A. J. van Rossem.

In 1944 van Rossem and Loye Miller began a series of special trips into the deserts of California, Arizona, and Sonora in order to collect Screech Owls and pursue a revisionary study of the group. Van Rossem assembled loan material at the Dickey Collections in Los Angeles with the result that by 1949 there was present there a total of 365 adult specimens pertaining to the deserts and their peripheries, almost half of which had been taken by Loye Miller and van Rossem in recent years. The untimely death in 1949 of van Rossem, who was to have prepared the report, left on record only a partial set of measurements and occasional indications of his views on identifications on the measurement sheets. Some of these were interpretable from verbal comments he had made to the present authors. Utilization of the unique assemblage of Screech Owls seemed not only mandatory but challenging, and accordingly Alden Miller began periodic study of it in 1949. Use was made also of 73 specimens at the Museum of Vertebrate Zoology additional to those previously borrowed by van Rossem. Thus a total of 438 birds bearing on problems in the area has been employed.

For the loan of specimens we are greatly indebted to the following persons and institutions: The University of Arizona, the Museum of Northern Arizona, Joseph Brauner, the Chicago Natural History Museum, Robert G. Hannum, Lyndon L. Hargrave, Lawrence M. Huey, Randolph Jenks, the Los Angeles Museum, the Museum of Zoology of the University of Michigan, Gale Monson, Allan R. Phillips, the late Max M. Peet, the San Diego Society of Natural History, William J. Sheffler, the United States National Museum (Biol. Surv. Coll.), and the University of Utah.

The large group of specimens available to us has served to develop an appreciation of the great range of individual variation in Screech Owls, both in color and dimensions, which early workers with small series could scarcely gain. As a consequence certain names based on small samples and slight individual variations can now be assigned to synonymy with some confidence. It is thought that naming of such variants and of intergrading stages badly obscures and distorts the main pattern of geographic variation.

The sex ratio in the collections is influenced by the greater readiness of males to respond aggressively to imitated calls. The most thorough comparison of geographic samples can, therefore, be made in this sex. However, in some areas, such as the Tucson district and the Cape district of Baja California, many Screech Owls were taken by climbing to nest and roost holes before nocturnal hunting was much in vogue. Consequently females are better represented or even predominate slightly in the samples from these areas.

GEOGRAPHICALLY VARIABLE CHARACTERS

Color and pattern.—In dealing with the extremely variegated and complex color patterns of owls, it is difficult to make comparisons and focus attention on comparable parts in different specimens and series. Mass effects of contrast are often readily seen but are troublesome to analyze. On the dorsal surface the principal geographic variables are: (1) the width and intensity of the dark shaft streaks, which are always more prominent on the head than on the back and which especially on the head increasingly dominate the pattern as seasonal wear proceeds; (2) the hue and shade of the grays and browns that chiefly in mottled form make up the principal background color of the back; and (3) the hue and tint of the light tawny or essentially white areas, especially where they are prominent in the neck region.

On the face and ventral surfaces the variables are: (1) the amount and purity of the white which predominates in the face, especially at the margins of the ocular-auditory disc; (2) the width of the black shaft streaks of the ventral surface, which are always two to three times wider on the breast than on the flanks; those of the same section of the flanks, for example, may vary geographically from 0.5 to 2.5 mm. in width; (3) the

number and width of the black cross bars lateral to the shaft; a given flank feather may have as few as four irregularly spaced and curved bars to as many as eight, either solid or partly broken bars; (4) the presence or absence of a brown or yellow-brown area bordering the shaft; (5) the light background color, which may be light gray, nearly pure white, or slightly tawny. The crural feathering, and to less extent that of the lower flanks shows a greater amplitude of variation in background color than other ventral parts; it ranges from white to dark gray or to rich tawny or brown. Also the bars and spots of the crural area, usually in correlation with the background color, may be sparse and small or heavy to a degree that they dominate the area.

Among the Screech Owls of the deserts, we have seen no instance of phase or polymorphic color variation like that well known in the eastern races of the species. The bright red-brown phase is lacking. On a very different level of magnitude is graded indi-

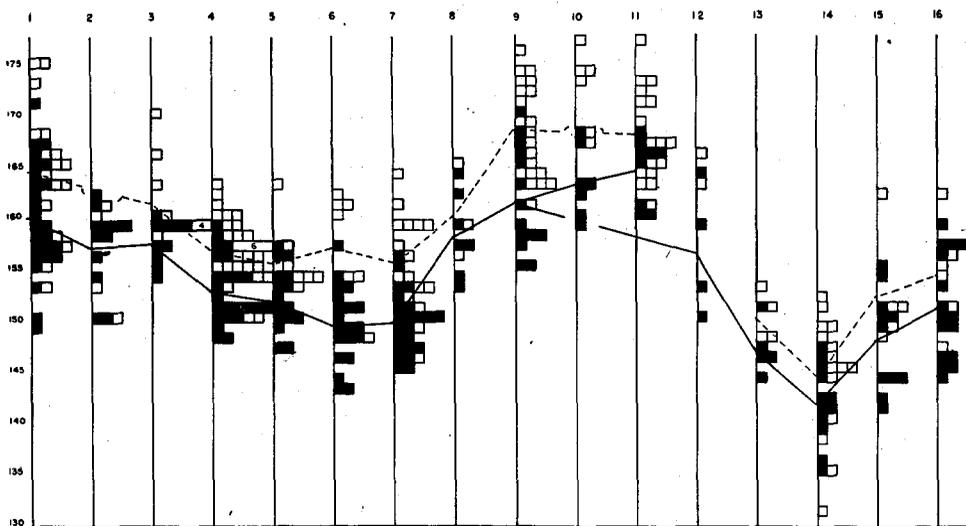


Fig. 1. Wing lengths of Screech Owls in millimeters. Solid squares individual males, open squares females. Each vertical line with number marks a separate geographic sample (see fig. 2 and note on page 164). Solid lines connect averages of males, broken lines females.

vidual variation in most western races involving gray and somewhat more tawny or brownish extremes (see p. 174). This variation is of the same order as that found in large samples of many bird species. It is equivalent to that in races of Song Sparrows and Savannah Sparrows.

Size.—Wing length, taken as the chord, proved to be the only worthwhile measurement to analyze. All specimens were remeasured by Alden Miller; his measurements were found to parallel but not always duplicate those made by van Rossem. Van Rossem had measured the tail, tarsus and middle toe without the claw on about half the assemblage. His record of foot measurements showed almost no hint of significant geographic variation except for slight tendencies parallel to the general size variation that is reflected by the wing measurement and some few weight records. Because of this and the great difficulty of making consistent foot measurements on a feathered foot surface, these variables were not further studied. Van Rossem's measurements of tail showed a parallel, individually and geographically, with wing length such that it did not seem profitable to undertake an independent set of measurements of this member.

The wing length apparently reflects a general size variation, although we must warn that this is only broadly true and the relation can not be established precisely without correlating wing length with some adequate set of measurements of body mass. Weight records are few, as they were not made by van Rossem and Loye Miller. Where they are available a strong parallel to wing length variation is indicated. For example, males and females of *inyoensis* average 164.5 and 168.0 mm., respectively, in wing length and 130.8 and 157.1 grams in weight; in *xantusi* males and females are 141.7 and 144.5 in wing length and 89.4 and 113.9 grams in weight. Thus in size (weight) *inyoensis* and some others of the larger races in this region are approximately 40 per cent larger than the dwarf *xantusi*, a rather amazing differential. The wing length differential is similar

Wing Length and Weight in Desert Populations of *Otus asio*

Population number (see names ¹)	Wing length in millimeters			Number of specimens	Weight in grams	
	Number of specimens	Average	Standard deviation		Average	Standard deviation
Males						
1	21	160.0	5.38
2	12	157.1
3	10	157.5
4	26	152.8	3.08
5	16	151.9	3.03
6	20	149.5	3.70
7	23	149.7	3.00	6	102.7	11.35
8	7	158.0	4	115.9
9	14	161.4	5.02
10	7	163.1
11	9	164.5	3.13	8	130.8	9.20
12	4	156.5	3	118.9
13	5	146.8
14	12	141.7	3.64	2	89.4
15	11	147.8	4.85
16	16	151.1	5.06
Females						
1	17	164.6	6.37	2	133.5
2	4	156.0
3	9	161.4
4	30	156.8	3.09
5	8	155.6
6	7	157.1
7	16	155.6	4.73
8	3	160.0
9	21	168.4	4.40
10	6	172.2
11	17	168.0	4.32	2	157.1	12.32
12	2	164.5
13	4	150.0
14	15	144.5	5.72	3	113.9
15	5	152.2
16	6	154.2

¹ *Geographic groupings used for measurements* (for outlines of areas see corresponding numbers on map, fig. 2).—1, southeastern Arizona and southwestern New Mexico, largely the Chiricahua Mountains; 2, Huachuca; 3, Prescott; 4, Tucson and Phoenix; 5, Álamo, Salome and Harquahala; 6, Sonoyta; 7, Colorado River valley; 8, Little San Bernardino Mountains; 9, coastal southern California; 10, Tehachapi and Walker Pass; 11, Owens Valley and Carson Sink; 12, northwestern Baja California; 13, El Rosario, Baja California; 14, Cape district, Baja California; 15, Guaymas area and southern Sonora; 16, central Sonora.

but does not reflect fully the magnitude of the difference in mass in these extreme races.

Sexual differentiation in plumage has not been detected. The greater average size of females has long been known, but we had not realized how extensively males and females overlap in wing length until the large series of measurements now assembled were compared (fig. 1). Females average only about three per cent longer winged in most populations. Weight also overlaps, although apparently to less extent, but the record is insufficient to establish the relationship precisely.

No means has been found of determining the age of owls subsequent to the period in the early fall when all remnants of juvenal body plumage are lost.

CLINES

Wing length shows a striking cline in which there is decrease from north to south and from higher terrain east and west of the lower Colorado River valley down slope into the trough of the valley. The resultant axes of the cline in Arizona and eastern California are therefore southwest and southeast to a point of low value in the Colorado River valley at elevations below 500 feet. The more southern populations of central coastal Sonora are not significantly smaller, and those of extreme southern Sonora are but slightly further reduced in wing length. Southward along the peninsula of Baja California wing length drops to a low extreme in the Cape district. As indicated earlier wing length reflects body size and the cline of decreasing wing length probably has chief significance as an imperfect index of change in body size; independent modification of wing length, although probably extant, is not readily made out and in any event appears not to be large. Thus, there is no basis for relating the wing length cline to Allen's principle, positively or negatively. The evident size cline reflected by wing and weight is, however, strikingly in accord with Bergmann's principle. Decreased size correlates both with southern warmer latitudes and lower warmer elevations in the desert.

Screech Owls throughout the area under consideration feed chiefly on arthropods, especially large ground-dwelling forms. Only occasionally are small rodents taken. Possibly rodents are more often depended on, especially in winter, in the populations at more northern points and at higher elevation. Conceivably large size would be an advantage in this connection, but diet differential is at this time only surmised and remains to be established.

Screech Owls, so far as evidence indicates, are essentially nonmigratory (there may be some rather local shifting). In winter in cold areas the birds seem to be very inactive on many nights and especially when there is wind and storm. At these times they respond poorly to calls. We can not escape the notion that owls that must move about at night and be subject at that time to the convectional factor to great degree have more of a problem of heat loss than do diurnal animals in the same latitude or climatic area. Also it is noted that heavy fat deposition is frequent in them by late fall. These several circumstances suggest that there is a particularly acute need for heat and energy conservation in winter. If a Screech Owl is to be quiescent for many days during unfavorable weather and consequently feed but little, a favorable surface-mass ratio, such as exists in large-sized individuals, would be distinctly advantageous. Certainly the winter nights at 4000 feet in the Great Basin and in the desert mountains of California and Arizona are more severely cold than those of the Cape district of Baja California where frosts are rare indeed at low elevations.

Coloration shows several independent gradations. Brownish hue in the dark background color of the back, in the crural area, and on the borders of the shaft streaks of the ventral tract diminishes fairly abruptly eastward across the desert divides of southern California and gives way to light gray back and to light tawny or yellowish shaft-

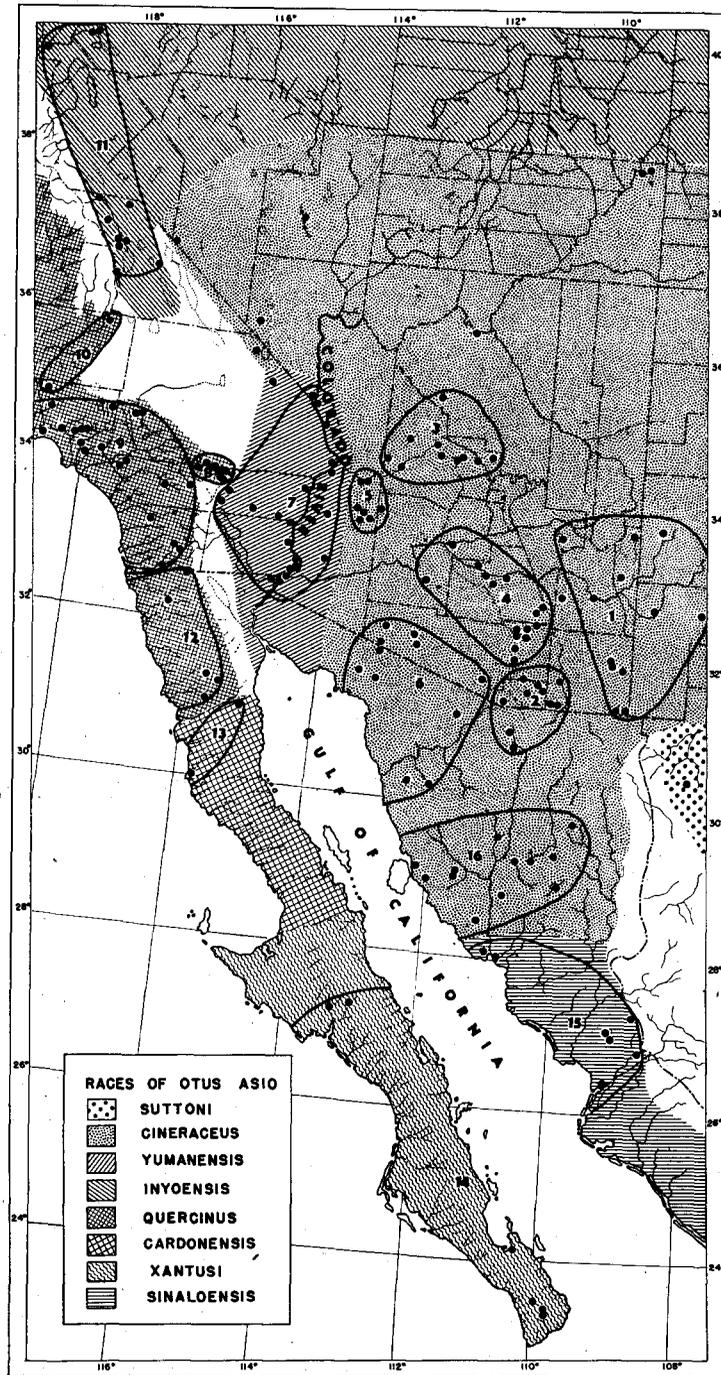


Fig. 2. Distribution of desert races of Screech Owls, each race marked by style of shading. Dots show localities from which specimens were examined. Encircled areas with numbers mark geographic units used in comparisons (see page 164).

streak borders and crural background color. At the same time the whitish background of the underparts becomes whiter. Immediately east of the Colorado River valley, the back begins to be more neutral and darker gray, and ochre and tawny hues disappear from the lighter areas both above and below. Cold dark grays combined with light gray background colors gradually becomes more dominant in the populations farther eastward and occasionally are more extremely manifest. A considerable increase in this tendency results in the race *suttoni* of the plateau of Chihuahua.

Northwestward in the Inyo district and on into western Nevada, white background becomes purer and white facial marks are whiter and more extensive; otherwise the birds are similar to those of Arizona east of the Colorado River and to intermediate stages along the gradient from coastal southern California to the Colorado River valley. South of Arizona, dark, neutral grays and dull whites prevail until in central Sonora the grays become darker and browner, and rufous brown appears in the crural area and flanks. On the peninsula of Baja California grays become paler in the southern half.

Viewed broadly, then, colors are less brown and tawny and grays are lighter and whitish areas purer in the most arid regions, as in the Colorado River valley, the Owens Valley and the southern part of Baja California. Darker grays with even less tawny or brown hues prevail eastward in the less severely arid regions both at low elevations and in the mountains.

The breadth of the shaft streaks on the crown and on the underparts shows gradients that parallel size; large Screech Owls are boldly marked, small ones narrowly striped. It is not impossible that there is a partial common regulation or genetic determination of these features, yet there is at the same time no perfect correlation of the two in intraracial variation and each may be presumed to be independently modifiable to a degree. Shaft streaks are broad in all groups bordering the Colorado basin, including *inyoensis*, and diminish in converging gradients toward the lower valley; the streaks are also narrow in *xantusi* of the Cape district and in *sinaloensis*. More or less associated with this cline is the condition of the lateral feather bars on the ventral surface; these bars are broader and more continuous in correlation with broader shaft streaks. The number of lateral bars per feather is independent of width. The number is low in *mccallii* of Texas and is consistently high in *sinaloensis*, but there is considerable individual variation in number through most of the populations in the area under study. In *sinaloensis* the lateral bars are disproportionately heavy compared with the shaft streaks and are also numerous, giving a densely barred, almost reticulate effect in extreme individuals.

The broad aspects of the color cline and that of the streaking have a measure of environmental correlation which in turn may reflect adaptive significance. This significance probably does not extend to local aspects of the gradients nor to the precise combinations of pattern and color features. These details may be influenced by infiltration or flow effects from adjoining faunal areas, by historic factors, and by the chance availability of mutants and the chance fixation of them. Paler, duller colored, less boldly striped Screech Owls should be less conspicuous on their daytime roosts (not all roost in holes) in the desert vegetation and at crepuscular hours than birds possessing the opposite extremes of coloration and pattern which should in turn be less conspicuous in oak or oak-pine woods by reason of their dark, bold and varied markings.

In the elaborate immobile concealing posture assumed by alarmed Screech Owls, the ear tufts are extremely elevated (perhaps this is the main reason for their existence) and the facial disc and eye slits are arranged so as to distort the normal strigine outline and pattern. This can scarcely have been evolved except under considerable selection pressure. Anyone encountering this posture in an alarmed owl on a daytime roost, or for that matter at night, can not escape noticing the strong concealment aspect of it. Re-

semblance to odd-shaped masses of foliage or to bark fragments or trunk surfaces is striking. In a certain percentage of cases, and the percentage need not be large to be effective, this concealing aspect must lead to failure to detect on the part of carnivores and man. Wildcats, coyotes, foxes, and larger owls that could get at Screech Owls in low desert vegetation must surely be deceived occasionally. And Screech Owls, unlike Pigmy and Horned owls, are easily struck down and injured once they are detected. They do not have the stamina of some of their relatives to survive minor injury and escape.

General resemblance in color to the prevailing light gray of desert foliage must be an effective part of this general concealing mechanism no matter how the owl's pattern is worked out in detail. Fine striping more generally corresponds with the shadows of bare twigs and narrow, reduced desert leaf types than it does with those cast by broad-leaved trees.

The gradients in color and pattern do not break sharply at zonal or plant-belt borders, yet there is a rough or partial correspondence, as through the Joshua Tree National Monument in passing from the piñon-oak belt down into the mesquite and ironwood to the eastward, or in Arizona in passing down mountain slopes from the oak-pine country into the palo verde, mesquite and sahuaro association. Imperfections are evident, for the darker gray, broad striped, *cineraceus* types spread far out westward in Arizona beyond the larger mountains, but in a sense such an imperfect correlation is what one would expect where selection for concealment is in no sense absolute and full continuity of populations permits gene flow.

The color clines have a general correspondence with the trends subsumed under Gloger's principle. But more important than the mere correspondence with this dictum is the fact that in this instance we may reasonably interpret the correspondence as one directed by selective forces working in favor of concealing coloration. The correlation of color with temperature and humidity as outlined by Gloger's principle is only secondarily causal, the background colors being determined by these climatic factors, and these in turn setting up selective forces working on the owls. This sort of relation is probably general, as now often assumed, in instances of variation that conform to Gloger's principle.

GEOGRAPHIC RACES

Otus asio suttoni Moore

Otus asio suttoni Moore, 1941:154.

Type locality.—Portezuelo, Hidalgo, México, about 5800 feet (type in coll. R. T. Moore).

Range.—Central Plateau of México, from Hidalgo northwest to Chihuahua.

Characters.—Resembles *Otus asio cineraceus* of Arizona and New Mexico but ventral markings coarser and more sharply contrasting black and white; back darker, more neutral, "colder," gray. Wing length and weight same as in *cineraceus* of eastern Arizona and western New Mexico.

Specimens examined.—Two. CHIHUAHUA. Ramos, 4800 feet [near Casas Grandes].

The distinctness of this form from races bordering it to the south and east has not been investigated, but we have no reason to doubt its validity. The large size claimed for it by Moore is not substantiated, however, particularly in comparison with *cineraceus*. The understanding of wing length variance in *cineraceus* developed in the present study and the measurements of the two Chihuahuan examples of *suttoni* we have had at hand indicate that the dimensions of *suttoni* fall well within those of *cineraceus*.

No light can be thrown on the relations of *suttoni* to *O. a. vinaceus* of the mountains of central western and southwestern Chihuahua. The coloration of the specimens from Ramos in the Chihuahuan desert plateau does not in any way suggest that ascribed to *vinaceus*.

Although the area east of the continental divide has been given little consideration,

examples of *cineraceus* have been examined from Dona Ana County, southern New Mexico, and from Culberson and Jeff Davis counties in western Texas. These birds and those from the area about the border junction of Arizona, New Mexico, and Sonora as a group are not as extremely black and white nor as cold gray as the specimens from northern Chihuahua. They agree well with *cineraceus* of the Chiricahua mountain area (see also Van Tyne and Sutton, 1937:36). One of three individuals from Jeff Davis County does, however, approach the Ramos specimens. Although intergradation of *cineraceus* with *suttoni* is not adequately localized by these specimens, it is evident that the most definite change in coloration takes place at or slightly south of the international boundary in Chihuahua.

Otus asio cineraceus (Ridgway)

Megascops asio cineraceus Ridgway, 1895:390.

Otus asio gilmani Swarth, 1910:1.

Otus asio mychophilus Oberholser, 1937:356.

Type locality.—Northwestern Mexico and contiguous border of United States, in Arizona and New Mexico . . . Lectotype from Fort Huachuca, [Cochise County,] Arizona (in U. S. Nat. Mus).

Range.—Southern Nevada south of latitude 38° (exclusive of lower Colorado River valley), southern Utah (northeast at least to northern San Juan County), probably southeastern Colorado, and southwestern New Mexico (south and west from Socorro County), south throughout Arizona, except the Colorado River valley south of Fort Mojave area, to central Sonora (intergradation with *sinaloensis* occurs in the Guaymas area) and to western Texas west of the Pecos River.

Characters.—A gray and black, moderately large form with finer, more numerous dark cross bars on ventral plumage than in *aikeni* and *mccallii* to the eastward and with coarser shaft markings than in the smaller desert races to the southwest. Brownish and tawny hues less evident than in the Colorado River valley and Pacific coastal forms of California and than in *aiken* and *mccallii*. Crural barring heavier and background darker, less white or pale tawny than in Colorado River valley form and *inyoensis*, but less extensive and less brown than in *sinaloensis*.

Specimens examined.—Two hundred and forty-seven. NEVADA. Nye County: 2½ mi. E, 1 mi. S Grapevine Peak, 6700 ft. (2 specimens). Lincoln County: Ash Spring, 3800 ft., Pahrangat Valley (1). Clark County: north side Potosi Mt., 5800 ft. (2). CALIFORNIA. San Bernardino County: southeast side Clark Mt., 6300 ft. (1). UTAH. San Juan County: 16 mi. S Moab (1); 19 mi. SE Moab (1). ARIZONA. Yuma County (intermediates): Alamo Crossing, Bill Williams River, 1200 ft. (6); 3 mi. E Alamo Crossing (3); Salome (1); 10 mi. S Salome (1); Reed Ranch, 6 mi. SE Salome, 1650 ft. (7); 8 and 13 mi. SE Salome (2). Coconino County: Grand Canyon Village (1); 10 mi. N Ashfork, 6000 ft. (2). Yavapai County: 3 mi. E Big Sandy River (Crosby Ranch), 3200 ft. (1); Bagdad Bridge, Santa Maria River, 2300 ft. (2); Camp Wood (1); Williamson Valley, 4837 ft. (1); Prescott (1); Ash Creek, 4500 ft. (10); Dewey (1); Camp Verde (1); 2 mi. E Montezuma Wells, Palo Verde Valley (1 jv.). Maricopa County: Golden and North canyons, Harquahala Mts., 2600 ft. (8); Gila Bend (1); Phoenix (6). Pinal County: Santan (1); Blackwater (2); 3 mi. W Coolidge (2); 8 mi. S Coolidge (1); Florence (2); Mammoth (2); 2 mi. E Oracle, 4500 ft., Santa Catalina Mts. (1); Pepper Sauce Canyon, lower Santa Catalina Mts. (1). Pima County: east slope Santa Catalina Mts. at "lower control" (1); 12 mi. NE Tucson, Sabino Canyon (4); 5 mi. N Tucson (3); Fort Lowell (14); Tucson (17); 9 mi. E Tucson (1); San Xavier (2); 20 mi. S Tucson (1); Thomas Canyon, Baboquivari Mts., 4100-4700 ft. (6); 9 mi. N Menager's Dam (1); Alamo Canyon, Ajo Mts. (4); southeast end of Growler Valley (1); 1 mi. N Int. Boundary at Sonoyta (4). Santa Cruz County: Santa Rita Mts. (1); Florida Canyon, Santa Rita Mts. (1); Madera Canyon, Santa Rita Mts. (1); Sonoita (1); 10 mi. E Patagonia (1); 2 mi. S Patagonia (1); Peña Blanca Spring (6). Cochise County: Carr Canyon, 5300 ft., Huachuca Mts. (2); Sunnyside Canyon, 5800 ft., Huachuca Mts. (1); 1 mi. S Fairbank (1); Bonita Canyon and Pinery Canyon, Chiricahua Mts. (9); Chiricahua Mts. (6); Paradise (2); San Bernardino Ranch, 3717 ft., Mon. 77 (4); extreme southeast Arizona at Sonora boundary, 4000 ft. (2); Guadalupe Mts., 5200 ft., at Arizona-Sonora corner (1). Gila County: Casadero Spr., 23 mi. ENE Globe, 4050 ft. (1). Graham County: Aravaipa Creek [Klondyke] (2); 3 mi. NW Safford (1). Greenlee County: Blue (1); ½ mi. S Granville, 6500 ft. (1). NEW MEXICO.

Socorro County: 2 mi. N Valverde, Rio Grande River (2). Catron County: Reserve (13). Grant County: Redrock (3); Mimbres River (2). Dona Ana County: Cox Ranch, west side Organ Mts. (1). TEXAS. Culberson County: McKittrick Canyon, 8 mi. NE Guadalupe Peak, 5300 ft. (1). Jeff Davis County: 1 mi. N Fort Davis, 4800 ft. (3). SONORA. Quitobaquito (2); 37 mi. SW Sonoyta (1); 19 mi. S Sasabe (2); 12 mi. W Caborca (1); 3 mi. E Caborca (5); Casita, 40 km. S Nogales (2); Quelita (1); 4 mi. N Moctezuma (2); 5 mi. E Masocahui (2); 15 mi. W Ures (1); 27 mi. W Ures (2); 5 mi. W Carbo (2); Sierra de Mazatan, 6 mi. N Nácari (1); 16 mi. S Hermosillo (1); 35 mi. W Hermosillo (3); 27 mi. E Kino Bay (5); 6 mi. NE Kino Bay (2); Sierra Seri (1); 15 E Estero Tasiota (4).

The boundaries of this form to the north and east have not been extensively investigated and they are only approximately indicated by a scattering of specimens available. If the range is incorrectly indicated in these directions, the error probably consists of not extending it far enough. In Nevada the junction with *inyoensis* must take place north and west of Death Valley, but there is a gap in the representation of specimens between the piñon belt east of Death Valley, whence two worn birds seem a little closer to *cineraceus* than to *inyoensis*, and the northern Owens Valley and Carson Sink areas where *inyoensis* is typical. We have seen nothing to indicate the point of junction of these races in Utah.

Oberholser described *Otus asio mychophilus* from the south rim of the Grand Canyon and indicated its extension far into Utah to Provo and Moab. We have had available one topotype of *mychophilus* and one of us has seen the type specimen in the United States National Museum. Also, two birds from near Moab in San Juan County, Utah, have been carefully compared. In none of these can we see any significant departure from the normal types of variants in *cineraceus*. Oberholser's principal comparison of *mychophilus* was with *inyoensis* and the points of difference he indicates are among those by which *cineraceus* differs from *inyoensis*. Contrasted with *cineraceus*, he claims it to be of much larger size, with darker and usually more uniform and more finely vermiculated upper [*sic*] surface. The color characters may have been indicated in the particular samples Oberholser had before him, but are completely encompassed within the range of individual variation of *cineraceus* as adequately demonstrated in large series. Indeed the direct comparison of the types of *cineraceus* and *mychophilus* in Washington failed to show any color differences other than those of a normal sort that may be seen in many different population samples of *cineraceus*.

In size the topotype male of *mychophilus*, by our measuring, shows a wing of 162 mm. and the two females from the Moab area, Utah, are 168 and 173 mm., respectively. A comparison of these with values shown in the table (p. 164) and figure 1 indicates that they fall well within the range of *cineraceus* of the southeastern Arizona area, a population which in size is but slightly larger than that in the vicinity of the type locality of *cineraceus*. Although no two workers' measurements can be expected to conform minutely, Oberholser's published figures for *mychophilus* also appear to agree well with the larger eastern and northern extreme populations of *cineraceus*. These slight trends in size, part of extensive clines, are not at all adequate for definition of separate races in a practical nomenclature.

Cineraceus at its eastern limits gives way to more openly barred and streaked and less pure gray populations—the *aikeni* and *mccallii* types; these limits can not be localized now. The samples of *cineraceus* from southwestern New Mexico represent no trend in this direction but merely a slightly higher proportion of the more heavily striped and neutral gray variants than in central Arizona; there is no major alteration of pattern in them that approaches the condition in *mccallii* which, for example, regularly develops flank feathers with only four or five cross bars. (See p. 169 concerning approach to *suttoni*.)

For a great many years there has been the assumption that in Arizona one race of Screech Owl, the *cineraceus* type as now understood, occupied the oak and lower pine country—the Upper Sonoran Zone—of the mountains of the central and eastern sections and that a low desert race, which Swarth named *gilmani*, occupied the mesquite and sahuaro belts westwardly to the Colorado River. Swarth at various times (1904, 1910, 1914) developed this picture and there is a fundamental truth in it, for a comparison of opposite extremes of birds from the oak belts of the Chiricahua and Huachuca mountains and the bottom lands of the Colorado River valley show a strong contrast in size and in depth of coloration, hue, and fineness of markings. What could not be well seen until large, geographically diversified samples were assembled was that there was no sharp correspondence of these characters with zonal boundaries and that in the central lowlands there are mixtures of the types of color and pattern, these mixtures shifting gradually in proportion toward one extreme to the west and another to the east. Indeed the extreme populations show similar ranges of individual variation but each has a different assemblage of variants which does not overlap the extreme at the opposite end of the cline.

It becomes evident that in size and color the population of eastern Arizona and western New Mexico is on the average slightly more extreme than that centering about the type locality of *cineraceus* in the Huachuca district and than that of the Prescott district. But the Chiricahua and Huachuca groups so fully overlap that no distinction at the level of a two-thirds separation exists and thus no distinction of taxonomic worth is present.

Similarly in comparing the Huachuca group with that of the Tucson area (formerly classed as *gilmani*) a moderate average decrease in wing length is noted and a number of lighter gray and some earthy gray birds appear as well as those with finer shaft stripes, yet there are in the Tucson group many, including proved breeding birds, that in color and size are identical with examples from the Huachuca and even the Chiricahua and New Mexican areas. The size and average color make-up of the population in the Phoenix area is so similar to that of the Tucson group that the samples were combined for the plotting of wing length.

Farther westward toward the Colorado River trough and southward to the Sonoyta area size further diminishes gradually, but coloration changes rather little until close to the Colorado River. The birds of the Alamo area on the Bill Williams River and those from the vicinity of Salome are essentially the same in range of color as the Phoenix and Tucson groups, but coarsely striped and dark gray variants are few. Then, rather abruptly in the Colorado River valley proper, dark gray, heavily striped birds disappear from the samples and even more extremely pale, fine striped and light buffy gray variants appear. There is then a fairly distinct break in the general color cline within twenty-five miles of the river valley and only about 25 per cent of the sample from the Colorado Valley overlaps in color the paler, more finely striped extremes of the Salome, and Alamo intermediate groups. It is at this point that the race boundary must logically be set as it is the one steep section in the color cline; there is no sharp break anywhere in the wing length cline.

It is most unfortunate that Swarth in perceiving the general outlines of this geographic variation and intending to name the desert race of the area did not select a type from the Colorado River valley. The reason probably is that he had very scant material from this valley in 1910. Thus he chose a type from Blackwater, some 35 miles southeast of Phoenix, from which vicinity he had several recently taken specimens provided by M. French Gilman. The type of *gilmani* has been compared many times by van Rossem and by us with the present assemblage of Screech Owls. Two main points emerge:

(1) it is not representative of the average of the Phoenix and Tucson groups, most of which are purer gray dorsally, but it is one of the somewhat earthy brown variants of these groups of Screech Owls which are uncommon yet present throughout most of the populations of *cineraceus*. (2) It does not possess the light tawny hues of the Colorado River valley birds nor the nearly pure white background of the underparts and the fine striping. In other words the type is not identifiable with the Colorado River valley form although it shows in its brownish gray color some parallel to the light warm gray color of that race. No alternative exists but to relegate *gilmani* to the synonymy of *cineraceus* even though it is a fairly well known name and was intended by its describer to include the Colorado River bird, the extreme differentiation of which he did not, and probably could not, at that time discern. A new name is therefore supplied (see below) to represent the extreme or end point of the color and size clines running both from the northwest and northeast into the Colorado River trough.

South of Arizona through the coastal and lower mountain districts of northern Sonora coloration does not seem to alter significantly. Occasional pale, fine-striped birds suggestive of the Colorado Valley form appear, but they are rare. The size remains at the low level of the Sonoyta group. Thus, we encounter owls of the general coloration of *cineraceus* and the small size of the Colorado Valley form. However, the size (or wing length) so broadly overlaps that of the typical populations of the Huachuca area as to rule out nomenclatural distinction.

Size further declines a little grading into *sinaloensis* of southern Sonora. Beginning even as far north as Moctezuma, near latitude 30°, occasional birds appear that are darker and browner above and below than *cineraceus* and suggest *sinaloensis*. Not until the Guaymas area is reached, however, do several dark colored, fine striped and densely barred birds appear. The population here may be regarded as intergradient, perhaps as a whole closer to *sinaloensis*. Even in extreme southeastern Sonora in a *sinaloensis* population, one *cineraceus*-like individual has been taken 17 miles northeast of San Bernardo. This bird may be a migrant but just as probably it is an individual variant of a resident population.

Otus asio yumanensis new subspecies

Type.—Male, no. 52107 Museum of Vertebrate Zoology, taken 10 miles west of Pilot Knob, 1 mile south of Mexican Boundary, Baja California, March 15, 1928, by Chester C. Lamb; weight 102.5 gm.

Range.—Lower Colorado River Valley from vicinity of Fort Mojave in extreme southern Nevada and western Arizona south to the delta in Sonora and Baja California and the Colorado Desert of California west to Shaver's Well (near Mecca).

Characters.—Similar to *Otus asio cineraceus* but size smaller (see fig. 1 and table); back light, less neutral gray, and the light areas of nape more ochraceous. Stripes of crown narrower and dark wing bars paler. Ground color below less gray and more yellowish, the flanks and legs usually yellowish or pale tawny. Dark stripes of breast narrow, usually bordered slightly with yellow-brown.

Specimens examined.—Forty-three. NEVADA. Clark County: Fort Mojave (2); ½ mi. N Nev.-Calif. line (1). ARIZONA. Mohave County: Fort Mojave (1); Mellon (1, probably migrant *cineraceus*). Yuma County: Cienega Spring, 5 mi. NE Parker (1, migrant?); Quartzite (1); 40 mi. S Quartzite (1); Yuma (1); 11 mi. SW Yuma (1). CALIFORNIA. San Bernardino County: Cedar Canyon, 5000-5300 ft., Providence Mountains (2, intermediates); 5 mi. N Earp (5). Riverside County: 25 mi. N Blythe (1); 8 mi. SW Wiley Well (1); Aztec Well (1); Shaver's Well (2); Cottonwood Springs (4). Imperial County: 2 mi. E Palo Verde (1); 20 [= 10 ±] mi. N Picacho (1); 4 mi. above [= north; also Sahuaro patch] Potholes (4); Potholes [also Laguna Dam] (3); Bard (7). BAJA CALIFORNIA. Type locality (see above; 1).

Yumanensis may extend north along the Colorado River above the open part of the valley of the Needles and Fort Mojave district but probably for no great distance, for

at the latitude of Las Vegas *cineraceus* is present in the mountains not far west of the river. The sample from the northern half of the known range of *yumanensis* is slightly less extreme in the development and proportion of pale-backed, yellowish and narrow striped variants than the group from near Yuma. A dark-colored winter-taken bird from Mellen probably is a migrant from the not distant range of *cineraceus*.

To the west of the Colorado River valley *yumanensis* apparently extends to the Imperial Valley area, to judge from the presence of typical specimens in the mountains bordering this valley on the north in Riverside County.

West of Cottonwood Springs in the Little San Bernardino Mountains of Riverside and San Bernardino counties a sparse population occurs in the piñon and scrub oak belt which is intermediate in color and size between *yumanensis* and *quercinus* of the coastal slopes. These fall in line with the wing-length cline (see fig. 1). In color they are variable, some being close to *yumanensis* and others as dark and coarsely striped as the grayer types of *quercinus*. None of the richly brown type of *quercinus* occurs. Several of these intermediates that are dark gray, fairly large, and broadly striped essentially duplicate *cineraceus* from the opposite side of the Colorado River. However, it seems fairly evident that the history of such birds is independent of *cineraceus* populations although they may have much the same set of genes and characters. They do not represent a type occurring across a broad area nor the terminal point in a cline but only a sector in a cline.

Apparently *O. a. clazus* Oberholser (1937), described from two specimens from the San Jacinto Mountains of Riverside County, is a similar stage in intermediacy along the western border of the deserts, or is even equal to the gray variants normal in *quercinus*. The latter situation is the most likely, since a bird from Palm Springs at the east base of Mount San Jacinto is a normal, moderately brown *quercinus* and another from the the same place is like the extreme gray variants of *quercinus*.

Otus asio inyoensis Grinnell

Otus asio inyoensis Grinnell, 1928a:213.

Type locality.—Independence, Inyo County, California (type in Mus. Vert. Zool.).

Range.—The Inyo region of California, principally Owens Valley, and the mountains west of Death Valley north to the Carson Sink area of Nevada; apparently extends across central Nevada to northwestern Utah (Oberholser, 1937:356; Behle, 1944:75).

Characters.—Size large, although no larger than *quercinus*. Coloration similar to *cineraceus* but background colors of underparts whiter and white areas about face and on legs more extensive. Shaft stripes of breast broad and boldly contrasted with white background, the cross bars more widely spaced and averaging slightly less numerous. Dorsal coloration usually more buffy or brownish gray.

Specimens examined.—Twenty-nine. NEVADA. Churchill County: 3 mi. N, 1 mi. E Fallon (2); 3-4 mi. WSW Fallon (7). Lyon County: 2 mi. ENE Dayton (1). CALIFORNIA. Inyo County: Roberts Ranch, Wyman Creek, White Mts., 8250 ft. (1 skel. only); 2 mi. N Bishop (1); 1½ mi. SW Big Pine [also Big Pine] (8); 5 mi. N Independence (1); Independence (2); Mazourka Canyon, Inyo Mts. (1); 1 mi. S Lee Pump, 6000 ft., Panamint Mts. (1); Walker Creek, 4 mi. SW Olancho (4).

The northern and northeastern limits of the range of *inyoensis* are but slightly known. A single bird from central Washoe County, Nevada, and birds from Cassia and Gooding counties, southern Idaho, in the collection of the Museum of Vertebrate Zoology are slightly darker about the head and more brownish on the back than *inyoensis* and have been identified as *macfarlanei*. However, they are much paler and grayer than many *macfarlanei* and may actually be nearer *inyoensis* than typical *macfarlanei*. The reported *inyoensis* from Utah may be of like nature. We have not at this time sought material to determine this.

In the Mohave Desert basin are great areas unrepresented by specimens and in which Screech Owls may actually be absent. Aside from *cineraceus* and *yumanensis* along the eastern edge of this basin and their intergrades in the Providence Mountains, we have material only from the coastal or western and southern borders of the Mohave Desert. Three specimens from the vicinity of Victorville are normal *quercinus*; a fourth is paler and less brown yet is not quite as gray as any of the intergrade group of the Little San Bernardino Mountains.

From the Tehachapi Mountains and Walker Pass areas, particularly the former, are good samples which are normal for *quercinus* and *inyoensis* in wing length (see fig. 1) and which show some approach to *inyoensis* in color. Four out of thirteen are close to *inyoensis* in reduced brown hues and general paleness, so much so that some or all would go undetected in a sample of *inyoensis* as darker extremes of that race. Such does not occur in populations of *quercinus* located on the Pacific drainages more remote from the desert divides.

Otus asio quercinus Grinnell

Otus asio quercinus Grinnell, 1915:60.

Otus asio clazus Oberholser, 1937:357.

Type locality.—Pasadena, Los Angeles County, California (type in Mus. Vert. Zool.).

Range.—Sacramento and San Joaquin valleys of California, below the continuous coniferous forest belts of the mountains and coast ranges, and coastal slopes from Monterey Bay south to latitude 31° in northwestern Baja California.

Characteristics.—Size large, as in *inyoensis* and the eastern populations of *cineraceus*. Coloration darker gray in background areas, above and below, than in *inyoensis* and brown hues much more prominent. At least narrow brownish areas always present beside shaft streaks of breast feathers and brown usually conspicuous in crural area. Shaft streaks broad as in *inyoensis*, and cross bars similar but less boldly contrasting with background gray than with the white of that form.

Specimens examined.—Forty-nine. Only those from coastal southern California and Baja California are here listed. No effort has been made to assemble all available material from southern California, as adequate samples were at hand for comparison with the desert races which have been our primary concern. CALIFORNIA. Kern County: ½ mi. W Summit Walker Pass (1); west slope Walker Pass, 4600 ft. (2). Los Angeles County: Sandberg, Liebre Mts. (10); Castaic (1); Calabasas (1); Toluca (1); Pasadena (10); Altadena (3); Mt. Wilson, San Gabriel Mts. (1); El Monte (2); Bassett (1); Claremont (3); 25 mi. W Hesperia (1). San Bernardino County: Mojave River, 6 mi. above Victorville (3); Hesperia (1). Riverside County: Riverside (1); near Corona (1); 10 mi. E Hemet (1); Palm Springs (2). San Diego County: Pine Mt. (1); Cuyamaca Mts. (1); Laguna Mt., 6000 ft. (1); 4 mi. S Barrett Lake, 900 ft. (1). BAJA CALIFORNIA. North end Nachogüero Valley, 3400 ft. (1); south end Valle de Las Palmas, 1200 ft. (1); Valle de la Trinidad (2); San Matias Pass (1); San Jose, 2500 ft., latitude 31° (1).

Intermediate group between *quercinus* and *yumanensis* in Little San Bernardino Mountains.—Ten. San Bernardino County: Black Rock Spring, 4500 ft. (1); Quail Spring, 3900–4500 ft. (3). Riverside County: 1 mi. W, 2½ mi. N Desert Hot Springs, Little Morongo Valley, 1500 ft. (1); Stubby Spring, 4750 ft. (1); 1 mi. E Key's View, 5000 ft. (1); Live Oak Tank (1); Pinyon Wells (2).

Quercinus shows a considerable range of color variation, some individuals being distinctly brown dorsally whereas others are gray, although not as purely gray as in the adjoining desert races. Especially gray-backed variants that apparently reflect intrusion of characters from grayish desert populations occur around the eastern or desert periphery of *quercinus* south of the Sierra Nevada.

The population in northwestern Baja California as a group is rather atypical; richly brown individuals are lacking, at least in the small sample available. Wing length diminishes in a gradient through this area toward *cardonensis* to the south.

Otus asio cardonensis Huey

Otus asio cardonensis Huey, 1926:360.

Type locality.—Canyon San Juan de Dios, about 10 miles east of El Rosario, Baja California, Mexico (type in coll. San Diego Soc. Nat. Hist.).

Range.—Baja California from latitude 30° 30' on the west coast and latitude 31° on the east coast south to latitude 29°. May range considerably farther south, to latitude 28°.

Characters.—Wing short and size small, on the average slightly smaller than in *yumanensis* and equivalent to *sinaloensis*. Coloration darker, sootier gray dorsally than in *cineraceus* and lacking the brownish and buff hues of *quercinus*, even of the grayer extremes of *quercinus*. Ventral background color darker and shaft stripes and cross bars broader than in *xantusi* and *yumanensis*. Ventral cross barring prominent and close set. Crural area browner and more heavily marked than in *xantusi* and *yumanensis*.

Specimens examined.—Nine. BAJA CALIFORNIA. 6 mi. E El Rosario (8); El Cajon Canyon, 3200 ft., east base San Pedro Mártir Mts. (1 intermediate).

Cardonensis represents a level in the size cline running south through Baja California from both *quercinus* and *yumanensis* toward *xantusi*, but its color characters are not precisely intermediate. The dark, dull gray dorsal color is fully as dark as in *quercinus* but lacks the brown hue of *quercinus* and the buffy gray of *xantusi*. The dense ventral markings are not quite like those in either *quercinus* or *xantusi*. Probably the *cardonensis* type of coloration and stage in wing length prevails over a wide segment of middle Baja California, but between latitude 30° and the vicinity of San Ignacio, latitude 27° 17', no specimens are available.

A bird from the east slope of the Sierra San Pedro Mártir is intermediate toward *yumanensis*, its color essentially duplicating that of *cineraceus* as Grinnell (1928b:116) indicated; but as in the case of the intermediates in the Little San Bernardino Mountains, this should not be taken to mean immediate derivation from, or population-affinity with, *cineraceus*.

Otus asio xantusi (Brewster)

Megascops xantusi Brewster, 1902:93.

Type locality.—Santa Anita, Baja California (type in Mus. Comp. Zool.).

Range.—Baja California from about latitude 27° 30' south to the Cape.

Characters.—Smallest of all the races of *Otus asio*. Coloration paler, warmer gray above and whiter below than in *cardonensis* and crural areas less brownish; light areas of dorsal surface usually yellowish. Shaft streaks narrow as in *yumanensis*, the lateral bars similar. Color similar to *yumanensis*, but less extremely white below and darker, warmer gray above.

Specimens examined.—Twenty-eight. BAJA CALIFORNIA. San Ignacio, 400 ft. (1); Campo Los Angeles (1); La Paz (1); Laguna Valley, 6000 ft., Victoria Mts. [also called Sierra de Laguna Mts.] (2); Agua Caliente, 800 ft. (5); Miraflores, 600 ft. (18).

Although *xantusi* has been compared with *sinaloensis* by Moore and Peters (1939: 42) in a way that would suggest close affinity, this may be misleading. *Sinaloensis* is darker on the legs and in the gray of the underparts and has even narrower ventral shaft streaks coupled with dense lateral cross bars, which gives a reticulate effect. The small size in which the two forms are alike is best regarded as a parallelism, under the influence of the Bergmann principle, rather than as a sign of immediate common derivation. Probably *xantusi* is a geographic modification of a northern stock. Actually it is close to *yumanensis* in most features, between which the darker *cardonensis* intervenes.

Otus asio sinaloensis Moore

Otus asio sinaloensis Moore, 1937:64 (type in coll. R. T. Moore).

Type locality.—Guamuchil, 45 feet, northwestern Sinaloa, México.

Range.—Southern Sonora from about latitude 28° southward and coastal plains and foothills of northwestern Sinaloa.

Characters.—Differs from *cineraceus* in darker gray coloration dorsally, less pure white ventrally, and in frequent tawny washes (vinaceous effect) and brown and tawny areas bordering shaft streaks; shaft streaks finer, contrasting less with dense, though fine cross bars of ventral feathering. Crural areas heavily marked and rich brown. Toes bristled to greater extent than in *cineraceus* with consequent reduction in normal feathering. Wing length slightly less than in neighboring *cineraceus* of northern Sonora.

Specimens examined.—Fourteen. SONORA. 10 mi. N Guaymas (2 intermediates); 3 mi. N Empalme (1 intermediate); 15-17 mi. NE San Bernardo, 2000 ft. [Los Algodones] (4); 10 mi. N Alamos (2); 5 mi. N Alamos (1); Alamos (1); Guirocoba (2); Agiabampo (1).

For discussion of intergradation with *cineraceus* in the Guaymas area of central Sonora, see p. 172. Moore (1941) has described a situation in Jalisco and Michoacán which suggests that the *sinaloensis-vinaceus* group of races of Screech Owls occurs in the same general region where a series of *cineraceus*-like races is present. This situation is still imperfectly known, but even if two chains of races here react as species, one should not lose sight of the fact that in Sonora a gradual intergradation of *cineraceus* and *sinaloensis* occurs in which the proportion of dark colored, finely streaked types increases progressively southward. This is the type of racial intergradation found between many races of Screech Owls. There may then be overlapping of races without interbreeding in southwestern México, but these end groups are certainly connected in the north as normally intergrading units and the whole complex should therefore be treated as one species.

SUMMARY

Screech Owls (*Otus asio*) are abundant and successful nocturnal raptors in the desert areas of western North America. They feed chiefly on large ground-dwelling arthropods.

A large group of specimens has been assembled by persistent nocturnal hunting in which advantage is taken of aggressive response of the owls to imitated calls. The series of skins reveals a wide amplitude of individual variation, appreciation of which justifies synonymizing certain races that have been proposed. Eight races are recognized in or bordering the lower Colorado River basin and the Gulf of California, one of which requires renaming.

A conspicuous difference in size, in the order of forty per cent, exists between the smallest and the largest owls of the desert areas. The clines in wing length, reflecting size in considerable degree, conform with Bergmann's principle, the smaller dimensions occurring in the warmer areas to the southward and at low elevations. Nocturnal habits and the cold winter nights at higher elevations in the north pose special problems of heat conservation for this non-migratory species. Large size, with a more favorable surface-mass ratio, appears to have definite selective advantage in the more northern and montane populations.

Clines in the general aspect of coloration coincide with environmental background colors and patterns and apparently contribute importantly to concealment. Concealment in these moderately small and easily captured owls is elaborately furthered by special posture and by the extreme elevation of ear tufts in addition to coloration.

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